Response of penguins to environmental changes across the Southern Ocean:

from individuals to population trends

Presented by Claire Saraux

Defended on the 18th of October 2011 in front of:

Yvon Le Maho	(Research Director, CNRS, Strasbourg)	PhD director
François Gauer	(Professor, University of Strasbourg)	President of the jury
Phil Trathan	(Professor, British Antarctic Survey)	Reviewer
Jean-Michel Gaillard	(Research Director, CNRS, Lyon)	Reviewer
Nigel Yoccoz	(Professor, University of Tromsø)	Examiner
André Chiaradia	(Researcher, Phillip Island Nature Park)	Invited member
Céline Le Bohec	(Post-doc, University of Oslo)	Invited member
Cyril Kao	(Assistant scientific director AgroParisTech)	Invited member

Acknowledgements

> *« I am among those who think that science has great beauty. A scientist in his laboratory is not only a technician; he is also a child placed before natural phenomena which impress him like a fairy tale »* **Marie Curie**

First page and still it's not easy to realize. This is the end already. Everything went so fast but as they say *all good things come to an end*. Three years to discover the behind the scenes of penguins. I should say I was pretty lucky, 3 different field works, 3 penguin species to love, loads of very interesting people, and a single downside: only 3 years to enjoy it all! There are a lot of people who made this possible and I would like to thank them all. For a few, I would never be able to say how grateful I am for you know writing is not my favourite thing but I hope you'll still see it through these lines. By the way, I apologize to everyone for switching between French and English in these first pages.

First, I wish to express how grateful I am to Pr. François Gauer, Jean-Michel Gaillard and Phil Trathan for accepting to evaluate this work.

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Of course, I have trouble finding my words, to say how much I valued to have you at my side, Vincent. Nothing would have been the same without you. I learned so much with you and still do every day. Your comments, suggestions, loads of ideas improved greatly this PhD of course. But mostly, thank you for making my life easier and happier, for supporting me all along, for always being here, for truly believing in me, giving me strength and self-confidence. Everything becomes possible with you and that helps me so much.

Cette thèse aurait été bien plus compliquée sans la présence d'une base de données et je souhaite donc remercier tous ceux qui se sont investis pour transformer des centaines de fichiers txt en une belle base Mysql et le logiciel qui va avec, le désormais célèbre Sphénotron ! Merci donc à Ben, Loïc et David pour ce travail. Ben t'aurais quand-même pu attendre qu'on finisse pour partir… David merci beaucoup pour l'aide en Mysql. Sans vous deux, je pense que certaines de mes requêtes seraient encore en train de tourner !

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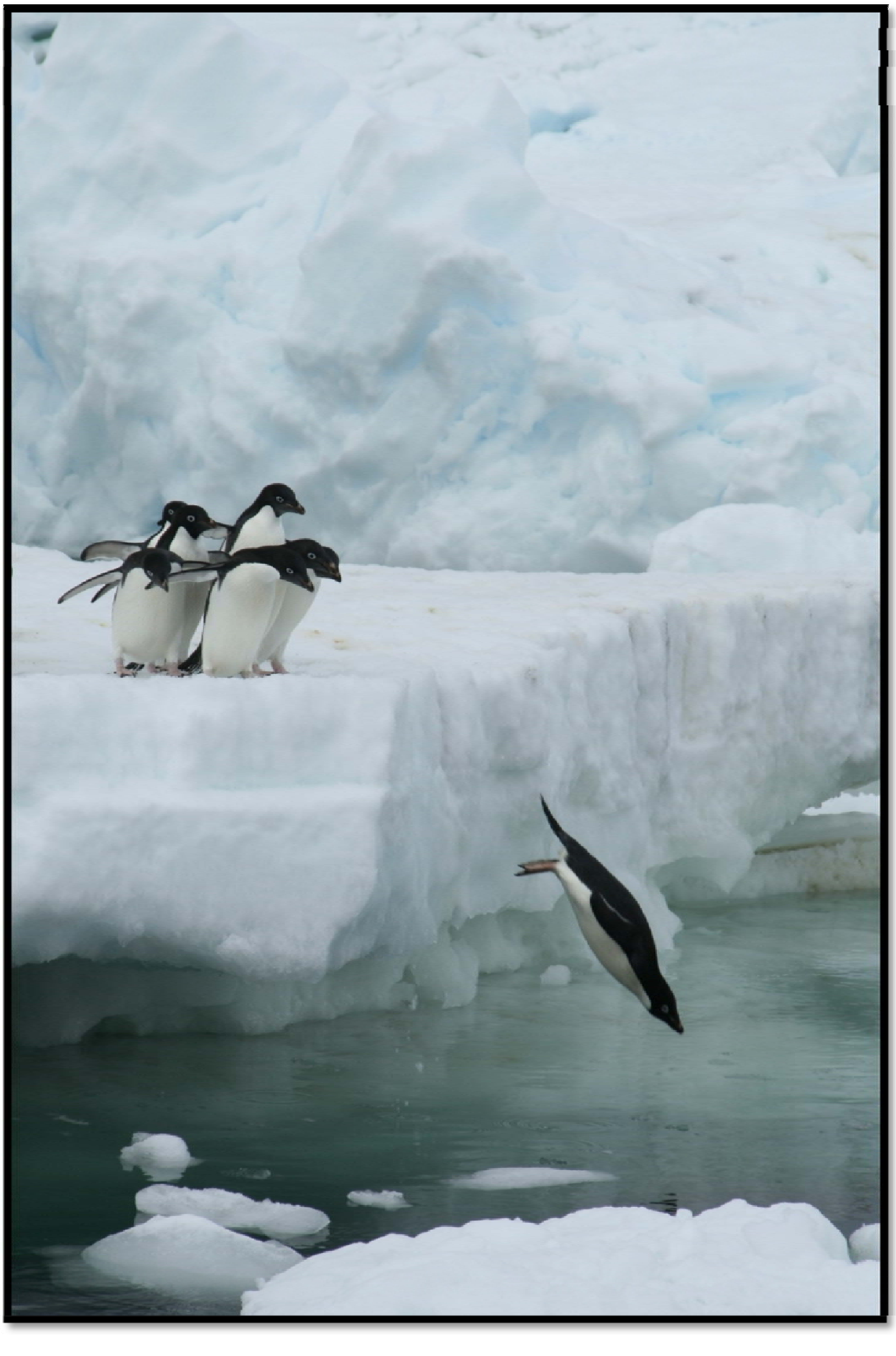
And what better than to finish by acknowledging the core of this work itself!

Penguins are amazing. I've enjoyed so much the chance I was given to go in these different places to observe them. All those experiences were unique. Just sitting there looking at the colony, at specific behaviours. This was simple and pure beauty, nature at its prime.

Articles & Communications



ARTICLES

List of articles on which this manuscript is based

Ropert-Coudert Y., **Saraux C.,** Kato A. IPCC: Integrating Penguins in Climate Change. *Ready to be submitted*

Saraux C., Le Bohec C., Durant J., Viblanc V. A., Gauthier-Clerc M., Beaune D., Park Y.-H., Yoccoz N., Stenseth N. Ch., Le Maho Y. 2011. Reliability of flipper-banded penguins as indicators of climate change. *Nature* **469**: 203-206

Saraux C., Viblanc V.A., Hanuise N., Le Maho Y., Le Bohec C. 2011. Effects of Individual Pre-Fledging Traits and Environmental Conditions on Return Patterns in Juvenile King Penguins. *PLoS ONE* **6(6)**: e20407. doi:10.1371/journal.pone.0020407

Saraux C., Chiaradia A., Le Maho Y., Ropert-Coudert Y. 2011. Everybody needs somebody: unequal parental effort in little penguins. *Behavioral Ecology* **22**: 837-845.

Saraux C., Chiaradia A, Nisbet I. Which time-scale to use to study the impact of climate on breeding success in little penguins? *In prep*

Saraux C., Bordier C., Viblanc V.A., Gachot-Neveu H., Beaugey M., Le Maho Y., Le Bohec C. Inter-annual variability of sex-ratio in king penguins: a result of climate? *In prep.*

Saraux C., Robinson-Laverick S., Le Maho Y., Ropert-Coudert Y., Chiaradia A. 2011. Plasticity in foraging strategies of inshore birds: How little penguins maintain body reserves while feeding the chicks. *Ecology* **92**: 1909-1916.

Saraux C., Friess B., Le Maho Y., Le Bohec C. Foraging strategies in chick-rearing king penguins. *In prep*

List of articles in supplementary material

Le Maho Y., **Saraux C.,** Durant J., Viblanc V. A., Gauthier-Clerc M., Yoccoz N., Stenseth N., Le Bohec C. 2011. An ethical issue on biodiversity science: The monitoring of penguins with flipper-bands. *Comptes Rendus Biologie* **334**: 378-384

Le Bohec C., Sabarros P., Durant J., **Saraux C.,** Ergon T., Pradel R., Yoccoz N., Friess B., Gauthier-Clerc M., Park Y.-H., Le Maho Y., Stenseth N. King penguins on the verge of extinction? *In prep.*

List of articles not included in the manuscript

Saraux C., Chiaradia A. Effect of age on little penguins' reproduction: evidence of both a learning phase and senescence. *In prep.*

Viblanc V. A., **Saraux C.,** Malosse N., Groscolas R. Physiological and behavioural adjustments during courtship and incubation in fasting male king penguins (*Aptenodytes patagonicus*). *In prep*

Le Vaillant M., **Saraux C.,** Hanuise N., Prud'homme O., Kato A., Le Bohec C., Le Maho Y., Ropert-Coudert Y. King penguins become better managers of their air load with age. *Ready to be submitted*

Mubalegh N., **Saraux C.,** Durant J.M., Beaune D., Le Vaillant M., Le Maho Y., Stenseth N.C. & Le Bohec C. Role of seabird colonies on nutrient cycle processes in the oceanic ecosystems: the case of the King penguin in the Southern Ocean. *In prep*

Viblanc V. A., Mathien A., **Saraux C.,** Viera V. M., Groscolas R. It Costs to be Clean and Fit: Energetics of Comfort Behavior in Breeding-Fasting Penguins. *PLoS ONE* **6(7)**: e21110.

Salton M., Chiaradia A., **Saraux C.,** Dann P. The link between non-breeding season and subsequent reproductive performance in an income breeder: the Little penguin Eudyptula minor. In *Revision for Ibis*

Toscani C., Le Bohec C., **Saraux C.,** Whittington J., Stenseth N.C., Le Maho Y. & Gauthier-Clerc M. Divorce in king penguins: a trade-off between timing of reproduction and mate choice. *In prep*

COMMUNICATIONS

Oral Presentations

1. 7th **International Penguin Conference**. August 2010, Boston, USA.
   Saraux C., Chiaradia A., Le Maho Y., Ropert-Coudert Y. "*Unequal parental investment in little penguins*".
2. 5th **Doctoral School Day.** December 2010, Strasbourg, France.
   Saraux C., Le Bohec C., Durant J., Viblanc V. A., Gauthier-Clerc M., Beaune D., Park Y.-H., Yoccoz N., Stenseth N., Le Maho Y. "*Using penguins as sentinels of climate change: are banding data reliable*" awarded as the 2nd best presentation.
3. 7th **Ecology & Behaviour meeting.** May 2011, Rennes, France.
   Saraux C., Robinson S., Ropert-Coudert Y., Le Maho Y., Chiaradia A. "*Plasticity in foraging strategies of inshore birds: How little penguins maintain body reserves while feeding the chicks?*"

4. **IPY Conference**. June 2010, Oslo, Norway.
   Le Bohec C., **Saraux C.,** Friess B., Gauthier-Clerc M., Beaulieu M., Chatelain N., Le Maho Y. *"Long-term data on unbanded penguins as indicators of climate impact on sub-Antarctic and Antarctic ecosystems."*
5. 7th **International Penguin Conference**. August 2010, Boston, USA.
   Salton M., Chiaradia A., **Saraux C.,** Dann P. "*The link between non-breeding season and subsequent reproductive performance in an income breeder: the Little penguin Eudyptula minor."*
6. 7th **International Penguin Conference**. August 2010, Boston, USA.
   Le Vaillant M., Prud'homme O., **Saraux C.,** Kato A., Le Bohec C., Le Maho Y., Ropert-Coudert Y. "*King penguins become better managers of their air load with age."*
7. 7th **International Penguin Conference**. August 2010, Boston, USA.
   Le Bohec C., Pradel R., **Saraux C.,** Durant J. M., Gauthier-Clerc M., Friess B., Le Maho Y., Stenseth N. "*How climate affects juvenile survival and recruitment in the king penguin?"*

8. 1st **World's Seabird Conference**. September 2010, Victoria, Canada.
   Viblanc V. A., **Saraux C.,** Malosse N., Groscolas R. "*Holding the fast: energetic and behavioral adjustments in courting and incubating male King Penguins.*"
9. 1st **World's Seabird Conference**. September 2010, Victoria, Canada.
   Le Bohec C., Durant J., Sabarros P., Stenseth N., **Saraux C.,** Gauthier-Clerc M., Pradel R., Beaune D., Hjermann D., Le Maho Y. "*Modelling demography and extinction risk in the King Penguin under climate warming scenarios.*"
10. 1st **World's Seabird Conference**. September 2010, Victoria, Canada.
    Le Maho Y., Friess B., **Saraux C.,** Gauthier-Clerc M., Le Bohec C. "*Colony studies: The importance of technological innovations on long term monitoring of individuals and populations in colonial species*"
11. 7th **Ecology & Behaviour meeting**. May 2011, Rennes, France.
    Viblanc V. A., Smith A., Valette V., **Saraux C.,** Malosse N., Kauffmann M., Gineste B., Groscolas R. "*Sociality, colonial density and stress : effects of social context and breeding status on the behaviour and physiology of fasting penguins.*"
12. **SFECA.** May 2011, Tours, France.
    Viblanc V. A., Valette V., **Saraux C.,** Malosse N., Kauffmann M., Groscolas R. "*Agressiveness and social stress in a colonial seabird: is there an energy cost to group-living?*"

Posters

1. **7th International Penguin Conference.** August 2010, Boston, USA.
   Saraux C., Le Bohec C., Viblanc V.A., Hanuise N., Le Maho Y. "*Babies come back! Environmental conditions, individual quality and juvenile survival in king penguins*."
2. **1st World's Seabird Conference.** September 2010, Victoria, Canada.
   Saraux C., Le Bohec C., Durant J., Viblanc V. A., Gauthier-Clerc M., Beaune D., Park Y.-H., Yoccoz N., Stenseth N., Le Maho Y. "*Using penguins as sentinels of climate change: are banding data reliable*".
3. **5th Doctoral School Day.** December 2010, Strasbourg, France.
   Saraux C., Le Bohec C., Viblanc V. A., Hanuise N., Le Maho Y. "*Babies come back! Environmental conditions, individual quality and juvenile survival in king penguins*" awarded.

4. **10th SCAR International Biology Symposium.** July 2009, Sapporo, Japan.
   Ropert-Coudert Y., Le Maho Y., Ancel A., Beaulieu M., Chatelain N., Chiaradia A., Friess B., Geiger S., Gilbert C., Kato A., Le Bohec C., Le Vaillant M., Raclot T., **Saraux C.,** Spée M., Zimmer I. "*PICASO: Penguins as Indicators of Climate Anomalies in the Southern Ocean*."
5. **7th International Penguin Conference.** August 2010, Boston, USA.
   Viblanc V. A., **Saraux C.,** Malosse N., Groscolas R. "*Stop pushing I'm breeding! Physiological and behavioural adjustments during courtship and incubation in fasting male king penguins.*"
6. **Biologging IV.** March 2011, Hobbart, Australia.
   Le Vaillant M., **Saraux C.,** Prud'homme O., Kato A., Le Maho Y., Le Bohec C., Ropert-Coudert Y. "*King penguins learn respiratory air load management with age.*"
7. **7th Ecology & Behaviour meeting.** May 2011, Rennes, France.
   Bordier C., **Saraux C.,** Le Bohec C., Viblanc VA., Beaugey M., Gachot H., Le Maho Y. "*Is sex ratio in king penguin populations biased at hatching, or is it a result of postzygotic mechanisms?*"
8. **8th European Ornithologist Union Conference**. Aout 2011, Riga, Latvia.
   Viblanc V. A., Valette V., **Saraux C.,** Kauffmann M., Malosse N., Groscolas R. *"Agressiveness and social stress in a colonial seabird: is there an energy cost to group-living?"*

GENERAL STRUCTURE OF THE MANUSCRIPT

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FOREWORD *(AIMS and STRUCTURE of the THESIS)*

Climate change is part of planet Earth's natural history. The mean surface temperature of our globe has always varied through geological times. Yet, now unequivocally acknowledged, climate change is presently occuring at a pace never seen before. Additionally, whatever the economic scenarios considered, climate change and warming should continue in the next centuries (*a review of climate change can be found in chapter I*). Every living organism is thus facing new selective pressures from the environment. We already know that an important number of biological systems are affected by perturbations resulting from environmental changes (*see effects of climate change in chapter I*). However, it remains difficult to mechanistically link climate change and observed upheavals in many ecosystems not only given the actual complexity of ecosystems but also because of methodological limitations, such as for instance a lack of long-term datasets on physiological, behavioural, and evolutionary responses of specific organisms to a changing environment. At the dawn of the 6th extinction crisis, it is thus indisputably necessary to increase our understanding of ecosystems and their responses to climate. This is especially true for the important but poorly known marine ecosystems. In particular, lying under high latitudes, the Southern Ocean should endure strong climate change imposing new selective pressure on its productive ecosystems (*the case of marine ecosystems and more particularly the Southern Ocean is reviewed in chapter I*).

However, acquiring data on Southern Ocean ecosystems is especially difficult due to their remoteness. One solution consists in investigating the effects of climate on a few species, taken to be representative of the whole ecosystem which they inhabit. Here, we propose to investigate the effects of this rapid climate change on Southern Ocean ecosystems through the monitoring of top-predators. Situated at the top of the food chain, top-predators are indeed considered as being relatively good indicators of the ecosystem's health. They integrate changes that occur at lower levels of the food chain (*the role of top-predators as indicators of ecosystem is detailed in chapter II*) and thus are considered reflective of the overall impact climate change may have on the ecosystem. In particular, penguins appear as models of preferred choice as they are both widespread and easy to monitor (*advantages of penguins are explained in chapter II*). Population trends have been recorded for a long time and changes have been frequently observed in these last 40 years. However, demographic studies allowing the modelization of future population trends rely on a good knowledge of vital rates of a population, and until now only few demographic studies have been conducted. Further, mechanisms underlying these changes are poorly known (*state of the art on climate study on penguins can be found at the end of chapter II*).

Thus the main objectives of this work were to acquire a better knowledge of the ecolgy of several species of the spheniscidae family in order to unravel the effect of climate on life-history traits. It is based on three different penguin species (little penguins, king penguins and Adélie penguins), which live under highly different latitudes from temperate to polar areas. Additionally, they exhibit differences in size, foraging behaviour (inshore *vs.* offshore) and position along the slow/fast life-history continuum (growth, longevity and reproductive rates, *the particularity of each species and study sites are presented in chapter III).* Comparing these three different species will thus provide insight into the effects of climate change on (1) the responses of ecosystems varying in latitude, (2) the differences in foraging strategies of inshore and offshore birds, and finally (3) the plasticity and flexibility of each species and their potential for adaptation.

After investigating how to monitor penguins and their response to climate (*chapter IV and Article 2 Saraux et al. 2011a*), we investigate the effect of climate on different life-history traits. As penguins are long-lived species, adult survival should vary only slightly. Consequently, our work focused on the other important vital rates that are juvenile survival (*Chapter V, Article 3 + complementary results*) and adult reproduction (*chapter VI, Articles 4, 5 and 6*). Additionally, in order to better understand the mechanisms involved in these responses, we also address questions on foraging strategies (*Chapter VII, Articles 7, 8*).

After summing-up the main results, I compare the responses to climate both across and within species (*Chapter VIII*). Then, we integrate results on vital rates in an age-class population model and discuss the results, with in mind an appraisal of the potentiality and efficiency of adaptative responses of penguins to climate changes (*Chapter VIII*). Finally, I provide a personal critical view of the work accomplished (*Chapter IX*) and possibilities to further extend this work (*Chapter X*).

Chapter I ●○○○○○○○○○

Why study the effect of climate on Southern Ocean ecosystems[1]?

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[1] ECOSYSTEM: term introduced by Tansley in 1935 is the basic unit of nature, representing the whole system including not only the organism complex but also the whole complex of physical factors forming what we call environment of the biome, the habitat factors in the wildest sense (Tansley 1935).

I. Climate change

July in Strasbourg. As I start writing the first sentences of this manuscript, the thermometer reads 35°C. No air in the office, 4 people and computers working add even a few degrees. The only thing I can think of is cold water. How can it be so hot? And the simple response I get everywhere I go: "*climate change*" or "*global warming*". Funny how a scientific question can become societal! Funny also, how these very same people were saying the opposite just a few months ago. It was December in France and it snowed as we had not seen it for a while, people were blocked everywhere on the road. "*And they say climate is warming… look at that*!" This is when it struck me, how would I write about climate change without all these clichés, how to let people understand this is a real scientific problem and not just some excuses for everything that happens.

Climate change refers to a change in the state of the climate that can be identified (*e.g.* using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer. It refers to any change in climate over time, whether due to natural variability or as a result of human activity. (*IPCC usage*)

1) Climate change through history

Life on Earth has existed for hundreds of millions of years. However, this does not imply that the climate has been stable throughout this time (Figure I - 1). From glacial periods (or "ice ages") where ice covered significant parts of the Earth to interglacial periods where ice retreated to the poles or melted entirely, the Earth's **climate has continuously changed through history**.

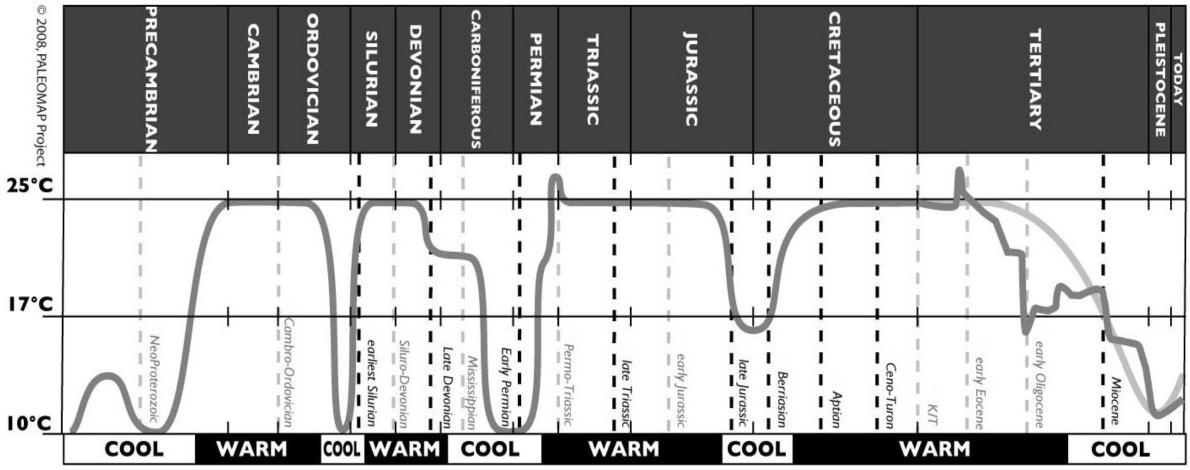

Figure I - 1 : *Evolution of temperature through history. Alternation of ice and interglacial periods. (from Paleomap Project, C. Scotese)*

Paleoclimate science has made considerable advances lately and the use of a number of proxies enabled scientists to build a picture of the Earth's climate as far as millions of years ago. Atmospheric composition can be known from air trapped in polar ice and from the ice itself for the last 650 000 years, while climate forcing can be inferred from celestial mechanics (Jansen *et al.* 2007). At a large time-scale, most of the climatic variations occur under the influence of changes in the Earth's orbit, the sun's intensity, volcanic eruptions or collisions with large celestial objects.

Changes in the shape of the Earth's orbit, tilt and precession affect the amount of sunlight received by its surface (Figure I - 2) and are thought to be the main drivers of ice ages according to the theory of Milankovitch, explaining the mean periodicity of about 100 000 years in the cycle (Bard 2003; Vimeux *et al.* 1999). The amplitude and speed of these transitions between ice and inter-ice ages result from complex interactions between oceans, atmosphere and cryosphere (Hays *et al.* 1976; Jouzel *et al.* 2007). Changes occurring within the sun itself can also affect the amount of sunlight received by the Earth. Reduced solar activity is thought to be the key factor explaining the "Little Ice Age" of the middle of the last millennium for instance. Volcanic eruptions can also play a role in climate forcing through the emission of aerosols (tending to block sunlight but for a short-term) and carbon dioxide.

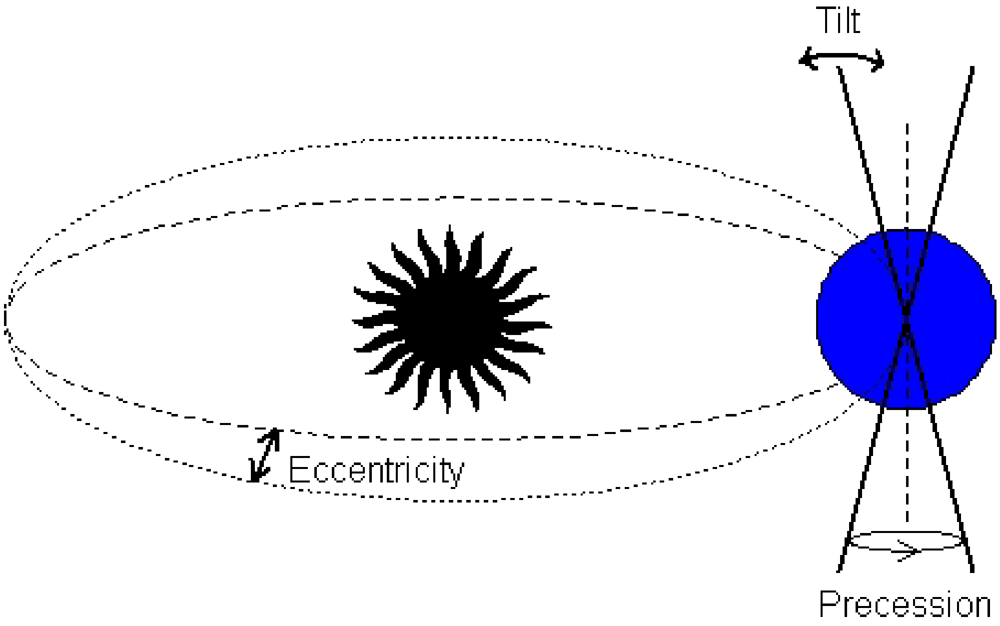

Figure I - 2 : *Schematic of Earth's orbital changes that drives the ice age cycles through the amount of sunlight received.*
Milankovitch cycles with periodicity of 100 000 yrs, 41 000 yrs and 19 000 to 23 000 yrs respectively for eccentricity, tilt and precession.

However, since 1850 and the industrial era, temperatures at the Earth's surface have increased at a pace never seen before (Petit *et al.* 1999). "***Warming of the climate system is unequivocal****, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice and rising global average sea level"* (IPCC 2007; Figure I - 3). The increase in the last 100 years (from 1906 to 2005) in air temperature of 0.74°C (95% CI: 0.56 – 0.92°C) is already very important but the rate of warming keeps on increasing all the time: the linear trend (0.13°C per decade) over the 50 years from 1956 to 2005 is almost twice that of the 100 years 1906-2005. However, one needs to be careful as these values and trends are averages on the whole planet and hide much more complicated changes at a local scale.

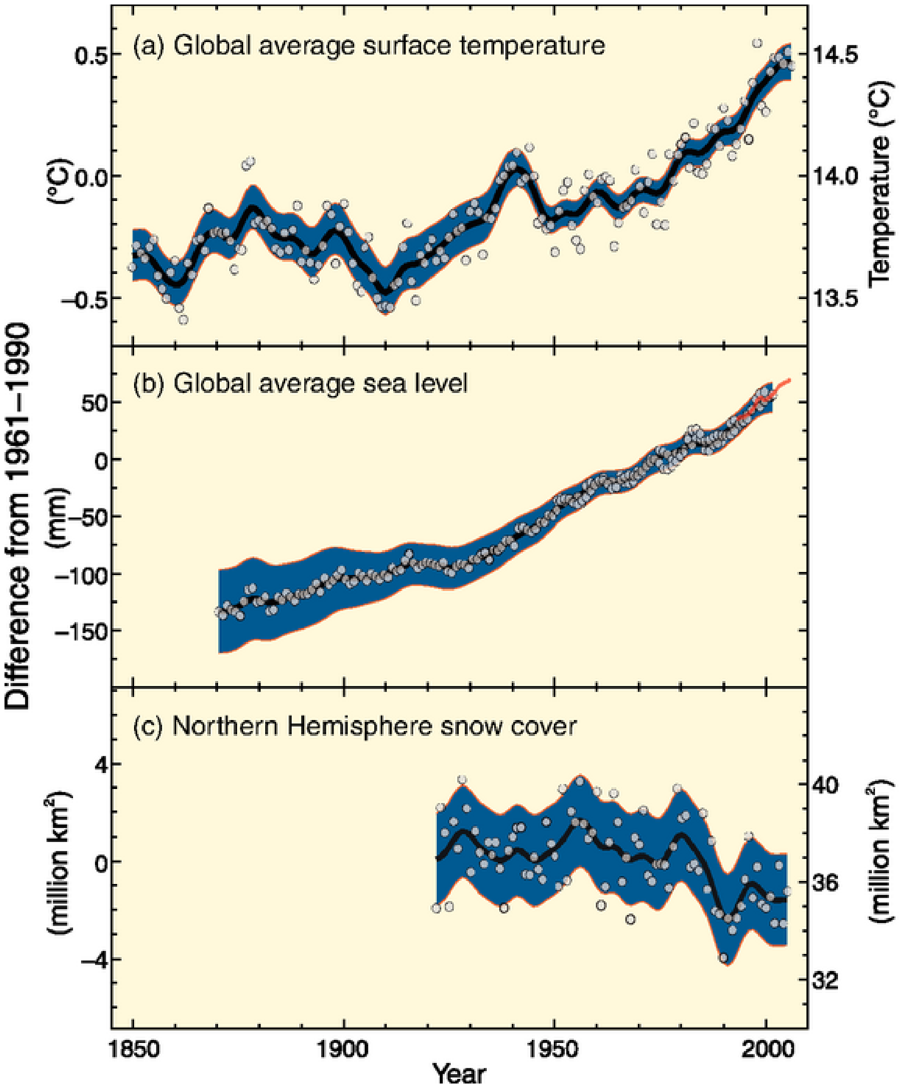

Figure I - 3: *Changes in temperature, sea level and snow cover since the beginning of the industrial era. (from IPCC 2007).*

All differences are relative to corresponding averages for the period 1961-1990. For graph (b) sea level was estimated by tide gauge (black line) and satellite (red line). The snow cover corresponds to the period March - April.

2) Causes of the recent climate change

Causes of climate change are diverse as the Earth's energetic balance is altered by changes in land cover, solar radiation and atmosphere composition in greenhouse gas (GHG) and aerosols. Such changes affect the absorption, scattering and emission of radiation within the atmosphere and at the Earth's surface. The resulting positive or negative changes in energy balance are expressed as radiative forcing[2], which is used to compare cooling or warming influences on global climate.

However, **the anthropogenic origin of the present climate change makes no more doubts** apart for a few climate skeptics (~97% of climate researchers support it according to Anderegg *et al.* 2010). In particular, most of the warming over the past 50 years is very likely to be due to anthropogenic GHG emissions (IPCC 2007). Global GHG emissions due to human activities have increased continuously since pre-industrial times, reaching 70% more emissions in 2004 compared to 1970 for instance (IPCC 2007; Figure I - 4).

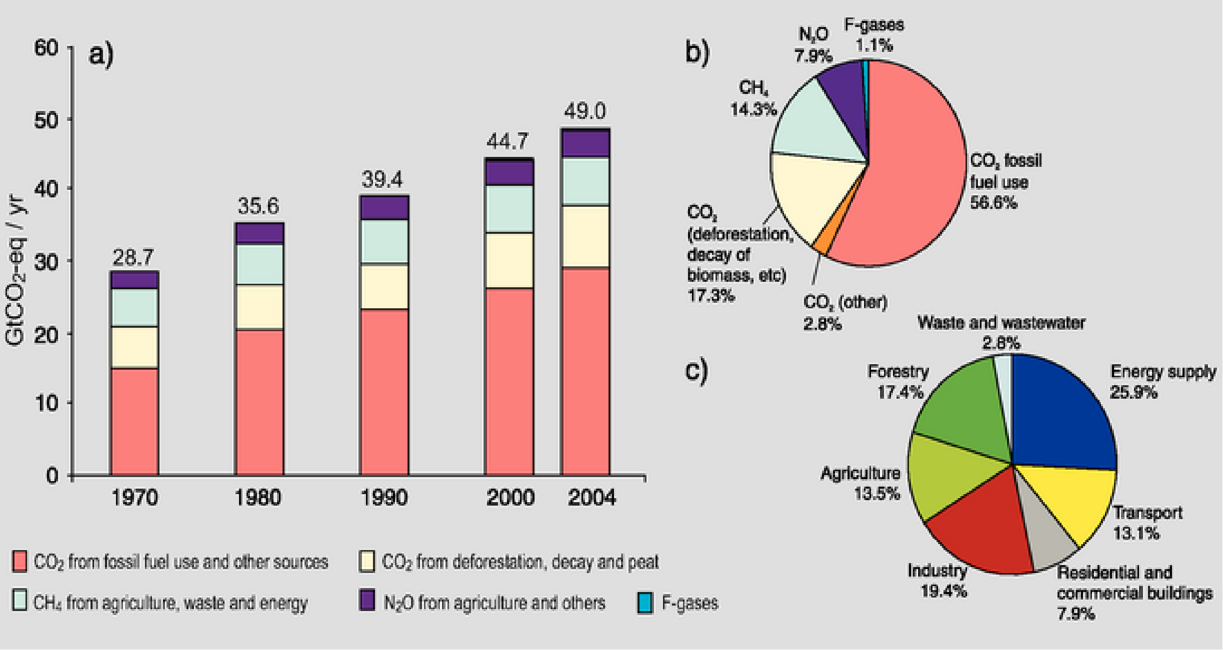

Figure I - 4: *Global anthropogenic GHG emissions. a) Evolution of these emissions from 1970 to 2004, b) share of different GHG in total emissions of 2004, c) share of different human activities in total emissions of 2004. (from IPCC 2007).*

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[2] RADIATIVE FORCING: measure of the influence a factor has in altering the balance of incoming and outgoing energy in the Earth-atmosphere system and is an index of the importance of the factor as a potential climate change mechanism. (definition from IPCC 2007)

Global atmospheric concentrations of CO_2, CH_4 and N_2O have increased considerably since 1750 under human activity influence to reach levels outside of the natural range observed over the last 650 000 years (IPCC 2007; see Figure I - 5 for CO_2 as an example).

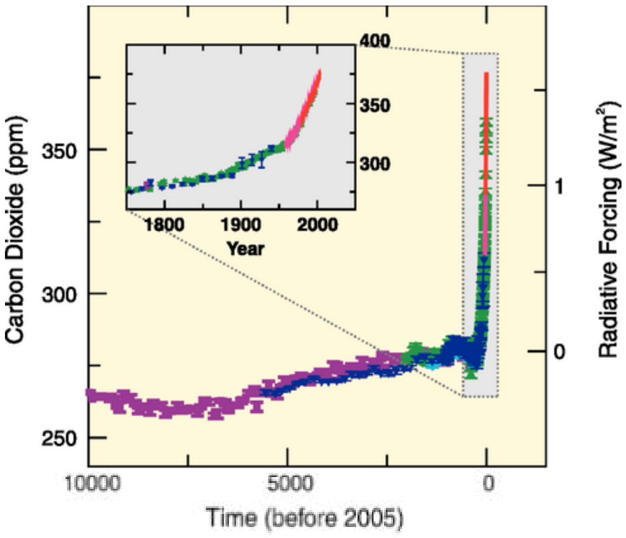

Figure I - 5 : *Atmospheric concentration of CO2 over the last 10 000 yrs. (from IPCC 2007) Measurements come from ice cores (points) and atmospheric samples (red line).*

These increasing emissions change the radiative forcing and consequently the energetic balance of the Earth. According to the IPCC (2007), there is very high confidence (*i.e.* Probability > 0.9) that the total net anthropogenic effect has been one of warming, with a positive radiative forcing of +1.6°C [+0.6 - +2.4] (IPCC 2007).

3) Predictions of future climate

> *« Prediction is very difficult, especially about the future »*
> *Niels Bohr*

Predicting oncoming climate is extremely difficult given the uncertainties on the evolution of the world population, economic growth and climate understanding. Yet, whatever the scenarios, **climate models predict that the 21st century will see an increase of the mean global surface temperature, a regime shift of winds and precipitations, a large reduction of the arctic sea-ice and an increase in both the frequency and amplitude of extreme events** (Meehl *et al.* 2007; Figure I - 7). Even if we stopped emitting GHG now, the time-scale at which climate processes occur is so important that warming would go on for numerous years (Figure I - 7). Yet, there are strong evidences that GHG emissions will continue to grow over the next few decades (IPCC 2007). The question is then: ***how many tons of GHG are we going to emit in the future?***

Emissions rely mostly on demographic and economic growth (number of people on this planet along with their life style) and technological change. To predict the GHG emissions, economists have worked on several economic scenarios simulating various ways of development (IPCC Special Report on Emissions Scenarios, SRES 2000, see box below).

SRES SCENARIOS

"*Scenarios are alternative images of how the future might unfold and are an appropriate tool with which to analyze how driving forces may influence future emission outcomes and to assess the associated uncertainties.*" (SRES 2000). The SRES scenarios are divided into four families (A1, A2, B1 and B2) that explore alternative development pathways covering the widest range of demographic, socio-economic and technological driving forces, excluding only the outlying "surprise" or "disaster" scenarios of the literature (Figure I - 6).

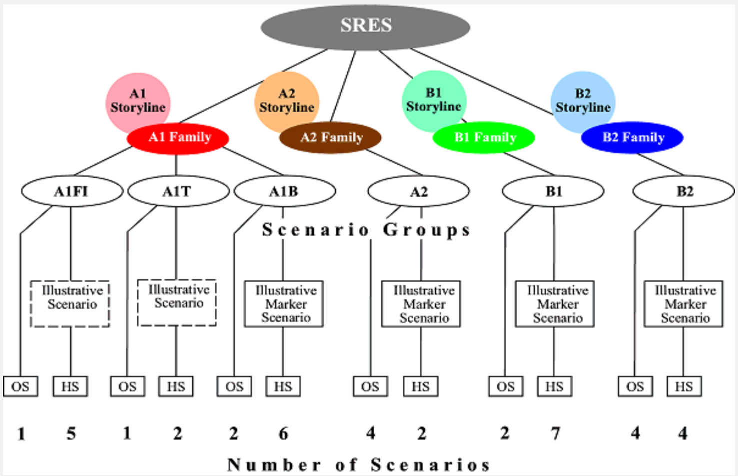

Figure I - 6 *: SRES Scenarios divided in 4 families. (from SRES 2000)*

In total, 40 scenarios have been created by 6 modelling teams.

A1 family: very rapid economic growth, peak of global population in mid-century and rapid introduction of new technologies. This family is divided into three groups according to the types of these new technologies

- **A1F1**: intensive use of fossil energy
- **A1T**: non-fossil energy resources
- **A1B:** balance of energy across all sources

B1 family: with similar world population as A1, but more rapid changes in economy structures towards services and information.

B2 family: intermediate population and economic growth, local solutions preferred to ensure economic, social and environmental sustainability.

A2 family: heterogeneous world with high population growth, slow economic development and technological change.

It is important to note that the possibility that any of this path occurs is highly uncertain, explaining why no likelihood has been attached to the scenarios. However, what actually happens in terms of worldwide economy ought to lie within the range of these scenarios.

Even if we were able to predict the exact future emissions of GHG, the relation between emissions and climate response is not direct. Intermediate calculations of the radiatively active species concentration and radiative forcing are needed, and those introduce small cumulative uncertainties on each step, resulting in large variability around the projected response of climate. Several models were computed for each scenario in order to predict climate responses such as temperature change. According to the IPCC, **the mean surface temperature should increase at least by 0.2°C per decade in the next 20 years** (Figure I - 7). Additionally, **climatic events such as El-Niño should become more frequent** (Timmermann *et al.* 1999).

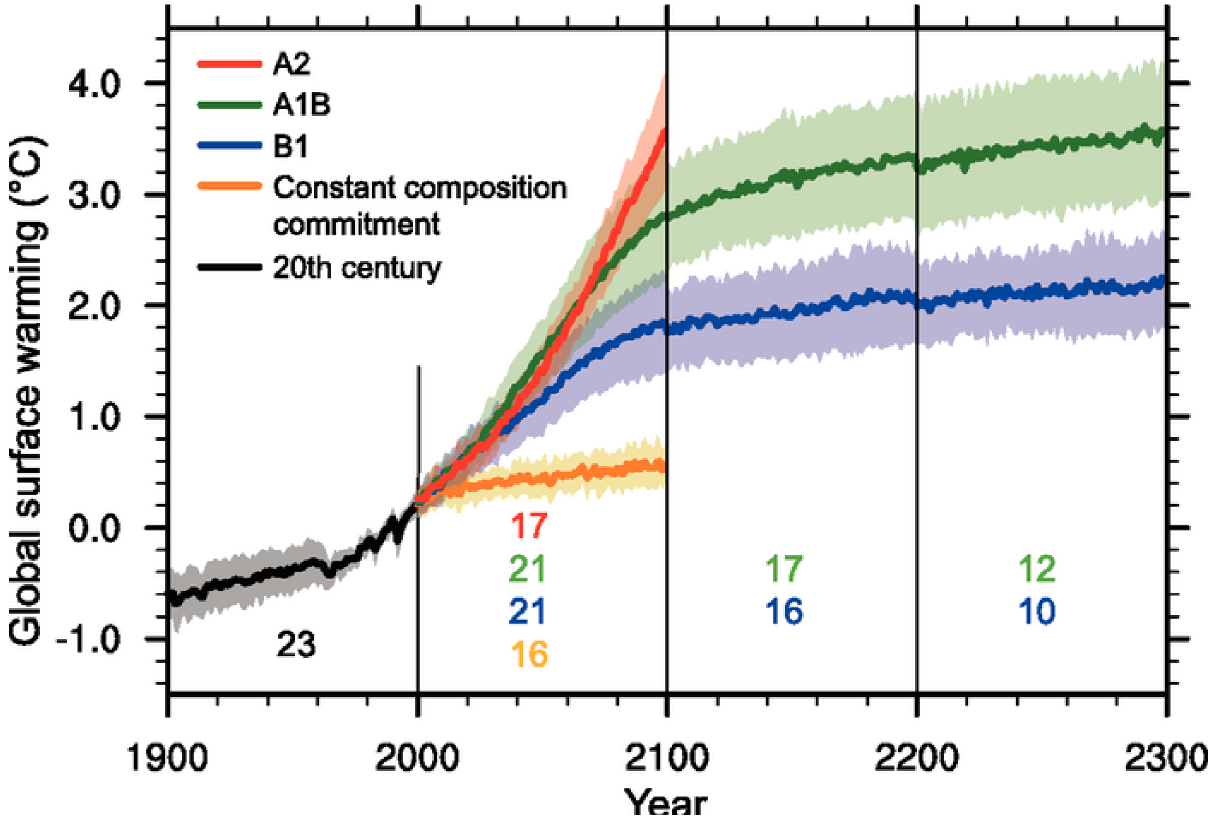

Figure I - 7: *Projected surface warming according to different scenarios.*
Lines show the multi-model means corresponding to one scenario. Figures indicate the number of models used to calculate these means. Discontinuities exist as the number of models is not constant across time. Shaded zone: ± SD range of individual model means.

Of course, the further away the predictions the most associated uncertainties are obtained. As an example, the table below shows the projected warming at the end of the 21st century. We see that if every scenarios lead to a warming, the range of this temperature increase is large within scenarios (variability between models, see A1F1 for instance) and between the scenarios (from 1.8 to 4.0°C in the scenarios presented here, if we remove the non-realistic constant scenario; Table I - 1).

Table I - 1: *Projected global surface warming at the end of the 21st century according to different scenarios*

Case	Temperature change (in °C, 2090-2099 relative to 1980 – 1999)	
	Best estimate	**Likely range**
Constant	0.6	0.3 - 0.9
B1 scenario	1.8	1.1 - 2.9
A1T scenario	2.4	1.4 - 3.8
B2 scenario	2.4	1.4 - 3.8
A1B scenario	2.8	1.7 – 4.4
A2 scenario	3.4	2.0 – 5.4
A1F1 scenario	4.0	2.4 – 6.4

In conclusion, whereas climate has been continuously fluctuating over geological times, its current change has been both amplified and accelerated by human activities, and rapid changes will continue to occur in the future whatever scenarios of economic and population growth we consider. What will be the consequences of such changes? In this PhD, I set out to understanding how organisms and ecosystems might cope with a changing environment.

II. Impact of climate on ecosystems

Many people accord to say that the earth is facing its 6th big extinction crisis and that this crisis results mostly from anthropogenic activities (Thomas *et al.* 2004). However, human activities are numerous and their consequences on biodiversity difficult to disentangle (Parmesan & Yohe 2003). In comparison to other human-induced environmental changes, such as land use or pollution, which dominate short-term local biological changes, direct effects of climate change should be slow and difficult to measure (Kappelle *et al.* 1999). However, processes linked to climate are global and practically irreversible. Moreover, as explained by Kappelle and colleagues (1999), climate change will exacerbate the stresses already imposed by human activities on the environment. For instance, in a fragmented environment, species may be unable to move to climatically more profitable areas, as they may not cross the barriers between the remaining natural areas.

> *« Climate change poses a potential threat to the earth's biodiversity »*
> *Kappelle et al. 1999*

Though climate seems to us an important driver of the recent and future changes in ecosystems, many scientists are still skeptical (see for instance Forchhammer & Post 2000;

Kozlov 2000 both in response to Hughes 2000). This is probably the result of two different processes. First, as stated above climate change occurs on a long-term perspective and as such is not responsible for most of the recent short-term biological changes and is difficult to observe, as one needs long-term datasets to scientifically investigate the effect of climate. Second, most of the studies rely on correlation approaches stating that populations changed concomitantly to climate changes, but with no proof of causality. Mechanistic approaches focusing on individual biology, are needed to test the reality of the effect of climate on living organisms and population dynamics (Kearney & Porter 2009).

However, there is an accumulating and ever increasing body of evidence that climate affects a wide range of biological systems, from polar terrestrial to marine tropical environments (Hughes 2000; McCarty 2001; Stenseth *et al.* 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006). In its last report the IPCC reviewed data from 75 studies and 29 000 data series, showing that more than 89% of the changes in physical and biological systems observed were consistent with the direction of change expected as a response to warming (IPCC 2007). **Climate impact on individuals and populations may operate (**Ottersen *et al.* 2001) **either directly** mostly through physiology (metabolic and reproductive processes), **indirectly** through changes in habitat or food supply (McCarty 2001; Stenseth *et al.* 2002) or even **in an integrated way** through delayed long-term effects of environmental conditions experienced early in life on later survival and breeding performances (Albon *et al.* 1987; Gaillard *et al.* 1997; Lindström 1999; Forchhammer *et al.* 2001).

1) Direct effects

Direct immediate effects of climate are the most documented ones and **can result from changes in temperature, precipitations and atmospheric composition**. The direct effect of ambient temperature on **physiology** through metabolism is well-known (Louw 1993). All organisms live within a limited range of body temperatures and thermal windows evolved to be as narrow as possible to reduce costs (Pörtner & Farell 2008). Climate warming can thus have direct consequences on growth, reproduction, foraging, immune competence, behaviour and competition (Pörtner & Farell 2008). This is especially true for ectotherm species, whose metabolism relies on ambient temperature (see for example Tewksbury *et al.* 2008), while the amplitude of the recent warming may be too small compared to the thermoneutrality range of endotherm species to affect them directly (Porter & Kearney 2009). Photosynthesis and hence plant growth and productivity are directly affected by temperature and atmospheric CO_2 concentration. The increase in CO_2 concentration along with the warming thus leads to an increase of photosynthesis activity. Since 1960, this activity has for instance increased by 20% in Hawaï and 40% in the Arctic (Keeling *et al.* 1996). Precipitations can also affect directly organisms through water stress, which is one of the main drivers of vegetation distribution for instance (Woodward 1987). Snow can also affect foraging capacities of grazers, such as deer (Post & Stenseth 1999).

Climate change is also responsible for changes in **phenology**[3] both in plants and animals. In general, spring activities have occurred earlier (Parmesan & Yohe 2003), while autumnal events may have been delayed (even if autumnal shifts are less pronounced; Walther *et al.* 2002). Vegetation duration has for instance increased by more than a week since 1970 (Myneni *et al.* 1997; Menzel & Fabian 2004). Datasets on 677 species have been reviewed by Parmesan & Yohe (2003) and 62% have shown an advance in spring activities. Observed trends include earlier first flowering, tree budburst, frog breeding, bird nesting and arrival for migrant birds and butterflies (Parmesan & Yohe 2003).

Many studies have focused on **abundance and distribution** of species. The local abundance of species, especially those living in high latitudes or altitudes and marine environment is affected by climate change (Hughes 2000). As an example, abundance of zooplankton has been reduced by 70% between 1951 and 1993 along the coast of California. This reduction is associated with an increase in sea surface temperature, which led to a reduction of water mixing and nutrient income in the euphotic zone. But most of these changes are associated with shifts in distribution. Species distributions are influenced by climatic regimes through physiological thresholds of temperature and precipitation tolerance (Woodward 1987; Hoffman & Parsons 1997). Thus, 'climate envelopes'[4] are expected to shift towards higher altitudes or latitudes in reaction to climate warming. However, these shifts can be limited by factors such as light tolerance and dispersal abilities (Walther *et al.* 2002). Additionally, species that already live under extreme climatic conditions (in mountains or poles) may not have any more favourable areas to go to. Studies have documented poleward and upward shifts of species ranges across a wide range of species and geographical locations

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[3] PHENOLOGY corresponds to the timing of specific activities.
[4] CLIMATE ENVELOPE: area where a species is to be found in the future to live in the same climatic conditions

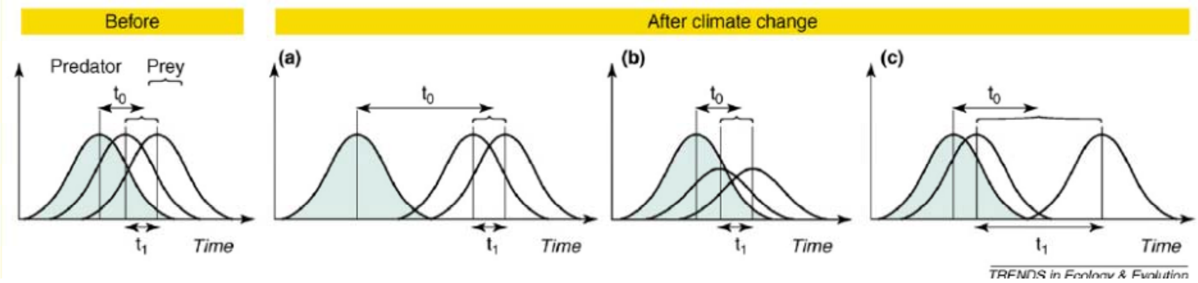
during the last century (Hughes 2000; McCarty 2001; Parmesan & Yohe 2003; Root *et al.* 2003). Of the 893 species reviewed by Parmesan & Yohe (2003), less than a third has exhibited a stable distribution across time. The maximal amplitude of these distribution shifts varies across species from 200km (butterflies) to 1000km (copepods) over the past 40 years (Parmesan & Yohe 2003).

2) Indirect effects

A shift in distribution, as a shift in phenology, can appear relatively benign if not a good sign. Indeed, this indicates that species have the ability to respond to climate changes by modifying the timing of their life-history events or by moving towards better conditions. However, this could be the source of **more complicated indirect effects** on their demographic parameters. A shift in phenology may for example disrupt important correlations with other ecological factors (McCarty 2001). Migratory species may have to face different rates of climate changes according to areas and not be able to adjust phenology for each one. But mainly, "*responses by individual species may disrupt their interactions with others at the same or adjacent trophic levels*" (Walther *et al.* 2002). When two competing or interacting species react differently, the outcome of their interactions may be altered, often resulting in changes in abundance of at least one of the two species.

> *« What escapes the eye… is a much more insidious kind of extinction: the extinction of ecological interactions »*
> ***Janzen 1974***

Changes in phenology could create an asynchrony (or mismatch) between species, resulting in changes in inter-specific interactions such as predation (Figure I - 8). Trophic interactions between predator and prey have been reported to be altered (see review in Durant *et al.* 2007) in fish-plankton (Cushing 1990; Ottersen *et al.* 2001), insect-plant (Visser & Holleman 2001) and bird-insect systems (Thomas *et al.* 2001; Visser *et al.* 2003). The temporal **match-mismatch** hypothesis (Cushing 1990) predicts that predator's recruitment would be high if the peak of prey availability temporally matches the most energetic period of predators' breeding phenology. Conversely, a mismatch (situation when there is no overlap between the two peaks) will lead to poor recruitment. Depending on systems, species will either respond to climate change similarly and be able to maintain this synchrony (Buse & Good 1996) or respond differently and disrupt the system. Similarly, shifts in distribution area or decline in abundance of a species may well mean the disappearance of a competitor or important prey for another species of the ecosystem.



TRENDS in Ecology & Evolution

Figure I - 8: *Potential indirect effects of global change on predators (from Cury et al. 2008)*
a) mismatch due to desynchrony of the predator and its prey. b) decrease in prey abundance, leading to poor resources even if the species are synchronized. c) maintained synchrony and abundance of the prey but increase in variability and thus previsibility of prey timing, leading to mismatch on certain years.

3) Long-term integrated effects

Finally, climate could impact population dynamics through **delayed long-term cohort[5] effects**. Adverse conditions during early development[6] may affect growth, metabolism and immune-competence (Lindström 1999). The resulting phenotypes should endure adult life differently than those produced under favourable conditions (cohort effects; Figure I - 9). Conditions experienced early in life may thus affect later survival and reproductive performance (Gaillard *et al.* 1997; Lindström 1999; Forchhammer *et al.* 2001), through long-term changes in metabolic rate for instance (Criscuolo *et al.* 2008).

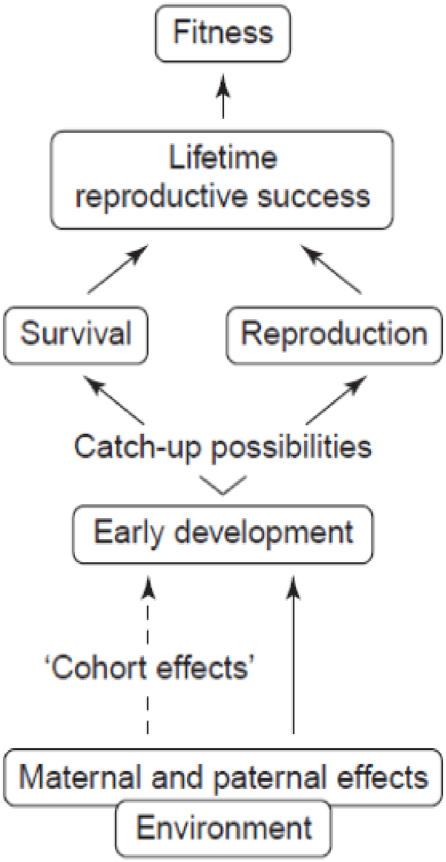


Figure I - 9: *Early-life condition consequences on fitness (Lindtsröm 1999)*

Other physiological direct effects of temperature may present unexpected challenges in later life-history traits (McCarty 2001). For instance the sex of turtle embryo is entirely determined by environmental temperature (Bull 1980), with eggs under warmer conditions producing males and in cooler conditions females (Janzen 1994 for the painted turtle). As a

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[5] COHORT: group of individuals born during the same breeding season under similar environmental conditions
[6] EARLY DEVELOPMENT: period from conception to developmental maturity

consequence, the sex-ratio of produced offspring is explained by the mean temperature in July (Janzen 1994). Under climate warming, turtle may suffer extinction risk or at least important changes in abundance only as a result of skewed sex-ratio.

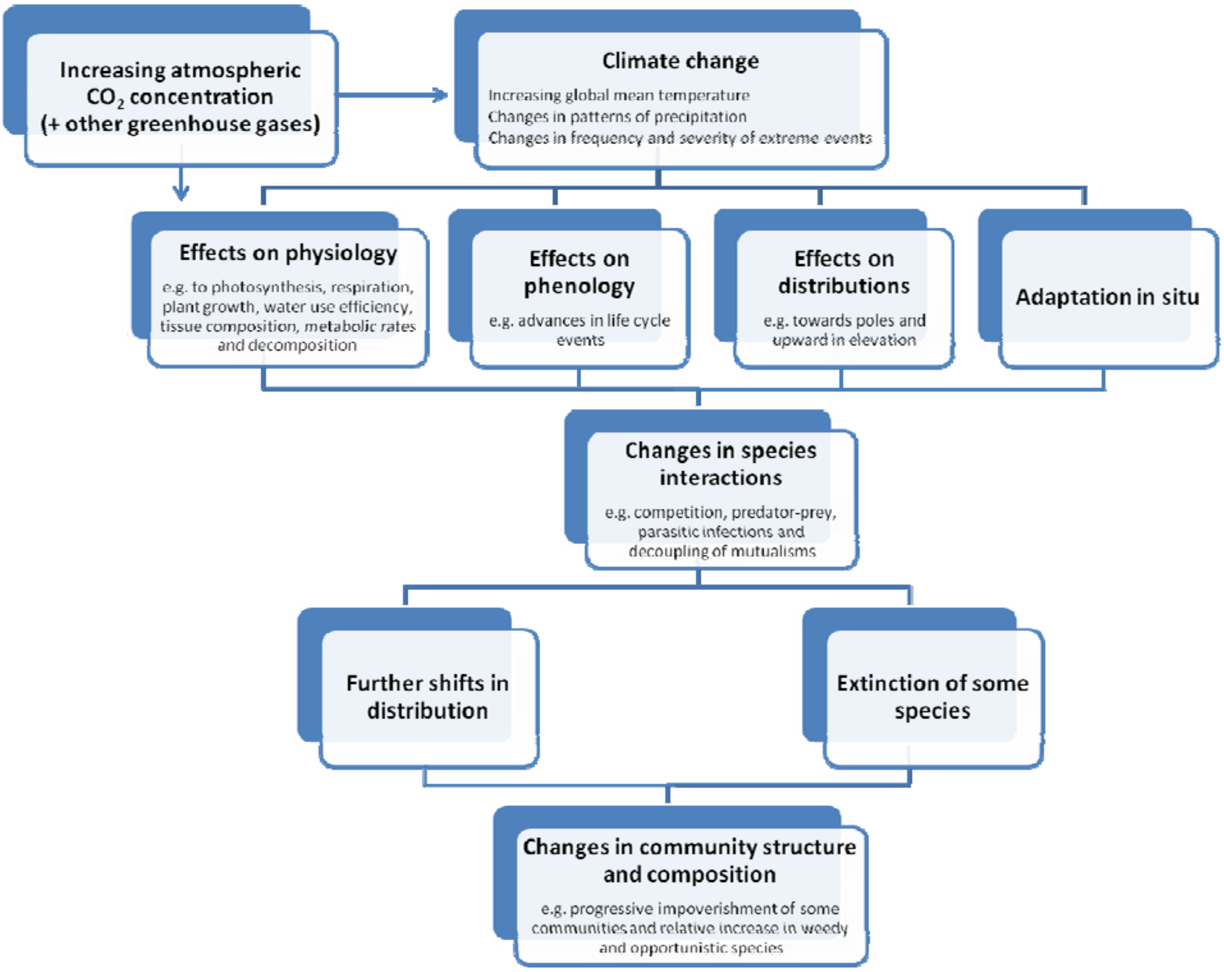

Figure I - 10: *Summary of the effects of climate on organisms (copied from Hughes 2000 in TREE)*

Biological changes are now well documented across taxa and geographic locations, leaving no doubt on the detrimental effects of climate change on biodiversity, though the mechanistic link can be difficult to establish. In this PhD, I try to understand the direct, indirect and integrated effects of climate (Figure I - 10) **on ecosystems and to define the nature of the mechanisms underlying these effects. Ultimately, such knowledge may help to better predict population trends in the future and help with conservation or management measures.**

III. Predicting the impact of climate on populations

Predicting the possible impact of climate changes on populations and biodiversity is a critical task assigned to scientists nowadays. Society has indeed to face increasingly global environmental changes, mostly human-induced, and decision-makers accordingly need scientific information to make previsions and anticipate the effects of these changes. Knowledge and understanding of consequences of climate change on population dynamics are therefore indisputably necessary to fathom the future of populations, species or ecosystems.

Temporal changes in population can be monitored through counts realized frequently enough, at similar dates and similar periods in terms of phenology[7] of the species. Indeed, long-term datasets of counts give population trends that can be correlated to climate and even projected according to climate predictions. However, this gives no information on the mechanisms involved in the observed changes. Population changes reflect the balance between gains (reproduction and immigration) and losses (mortality and emigration), which can all be affected by climate (Figure I - 11).

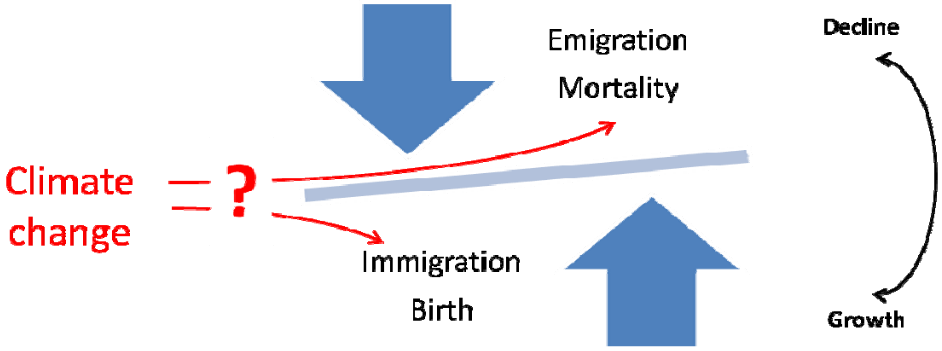

Figure I - 11: *Balance between gains and losses in the population, resulting in decline or growth of this population.*

In order to better understand and predict population dynamics, one needs to find a way to differentiate between these different components. One way is thus to monitor a sufficient number of individuals, their survival, reproduction, *etc.* and then to link these individuals to the population.

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[7] PHENOLOGY: time frame for any seasonal biological phenomenon. This could include a variety of parameters such as dates of first appearance of leaves in plants, of egg-laying in birds and reptiles, of migration, *etc.*

1) Demography: from individuals to populations

> *Not only the adult, but the whole life cycle will be considered the organism. This is an ancient notion, for philosophers have often pointed out that an individual conventionally means an organism in a short instant of time (...) For example, if we refer to a "dog" we usually picture in our minds an adult dog momentarily immobilized in time as though by a photographic snapshot. (...) [But] is the dog not a dog from the moment of fertilization of its egg, through embryonic and foetal development, through birth and puppyhood, through adolescence and sexual maturity, and finally through senescence?*
> **Bonner, 1965**

To infer population trends from individuals, one needs a sufficient number of individuals that are representative of this population. The simplest population model considers that all individuals are identical and behave the same way. Monitoring of a few (even 1) individuals should thus be enough. The other extreme would be to consider that every individual in the population is different, which is true for most organisms but would mean to monitor every individual of the population. This is one of the most complicated dilemmas of science: ***how to keep it simple (or at least feasible) but also realistic?*** Scientists try to solve this trade-off by categorizing the population into different states. Most often these states are defined on the basis of the life-cycle. The assumption is that every member of a state responds the same way, thus discarding any intra-class variability. A general example of such a life-cycle graph is given in Figure I - 12. Note that such a graph does not allow taking into account new individuals from immigration, one of the most difficult parameter to estimate (Forero *et al.* 2002). The ecology of the species will then enable to estimate the different probabilities associated to enter in the population model to calculate population growth rate and infer population trends.

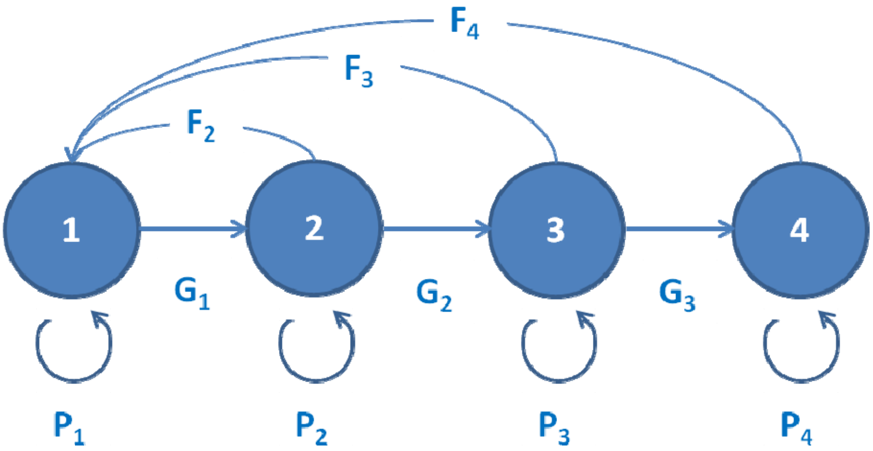

Figure I - 12: *General life-cycle graph with 4 different states.*
Individuals survive and stay in their state with probability P_i or enter the following unit with probability G_i, they reproduce with fertility F_i producing new individuals in class 1.

An important consideration to build this group is the reproductive status of individuals. Reproductive maturity can be reached at a certain age or a certain size (*e.g.*, trees Zon 1915; fish Alm 1959). Consequently, age and size but also reproductive modes (for species that exhibit several modes of reproduction, *e.g.*, sexual and vegetative or clonal reproduction; Jackson 1985) have often been chosen as the variables driving the different categories. For instance in the graph above, if class 2 has not reached sexual maturity (either because they are too small or too young) F_2 would be equal to 0. Age and size can also govern reproductive performances and survival probabilities (Schmidt-Nielsen 1984). As an example, some studies have shown the importance of senescence in reproductive capacities of organisms (see Nussey *et al.* 2008 for a review). The fourth class could well represent a group of senescent individuals with a lower fecundity $F_4 < F_3$. Similarly, juvenile survival is often considered to be smaller than adult survival due to inexperience (Lack 1954; Sullivan 1989; Grüebler & Naef-Daenzer 2010), so that $P_2+G_2 < P_3+G_3$.

In some cases, the unidirectional arrows between the states are not adapted and individuals could go back and forth in between stages. For instance in an adult population, individuals facing trade-offs between their survival and reproduction (Stearns 1992) may decide not to reproduce. This could be modelled by two different classes of adults, one breeding the other not with the possibility for each individual to stay in its group or go in the other one (Figure I - 13).

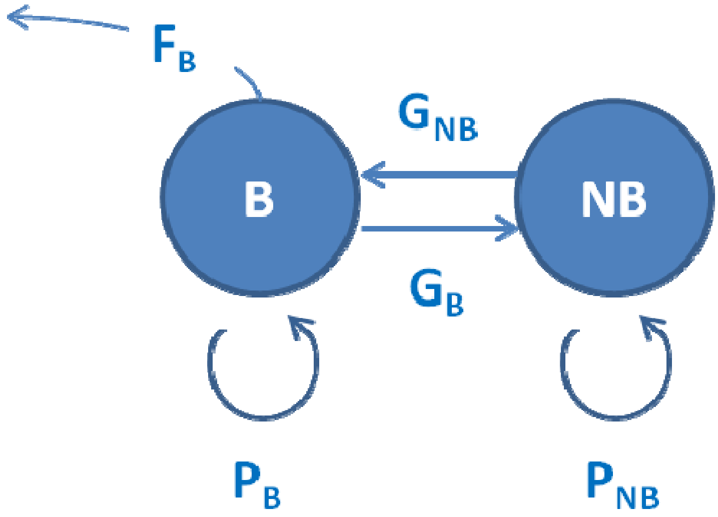

Figure I - 13: *Life cycle integrating 2 groups of adults, one breeding and the other not.*
B stands for breeders and NB for non-breeders. P and G indicate the probability to stay in the group or to change. The fecundity is indicated only for group B, as the other does not reproduce.

Mathematic bases of population modeling

Life-cycle graphs are very handful to build population models and are isomorphic to the population projection matrix A in the equation

$$\boldsymbol{n}(\boldsymbol{t}+\mathbf{1}) = \boldsymbol{A}\,\boldsymbol{n}(\boldsymbol{t}) \qquad \textbf{(Equation 1)}$$

where n(t) represents the vector of abundance of each stage determined earlier with the life-cycle graph (Caswell 2001).

The coefficients of the matrix $a_{i,j}$ correspond to the transition probabilities from the nods N_j to N_i. The matrix corresponding to the graph (Figure I - 12) is the one below.

$$\mathbf{A} = \begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

If this matrix is invertible, there is an orthogonal base of d eigenvectors $\mathbf{v_i}$ so that $\boldsymbol{A}v_i = \lambda_i \boldsymbol{v_i}$ where d is the dimension of the matrix and λ_i are the eigenvalues of the matrix, *i.e.* the solution of det $(\mathbf{A}-\lambda\mathbf{I}) = 0$. By decomposing *n(t)* on this base, we obtain

$$n(t) = \sum_{1}^{d} c_i(t)\mathbf{v_i} \qquad \textbf{(Equation 2)}$$

$$n(t+1) = \mathbf{A}\sum_{1}^{d} c_i(t)\mathbf{v_i} = \sum_{1}^{d} c_i(t)\mathbf{A}\mathbf{v_i} = \sum_{1}^{d} c_i(t)\lambda_i\,\mathbf{v_i}\,. \qquad \textbf{(Equation 3)}$$

Based on common geometric series, we obtain

$$n(t) = \sum_{1}^{d} c_i \lambda_i^t \mathbf{v_i} \qquad \textbf{(Equation 4)}$$

where c_i represent the initial conditions (*i.e.* the decomposition of n_0 on $(v_1 \ldots v_d)$). **A** being a non-negative matrix, there is at least one real strictly positive eigenvalue and this eigenvalue, called the dominant eigenvalue, is greater than or equal to the others in magnitude. If we order the eigenvalues such as $\lambda_1 \geq |\lambda_2| \geq \ldots \geq |\lambda_d|$, we obtain

$$\frac{n(t)}{\lambda_1^t} = c_1\mathbf{v_1} + c_2\left(\frac{\lambda_2}{\lambda_1}\right)^t \mathbf{v_2} + \ldots + c_d\left(\frac{\lambda_d}{\lambda_1}\right)^t \mathbf{v_d} \qquad \textbf{(Equation 5)}$$

If $\lambda_1 >| \lambda_2|$

$$\lim_{t\to\infty} \frac{n(t)}{\lambda_1^t} = c_1\mathbf{v_1} \qquad \textbf{(Equation 6)}$$

The case where the dominant eigenvalue has the same magnitude as other complex eigenvalues is more complex, as the limit is periodic. However, this means that the limit exhibits some cyclicity in the population dynamics (which reflects the cyclicity of the life cycle) and that the average over the period of oscillation grows at a rate λ_1.

Population growth rate is thus defined as this dominant eigenvalue and is the result of asymptotic analysis. Therefore, it assesses the long-term behaviour of a population. When $\lambda > 1$, the population grows, while $\lambda = 1$ means that the population is stable and $\lambda < 1$ that the population declines. Further, one of the strong assumptions made in the model presented above is that the projection matrix **A** is time-invariant. This means that the projections we obtain correspond to the future of populations if the present conditions were to be maintained indefinitely. This seems absurd as vital rates of most organisms vary in time, especially in the present context of climate change. In order to predict the response of populations to climate change, the equation needs to be transformed in $n(t+1) = A_t\, n(t)$, where each component of the matrix can vary according to time. The usual solution is to allow vital rates to depend on climate parameters such as temperature or precipitations (relations estimated over past data) and use temporal predictions of these parameters to build A_t (Figure I - 14).

> *« The use of deterministic rather than stochastic models can only be justified by mathematical convenience »*
> *Maynard-Smith*

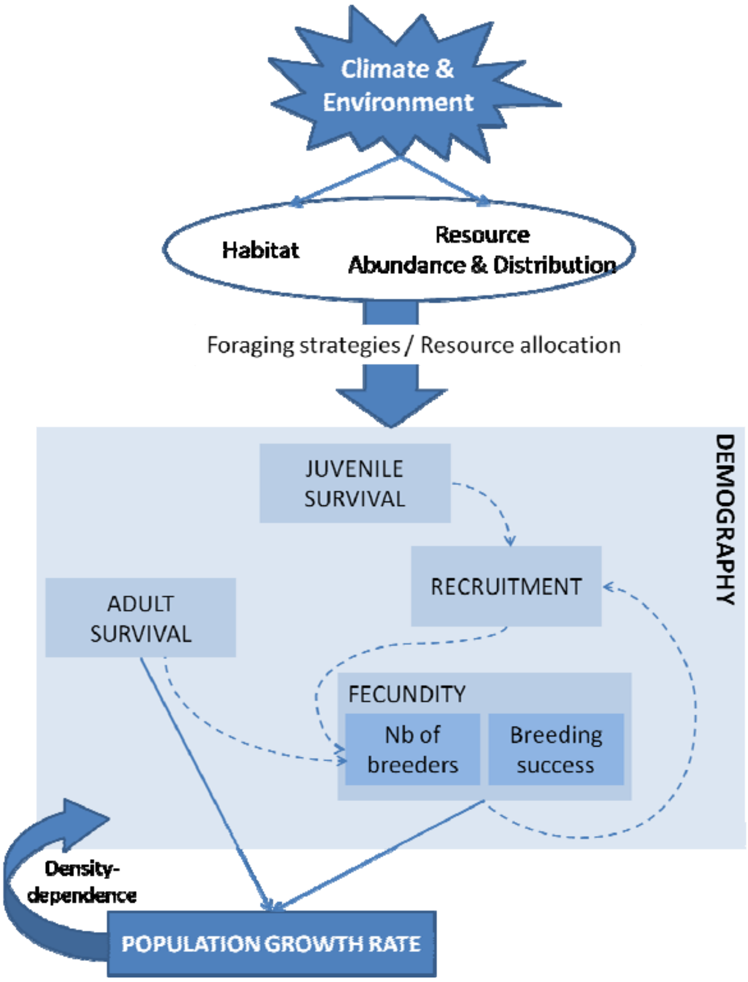

Figure I - 14: *Main vital rates, their sensitivity to climate and their contribution to population growth rate*

In summary, **to predict future population responses to climate** through demographic models, one **needs to assess first the vital rates of this population** (survival and fecundity of the different classes in population) and **the effects of climate on these vital rates**.

2) Life-history theory

Vital rates, such as survival and fecundity depend on several life-history traits[8]. According to Stearns, "*the key life-history traits are brood size, size of young, the age distribution of reproductive effort, the interaction of reproductive effort with adult mortality and the variation in these traits among an individual's progeny*" (Stearns 1976). For instance, fecundity of the population is function of the brood size, the actual success of raising offspring but also of the number of breeders in the population, which depends on recruitment and adult survival (Figure I - 14). According to natural selection genotypes that enable organisms to better survive and reproduce should increase the fastest and dominate the population. Thus, natural selection should favour genotypes that enable organisms to have more offspring that survive well and mature fast (*e.g.* high number of offspring per reproduction and as many reproductions as possible by starting to reproduce early, having a lot of reproductive episodes per unit time and continuing to reproduce late in life with a high longevity). In that optic, we might expect ever-greater fecundity, ever-longer life and ever-earlier maturation. *Why then are organisms limited in their capacities for high reproduction and survival?* Why do we observe Pacific salmons to reproduce a single time and die after, or bats to have single offspring? Energy is not unlimited for organisms and energy invested in reproduction for instance is lost for other functions. These physiological constraints lead to energy allocation trade-offs between the major life functions and in particular between growth, reproduction and maintenance (Williams 1966). Life-history theory has then as main goal to unravel the combinations of traits that will evolve in organisms living in specified conditions (Stearns 1976). The most important trade-off concerns the cost of reproduction (Williams 1966), both in terms of cost on survival and costs on future reproductions (Stearns 1989). Organisms have evolved different strategies to

> *« The central biological problem is not survival as such, but design for survival »* ***Williams 1966***

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[8] LIFE-HISTORY TRAITS: morphological, behavioural and physiological characteristics that affect the fitness of an individual and represent different investments into growth, reproduction and survival and which are submitted to natural selection.

maximize their fitness[9]. Some abandon reproduction in favour of propagation of their genes through siblings, while others decide to invest all their energy in one reproduction or in the contrary to reproduce at the lowest cost possible but several times. Demographic tactics describe complex co-evolution of demographic parameters in response to environment (Stearns 1976).

Two extreme life-history strategies have been defined in the 60's as a result of density dependent natural selection (MacArthur 1962). McArthur and Wilson first coined the terms r-selection and K-selection to represent the quantitative extreme corresponding to an absence of density effect and competition and the qualitative extreme in which density effects are maximal and the environment is saturated by organisms, respectively (MacArthur & Wilson 1967). As most species under one of these two selections are characterized by similar life-history traits, these terms of r and K have been often used as labels since. K-label corresponds to the "*label applied to the combination of late maturity, few, large young, a long life and small reproductive efforts*", while r-label is a "*label applied to the combination of early maturity, many small young, a short life and large reproductive efforts*" (Stearns 1976). Surely, there is no clear dichotomy between r- and K-labels rather these two extreme strategies set the life-history strategy range, in between which organisms have to compromise (the so-called r-K gradient; Pianka 1970). These theoretical strategies have been evaluated through empirical data on birds and mammals (Gaillard *et al.* 1989). Body mass appeared as one of the main drivers of life-history traits (*first order tactics* Western 1979; allometric component Lebreton 1981; Dobson & Oli 2007) but after correcting for this factor, species always ranked along a gradient from the slowest to the fastest turnover rate (*second order tactics* Western 1979). Finally a last gradient has been highlighted from iteroparity[10] to semelparity[11] (mostly in mammals). Importantly, we should note that these demographic tactics are not set. We often refer as a species as slow or fast giving the impression that it cannot change. Yet, we just highlighted that they evolved in response to their environment and any change in environment may lead to a new equilibrium of demographic parameters.

Vital rates of organisms are not independent from each other but follow a global strategy resulting from complex trade-offs of resource allocation and that has evolved in response to environment as to maximize fitness. Depending on its strategy, climate change should affect a species through different vital rates.

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[9] FITNESS: "*something everyone understands but no one can define precisely*" (Stearns 1976). Still it may be viewed as the ability of an individual's genotype to propagate into the population and into the future through kin (offspring and siblings).

[10] ITEROPARITY: Reproductve strategy in which organisms produce offspring in successive breeding cycles.

[11] SEMELPARITY: Reproductive strategy in which organisms reproduce only once in their lifetime.

3) Relative importance of life-history traits to population growth

Relative contribution of life-history traits to variation in population growth is especially important for ecologists, because knowledge of these contributions is required for conservation or regulation purposes (Dobson & Oli 2001). To develop management strategies, one needs first to identify the main cause of the decline or increase in the population to know on which parameter to concentrate its effort. For instance, is it better to reduce mortality by limiting predation or to favour measures directed to improve breeding conditions? This is the situation that decision-makers face every day. Further, as one cannot monitor and study everything, relative importance of life-history traits in demography may help researchers to make relevant choices on their protocols.

Several methods to infer this relative importance have been developed and used widely (see references in Coulson *et al.* 2005). Mainly, the first method developed was that of k-value analysis, which contain several problems and was rapidly abandoned in favour of demography approaches, such as structured accounting of the variance of demographic change or the matrix model based on elasticity analyses (Caswell 2001).

When looking at the effect of different life-history traits on population growth through elasticity analyses, Oli & Dobson (2003) showed that age at last reproduction has consistently the lowest effect through species. However, there are no data to support the theory that age at first maturity or any other parameters actually (Cole 1954; Lewontin 1965; Stahl & Oli 2006) had the largest relative influence in the majority of populations. Evidence for the importance of the slow-fast continuum (assessed by the ratio fecundity / age at maturity) in the relative influence of life-history traits on population growth appeared in this study on mammals. Population dynamics of slow species (or K-selected also called long lived) are more sensitive to adult and juvenile survival than other life-history traits, while fast species are more sensitive to fecundity and age at first reproduction (Gaillard *et al.* 1989; Oli & Dobson 2003; Stahl & Oli 2006).

However, natural selection should drive individuals towards a maximization of the selective value or fitness and a minimal variance associated especially in the case of traits to which this selective value is highly sensitive (Pfister 1998). Demographic parameters that strongly affect population dynamics should thus vary less compared to those which have a low impact on population growth (Horvizt *et al.* 1997 in plants; Gaillard *et al.* 1998 in ungulates; Rochet *et al.* 2000 in fish). Thus, fitness components that strongly affect population growth are expected to be canalized against temporal variability. This canalization hypothesis (Gaillard & Yoccoz 2003) is supported by data on different populations of ungulates. In birds, Saether & Bakke (2000) also highlighted a negative relation between sensitivity of population growth rate to a demographic parameter and temporal variation of the latter. Finally, Coulson and colleagues (2005) confirm that demographic rates with the highest elasticity were not often those showing the largest contributions to variation in population growth.

The relative contribution to population growth also differs according to the selective pressure that applies on the populations. As an example, by comparing two populations of bighorn sheep, Coulson and colleagues (2005) observed very different roles of adult survival in population growth. Adult survival had three times more effect on the growth of the population that faced pneumonia and predation than that controlled by density dependence. "*The large diversity of ecological processes that affect populations of large vertebrates generates different demographic responses that potentially allow all life-history stages to play a substantial role in contributing to distributions of population growth characterized from a time series*" (Coulson *et al.* 2005).

Vital rates all contribute to population growth rate. However, some will affect it more than others and their response to climate change is thus essential to investigate. Yet, these traits should be the less variable as a result of evolution towards optimization of fitness (mechanism of canalization). In that case, the effect of climate may be visible only on the less contributing vital rates. For instance in long lived species, adult survival is usually the vital rate affecting most population growth rate but also the one exhibiting the smaller inter-annual variability. In this thesis, I investigate the effect of climate on vital rates that should react importantly to climate (mainly reproduction in long lived species) and also on vital rates that contribute importantly to population growth rate to check whether the 'canalization hypothesis' is verified facing such drastic changes as those caused by climate change.

4) Potential adaptations[12]

Another important point to underline is that previsions assume that animals will react in the future to the same extent as they did during the past, *i.e.* they will **not** adapt in response to predicted changes. Yet, in many instances adaptation is likely to mitigate the impacts predicted by models (Skelly *et al.* 2007). When facing a new selection pressure, such as global warming, animals can either move towards a more favourable area, adapt to the new conditions through micro-evolution mediated by genetic changes and natural selection, or adapt their phenotypic reaction norm to their new environment (Davis *et al.* 2005). The relative importance of these three ways of coping with climate change depends on the timescale considered, the rate and extent of climate change, life-history strategies and availability of alternative habitats in regard to species dispersal ability (Gienapp *et al.* 2008).

> *«In the struggle for survival, the fittest win out at the expense of their rivals because they succeed in adapting themselves best to their environment. »*
> ***Charles Darwin***

Individuals might indeed react differently to global warming and be able to cope with climate change if they could adapt by micro-evolutionary changes or phenotypic plasticity (Nussey *et al.* 2005; Nussey *et al.* 2007; Visser 2008, Charmantier *et al.* 2008). Micro-evolution modifies the gene frequency within a population by decreasing the frequency of genotypes that have the lowest fitness, while phenotypic plasticity corresponds to the situation when a single genotype express different phenotypes according to environmental pressure (Gienapp *et al.* 2008; Visser 2008). Population models or climate envelope models typically assume that the relationships established between organisms and their environments do not evolve through time (Grémillet & Boulinier 2009). However this is highly unlikely to be the case as functional relationships may shift due to phenotypic plasticity. Such plasticity can either be fixed after exposure to environmental conditions during development (*e.g.* body size) or can be reset every year (*e.g.* laying dates). Flexibility in behaviour is often a pre-requisite of phenotypic plasticity.

The effects of climate change monitored in a species could well be attenuated by adaptations of this species to its new environment. Therefore, in this thesis I also investigate behavioural plasticity as an indicator of adaptation potential.

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[12] ADAPTATION: change in a phenotype that occurs in response to a specific environmental signal and has a clear functional relationship to that signal that results in an improvement in growth, survival or reproduction (Williams 1966).

IV. Marine environment

1) Oceans are important but poorly studied ecosystems

Oceans cover more than 70% of the earth planet and contribute to most of the world biological production (Mann & Lazier 1991). Additionally, oceans play an extremely important role in the world climate regulation through currents and the interaction between sea and atmosphere dynamics (Minster 1998). Finally, ocean biodiversity constitutes resources of an enormous socioeconomic value through alimentary production, nutrient recycle and gas regulation, even estimated at 21 trillions of dollars (Costanza *et al.* 1997). In this context, the monitoring of climate perturbations and their impact on marine ecosystems is a scientific but also socioeconomic priority (Parmesan & Yohe 2003).

Oceanographic features and large scale climate fluctuations, such as El-Niño or the North Atlantic Oscillation (Stenseth *et al.* 2002) show important inter-annual variability and strongly impact marine ecosystems (Ottersen *et al.* 2001; Schreiber 2001). Important regime shifts have for instance been observed in Atlantic, Pacific and Southern Oceans (Hare & Mantua 2000; Weimerskirch *et al.* 2003; Alheit & Niguen 2004; Ainley *et al.* 2005; Jenouvrier *et al.* 2005a). Marine species seem to be very sensitive to climatic fluctuations and global warming has already significantly affected marine ecosystems (Hughes 2000; Richardson & Schoeman 2004; Behrenfeld *et al.* 2006; Halpern *et al.* 2008). This impact is expected to increase in the near future owing to the current acceleration of warming (Trenberth *et al.* 2007).

A thorough understanding of marine and coastal ecosystems is thus a global priority if we are to detect early signs of climate changes and more importantly if we wish to predict the response of animal populations to these changes. Yet, marine environments are those, on which we possess the least information. The 2007 Intergovernmental Panel on Climate Change report indeed highlighted our limited knowledge on the response of marine environments to climate changes and an urgent need to remedy to this lack of information (*cf.* Richardson & Poloczanska 2008; Figure I - 15).

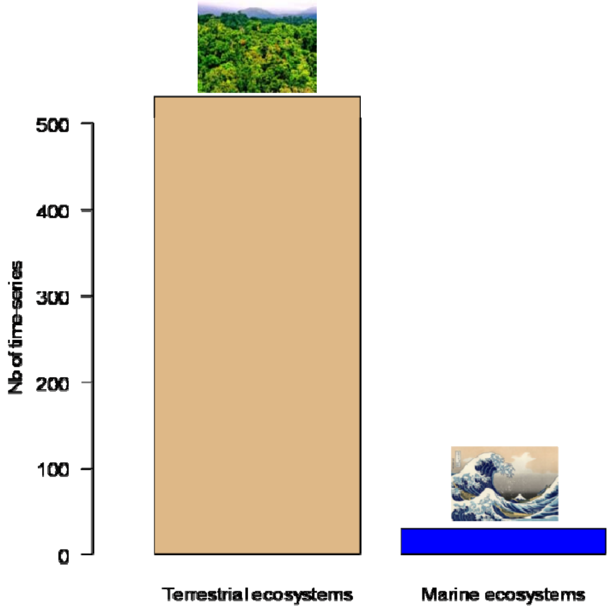

Figure I - 15: *Number of time-series published before the 2007 IPCC report in both terrestrial and marine ecosystems. (The numbers come from Richardson & Poloczanska 2008)*

Whereas substantial information may be collected at the level of primary producers of the euphotic zone *via* remote sensing, the data on subsequent levels of the food-web (primary and sometimes even secondary consumers) are scarce. Indeed, humans are far removed from the ocean expense and most marine ecosystems are hardly accessible and poorly sampled (Richardson & Poloczanska 2008). Despite the efforts of international programs, such as the Census of Marine Life (Ausubel 1999), collecting data remains a tremendous challenge. We lack practical methods to examine and monitor the structure of marine ecosystems both at the spatial (most sampling is done only on some transects along the ships' roads) and temporal scales (difficulties of having repeatable measurements from year to year when using commercial ship trips or fisheries' data), that are appropriate to understand the consequences of climate changes on biodiversity erosion.

Though very important ecosystems, oceans are poorly known and knowledge on the impact of climate on marine ecosystems is lacking, mainly due to methodological difficulties.

2) Oceanic parameters affected by climate change

According to Hoegh-Guldberg & Bruno (2010), "*recent studies indicate that rapidly rising greenhouse gas concentrations are driving ocean systems toward conditions not seen for* *millions of years, with an associated risk of fundamental and irreversible ecological transformation*". Changes in oceanic parameters have been reviewed in great details in this study. Mainly, modifications of chemical properties have been observed in the oceans due to absorption of CO_2 resulting in a decrease in pH associated with a decline in carbonate ion concentration. Concerning the physical parameters, the most evident consequence of climate change on oceans is the increase of sea surface temperature (SST). According to the last IPCC report, the mean world SST has increased at a rate of 0.067°C per decade during the last century (1901-2005; Trenberth *et al.* 2007) and this warming has been common to every ocean basins since the 90's (Belkin 2009). These changes in SST have further repercussions on the climate through modifications of large-scale oscillations, such as the El-Niño Oscillation (Collins *et al.* 2010), or the North Atlantic Oscillation (Ottersen *et al.* 2001; Stenseth *et al.* 2002). For instance, El-Niño events were more frequent, longer and more intense between 1980 and 2000 than before (Kaplan *et al.* 1998; Timmermann *et al.* 1999).

Sea ice extent also seems to be affected by climate change, though the situation is very different in the Arctic and the Antarctic, the latter in which no clear trend appears (Zwally *et al.* 2002). Changes in sea ice extent and concentration appear at a regional scale but may have consequences on global parameters such as the Sea Surface Height (SSH), which has been increasing of 3.2mm per year between 1993-2010 according to TOPEX/Poseidon and Jason satellite altimetry data (Hoegh-Guldberg & Bruno 2010), consistently with tidal gauge data (Cazenave & Llovel 2010). This could even lead to a mean rise of sea levels up to 12m if both Greenland and the West Antarctic Ice Sheet melt completely (Cazenave & Llovel 2010).

Climate change is already visible in oceans through physical and chemical modifications. However, little is known about the consequences those changes may have on oceans' biological component.

V. The Southern Ocean: *a unique place to study the effect of climate on marine ecosystems*

1) A central ocean

« A natural laboratory for climate change study »
Le Quéré et al. 2002

The circumpolar Southern Ocean communicates with the three other oceanic basins through the Great Conveyor Belt (Figure I - 16). As a consequence, the Southern Ocean plays a **key role in the word climate regulation** as it spreads climatic anomalies among the major ocean basins (Busalacchi 2004). With no continental barriers, it corresponds to an oceanic division of 1000 to 4000 km width encircling Antarctica and flowing eastward under the effect of the Antarctic Circumpolar Current (ACC). The main feature of this ocean is its conspicuous frontal banding consisting of several circumpolar quasi-uniform belts divided by fronts[13], comparatively narrow zones of sharp changes in vertical structure temperature salinity and nutrients (Belkin & Gordon 1996).

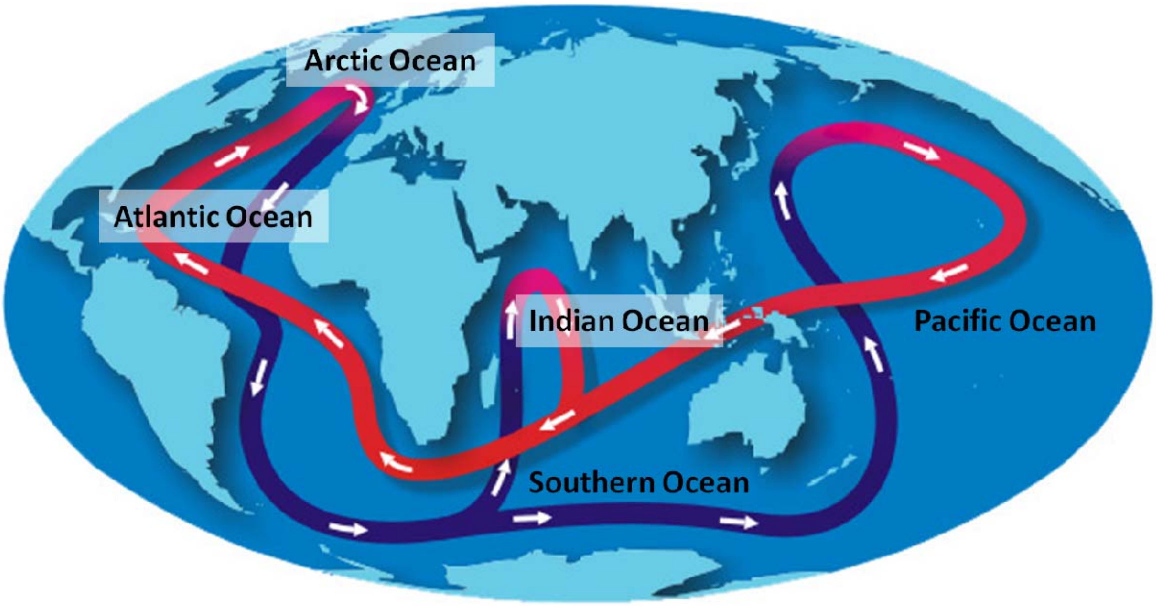

Figure I - 16: *Map of the world and its major ocean basins, with the Great Conveyor Belt. (Adapted from www.mi2g.com)*

Any climatic perturbation occurring in one of the other main oceans (except for the Arctic Ocean) will be transmitted to and thus detectable in the Southern Ocean, which thus make it a key location to study climate change.

2) A productive ocean

The Southern Ocean also supports one of the most productive marine ecosystems on the planet, accounting for *ca.* 20% of the world total marine primary production (Tynan 1998). This is mainly a result of short, intensive spring phytoplankton blooms (Smetacek & Nicol 2005). Because of restrictions on land–ocean–atmosphere interactions by the Antarctic ice cap, nutrient supply via rivers and dust is generally absent or limited to areas around islands (*e.g.* nutrient input by the Possession Island, Crozet Archipelago, Mubalegh *et al. in prep*).

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[13] FRONTS: Oceanic regions where horizontal gradients of temperature and/or salinity are conspicuous. Fronts emerge from various physical processes, such as tides, upwellings and currents, and range from small to large spatial and temporal scales (Cury *et al.* 2008).

Input of sedimentary nutrients is limited to coastal shelves, whereas pelagic waters over deep basins can be enriched via nutrient release from melting sea ice (Brierley & Thomas 2002), advection of nutrient-rich water masses from upstream shelf regions (Sullivan *et al.* 1993), or upwelling from distant sediment sources (Prézelin *et al.* 2000). The spatial and temporal distribution of nutrients is therefore highly influenced by interactions between bottom topography, water mass properties, ocean currents, and sea–ice dynamics. Significant phytoplankton blooms occur mostly on particular hydrologic structures, such as fronts and island shelves (Moore & Abbott 2000). Concerning higher trophic levels, the abundance of organisms in water mass is either the result of the primary production *in situ* and the energy transfer through the local food webs or the result of advection of species being produced elsewhere (Hunt *et al.* 1999). The biomass of this ocean is still little exploited, making it one of the most important on our planet (krill, pelagic fish, cephalopods, *etc.*). As an example, mesopelagic fish abundance has been estimated between 200 and 400Mt (Lubimova *et al.* 1987; Lancraft *et al.* 1989), while the total world commercial fisheries amount to 90Mt per year.

Besides its physical properties and its role in climate regulation, the Southern Ocean supports very productive ecosystems, on which the impact of global change needs to be assessed.

3) A pristine environment?

The Southern Ocean: a pristine environment? Sadly, no such thing remains on our planet. With an ever growing human population the planet currently bears almost 7 billion people (6.93 billion in 2009 according to the World Bank). Together with economic growth, rapid population growth has led to global changes worldwide (see the climate change discussed above as an example). No area has been spared and the so-called ozone hole is even situated on top of Antarctica.

However, a lot of human-induced changes in the environment occur at a more local scale, where the actual presence of humans has a direct impact on their surroundings (see the effect of habitat destruction on animal and vegetal species). In that, some places seem less affected by humans than others, particularly near the poles (Halpern *et al.* 2008). The Southern Ocean is a remote area enduring harsh environmental conditions from a human point of view and human occupation has then been almost absent. Antarctica, the only continent devoid of native populations, has been established as a scientific preserve by the Antarctic treaty and reinforced by the protocol concerning environmental protection signed in Madrid in 1991, which is running to 2048. As such the Southern Ocean is a crucial place to study climate as it should be easier to disentangle its effects from those of harvesting or fishing activities for instance.

However, human presence still exists and the protection offered by the harsh environmental conditions found below the 40° South is fragile. Already in the past, king penguin populations went down to extremely low levels when they were exploited for oil (and also as food items) during the 18th and 19th centuries. Exploitation probably ceased in the early 20th century when colonies were reduced or even extinct but they subsequently increased substantially at all breeding sites (Croxall *et al.* 1992, Weimerskirch *et al.* 1992). Yet, nowadays other factors are superimposing to the effects of climate in the Southern Ocean. Tourism, for example, is a rapidly developing activity in sub-Antarctic and Antarctic regions (Fraser & Patterson 1997). As such, tourists may – if not properly supervised – destroy habitats, approach wild breeding animals without care and increase animal stress (Woehler *et al.* 1994). In addition to tourism, oiling is still a vivid problem in many regions of the Southern Ocean. At lower latitudes, man's activities, both on land (habitat destruction) and at sea (fisheries and leisure boating), present an additional impact onto populations. For example, intense fishery activities occur in the Benguela ecosystem, where sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* progressively distribute further eastward, forcing top predators to either follow the move or to switch to new prey (Grémillet *et al.* 2008).

The productive ecosystems of the Southern Ocean are less affected by direct human activities than those of other oceans mainly due to the remoteness of this ocean. The study of the impact of climate should thus be easier, as effects may be less masked by other human disturbances.

4) A region undergoing strong climate change

Because it lies in a high-latitude region, the Southern Ocean is expected to be strongly affected by global warming (IPCC 2007). Some of the most striking evidences of climate change have indeed been observed in polar oceans, where temperatures and acidities are changing at more than twice the global average (Hansen *et al.* 2006; Bindoff *et al.* 2007). In fact, latitude seems an important factor to consider in the intensity of warming (Figure I - 17).

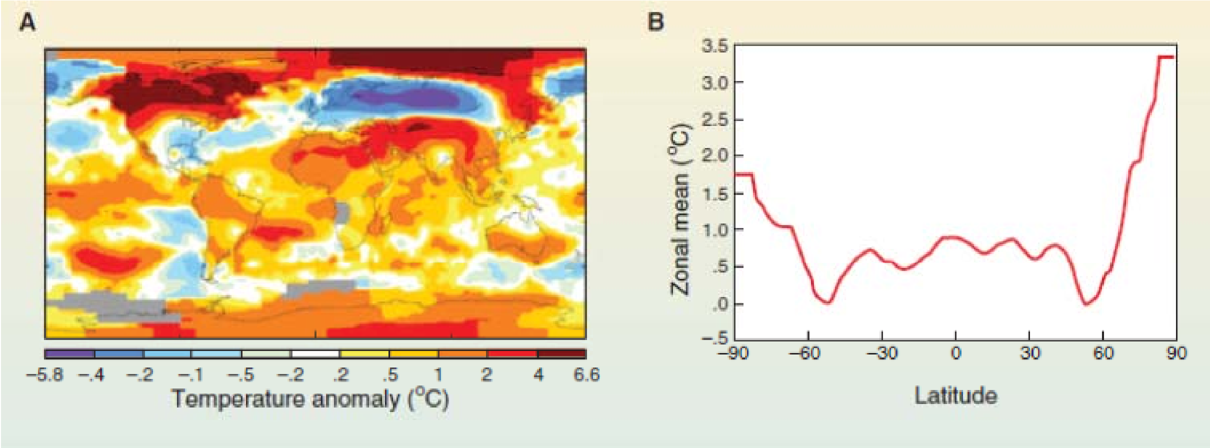

Figure I - 17 : *Surface temperature anomaly for January 2010 relative to the mean for 1951-1980. Figure from Hoegh-Guldberg & Bruno 2010, giving credits to NASA Goddard Institute for Space Studies.*

As an example, I investigated SST changes across the last century in one part of the Southern Ocean, the Crozet Archipelago. This is one of the most productive sectors of the Sub-Antarctic zone and also the home for one of the most diverse seabird community in the world. In this area, we can observe a mean increase of 1.27°C in SST between 1901 and 2005 (Figure I - 18). This corresponds to a 1.8 fold increase of the average sea warming observed (0.67°C; Trenberth *et al.* 2007; see what SST would have been like under the mean warming instead on the green line in Figure I - 18).

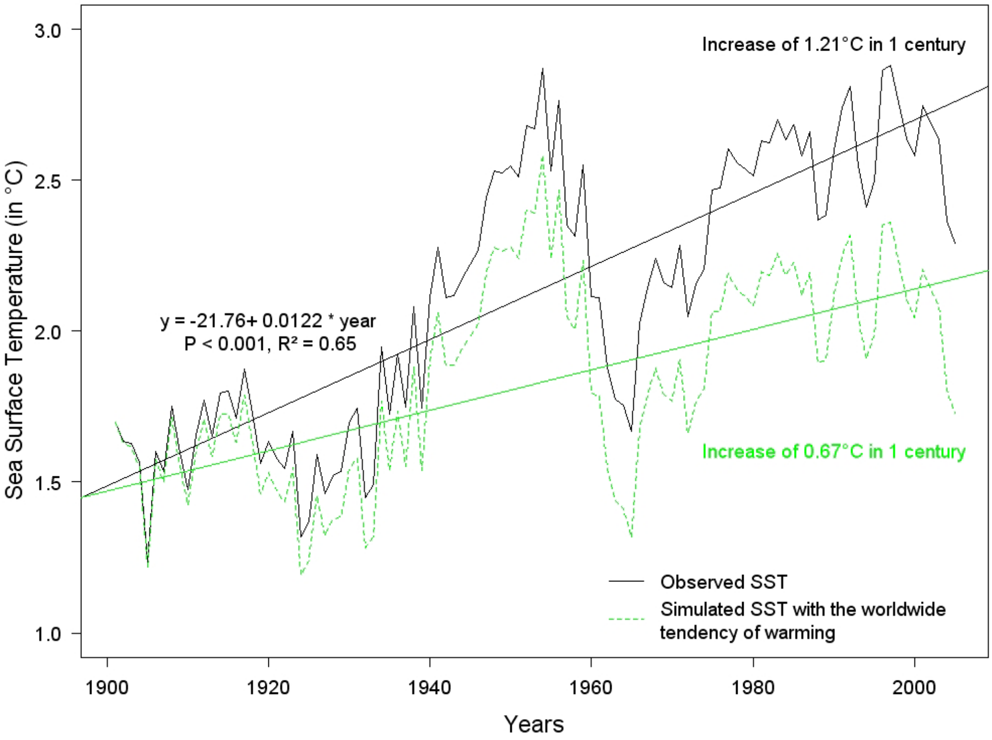

Figure I - 18: *Increase of Sea Surface Temperature around Crozet (46-56°E, 46-60°S) along the last century (1901-2005) compared to the mean world increase of SST.*

Green curve is given only as an indication of comparison and corresponds to the unreal situation in which variability of SST was that observed in Crozet but average trend was changed from that observed in Crozet (1.21°C per century) to that observed worldwide (0.67°C per century).

The Southern Ocean is thus enduring very strong climate change imposing a new selective pressure on its productive ecosystems. In this thesis, I investigate the effect of this new pressure on its ecosystems.

The fact that warming rates are higher at high latitudes does not necessarily imply that the impact of warming also ought to be stronger on high-latitude ecosystems. As I said above, to predict the impact of climate, one must know both the amount of change and how organisms are able to tolerate these changes (Le Maho 2002). According to Tewksbury and colleagues (2008), the most dramatic impact could actually be in the tropics. Organisms in the tropics do not experience much temperature variation normally, as there is very little seasonality in these regions and so even small temperature changes may have a very large impact in these low latitudes. By opposition, organisms living in higher latitudes experience more contrasted temperatures and may exhibit a greater tolerance to temperature shifts. If some datasets on terrestrial ectotherms seem to prove their point (Tewksbury *et al.* 2008), the authors acknowledge that this could be very different for endotherms and marine environments. **The question of differences in organism responses to climate change according to latitudes will be addressed in this thesis by the use and comparison of different species.**

5) The impact of climate change on Southern Ocean food webs

Climate change is likely to have impacts at all trophic levels and will be manifest in a variety of ways (Chambers *et al.* 2005).

Primary & secondary production (plankton)

Primary production is defined by the availability of light and nutrients. Consequently, it strongly depends on ocean circulation, mixed-layer dynamics, upwelling, atmospheric dust deposition, and the solar cycle (Behrenfeld *et al.* 2006). Climate changes that allow ocean surface warming cause an enhanced stratification of the water, suppressing nutrient exchange through vertical mixing. Similarly, the fresh water coming from ice melting can decrease vertical mixing. The availability of nutrients in the euphotic zone for phytoplankton is thus reduced and the Net Primary Production (NPP) decreases (Behrenfeld *et al.* 2006). Indeed, the NPP has been decreasing according to Sea-viewing Wide Field-of-View Sensor (SeaWiFS) data for the last decades, as a result from changes in upper-ocean temperature and stratification (Behrenfeld *et al.* 2006). Further, *in situ* data collected at the entire ocean scale indicate that NPP has been decreasing of about 1.5% per year since 1950 in the Southern Ocean (Boyce *et al.* 2010; note that the Southern Ocean in this study corresponds to a smaller part than that I consider in this thesis). Zooplankton abundance has also been reported to decrease in the Southern Ocean (see Hunt *et al.* 2001 for a decrease in the Indian part). Antarctic krill, *Euphausia superba,* a major grazer in the Southern Ocean which dominates the Antarctic food web (Croxall *et al.* 1988; Loeb *et al.* 1997), has been decreasing since the 70's (Atkinson *et al.* 2004). This decrease appears to be related to both climate change and the important Antarctic krill fishery, the largest fishery in the Southern Ocean.

In addition to changes in abundance, changes in distribution (range expansion for instance), community structures and bloom phenology also occur (reviewed in Hays *et al.* 2005). The acidification caused by an increase in dissolved CO_2 may indeed have an important effect on phytoplankton communities (Hays *et al.* 2005). Finally, bloom timing may be tightly coupled with SST and warming thus lead to earlier blooms. This may have strong consequences for energy flow to higher trophic levels by leading to a mismatch between trophic levels, *i.e.* de-synchronization of the different levels (see match-mismatch above in II). For instance, phytoplankton blooms have globally advanced more than have their zooplankton grazers in the North Sea (Edwards & Richardson 2004).

Intermediate levels

Changes in plankton will have repercussions on intermediate levels of the food webs. Changes in the abundance or distribution will modify the availability of food for fishes, while a change in the phenology may result in a mismatch situation between plankton and their predators. Changes in community structure mean changes in relative abundance of the different species of plankton. Depending on the new dominating species, a change in energy intake for a similar amount of food ingested by a predator may also occur.

Though all of these changes are expected from a theoretical point of view, no long-term datasets are available to confirm them and virtually nothing is known on the impact of climate on intermediate levels of the chains, such as myctophids.

Top-predators

The impact of climate change on top-predators of the Southern Ocean is more documented than on intermediate levels. Breeding performance variability and periodicity have been related to fluctuations of the environment, especially driven by physical forcing from the El-Niño Southern Oscillation in marine predators of the Southern Ocean (Trathan *et al.* 2007); these relationships appearing to be mediated by mid-trophic-level processes (Trathan *et al.* 2007). In particular, several long-term datasets collected in the Antarctic and sub-Antarctic ecosystems have shown changes in abundance, phenology and distribution.

Following the regime shift[14] caused by temperature increases, many sub-Antarctic seabird populations have declined around the 70's (Woehler 1996; Croxall *et al.* 2002 but see Ainley *et al.* 2003a; Weimerskirch *et al.* 2003; Jenouvrier *et al.* 2005a). Most seabirds and seals have declined with a certain delay (2 – 10 yrs) compared to the increase in temperature. For instance, elephant seal populations have decreased of 30% between 1950 and 1980 and now seem stable. Similarly, several populations of seabirds and marine mammals relying on krill stocks have declined in South Georgia, such as fur seals, albatrosses and penguins (Reid & Croxall 2001). In Antarctica, the decrease by half of the emperor penguin population at Adélie Land has been interpreted as the result of a prolonged warm period resulting in a contraction of sea-ice extent (Barbraud & Weimerskirch 2001; Barbraud *et al.* 2011a).

Changes in phenology have been observed in seabirds breeding in Adélie land (Barbraud & Weimerskirch 2006). Contrary to what has been observed in the northern hemisphere, the tendency observed was that of a delay in arrival and laying dates.

Finally, changes in distribution area have also been observed, in particular in penguins (Forcada & Trathan 2009). Everything that concerns penguins will be reviewed in greater details in the following chapter.

Biological changes due to climate change have already been observed at each level of the food chain in the Southern Ocean, though some remain less documented. In this thesis, I attempt to unravel the role of these mechanisms in driving population dynamics of our study species and I investigate the effect (direct, indirect and integrated) of climate on the life-history traits of these species.

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[14] REGIME SHIFT refers to a radical rapid change from a relatively stable state of an ecosystem to a new one.

Chapter II ○●○○○○○○○○

IPCC: Integrating Penguins in Climate Change as bio-indicators of the Southern Ocean ecosystems

As described earlier, we lack practical methods to examine and monitor the structure of marine ecosystems that are appropriate to understand the consequences of climate changes on biodiversity erosion (Richardson & Poloczanska 2008). Regarding the Southern Ocean, the assessment is even worse, probably due to its remoteness. Though the mechanisms of climate variability in the Southern Ocean are well investigated, the impacts of this variability on ecosystems and trophic chains are poorly known. Information about how these impacts affect biological communities is essentially limited to primary production and information on how the abundance or distribution of higher levels of the trophic chain are affected, is scarce. Thus, scientists **need to develop long-term observatories of the southern ecosystems** for a better understanding of the relations between climate and marine species, as recommended by the report of the International Geosphere-Biosphere Programme (de Young *et al.* 2006).

I. Top-predators

One way around consists in investigating changes related to climate through biological indicators that are taken to be representative of the ecosystem as a whole and are relatively easy to monitor. Because of their complexity, ecosystems are difficult to encompass in their integrity (Ciannelli *et al.* 2005). Such indicators are thus all the more required, especially for decision-makers and conservation programs (*e.g.* use of seabirds by the Commission for the Conservation of Antarctic Marine Living Resources, CCAMLR).

These representative species are often chosen at the top of trophic webs since the effects of climate forcing on primary and secondary production of the short oceanic food webs are integrated at higher levels of the food chain (Croxall *et al.* 1988, Le Maho *et al.* 1993, Boyd & Murray 2001; Boyd *et al.* 2006; Figure II - 1) and thus detectable in top-predators, such as seabirds or marine mammals. Top-predators are then sensitive indicators of environmental changes and reflect the trophic dynamics of their ecosystems (Verity *et al.* 2002), an illustration of this being the large-scale, top-down approach proposed by the Tagging Of Pacific Pelagics project (Block *et al.* 2003). As a consequence, seabirds and marine mammals are increasingly used as ecological indicators (*e.g.* Jenouvrier *et al.* 2003), *i.e.* as species that can reveal alteration in their environment through proximal (physiological or behavioural) or distal (population) changes.

The term bio-indicator is often used to characterize top predators in such a situation but it traditionally refers to species that reflect the level of pollutants in an ecosystem and not ecosystemic or trophic changes (*sensu* Karr 1981). Here, we extend this definition and **bio-indicators correspond to species that provide an integrative view of the consequences of environmental variability on ecosystems**.

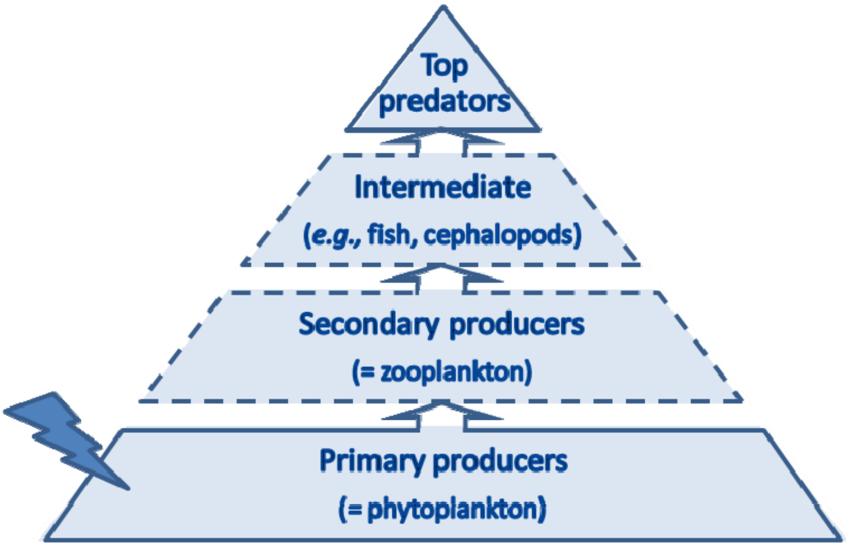

Figure II - 1: *Impact of a perturbation integrated along a simplified marine food chain*

Seabirds and marine mammals are particularly useful top-predators to study marine systems since most rely entirely on marine resources but breed and moult on land and are thus easily accessible for investigations during those periods ashore. "*Given their relative ease of study, seabirds have frequently been identified as useful indicators of the health and status of ecosystems (see Montevechi 1993; Furness & Camphuysen 1997)"* (Piatt *et al.* 2007). The *pros* and *cons* of the use of seabirds as ecological indicators have been reviewed by Durant and colleagues (2009; see also the special edition of Marine Ecology Process Series volume 352), while those of marine mammals can be found in Moore (2008). Seabirds have been used increasingly in recent years as bio-indicators of climate change and regime shifts. A paper by Aebischer and colleagues in 1990 reveals a remarkable parallel in long-term responses to climate variability across 4 trophic levels (namely phytoplankton, zooplankton, herring and kittiwakes). This supports the two main assumptions that are key to being good indicators: i) higher trophic levels are controlled by bottom-up[15] processes (Frederiksen *et al.* 2006) and ii) **seabirds or their life-history traits vary with ecosystem change**.

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[15] BOTTOM-UP CONTROL: regulation of the food web components by either primary producers or the input of limited nutrients through changes in the physical environment

In the Southern Ocean, the use of marine top predators seems particularly relevant. Indeed, its food chains are especially short (Figure II - 2), resulting in a rapid response of top-predators to modifications lower in the food chain. The Southern Ocean top-predator community is also one of the most numerous of the world, benefiting from the high biomass of their main prey (krill, cephalopods and fishes; Croxall *et al.* 1992). Indeed, the simplicity of the southern food webs results in a high quantity of the total productivity reaching the higher trophic levels compared to other ecosystems (Figure II - 2; Warham 1996).

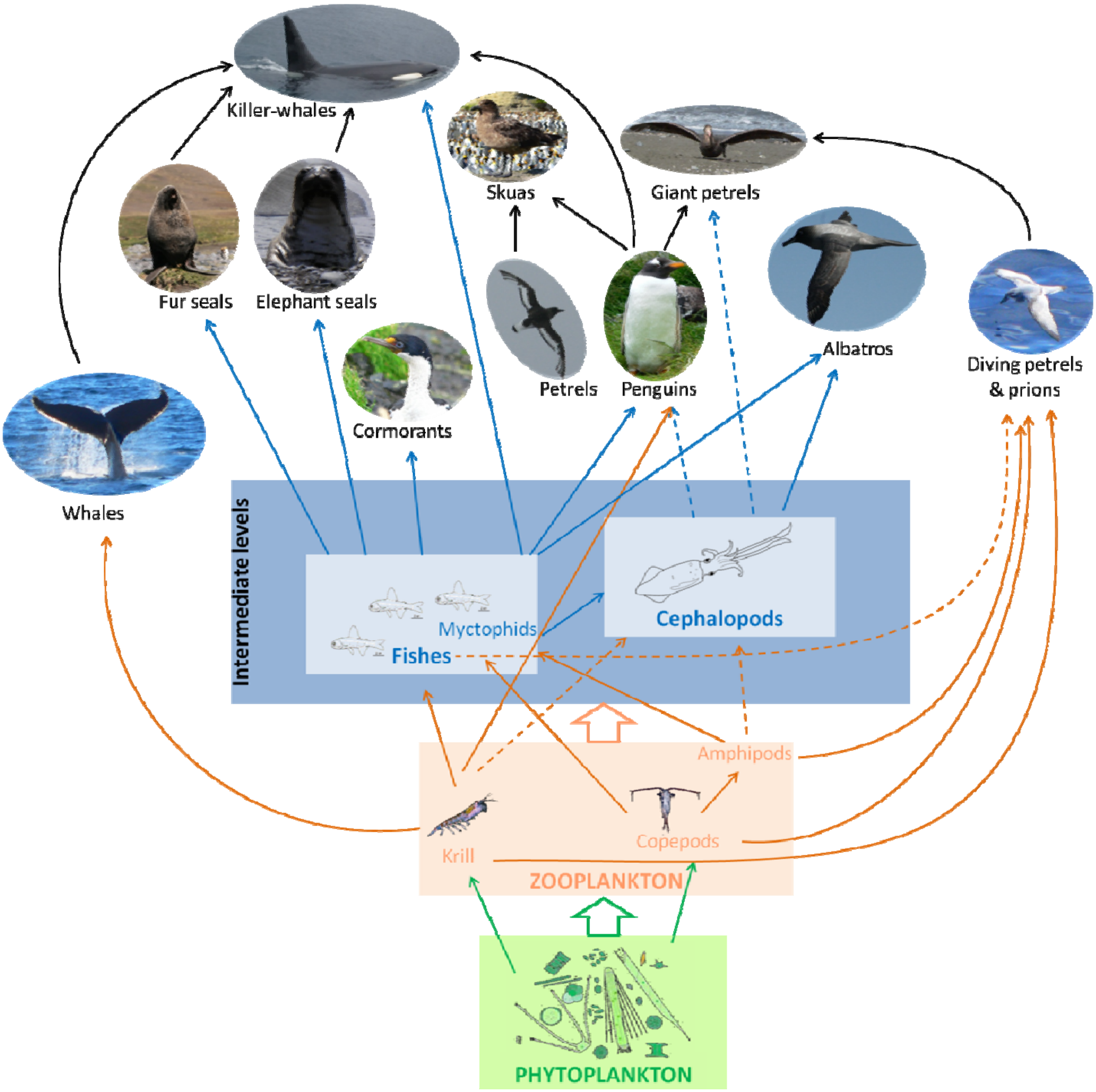

Figure II - 2 : *Simplified schematic view of the Southern Ocean food chains (Indian Ocean part here as an example).*
Drawings of phyto- and zoo-plankton and cephalopods were taken from Wikipedia websites, while myctophid drawing comes from the Fishes of Australia website, http://foa.webboy.net/family/myctophidae

Additionally, Southern Ocean top-predators cover huge distances (*e.g.* Jouventin & Weimerskirch 1990), therefore providing indications on a large part of the Ocean. Finally, they concentrate their at-sea activity to oceanographic features that are of key importance to the functioning of the world oceanic system, such as upwellings (*e.g.* Biuw *et al.* 2007), oceanic fronts (Bost *et al.* 2009), eddies (Cotté *et al.* 2007), or thermoclines (*e.g.* Boyd & Arnbom 1991, Ropert-Coudert *et al.* 2009).

As information on Southern Ocean ecosystems is scarce and difficult to obtain, I decided in this thesis to focus on top-predators and more precisely seabirds as relevant indicators of their whole ecosystems.

II. Penguins[16]

Penguins are an iconic family of seabirds most famously known for their impressive swimming performances (see Ropert-Coudert *et al.* 2006a), their extraordinary fasting capacities (Cherel *et al.* 1993a) or their remarkable resistance to extreme environments (*e.g.* emperor penguins, *Aptenodytes forsteri,* are able to withstand temperatures well below 0°C, Ancel *et al.* 1997). Penguins are also good models for climate change studies (see Boersma 2008 and Forcada & Trathan 2009), and represent, therefore, one of the main family of ecological indicators of the marine southern hemisphere (Ellis *et al.* 2007).

1) An abundant and widespread family

The 18 penguin species compose the family of the Spheniscidae. The whole penguin population, living in the Southern Hemisphere, is estimated at more than 24 million breeding pairs, *i.e.* a 250 000 ton biomass, accounting for the majority of seabird biomass in the Southern Ocean (Woehler 1995; Woehler *et al.* 2001). Penguins are equally important consumers of the marine ecosystems (de Brook 2004), taking about 85% of the energy consumed by seabirds in this region (Croxall 1984). Their populations are large and widespread, and distributed all around the southern hemisphere (Marchant & Higgins 1990; Figure II - 3), from the tropics to the south polar circle, although the Pacific sector of the southern hemisphere is probably less extensively covered than the Indian Ocean one.

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[16] This paragraph is partly based on Ropert-Coudert, Saraux & Kato (Article 1, ready to be submitted, see Apendix 1)

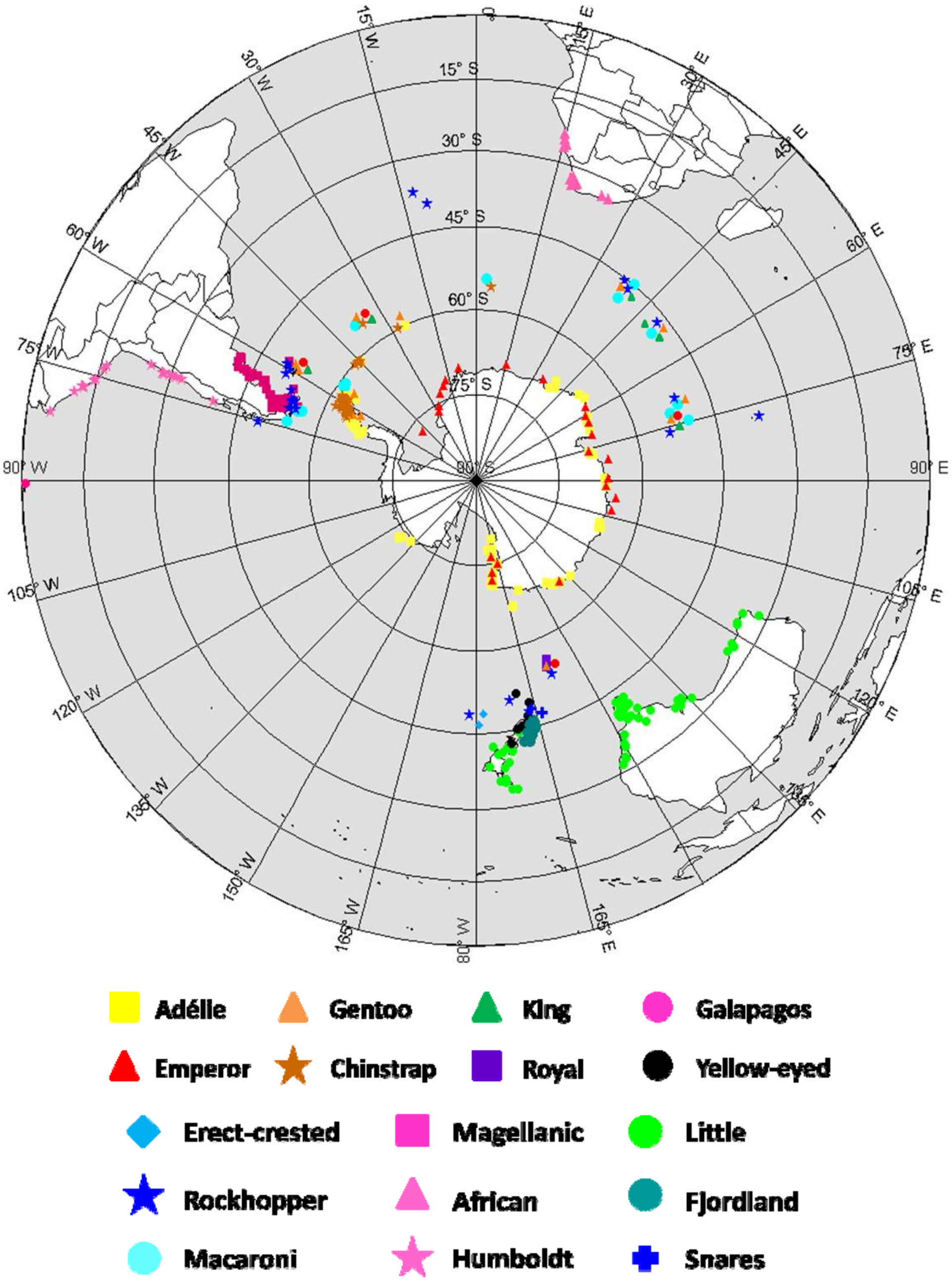

Figure II - 3 : *Penguin distribution all around the Southern Ocean*
(adapted from Ropert-Coudert et al. Article1 see Appendix 1). For clarity of presentation Northern and Southern Rockhopper Penguins, as well as New Zealand and Australian species of Little Penguins, have been merged into Rockhoppers and Little Penguins, respectively.

2) Good prospectors of the Southern Ocean

Adding to their extensive circumpolar on-land distribution penguins are extraordinary divers which enable them to prospect a large vertical volume of southern hemisphere oceans, from right underneath the surface (*e.g.* Watanuki *et al.* 1999) to the benthos (Rodary *et al.* 2000; Tremblay & Cherel 2000; Takahashi *et al.* 2003a). Despite being flightless - the horizontal distances travelled by penguins are on average 10 times less wide than that of flying species

(Wilson *et al.* 1989a) - they forage from coastal (*e.g.* Collins *et al.* 1999) to offshore areas (Bost *et al.* 1997), reaching sometimes distances as far as 1620km from the colonies in the case of king penguins, *Aptenodytes patagonicus,* in winter (round trip amounting to 4095km; Bost *et al.* 2004).

3) Relatively easy to monitor

Penguins need to go back on land to breed, and moult. Their life is thus characterized by alternations of feeding periods at sea and fasting ones on land, where they are accessible to scientists. Penguins are seabirds and as such present a high degree of philopatry[17] (>80% for seabirds in general; Grémillet & Boulinier 2009), *i.e.* they normally return to the same site throughout their entire life. This enables to study individuals on several consecutive years and even throughout their entire life by the monitoring of one single place.

Compared with other seabirds, penguins can be captured and recaptured at ease having lost the ability to fly. Information, however, remains scarce during the non-breeding period (immature period + non-breeding season), when individuals do not return regularly on land. The morphological adaptations to flightlessness represent a further enhancement to using them in scientific studies compared with Procellariforms for example: their bodies are dense and relatively large and can thus accommodate diverse recording systems that are either attached onto or implanted into them, an approach referred to as bio-logging (Naito 2004, Ropert-Coudert & Wilson 2005). Of course, such an approach requires specific guidelines to be strictly followed so as to limit the impact that devices could incur on the fitness or performances of the birds (*cf.* Casper 2009 and references on penguins therein, see also Chiaradia *et al.* 2005; Ropert-Coudert *et al.* 2007a, b).

Penguins are the major seabird biomass and consumers of the Southern Ocean. They are widespread around this ocean and prospect an important volume of this ocean (both vertically in the water column and horizontally as they cover huge distances to feed). Finally, they are probably the easiest seabirds to monitor given their inability to fly. Thus they represent ideal models that I will use all along this thesis.

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[17] DEGREE OF PHILOPATRY: "*likelihood that individuals breed at or near their place of origin*" (Weatherhead & Forbes 1994)

III. State of the art on penguins[18]

Most of the studies of the impact of climate variability on penguins have done so by investigating correlations between climatic variables and penguin population trends or demographic parameters. Such an approach is based on the indirect effects that climate change can have on an ecosystem (Stenseth *et al.* 2002), which are expected to be reflected in the penguins' responses. For instance, an increase in SST mediated by climate change may lead to a decrease in the ocean's productivity (Gregg *et al.* 2003), which, in turn, would affect the food webs via cascading bottom-up effects (see Frederiksen *et al.* 2006). Linking similarly long timescale climatic and penguin population datasets may provide clues to understanding ecosystem processes and also represents a powerful *a posteriori* approach to predict future trends as these can be extrapolated from the shape of the relationship established in the past (Jenouvrier *et al.* 2009a).

The impact of climate change on penguin populations in the Southern Ocean *sensu stricto*, *i.e.* south of the polar convergence (*i.e.* restricted to polar and sub-polar species) has been recently reviewed in great details (Forcada & Trathan 2009; see Table II - 1). The following will focus on principal trends and further expand the discussion to other penguin species and their respective environments.

1) Effects on population trends and distribution area

The impact of climatic anomalies has been mostly discussed at population scale where scientists correlate long-term datasets on population trends to long-term climate datasets (*e.g.* Kato *et al.* 2002, Croxall *et al.* 2002; Ainley *et al.* 2005; Jenouvrier *et al.* 2009a among others). At the population level, highly diverse trends have been observed in association with climate change both across and within species. At the South Orkney Islands for instance, Adélie, *Pygoscelis adeliae,* gentoo, *Pygoscelis papua,* and chinstrap, *Pygoscelis Antarctica,* penguins, which breed sympatrically[19], exhibit opposite responses to the current climate warming and associated ice-cover reduction (Forcada *et al.* 2006; see the box below). Further Adélie penguin responses depend on the location of the colonies, with decreasing populations

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[18] This paragraph is partly based on Ropert-Coudert, Saraux & Kato (Article 1, ready to be submitted, see Apendix 1)

[19] SYMPATRIC: Occupying the same or overlapping geographic areas without interbreeding.

at lower latitudes and increasing ones in southern Antarctica. Additionally, in contrast with the expected negative effect of warming, some penguins' declines have been linked to a decrease in SST such as in northern rockhopper penguins, *Eudyptes moseleyi,* on Amsterdam Island (Guinard *et al.* 1998). Similarly, opposite shifts in distributional range have been observed on the one hand in emperor and Adélie penguins (whose range has shifted poleward and contracted) and on the other hand in gentoo and chinstrap penguins (whose range has expanded southward; Forcada & Trathan 2009).

Galápagos penguin populations have declined because of changes in oceanographic conditions, paralleling an overall warming in the Pacific during the last twenty years of the twentieth century associated with more frequent El-Niño and less frequent La Niña events (Boersma 1998). The effect of periodic climatic events, such as the El-Niño Southern Oscillation (ENSO), can thus be highlighted (*e.g.* Boersma 1998). In this context, amplitudes of anomalies may often be more important in understanding population trends than the occurrence of the anomalies itself (Vargas *et al.* 2007). Thus studies are encouraged to investigate the effect of climatic indices on a continuous basis, in order to avoid subjectively fixed limits (for instance the use of Southern Oscillation Index instead of a categorical three-state variable Normal / El-Niño / La Niña). In addition, strong ENSO events can crash down populations but the subsequent succession of smaller-scale events can prevent the population to recover, as is the case in Galápagos Penguins (Vargas *et al.* 2006, 2007). Although correlations have been noted with climate parameters or primary production fluctuation, so far the mechanisms involved in generating these correlations have been poorly investigated. However, Murphy and colleagues (2007) showed that the relation between SST and breeding performances of krill predators (Antarctic fur seals, *Arctocephalus gazella*) was mediated by their prey. Similarly, a recent paper by Trivelpiece and colleagues (2011) attributes Adélie and chinstrap population changes to modifications in the abundance of their main prey, Antarctic krill, resulting both from climate change and harvesting. This offers explanations for the reduction of populations of these two different species, one 'ice-obligate' species and one 'ice-avoiding', contrary to the sea-ice hypothesis.

2) Effect on demographic parameters

Impact of climatic anomalies can also be investigated on life-history traits such as breeding success and/or individual survival. Spatial and time scales of climatic parameters used are of special importance in these studies. For instance, local SST anomalies may impact drastically the mean egg laying date, the number of successfully fledged chicks and the body mass of little penguin, *Eudyptula minor,* chicks at fledging, while the little penguins' hatching success is linked to global-scale ENSO related SST anomalies (Chambers 2004a). SST also presents an immediate effect on king penguins' breeding success but a 2-year time lag effect on survival (Le Bohec *et al.* 2008a but see Barbraud *et al.* 2008 and Le Bohec *et al.* 2008b). Interestingly, some contrasted results are observed on the phenology of penguin species: if climate warming is expected to delay the onset of breeding in emperor and Adélie penguins (Barbraud & Weimerskirch 2006), it should advance it in little penguins (Chambers 2004b, Cullen *et al.* 2009). Nonetheless, effects of climate on penguin life history traits will always remain difficult to interpret since they can be both direct and immediate (Fraser & Hoffman 2003) or indirect through modifications in the food chain for instance and appear only later.

Table II - 1: *Southern Ocean penguin population threats and responses to climate change (table from Forcada & Trathan 2009)*

Species	IUCN Criterium	Threats	Climate Change Response	Source
Emperor *(Aptenodytes forsteri)*	Least concern	Climate change Sea-ice loss SST warming	Poleward shift Range contraction Food web shifts	Barbraud & Weimerskirch (2001) Croxall *et al.* (2002) Ainley *et al.* (2005)
King *(Aptenodytes patagonicus)*	Least concern	Climate change SST warming	Food web shifts	
Gentoo *(Pygoscelis papua)*	Near Threatened	Climate change Tourism Pollution Fishing SST warming	Food web shifts Range expansion	Ellis *et al.* (1998) Fraser *et al.* (1992) Smith *et al.* (1999)
Chinstrap *(Pygoscelis Antarctica)*	Least concern	Climate change SST warming	Range expansion Food web shifts	Fraser *et al.* (1992) Smith *et al.* (1999)
Adélie *(Pygoscelis Adeliae)*	Least concern	Climate change SST warming Sea-ice loss Researchers / Tourists	Poleward shift Range contraction Food web shifts	Ainley (2002) Croxall *et al.* (2002) Ainley *et al.* (2005)
Macaroni *(Eudyptes chrysolophus)*	Vulnerable	Climate change SST warming	Food web shifts	Ellis *et al.* (1998)
Royal *(Eudyptes schlegeli)*	Vulnerable	Climate change Rats Researchers / Tourists Marine pollution Fishing SST warming	Food web shifts	Ellis *et al.* (1998)
Southern Rockhopper *(Eudyptes chrysocome)*	Vulnerable	Climate change Land predators Ecotourism Pollution Fishing SST warming	Food web shifts	Ellis *et al.* (1998)

3) Direct effects on behaviour

Compared with the growing body of literature linking large scale population trends to climate change, a mechanistic approach that would explain how environmental changes directly impact foraging efficiency and thus breeding success is clearly lacking. Yet foraging activity clearly conditions the success of reproduction and is thus an important parameter to understand penguins' responses to climate change (Fraser & Hoffman 2003). The difficulty of relating climate change to foraging activity is that the latter is often measured at short time scales that differ from climatic measurements. However, IPCC (2007) scenarios predict that an increase in extreme weather events will be linked to climate change. The influence of such severe conditions on foraging activity have, to the best of our knowledge, only been reported once: little penguins' foraging success – and consequently breeding success – has been shown to be reduced in years when violent storms mixed the water column, leading to a disappearance of the 25-m deep thermocline where prey of the penguins concentrate preferentially in years of good resource availability (Ropert-Coudert *et al.* 2009). These observations are yet to be investigated in other penguin species. As another example, SST anomalies can directly affect the location of penguins' feeding grounds, such as the polar front for sub-Antarctic penguins (Moore *et al.* 1999) and force them to migrate distances as long as 900 km in the case of the humboldt penguin, *Spheniscus humboldti,* to find new profitable grounds (Culik *et al.* 2000). This will thus impact directly chick provisioning.

Foraging activity can definitely tell us a lot about the plasticity of penguins to face climate change. For instance, recent studies on Adélie Penguins highlighted the interest of examining the match between the peak of penguin at-sea activity and the peak of resource availability (Beaulieu *et al.* 2009a).

Climate and especially temperature changes may also have a direct impact on the physiology of the birds. Indeed, as endotherms penguins are able to thermoregulate, *i.e.* regulate their body temperature to maintain it to a constant level whatever the ambient temperature. However, thermoregulation occurs at a great energetic cost and if ambient temperatures are out of the thermoneutrality range of the animals, their metabolism and thus energetic expenditure would increase (Louw 1993). For instance it has been shown that the resting metabolic rate of captive little penguins increase above 25°C (Baudinette *et al.* 1986). Yet, during the breeding season, penguins are faced with extended fasting periods (see Cherel *et al.* 1993a as an example) placing them in a strong context of energy limitations. While fasting, penguins mainly rely on fat stores built up during the previous foraging trip to sustain their metabolism and energy savings thus appear a critical issue to successful reproduction and chick survival. Increased ambient temperatures may then affect directly penguins. As far as we know, no study has investigated in this direction yet, but this should be accounted for in the future.

A CASE STUDY: THE SEA-ICE

Antarctic marine ecosystem appears intuitively fragile in facing global warming effects, as sea ice plays an important role there (Loeb *et al.* 1997). The ecology of the two penguin species living only in continental Antarctica, Adélie and emperor penguins, is highly associated with sea-ice conditions. Due to logistical difficulties of monitoring birds breeding on fast ice in the harsh Antarctic winter, relatively less information is available for emperor (but see Barbraud & Weimerskirch 2001, Jenouvrier *et al.* 2009b) than for Adélie penguins, for which a large number of studies have been conducted all around Antarctica over the past 50 years. For instances, modification in sea-ice conditions is known to affect foraging behaviour (Watanuki *et al.* 1999; Rodary *et al.* 2000), breeding success (Ainley & Le Resche 1973; Ainley *et al.* 1998; Irvine *et al.* 2000), winter survival (Wilson *et al.* 2001: Jenouvrier *et al.* 2006) and consequently population trends (Fraser & Patterson 1997; Wilson *et al.* 2001; Kato *et al.* 2002) of Adélie penguins, real "*creatures of the Antarctic pack ice*" (Ainley 2002).

Smith *et al.* (1999) proposed a conceptual model that links penguin population growth to sea-ice concentration for the three Pygoscelid species. The rapid warming in the lower latitudes of the Antarctic continent has induced the decline of sea ice extent and duration, alterations in phytoplankton and zooplankton community composition and changes in krill recruitment, abundance and availability to predators (Smith *et al.* 1999, Forcada *et al.* 2006, Ducklow *et al.* 2007). Concomitant to this reduction in sea ice at lower latitudes, a decreasing trend in Adélie population was observed (Fraser & Patterson 1997, Forcada *et al.* 2006, Carlini *et al.* 2009; Montaigne 2010). By opposition, Adélie penguin populations of Southern Antarctica are increasing (Ross Sea and East Antarctic regions, Jenouvrier *et al.* 2006, Woehler *et al.* 2001). Concerning closely related but ice-intolerant gentoo penguins, their populations are increasing in most of the Antarctic Peninsula (Forcada *et al.* 2006; Ducklow *et al.* 2007; Carlini *et al.* 2009; Ballerini *et al.* 2009; Montaigne 2010). The case of chinstrap penguins appears more complex since populations are either decreasing (South Orkney Islands 60°35′S, 45°30′W; Forcada *et al.* 2006; King George Island 62°06'S, 57°56'W; Sander *et al.* 2007a, b) or stable/increasing (Anvers Island 64°46′ S, 64°3′W; Ducklow *et al.* 2007; Hinke *et al.* 2007). Although penguins, like Adélie for instance, are able to adjust their behaviour to local change in sea-ice condition at least until some level (Beaulieu *et al.* 2009a), prolonged warming will inevitably lead to population decline and distribution changes. The recent production of giant icebergs in the Ross Sea has tremendously impacted Adélie and emperor penguin colonies in this region (Kooyman *et al.* 2007).

IV. Aims of the PhD

In summary, climate change is now unequivocal and should continue in the following centuries. Every living organism is thus facing new selective pressures from its environment. At the dawn of the 6th extinction crisis, it is indisputably necessary to increase our understanding of ecosystems and their responses to climate. This is especially true for the important but poorly known marine ecosystems and in particular the ones lying under the high latitudes of the productive Southern Ocean. Here, we propose to investigate the response to climate of Southern Ocean ecosystems through the monitoring of top-predators. At the top of the food chain, top-predators are often considered as good indicators of the ecosystem health integrating every modification occurring at a lower level. Due to their abundance, widespread localisation and easiness to monitor, penguins constitute models of preferred choice for such a study. Population trends of penguins have been recorded for a long time and changes across the last 50 years have been observed abundantly. However, few demographic studies have been conducted until now and responses of life-history traits to climate are still poorly known. The main goals of this study were thus to **obtain a better knowledge of the ecology of penguins** and to **study the impact of climate on their life-history traits.** The ultimate objective is to improve the predictions of their population dynamics. As penguins are long-lived species, adult survival should vary only slightly and thus **we decided to focus our work on** the other important vital rates that are **juvenile survival and reproduction**. Additionally, in order to better understand the underlying mechanisms and penguin potential for quick adaptation through behavioural plasticity, we also address questions on foraging strategies.

On a purely methodological note, differences in models and population estimators, as well as in monitoring means, among research teams add to the difficulty of establishing accurate censuses and predicting accurately the response of populations (*e.g.* Ellis *et al.* 2007). Homogenization of monitoring procedures is already a major goal of the CCAMLR Ecosystem Monitoring Program. Here we proposed to investigate the responses to climate of **three different penguin species** (**little, king and Adélie**) which have been monitored in a similar way, so that their responses could be compared.

The three studied species are penguin species living around the Southern Ocean. However, they exhibit several differences (Figure II - 4). First, they live under **very different latitudes** from temperate to polar areas (Figure III - 1). They also exhibit strong **differences**

in size, king penguins weighing 10 times more than little penguins. Such differences might partly be explained by adaptation to the different environments according to Bergman's ecogeographic rule (1847), which states that due to lower heat loss per unit mass, species of larger size should be found in colder environment, while species of smaller size should be found in warmer areas.

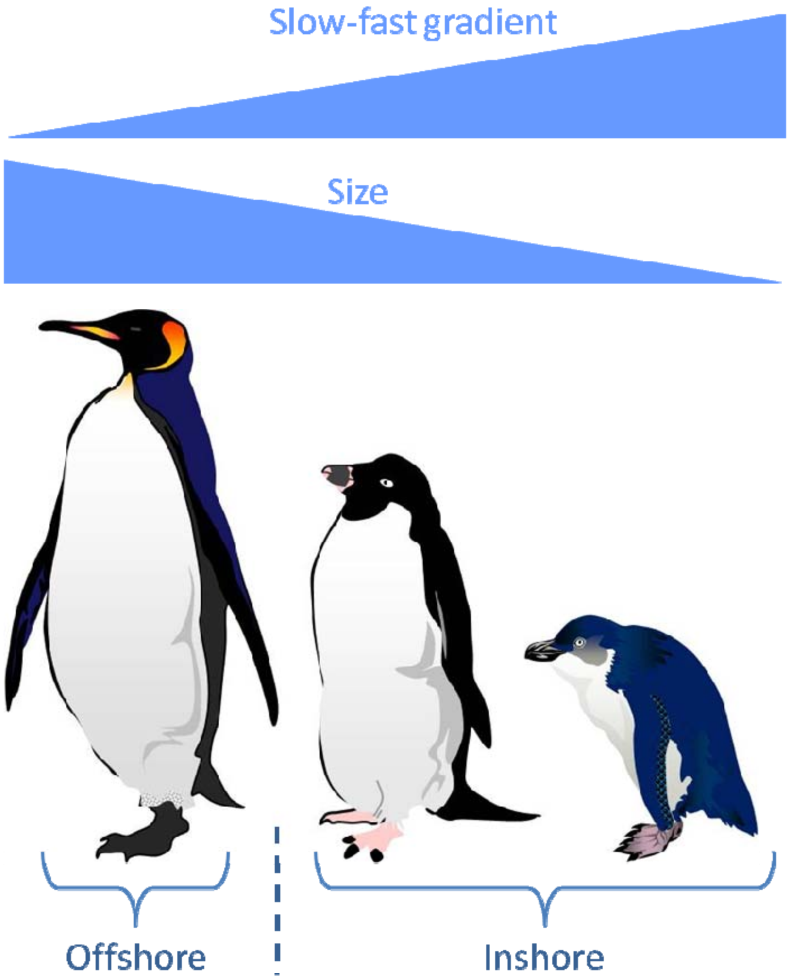

Figure II - 4: *Studied penguin species in relative size and their main differences.*

(drawings adapted from Ropert-Coudert).

As most seabirds, penguins are long-lived animals, which confer to them particular life-history strategies, such as a high longevity, a delayed sexual maturity and a low fecundity (K-species, MacArthur 1962). However, when classified along the slow-fast gradient, **little penguins present the highest turnover rate** with a higher mortality and fecundity than Adélie penguins and then king penguins. Little penguins often have a second clutch per year for instance (Fortescue 1995), while king penguins can breed successfully only once every two years or twice every three years because of the length of their breeding cycle (Stonehouse 1960; Barrat 1976).

Finally, penguins forage at sea but need to return on land for specific purposes, *i.e.* to moult and to breed. Penguins are thus considered as central-place foragers[20], when they breed, which adds an additional constraint to their foraging strategies. However, **king penguins are**

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[20] CENTRAL-PLACE FORAGING: behaviour of a forager that must return to a particular place in order to breed, consume its food, *etc.*

offshore seabirds foraging far from the colony while **little and Adélie penguins are considered inshore birds** foraging close to the colony (Figure II - 5).

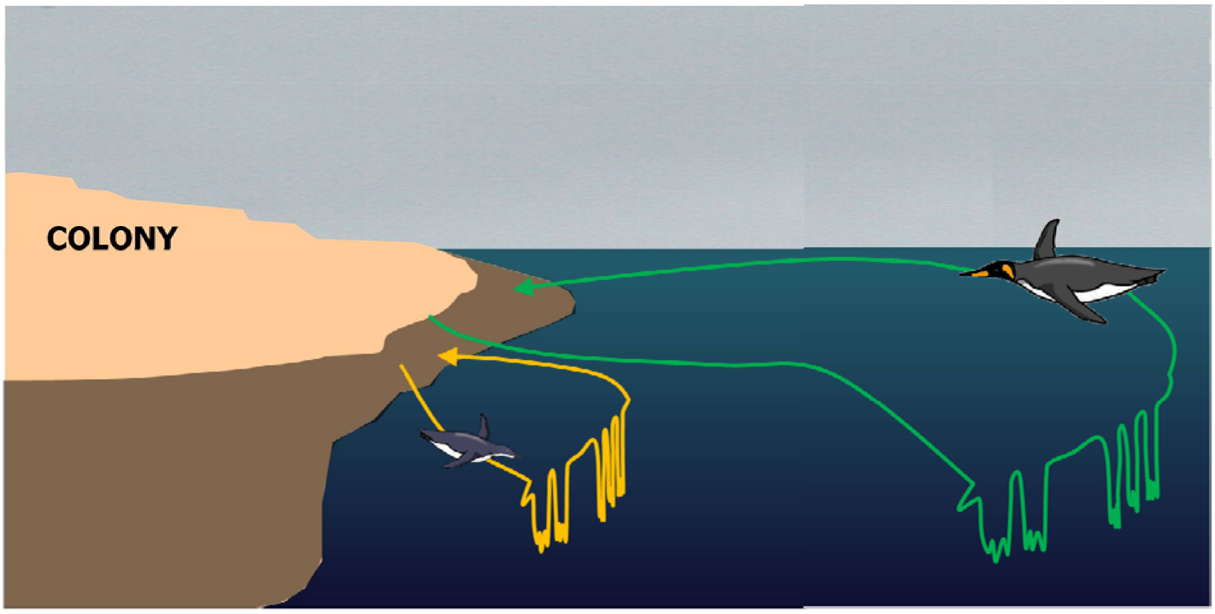


Figure II - 5: *Difference between offshore (in green represented by the king penguin) and inshore penguins (in yellow represented by the little penguin).*

The comparison of the three species thus enabled us to address the different following questions:

- **The role of latitudes in the response to climate**. The species chosen live along a latitudinal gradient from temperate to polar environment.
- **The difference in foraging strategies of inshore** (little and Adélie) **and offshore** (king) birds.
- **The plasticity and flexibility of the species and their different potential for adaptations (role of inshore *vs.* offshore birds, and slow-fast species gradient)**.

In **chapter IV**, I investigate **how to monitor penguin life-history traits** and their response to climate (**Article 2**).

In the following chapter (**Chapter V, Article 3 + complementary results**), we present results on **penguin juveniles**. Penguins exhibit a late maturation and information on the period between fledging and survival is scarce. In this chapter, we evaluate the return rates of the fledglings, the timing of their return and the effect of environmental conditions endured both during early development and later when at sea.

Then, I concentrate my work on reproduction. **Chapter VI** investigates **reproductive strategies** (**Article 4**), **breeding success** (**Article 5**) and **sex ratio of the fledglings produced** (**Article 6**), while **Chapter VII** concerns the **foraging strategies used while breeding** (**Article 7 & 8**). In particular I concentrated on the **plasticity and flexibility** of these strategies, elements that can affect the capacities of a species to adapt more or less easily to changes.

In **chapter VIII**, I **sum up the main results** and compare **the effect of climate between species** and **between life-history traits of a single species**. Then, I **discuss population trends** obtained when we integrated these results in an age-class population model before discussing **potential adaptations for penguins**, which may change these trends. Finally, I provide personal **critics of the work** presented in this thesis (**Chapter IX**) and **possibilities to further extend this work** (**Chapter X**).

Chapter III ○○●○○○○○○

Study models and environmental descriptors

I. Study sites

Penguins live all around the Southern Ocean at very different latitudes. Here, we studied 3 species representative of very different environments, along a latitudinal gradient from a polar area to a temperate one (Figure III - 1).

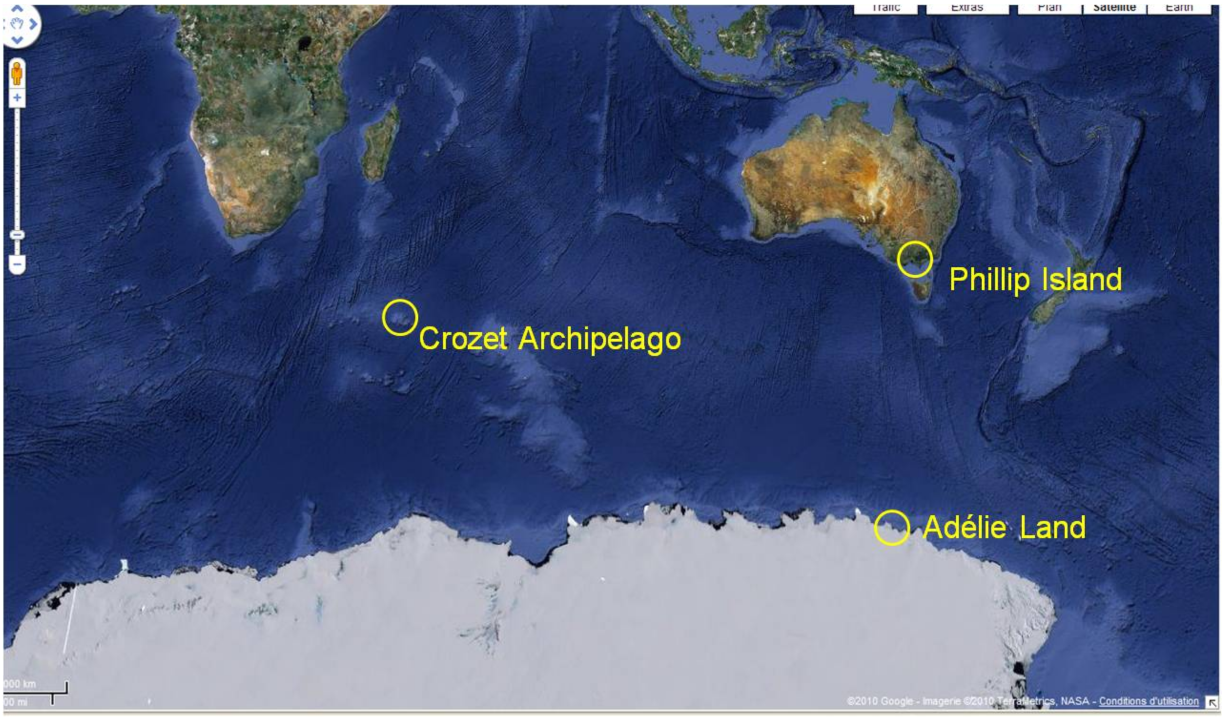


Figure III - 1: *Geographical situation of the three study sites. ©GoogleMap*

During these three years of PhD, I had the chance to work with each one of the three species over 3 field work sessions (a 5-month summer campaign in Crozet on king penguins and a 5-month period in Phillip Island followed by a 2-month summer campaign in Adélie Land, see the *a typical day in the field* box). Summer campaigns in Crozet and Adélie Land were part of the 137 polar program and I had the chance to participate in the long-term monitoring of the population, that implicate very diverse protocols concerning directly my PhD or not.

A typical day in the field *(Crozet, 2009-01-10)*

4am: *Drrrrringggggg*! Time to wake up already after a short night... After dressing into my nice smelly penguin clothes, I'm on my way to the colony cautious not to fall on the vicious rocks which pave the path, invisible to eyesight in the night. As I arrived safe and sound at the shelter (situated directly amongst the thousands of king penguin pairs, the shelters give us great facility to work), the first thing I do is check the computer to find out which penguins have returned or left the colony during the night (we wait for penguins we have equipped days earlier to retrieve their loggers). Then I take a moment to enjoy the beautiful sunrise on the Ile de l'Est. What a chance to be here! A lot of work for sure, but nature in its plain realm seems almost undisturbed, all everyday worries forgotten and just time to enjoy it all. I take my first tour of the colony to check on all the penguins we monitor, which parent is here, did the egg hatch…? I catch a marked chick in advanced moult to transpond it. Most of the cohort (around 600 chicks) has already been transponded and we chase the few remaining ones. I return to the shelter and it is time for observations (with binoculars) of a hundred random penguins entering and leaving the colony to determine infestation by ticks.

7am: Time for breakfast with the *Nutella* we hide in the shelter! Mary and Oni arrive and manipulations start. One person always stays in the shelter to check the computer in case some missed bird tries to enter the colony without our noticing.

9am: The morning will be spent with one of our preferred activity: monitoring chick growth. We have a group of 40 chicks to weigh, measure and blood sample every week. Funny how these first hideous "downballs" became so cute and lovely as soon as we handle them!

1 pm: the sun is here and we are eating outside in order to keep an eye on which penguin returns. Lunch, time to discuss with people of other programs so that everybody is aware of what's going on in the colony, whatever help could be needed… But of course, here it is with its bright B2 paint with picric acid just coming out of the sea, one of the so expected penguins. Too bad for the meal! First step catching and hooding it, to keep it calm, then retrieve the logger, weigh it and when this is done, B2 is free again. A good day is on; we had been waiting for B2 for so long!

2pm: No bad surprise this time, the logger is not rusty and it is functional. We download the data before reseting it for a next deployment. Mary stays to look at the data, while we make another tour of the colony, looking for marked individuals.

3pm: The afternoon is calm, Oni takes care of the weekly monitoring of the colony and I decide to go and help Vincent to equip birds with heart rate recorders. An hour later, we exchange place with Mary in the shelter and she goes to help Nico.

6pm: the afternoon flew away, time for a last check of every penguin, up until the end of the river and we'll return to the base.

7pm: As usual, we are running late for the 7pm dinner with everybody (29 people are living on the base, from military to scientists) but we still choose the shower!

1) Phillip Island

Little penguins were studied at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (lat 38°15’S, long 143°30’E), where about 14 000 pairs of little penguins breed (Cullen *et al.* 2009).

One of the particularities of this site (compared to the others we studied) is the proximity with humans. The colony is part of a nature park and is home for the famous “Penguin Parade”, where people can come every night (up to half a million visitors a year) and enjoy for 50 minutes the returns of little penguins crossing the beach. This attraction is monitored by rangers who make sure people stay on the board walk out of reach of the penguins.

Figure III - 2: *Penguin Parade: the studied colony in Phillip Island Nature Park*

The study site is a part of this colony containing 100 artificial burrows (wooden nest boxes; Figure III - 3), with an annual nest occupancy of ~60%. These artificial burrows have been part of measures of conservation to provide habitat at degraded areas.

Figure III - 3 : *Wooden boxes used as artificial burrows.*
Over time, they have been covered by vegetation and well incorporated in the landscape. Each one bears a number and the two white stickers on the right picture indicate the presence of two eggs.

2) Possession Island, Crozet Archipelago

The Crozet Archipelago is constituted by 5 French sub-Antarctic islands (total area of 360 km²), part of the Terres Australes and Antarctiques Françaises (TAAF).

The Crozet basin is one of the most productive sectors of the Sub-Antarctic zone. The iron coming from these volcanic islands enhances the biological production (Bucciarelli *et al.* 2001). The phytoplankton biomass around the islands is thus three to eight times higher than what is usually observed in pelagic waters (Pakhomov *et al.* 1994). This high productivity of the surrounding waters is probably responsible of the fauna richness of these islands with one of the most diverse seabird community in the world (Jouventin *et al.* 1984). Particularly, more than 1 million pairs of king penguins breed in this archipelago, which corresponds to about 2/3 of the world population (Guinet *et al.* 1995).

The scientific base Alfred Faure is situated on the Possession island (46°25'S, 51°45'E), which is home for about 80 000 breeding pairs (Delord *et al.* 2004). The studied colony called 'La Grande Manchotière' is the second biggest of the island and holds around 20 000 breeding pairs.

***Figure III - 4**: Colony of 'La Grande Manchotière', Possession Island*

3) Adélie Land

The Adélie Land is part of the TAAF. The French scientific base of Dumont D'urville (66°40'S 140°01'E) is situated on the biggest island of the Pointe Géologie Archipelago, the Petrel island. This island, a few kilometers of Antarctica is home for about 12 000 Adélie penguin pairs. The studied colony of the project called 'ANTAVIA' corresponds to a relatively isolated part of the island, where approximately 300 pairs breed every year.

Figure III - 5: *Petrel Island with the penguin colonies all around the base. ©Marie Pellé*
All brown spots correspond to penguin colony. The picture was taken in summer when most of the snow had melt.

II. Species

Penguins are monogamous (at least at the scale of one breeding season) and exhibit bi-parental care strategies, as is the norm in most birds (Lack 1968).

1) Little Penguins

Little penguins
- Eudyptula minor -

40-45cm
700-1700 g

2 eggs

Inshore species

Temperate area (Phillip Island, Australia)

Little penguins, the smallest of the 18 penguin species (Williams 1995), are endemic to southern Australia and New-Zealand. Though they are considered long-lived, little penguins exhibit one of the highest mortality amongst penguins (Williams 1995).

Little penguins breed in small colonies. They are philopatric and tend to return to the same area of their colony every year. They usually establish their nest in a burrow within a few metres of that used the previous season (Reilly & Cullen 1981). Egg laying generally takes place from August to December, although it has been known to start as early as May and extend as late as February. The usual clutch size is 2 eggs, sometimes 3-egg clutches may occur. The breeding cycle is summarized in a schematic presented below (Figure III - 6). Briefly, after laying, parents take turn at incubating the eggs for an average period of 35 days, at what time eggs hatch (Chiaradia & Kerry 1999). Chick-rearing then takes 7 to 10 weeks to complete. At first (~ the 2 first weeks), one of the parents stays with the chicks while the other one forages at sea (Chiaradia & Kerry 1999). This guard period is followed by the post-guard when chicks are left alone in the colony and both parents go out at sea to forage. Parents usually make one-day trips during guard, while longer trips can be observed in post-guard (Collins *et al.* 1999; Chiaradia & Nisbet 2006; Saraux *et al.* 2011d). After fledging, chicks depart to sea and do not return to breed until they are 2-3-year old on average.

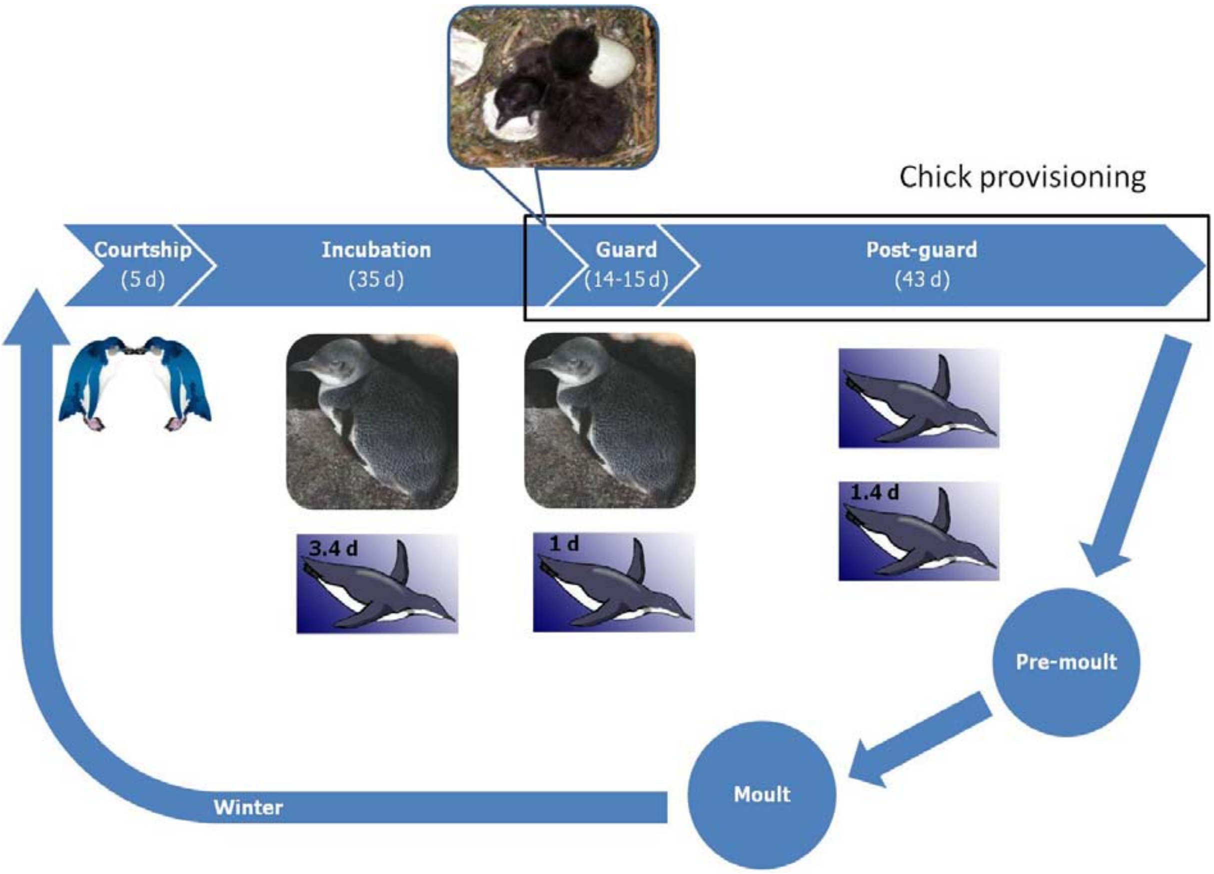


Figure III - 6: *Summary of the breeding cycle of little penguins.*
The number of days of each phase is indicated into bracket, while the average length of individual shifts is indicated on the foraging penguin scheme. These numbers come from Chiaradia & Kerry 1999 and personal observations.

Little penguins present a clear bill size dimorphism (Stahel & Gales 1987) that allow to sex them without genetic sampling (calibration for Phillip Island population in Arnould *et al.* 2004).

2) King Penguins

King penguins
- Aptenodytes patagonica -

90 cm
7-17 kg

1 egg

Offshore species

Sub-Antarctic area (Crozet)

King penguins are the second biggest penguins after the emperor penguins. They breed in dense colonies under sub-Antarctic latitudes (Stonehouse 1960). The breeding cycle of the king penguins has been well studied (Stonehouse 1960; Barrat 1976; Weimerskirch *et al.* 1992; Descamps *et al.* 2002). Its length is atypical and much longer than of other penguins, as it takes parents more than a year to fledge their single chick (around 14 months on Crozet archipelago; Barrat 1976; Weimerskirch *et al.* 1992; Descamps *et al.* 2002). Because of this especially long cycle, bird arrival at the colony depends on the success and timing of the previous year's breeding attempt (Figure III - 7). The laying period of king penguins therefore extends for over four months, with two peak periods (Stonehouse 1960; Barrat 1976): one for 'early breeders' (before the 1st January) and one for 'late breeders' (after the 1st January).

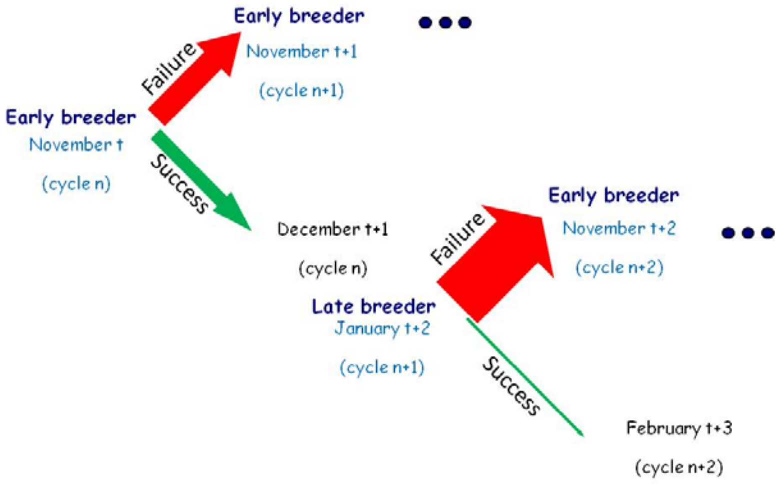


***Figure III - 7:** Successive breeding cycles of king penguins.* *Arrow width is proportional to the probability of the event. Breeding start is indicated in light blue, while its end is indicated in black. Note that for failures the end is not indicated as it may occur at any time.*

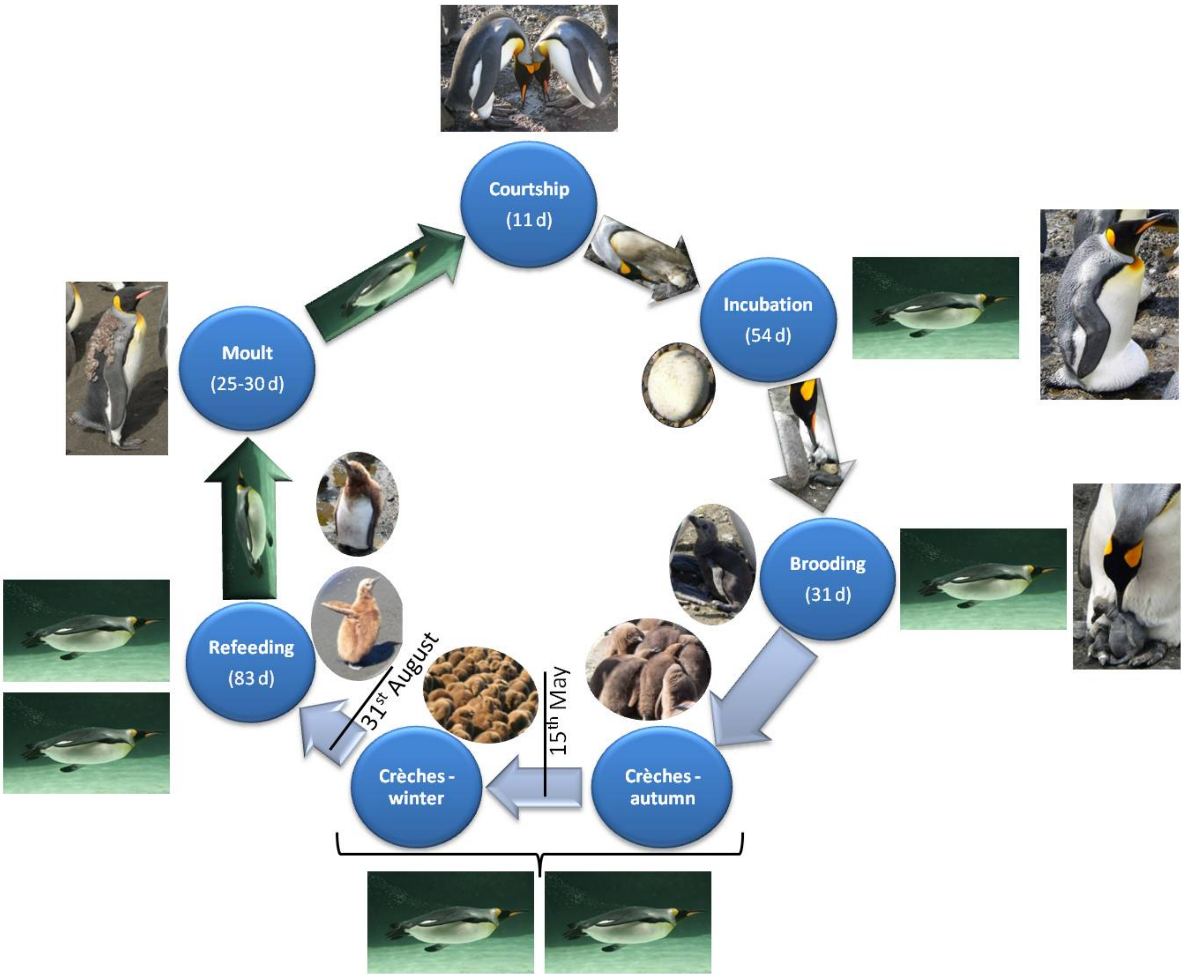


Figure III - 8: *Summary of the breeding cycle of king penguins.*
The average number of days of each phase is indicated into bracket (according to Weimerskirch et al. 1992 and Descamps et al. 2002). NB: two pictures have been kindly provided by M. Le Vaillant. The situation of the 2 parents (at sea or on land) is indicated with the pictures on the outside.

Before breeding, king penguins moult and change their old feathers to new ones (see Figure III - 8 for a summary of the whole breeding cycle). The moulting period is associated with a high rate of body fuel utilization, resulting from the combination of fasting on land for 2 to 3 weeks, the increased heat loss induced by the loss of old feathers and the body protein breakdown linked to the building of the new plumage (*e.g.* Gauthier-Clerc *et al.* 2002). An extended foraging trip follows moult in order to rebuild reserves before returning to the colony to breed. King penguins do not build nest but choose and settle in a specific territory when courting. After laying its single egg, the female goes at sea to replenish its reserves, leaving the male to incubate the egg. Incubation extends for a period of about 54 days, both parents taking turn to care for the egg (Stonehouse 1960). The newly-hatched chick cannot thermoregulate by itself, so that parents have to brood their chick (which is also a mean to face the elevated predation pressure at that time). After a period of about a month of brooding, the chicks are thermally emancipated and their parents can leave them alone in the colony (Barrat 1976). Day by day they begin to form crèches. Parents return often to feed the chick during this important phase of chick growth. The chicks indeed need to build up important body reserves to face the winter period, when the weather is at its worst and resources scarce and further from the colony. During the winter period, parents return less often to the colony and chicks have to fast, losing a third or half of their body mass (Stonehouse 1960; Barrat 1976; Cherel *et al.* 1987). The feeding frequency increases again with spring so that the chick completes its growth. After more than a year, the chick moults and finally fledges.

3) Adélie Penguins

Adélie penguins
- Pygoscelis Adeliae -

70 cm
3.5 - 6 kg

2 eggs

Inshore species

Antarctic area (Adélie Land)

Adélie penguins, together with emperor penguins are the only two penguin species that breed only in the Antarctica (Williams 1995). They usually breed in large colonies during the austral summer (from October to March, in between the retreat of the sea-ice and the next sea freeze-up). The breeding and life cycle of Adélie penguins have been extensively described by Ainley (2002). At the end of October, Adélie penguins get back to their colony, males arriving a few days earlier than females. Once the pair is formed, both members of the pair build a nest by piling small rocks, and copulate. After laying two eggs (average clutch size of 1.9; Ainley 2002), the female goes out at sea to feed, while the male begins incubating the egg. Both male and female thereafter take turns to complete the incubation, which lasts on average for 34 days. After hatching, the 3-week guard period begins. During that time, parents keep on taking turns in order to protect the chicks from predators and to keep them warm, and the foraging trips typically last 1 to 3 days. When chicks reach thermal emancipation, both parents leave the colony to forage at sea, while the chicks form small crèches. Parents then return to the colony every 2/3 days to feed their chicks until they fledge by the end of February or beginning of March.

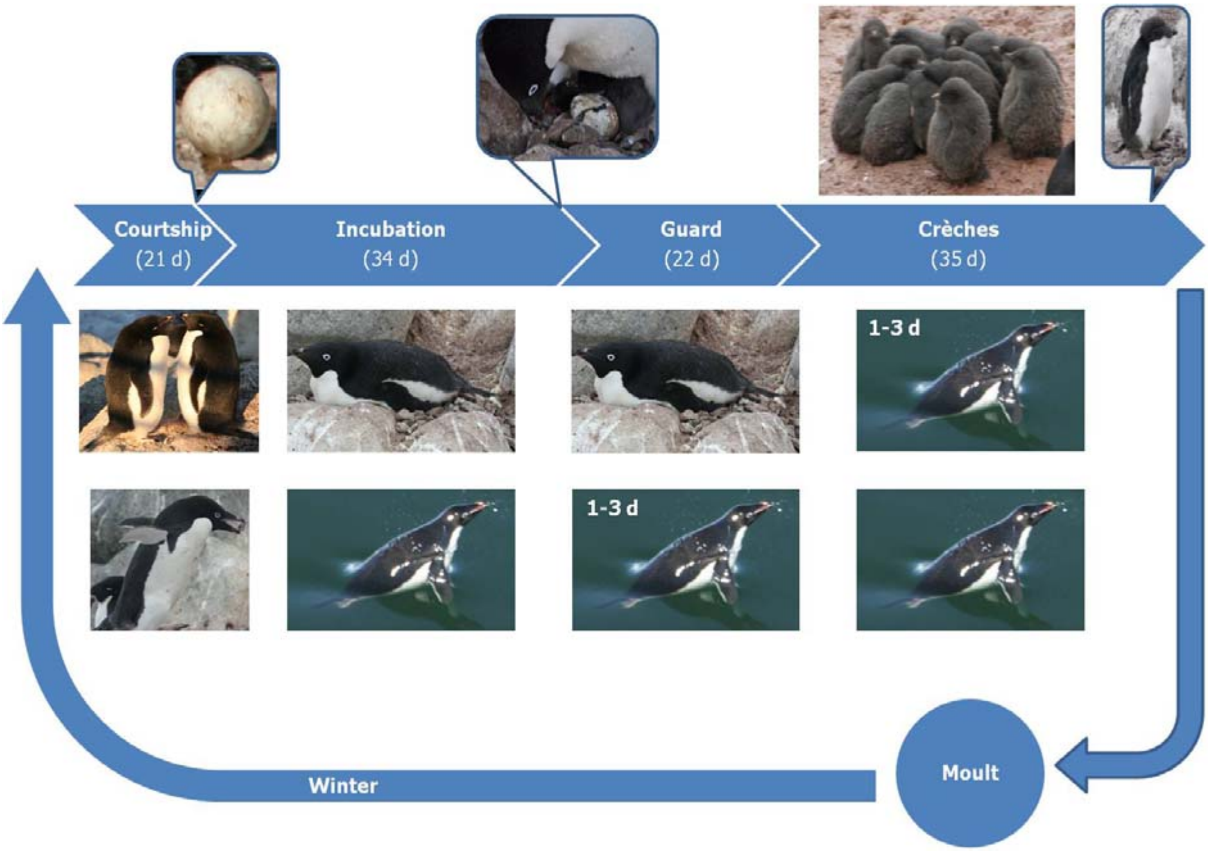


Figure III - 9: *Summary of the breeding cycle of Adélie penguins.*
The average number of days of each phase is indicated into bracket, while the average length of individual shifts is indicated on the foraging penguin scheme (Ainley 2002).NB: The picture of the hatching has been kindly provided by Manuelle Cottin.

Adélie penguins moult every year at the end of their breeding season. They replenish their reserves at sea before fasting for about two weeks, when they acquire their new feathers. Then they leave for their annual migration to be back the next summer.

III. Oceanographic context

1) Hydrologic structure of the Southern Ocean

The southern Ocean, which is usually associated with the Antarctic Circumpolar Current (ACC), is composed by several distinct water masses, separated by oceanographic structures such as fronts (Belkin & Gordon 1996; Figure III - 10).

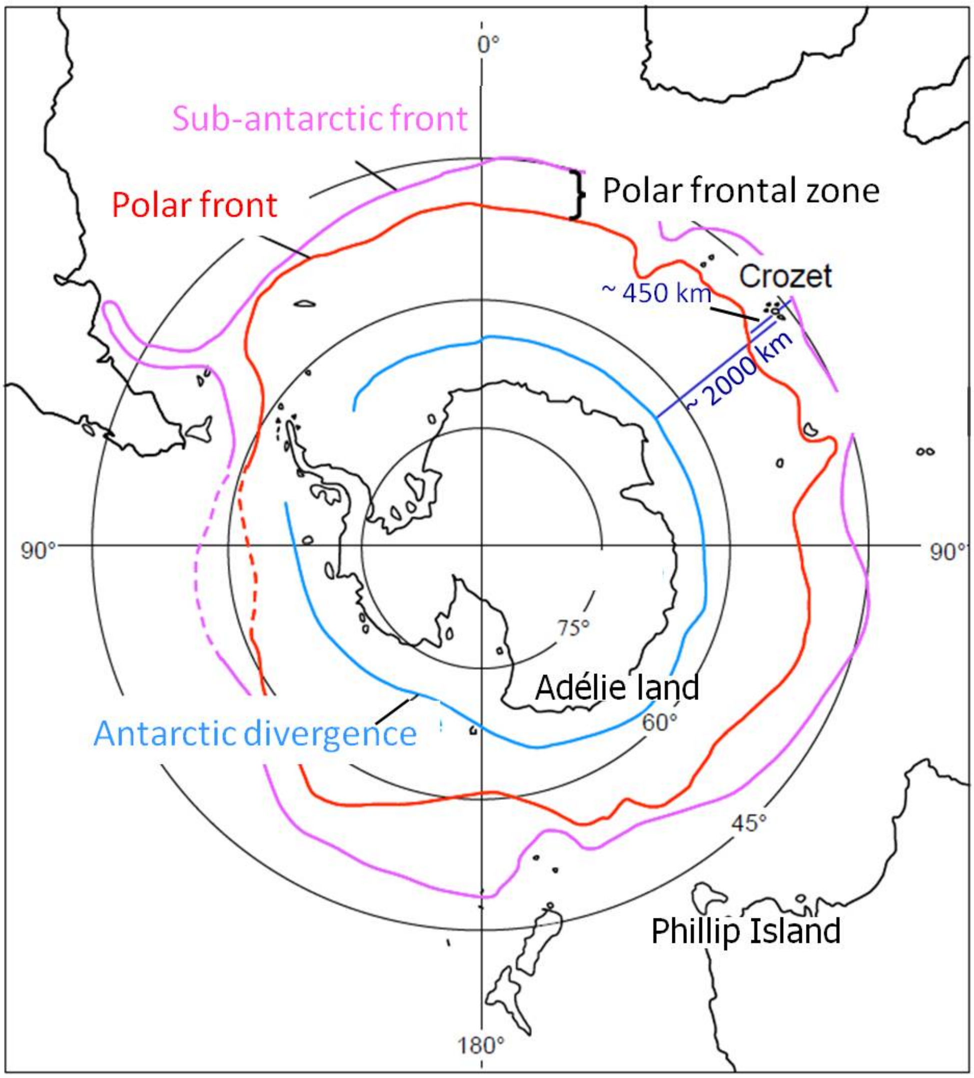


Figure III - 10: *Map of the main oceanographic structures of the Southern ocean. (from Belkin & Gordon 1996; Park & Gamberoni 1997).*

Fronts are identified by marked changes in vertical structures from one side to the other. Such changes are usually accompanied by enhanced horizontal property gradients at various levels, such as temperature and salinity and concentrated geostrophic flow. Going from south to north, the first encountered discontinuity is the Antarctic Divergence, resulting from the circumpolar deep waters rising, thus creating the surface Antarctic water. This water mass drifts north under the influence of the ACC (until around 50°S), at which it dives under warmer sub-Antarctic waters. The confluence of these two masses constitutes the Polar Front (PF). Finally, sub-Antarctic and sub-tropical fronts are situated north of this front.

The position of these different fronts can vary significantly according to longitudes, seasons and years (Park & Gamberoni 1997; Park *et al.* 1993; Moore *et al.* 1999). As the oceanographic structure of the ocean is not always available, we use satellite data of sea surface temperatures to estimate the position of the fronts. As an example, Park and colleagues (1993) evaluated that the polar front should stand where SST values reach 4°C.

2) Particularities for little penguins

Little penguins breed on grounds close to the food supply. They have indeed one of the shortest foraging ranges among seabirds (<20km, Collins *et al.* 1999) and therefore can be good models of inshore species, which constitute the majority of seabirds. Little penguins are thought to be visual hunters as they only feed at sea during daytime (Cannell & Cullen 1998, Collins *et al.* 1999, Ropert-Coudert *et al.* 2006b) and return ashore only after sunset (Klomp & Wooller 1991, Chiaradia & Nisbet 2006).

Little penguins from Phillip Island mostly forage in the Bass Strait (Weavers 1992). Bass Strait is a shallow continental shelf channel or sea between Victoria and Tasmania, with an average depth of 50 to 70 metres. This channel connects the Great Australian Bight to the Tasman Sea and is affected by water from both regions (Figure III - 11). The Bass Strait circulation is mostly regulated by three currents: the Leeuwin current bringing Sea Surface Temperature anomalies of the Indian Ocean Dipole (Yamagata *et al.* 2004), the Antarctic Circumpolar Current (ACC; Middleton *et al.* 2007) and the East Australian Current (EAC).

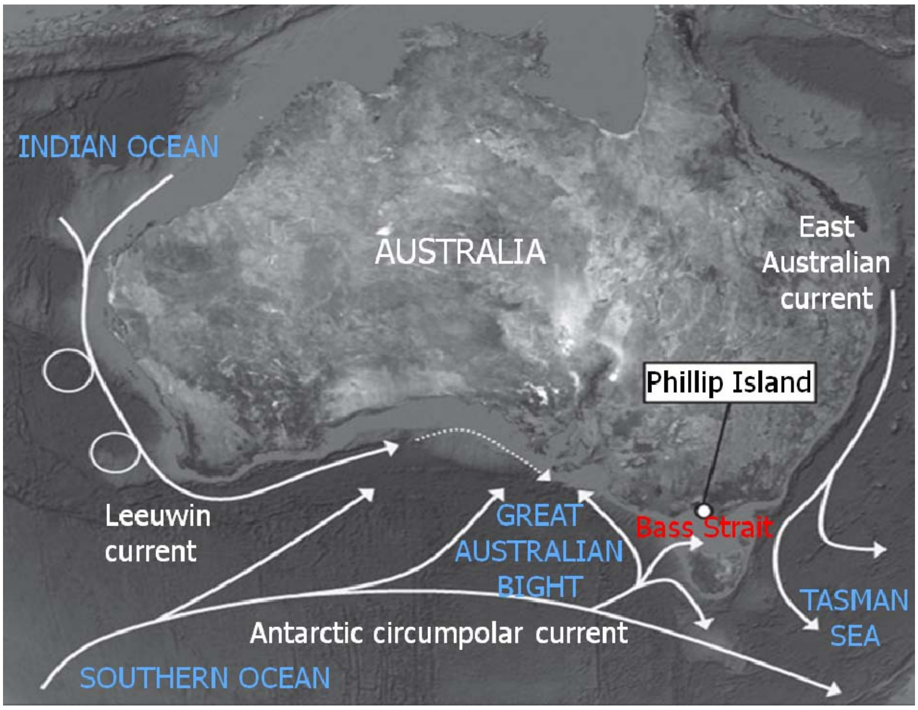


Figure III - 11: *Map of the main oceanic currents affecting the Bass Strait, area used by little penguins to forage. (modified from Ropert-Coudert et al. 2009)*

Little penguins have also been shown to be sensitive to the stratification of the water (Ropert-Coudert *et al.* 2009). Indeed, both foraging and breeding success increased with thermal stratification (Ropert-Coudert *et al.* 2009). When water is not stratified penguin prey may disperse widely while thermal stratification seems to create physical barriers that the prey cannot cross, easing penguin purchase. This thermal stratification can be observed through the presence or absence of thermoclines.

3) Particularities for king penguins

King penguins are offshore birds that forage in oceanic areas far from the colony and are specialized on mesopelagic fish and squids (Adams & Klages 1987; Cherel & Ridoux 1992). Satellite tracking indicated that king penguins from Crozet are foraging at the PF during summer in a sector comprising 48–52°S (about 450 km away from the colony). Myctophids, also called lantern fishes (Figure III - 12), then represent the quasi-totality of their diet since *K. anderssoni, E. carlsbergi* and *Protomyctophum spp*. amount to 99% of the ingested mass (Cherel & Ridoux 1992). The polar frontal zone is indeed characterized by very high concentrations of myctophids.

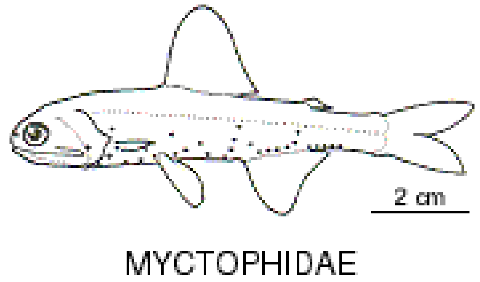


Figure III - 12*: Drawing of a myctophid (from the Fishes of Australia website, http://foa.webboy.net/family/myctophidae).*

However, when winter arrives, myctophids dive at greater depths (Kozlov *et al.* 1991) and become unavailable for king penguins. Their diet changes consequently, switching towards demersal cephalopods (~57%) and other species of myctophids (Cherel *et al.* 1996). The greater diversity of prey species and sizes suggests more opportunistic feeding behaviour in the winter period of food scarcity. In consequence, king penguins cross the northern limit of the light ice pack in winter to forage at the further southern latitudes of 56 – 62°S (Charrassin & Bost 2001). Thus breeding birds have to go as south as the Marginal Ice Zone (MIZ; more than 2000 km away from the colony; Bost *et al.* 2004), to replenish their reserves, while they fish for their chick on their way back close to the island.

4) Particularities for Adélie penguins

Adélie penguins are "*creatures of the pack ice*" (Ainley 2002). This quotation summarizes well the particularity of Adélie penguins. Indeed, Adélie penguins favour pack-ice habitat in winter and sea-ice maximal extent defines the at-sea range of this species (Ainley 2002). Consequently, the "sea-ice hypothesis" stated that Adélie penguin population trends should mostly result from sea-ice extent (Smith *et al.* 1999). However, a recent study proposed that sea-ice no longer drives penguin population trends in Antarctica through direct effects in habitat but rather that sea-ice is one of the factors affecting prey availability to penguins (Trivelpiece *et al.* 2011). Adélie penguins rely mainly on Antarctic krill, *Euphausia superba* (Volkman *et al.* 1980; Lishman 1985; Lynnes *et al.* 2004), whose abundance varied hugely across time. After the whaling era, during which humans depleted whale populations, thus widely decreasing predation pressure on krill, 150 million tons of krill were estimated to be available to support other krill predators (Laws 1977). Penguin populations seem to have increased up to fivefold following this period (Trivelpiece *et al.* 2011). Yet, recovering whale and fur-seal population along with increasing temperatures and reduction in sea-ice extent have now altered krill population (Atkinson *et al.* 2004).

IV. Environmental descriptors

Penguins are marine predators and as such should be affected by local climate through sea temperature, wind and currents (Ottersen *et al.* 2001). However, environmental conditions have been shown to affect population dynamics at both local and global spatial scales (Stenseth *et al.* 2002). Indeed, marine ecosystems exhibit a high inter-annual variability resulting from oceanographic process of a large spatio-temporal scale (Ottersen *et al.* 2001). 'Weather packages' and large-scale climate indexes (global indexes encompassing a combination of weather features, see Stenseth & Mysterud 2005) are thus good candidates for explaining the effects of large scale environmental variability on top-predators.

1) The Southern Oscillation Index: a global parameter

Global indexes, such as the Southern Oscillation Index (SOI), the North Atlantic Oscillation, or the Antarctic Oscillation Index are calculated at the scale of a whole ocean or even a hemisphere. That way they are good translators of global climatic mechanisms and general tendencies taking out the noise created by local fluctuations (Stenseth *et al.* 2003).

The famous El-Niño phenomenon has huge repercussions on the oceanic balance. On normal times, there is a vast area of low pressures in the South-West of the Pacific Ocean, while the east part is covered by a high pressure area. This pressure gradient leads trade winds from east to west along the equator. When an El Niño event occurs, the southern oscillation reverses this gradient and consequently the associated winds. This creates a lot of climatic modifications resulting in torrential rains in central pacific but a severe drought in Australia and Indonesia. La Niña is the reversed phenomenon, with an amplified gradient from east to west, resulting in a rise of cold waters in the east. El Niño / La Niña events occur irregularly with a cycle varying usually between 2 and 7 years and with variable amplitude.

The SOI is calculated from the monthly fluctuation in the air pressure difference between Tahiti and Darwin and gives a good indication of the phase of El-Niño Southern Oscillation (ENSO). Negative SOI values indicate El-Niño events, whereas positive values indicate La Niña events (Deser & Wallace 1987; Figure III - 13). This index has already been used several times to explain the effects of environmental variability on top-predators such as penguins (Jenouvrier *et al.* 2005a&b; Le Bohec *et al.* 2008a, Saraux *et al.* 2011a)

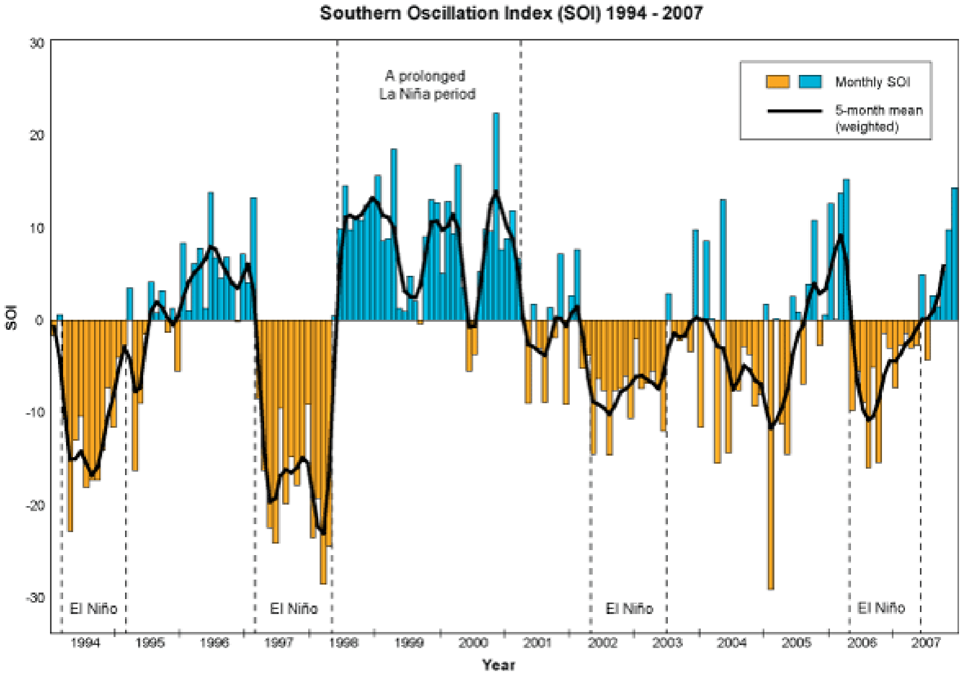


Figure III - 13: *Monthly values of Southern Oscillation Index from 1994 to 2007.*
Positive SOI values are shown in blue, with negative in orange. Sustained positive values are indicative of La Niña conditions, and sustained negative values indicative of El-Niño conditions. (from the Australian Bureau of Meteorology, http://www.bom.gov.au/).

Monthly SOI were obtained from the Australian Bureau of Meteorology.

2) Local parameters (SST, Chla)

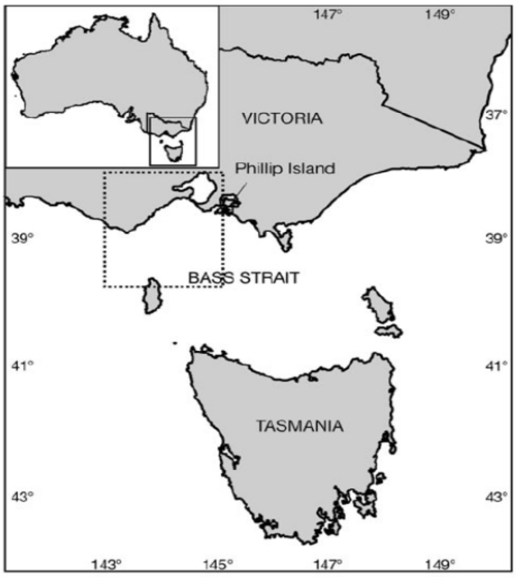
Sea Surface Temperature (SST) is known to influence the position of oceanic fronts, which along with areas associated with the seasonal sea-ice retreat are very productive regions (Moore & Abbott 2000) and important foraging grounds for top-predators (reviewed in Bost *et al.* 2009). Further, since changes in SST have repercussions on the primary production and the food chain (Gregg *et al.* 2003), SST has been used as a local proxy of abundance and distribution of prey for penguins (Jenouvrier *et al.* 2005b; Le Bohec *et al.* 2008a). Low SSTs in spring and summer (high photoperiod) might indeed favour phytoplankton bloom, yielding high levels of chlorophyll.

Chlorophyll *a* is at the basis of the food web and thus might impact apex predators through the availability of prey. The concentration in chlorophyll a ([Chl*a*]) is a local parameter to take into account. SST and [Chl*a*] have been shown to affect life-history traits of king and little penguins (Le Bohec *et al.* 2008a; Cullen *et al.* 2009).

Daily Sea Surface Temperature (SST, in °C), and weekly concentration of chlorophyll ([Chl*a*], in mg.m^{-3}) were obtained from satellite data of the National Ocean and Atmospheric Administration, and from the Sea-viewing Wide-Field Sensor (SeaWiFS), respectively. However, due to methodological problems (such as the presence of clouds), the [Chl*a*] dataset presents a lot of not available values, which renders its use difficult. This explains why SST is constantly used in each study but not [Chl*a*].

3) Spatial and temporal means

a) Phillip Island



Monthly averages of SST were calculated in an area of the Bass Strait, bounded by 38-40°S, 143-145°E (Figure III - 14). For analyses on breeding success, SST was averaged on different time periods, either before laying or during the actual breeding (mean on the whole breeding cycle, on the incubation or chick-rearing period, *etc.*).

Figure III - 14: *Area on which the SST was averaged (dotted rectangle). From Cullen et al. 2009*

b) Crozet

Monthly averages of SST were calculated in an area centred on Crozet Archipelago, bounded by 43–47°S, 46–56°E. This subsector corresponds to the yearly most productive subsector in the Crozet region, shallow shelves and weak currents acting as a retention zone (Perissinotto & Duncombe Rae 1990). SST in this area might therefore influence the primary productivity. Similarly, monthly averages of [Chl*a*] were calculated in this same subsector.

However, as stated above, penguin diet relies mostly on preys foraged on the polar front during summer and much further south until the MIZ during winter. SST south of Crozet influencing the position of fronts, monthly SSTs were also extracted at every two latitudes in the area south of Crozet bounded by 46–60°S, 46–56°E, encompassing the penguin's southernmost foraging range (Charrassin & Bost 2001). Additionally, we calculated monthly PF latitude as the latitude where SST value reaches 4°C using a linear regression between temperature and latitude. We also deduced from these PF latitudes the distance between Crozet Island and the PF and used this distance as a possible explanative variable in several models.

It is important to note that negative values of SOI are generally associated in our study area with warm SST anomalies (Park *et al.* 2004).

As indices of the environmental conditions during the breeding cycle, means on the breeding cycle of SOI, [Chla] and both SSTs (*i.e.* the mean centred on Crozet and the mean on the whole 46-56°S area) were used: for failing birds, the mean was calculated from the month of laying to the month of failure, whereas the mean was calculated over the 14 months of the breeding cycle for succeeding birds. Body condition being partly determined by environmental conditions (McNamara & Houston 1996), a mean of the SSTs during the winter (June to October) of each year was calculated and its impact on the arrival date and breeding success with a one-year lag was investigated.

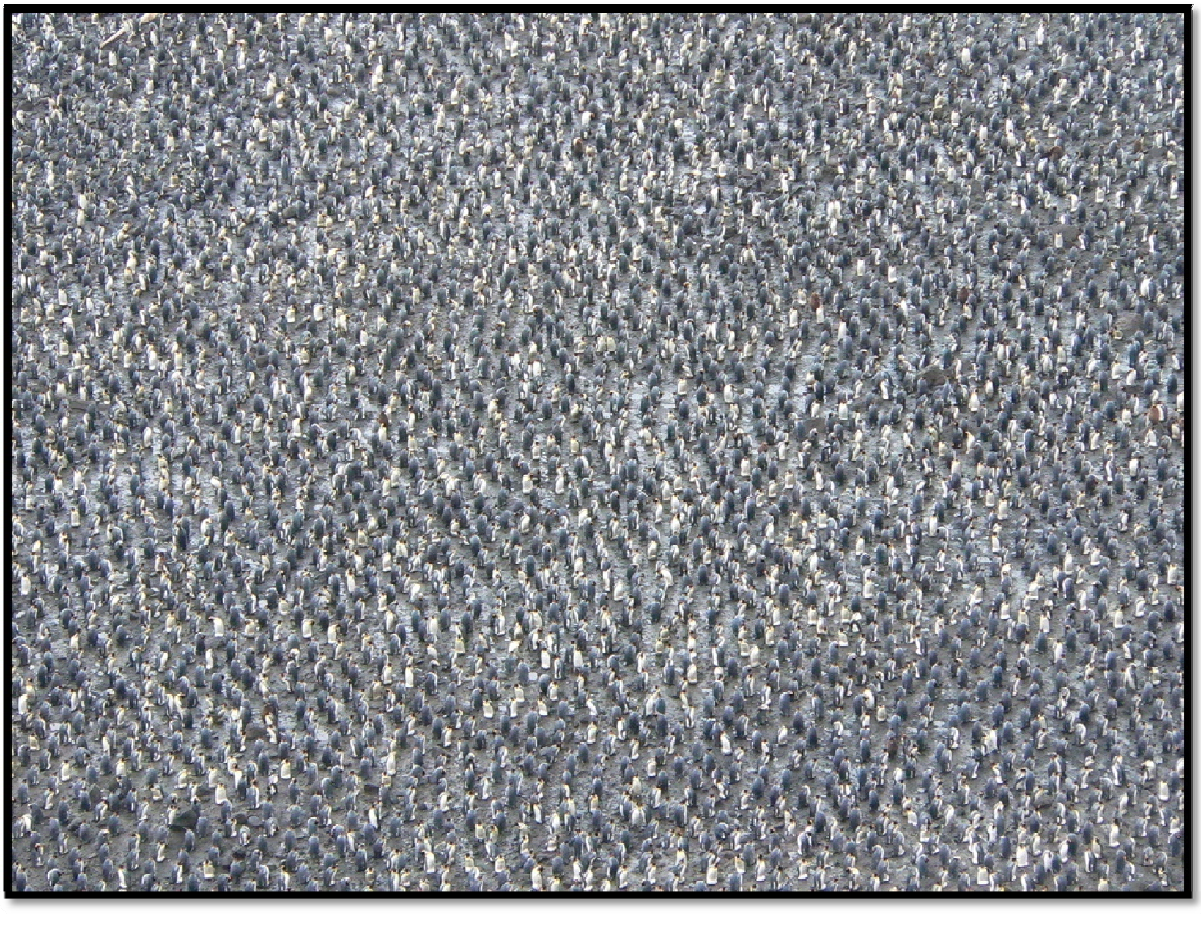
As little is known on the location of feeding grounds in sub-adult king penguins, we tested SST averaged on several areas when studying juvenile survival from the sub-tropical front to the MIZ (see Article 3 for details).

c) Dumont D'urville

According to the "sea-ice hypothesis", Adélie penguin population trends should mostly result from sea-ice extent (Smith *et al.* 1999). As an index of sea-ice extent, we used the distance from the colony to open water. Such a distance was calculated as the shortest straight-line distance between the colony and the nearest open water on cloud-free satellite images (resolution: 1 km; see Beaulieu *et al.* 2009a). These distances are calculated by Météo France several times a month (the number of times depending on the actual changes in sea-ice observed on these images). We used these distances averaged on the whole breeding season, *i.e.* from early October to late March each year. This average distance over the breeding cycle is highly correlated to the timing of sea-ice retreat (as inferred by the first date of open water reaching the colony; P = 0.01, r = 0.94 over the 5 years of data we have) and consequently probably mostly driven by this phenomenon. But it also accounts for differences in sea-ice extent when sea-ice retreated at similar times.

Chapter IV ○○○●○○○○○○

Monitoring individuals on the long-term



I. How to monitor penguins?

Much of our present knowledge on the ecology and behaviour of animals is derived from longitudinal studies of individuals. Long-term datasets are essential to study life-history traits (*e.g.* age-specific survival or reproductive success; Lebreton *et al.* 1992), and to understand how variations in those traits might impact population dynamics and behavioural strategies. However, the collection of such datasets requires the ability to repeatedly identify individuals over time. In some animal populations, this can become a real nightmare. Penguins live in huge colonies and bear no particular distinctive signs. As a little challenge for the reader, pick a penguin out of the picture on the previous page (the one you prefer of course). Close your eyes for a second open them again and try to spot it again. You will have to admit that this is far worse than finding Wally. This is what it can be like to monitor penguins.

Of course, several ways have been used to mark penguins. But the real challenge is to mark them with the smallest impact possible. One way consists in using animal dye such as Nyanzol®, picric acid or even Porcimark®. These techniques make them visible and exhibit no real danger for the birds (even if we do not know of the potential consequences on predation risk and mate choice). However, penguins moult every year and the marking then disappears, forbidding longitudinal monitoring.

At the start of my PhD, 3 different methods (flipper-bands, web-tags and transponder tags with Radio-Frequency-IDentification; Figure IV - 1) were known to monitor penguins on the long-term. All three methods consisted in catching the penguin to either attach something on it or insert it under its skin. External markings may imply an increased drag effect for penguins which are extraordinary swimmers and divers, as shown in Adélie penguins for instance (Culik *et al.* 1993). However, the consequences on penguin life-history traits on the long-term were poorly known. In the next part, we compare two ways of monitoring (flipper bands and transponder tags) in a 10-yr study conducted on king penguins.

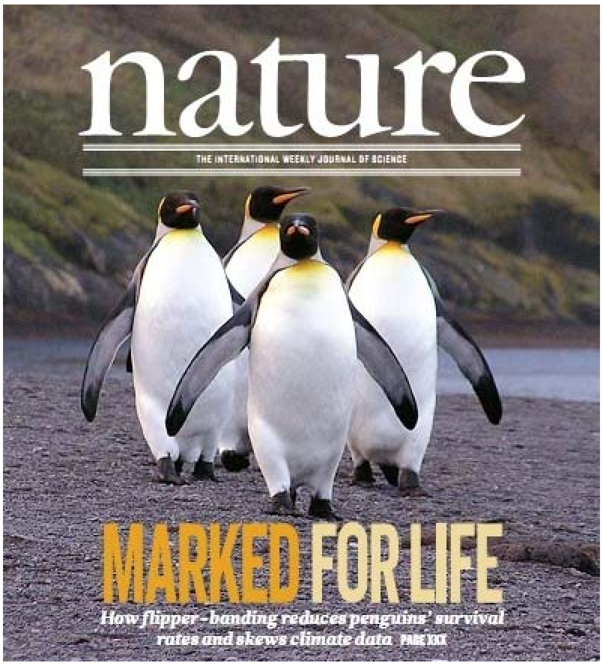
Figure IV - 1: *Stainless steel flipper band (on the left) and transponder tag (on the right).*

II. The use of flipper bands

Reliability of flipper-banded penguins as indicators of climate change

(Article 2)

Claire Saraux, Céline Le Bohec, Joël M. Durant, Vincent A. Viblanc, Michel Gauthier-Clerc, David Beaune, Young-Hyang Park, Nigel Yoccoz, Nils Chr. Stenseth & Yvon Le Maho



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In 2007, the Intergovernmental Panel on Climate Change highlighted an urgent need to assess the responses of marine ecosystems to climate change (Richardson & Polanczaska 2008)**. Because they lie in a high-latitude region, the Southern Ocean ecosystems are expected to be strongly affected by global warming. Using top predators of this highly productive ocean** (Tynan 1998)**, such as penguins, as integrative indicators may help us assess the impacts of climate change on marine ecosystems (**Croxall *et al.* 2002; Durant *et al.* 2009)**. Yet most available information on penguin population dynamics is based on the controversial use of flipper banding. Although some reports have found the effects of flipper bands to be deleterious (**Jackson & Wilson 2002; Gauthier-Clerc *et al.* 2004; Dugger *et al.* 2006; Fallow *et al.* 2009)**, some short-term (one-year) studies have concluded otherwise (**Hindell *et al.* 1996; Boersma & Rebstock 2009; 2010)**, resulting in the continuation of extensive banding schemes and the use of data sets thus collected to predict climate impact on natural populations (**Barbraud & Weimerskirch 2001; Jenouvrier *et al.* 2009a)**. Here we show that banding of free-ranging king penguins (*Aptenodytes patagonicus*) impairs both survival and reproduction, ultimately affecting population growth rate. Over the course of a 10-year longitudinal study, banded birds produced 41% fewer chicks and had a survival rate 16 percentage points lower than non-banded birds, demonstrating a massive long-term impact of banding and thus refuting the assumption that birds will ultimately adapt to being banded (**Barbraud & Weimerskirch 2001; Fallow *et al.* 2009)**. Indeed, banded birds still arrived later for breeding at the study site and had longer foraging trips even after 10 years. One of our major findings is that responses of flipper-banded penguins to climate variability (that is, changes in sea surface temperature and in the Southern Oscillation index) differ from those of non-banded birds. We show that only long-term investigations may allow an evaluation of the impact of flipper bands and that every major life-history trait can be affected, calling into question the banding schemes still going on. In addition, our understanding of the effects of climate change on marine ecosystems based on flipper-band data should be reconsidered.**

The effects of climate forcing on primary and secondary production of the short austral food webs may be integrated at higher levels (Croxall *et al.* 1988; Le Maho *et al.* 1993), and thus amplified in top-level predators such as seabirds. This has led to a strong interest in studying Antarctic and sub-Antarctic top predators (especially penguins, which are major consumers of the Southern Ocean ecosystem) as sensitive indicators of environmental changes (Croxall *et al.* 2002; Durant *et al.* 2009). To understand how variability in marine resources affects their demography over the timescale of years, simultaneous investigations of variation in breeding success and survival are necessary and require long-term individual monitoring at the population scale.

Most of our present knowledge on the population dynamics of penguins is based on large flipper-banding schemes. The key advantage is that bands can be identified from a distance, avoiding recapture stress for the birds. In the 1970s, however, bands were observed, both in zoos and in the wild, to injure flipper tissues severely (Jackson & Wilson 2002), especially during the moult. Although many research programmes consequently abandoned banding as a precaution in the late 1980s, massive banding schemes still continued (see references in Jackson & Wilson 2002). Yet, as penguins power their swimming exclusively with their flippers, there has been an increasing concern about the hydrodynamic drag effect that may be induced by flipper bands (for example a 24% increase in the energy cost of swimming in captive Adélie penguins; Jackson & Wilson 2002). The question was then whether penguins may compensate for such effects (Hindell *et al.* 1996; Boersma & Rebstock 2009) and whether the impact of flipper bands would be limited in time. Although it had been assumed that the effect of flipper bands lasted for a year at most (Barbraud & Weimerskirch 2001; until the bird got used to the band), the question remained to be addressed in the long term. In this context, medium-term studies revealed lower breeding success and survival in Adélie penguins (Dugger *et al.* 2006) and a reduced breeding success in king penguins (Gauthier-Clerc *et al.* 2004). However, those pioneering findings did not result in the cessation of ongoing banding schemes. Whether or not flipper bands have a deleterious impact in the long term is, nonetheless, a crucial issue, for ‘‘it raises practical and larger ethical questions about costs and benefits of procedures in field studies’’ (May 2004). In addition to possibly harming penguin populations already under threat (such as penguins rehabilitated after oil spills; see references in Gauthier-Clerc *et al.* 2004), the potentially negative effects of banding on demographic parameters may introduce a bias, which in turn might jeopardize any attempt to use data from banded birds to assess the impact of climate (Barbraud & Weimerskirch 2001) on population dynamics and to predict the future of breeding colonies according to scenarios of the Intergovernmental Panel on Climate Change (Jenouvrier *et al.* 2009a).

Using a decade-long data set, we analysed differences in reproduction and survival between two groups of electronically monitored king penguins (50 banded and 50 non-banded) breeding on Possession Island in the sub-Antarctic Crozet archipelago. These differences were investigated in relation to the birds' time of arrival for breeding and the duration of their foraging trips. Furthermore, we explored whether and how climate variability might differently affect banded and non-banded penguins.

Methods

We confirm that all work followed approval by an ethics committee and conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare.

Demographic survey

Our study was conducted on king penguins breeding in the colony of La Grande Manchotière at Possession Island (46°25'S, 51°45'E) on Crozet archipelago. We used automatic identification and data-logging systems (the ANTAVIA system; Gendner *et al.* 2005) to follow, from 1998 to 2008, 100 king penguins implanted with a passive transponder tag under the skin of their leg. The transponder tags weigh 0.8 g and have no known adverse effects. They were shown not to affect survival of king penguins (Froget *et al.* 1998) or breeding success, recruitment or survival of tits (Nicolaus *et al.* 2009). Furthermore, concerns about infections should be minimal, as transponder tags were kept sealed sterile in iodine capsules (Betadine) and were removed from the capsules only by the process of injecting them into the bird. Moreover, Vétédine soap and alcoholic antiseptic solutions were used to disinfect the skin and the injecting needle before each insertion. Flesh wounds did not seem infected thereafter (personal observations on recaptured birds). Penguins were randomly sampled in their breeding area (only breeding birds were taken, to make sure that they were mature birds). Fifty of them were also fitted with a metal flipper band (Gauthier-Clerc *et al.* 2004), with the simple rule of banding every second bird to randomize the treatment. Automatic identification systems allow for continuous, automatic data collection of bird movements into and out of the colony. The system is completed by video recording of the passageways over the antennas. Banded birds were thus monitored during the whole study, and only one bird lost its flipper band. This bird was not considered in further analyses.

Biological variables

The breeding propensities and phenologies of the birds were established by analysing recorded movements of the 100 studied penguins between the breeding area and the sea (Descamps *et al.* 2002). We assumed that those birds which were recorded leaving the colony went to sea. The specificity of the king penguins' breeding cycle allows us to determine whether and when birds attempted to breed, and whether and when they failed (stop in the sex-specific shifts). We were thus able to obtain arrival and laying dates, lengths of sojourns at sea and breeding variables, over all years and for each bird.

The sex of the birds was established by analysing the chronology of sex-specific incubating shifts (Descamps *et al.* 2002). Because sex had no significant effect on the date of arrival at the colony or on the propensity to breed, gender was not incorporated in our models. The presence of couples in the sample was controlled to avoid double-counting the same reproductive event and to keep independent our data on each individual. The data recorded during 1998 (that is, the year the birds were marked) were not included, to avoid eventual bias induced by handling.

Breeding success, sea trips and survival

We defined breeding propensity as a binary variable considering the onset of a breeding cycle (breeding propensity equals 1 if the bird attempted reproduction and equals 0 otherwise, that is, if no egg was laid). We defined breeding success as successful chick fledging for birds that laid an egg (breeding success equals 1 if the chick is fledged and equals 0 otherwise).

Lengths of sea trips were investigated for all birds still incubating or brooding, whether successfully fledging their chick or not. Different shifts have different mean durations (Descamps *et al.* 2002) and we thus separated them into different groups: one group per incubation shift, one for the first guard trip, one for all subsequent guard trips pooled together and a last one for all post-guard trips. To be able to run a single model on foraging trips, we standardized trips per group and then pooled them all together.

Yearly chick production was investigated as the number of fledglings (that is, 14-month-old chicks) produced per individual present in the colony each year. It combines breeding success and propensity into a single parameter representative of yearly reproduction at the population level. The total number of chicks produced over the 10-year period, integrating both breeding and survival over the number of penguins present in the colony, was also studied to give a better representation of the success of the considered sample (that is, banded or non-banded).

Survival was investigated as a function of decline in bird presence at the colony. We conducted analyses on both annual and overall survival. Overall survival corresponds to the number of studied birds present at the colony at the end of the period divided by the number of studied birds present at the colony at the beginning of the period.

Early breeders and late breeders

Because the king penguins' breeding cycle lasts more than 1 year (around 14 months on Crozet archipelago; Barrat 1976; Weimerskirch *et al.* 1992; Descamps *et al.* 2002), bird arrival at the colony depends on the success and timing of the previous year's breeding attempt. The laying period of king penguins therefore extends for over four months, with two peak periods (Stonehouse 1960; Barrat 1976): one for 'early breeders' (before 1 January) and another for 'late breeders' (after 1 January). To account for the dependence on the previous breeding attempt, we separated our data into two timing groups and conducted separate analyses on them. The first corresponded to penguins that did not fledge a chick the previous breeding season (failed or skipped reproduction) and which were thus free to arrive early in the summer (early group), and the second corresponded to birds that succeeded in fledging a chick the previous breeding season and which were consequently late breeders the subsequent season (late group).

As birds in the late group have a very small impact on the chick production of the colony, we did not present their data in our breeding analyses. Their late arrival almost always results in breeding failure as they do not breed early enough to allow their chick to meet normal phases of the chick growth period (Weimerskirch *et al.* 1992, Olsson 1996). Moreover, the pool of these birds is very small in comparison with the early group, and the production of chicks and, therefore, the renewal of the population is thus mostly dependent on the success of early breeders.

Environmental descriptors

The three environmental descriptors used in this study were the SOI, calculated from the monthly fluctuation in the air pressure difference between Tahiti and Darwin, Australia; the SST (in degrees Celsius); and the concentration of chlorophyll ([Chl a], in milligrams per cubic metre) (see Le Bohec *et al.* 2008a for details). Negative SOI values indicate a warm phase of El Niño/Southern Oscillation (Deser & Wallace 1987). SST and [Chl a] were used as a proxy of prey availability both around the breeding site and near the polar front, which are two locations known to affect the breeding of king penguins in the Crozet archipelago.

Growth rate estimates and simulations

To integrate breeding success and survival into one single parameter, we established population growth rates for both banded and non-banded groups, as the dominant eigenvalues of stage-structured population transition matrices (Caswell 2001). Different population matrix structures were tested and the obtained growth rates were almost identical, seeming insensitive to this structure. For simplicity, we present results of only one model. Briefly, we used a four-stage structured matrix with three first stages of immature birds and a last one of breeding adults. This supposes that every penguin began breeding at age five (average breeding age of the colony, unpublished data). An example of such a matrix is

$$M = \begin{pmatrix} 0 & 0 & 0 & GBS \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \\ 0 & 0 & \alpha & Adult\,Survival \end{pmatrix}$$

where GBS stands for global breeding success (that is, the product of breeding proportion and breeding success) and a represents annual juvenile survival.

As birds were followed only from adult age in this study, we fixed annual juvenile survival for both populations at 0.89 (C. Saraux *et al.*, unpublished observations, where the authors studied the return rates and survival of juveniles in king penguins). Breeding success is affected by the SST of the area around Crozet archipelago as far south as the polar front and survival is affected by SST at the MIZ with a 2-year lag (Le Bohec *et al.* 2008a). We computed two different models explaining breeding success in terms of SST around Crozet, one for banded birds and one for non-banded birds. Similarly, survival was modelled using the SST at the MIZ for banded and non-banded birds. Significant relationships were obtained in each of these four cases and were implemented in the matrix of each group as follows:

$$M_{non-banded} = \begin{pmatrix} 0 & 0 & 0 & \dfrac{1}{1+e^{4.1207 SST_{Cro} - 30.6312}} \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \\ 0 & 0 & \alpha & \dfrac{1}{1+e^{1.84 SST_{MIZ} - 8.6676}} \end{pmatrix}$$

$$M_{banded} = \begin{pmatrix} 0 & 0 & 0 & \dfrac{1}{1+e^{3.386 SST_{Cro} - 24.981}} \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \\ 0 & 0 & \alpha & \dfrac{1}{1+e^{1.1304 SST_{MIZ} - 5.5565}} \end{pmatrix}$$

SSTs averaged over the two different areas were highly correlated ($r = 0.97$, $P < 0.001$), and we thus decided to let both SSTs vary the same way, differing only by a constant: $SST_{Cro} = SST_{MIZ} + \text{Mean}(SST_{Cro} - SST_{MIZ})$. Finally, we simulated the variation of these population growth rates in relation to varying SST. Standard errors of growth rates were calculated using Caswell's method (Caswell 2001), by adding variance of all parameters of the matrix, these having previously been calculated bootstrapping over 1,000 repetitions of the models used in the matrix.

Statistics

All statistics were computed using the R-2.8.0 statistical environment (R Development Core Team, 2008). Survival was investigated using a Cox proportional hazards model with right censoring. Changes in survival over time were determined using breakpoints from segmented regression analysis ('segmented' package). Breeding data was analysed using a mixed-effect model fitted using maximum likelihood ('lme4' package; Bates & Maechler 2009). Generalized linear mixed models were computed with the individual (bird) as a random effect, enabling us to account for repeated measures, as birds were tracked over multiple breeding seasons. The most appropriate model was selected by using the Akaike information criterion. Variables were considered significant for $P < 0.05$.

Results & Discussion

First and foremost, our study underlines a strong negative impact of flipper banding on adult survival, to which population growth rate is most sensitive in long-lived species (Lebreton & Clobert 1991; Stearns 1992) such as king penguins. The average annual survival was 5% lower in banded penguins, leading to an overall 16 percentage point lower survival over a decade (Table IV - 1 and Figure IV - 2 a).

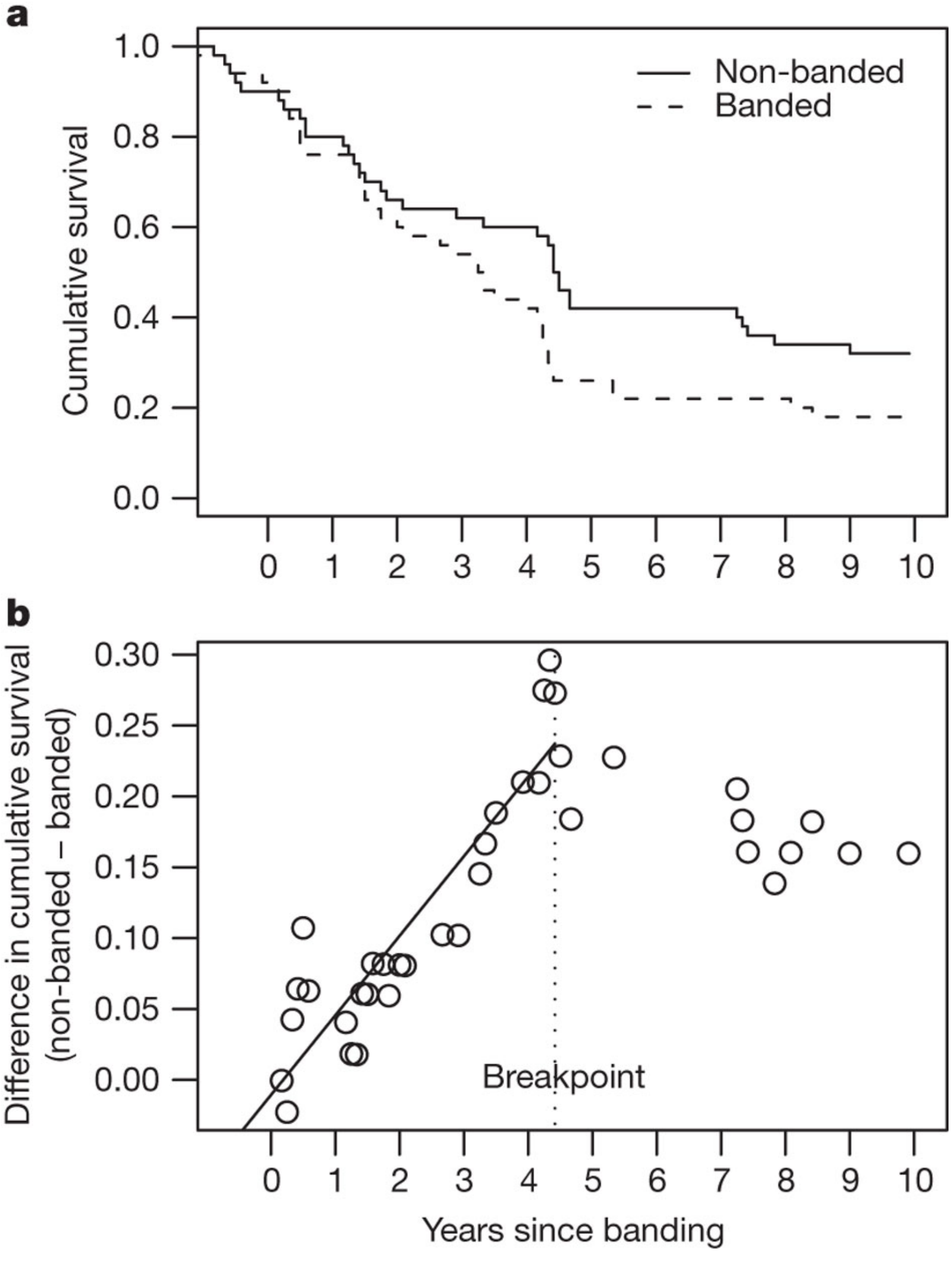

Figure IV - 2 *: Survival of banded and non-banded king penguins during the 10- year study period.* ***a****, Cumulative survival was lower for banded birds (dashed line) than for non-banded birds (solid line) (Cox proportional hazard model, P = 0.04; assumption of proportional hazards verified, P = 0.83).* ***b****, Difference between the cumulative survivals of banded and non-banded penguins over time. There is a breakpoint at 54 months (4.5 years) and the linear trend is indicated. Differences between banded and non-banded birds tended to disappear after the first 4.5 years.*

Yet a breakpoint analysis revealed that the difference between the cumulative survival of banded penguins and that of non-banded penguins had one breakpoint, after 4.5 years (54 ±

3 months; Figure IV - 2 b). Before that the mortality was 30% higher for banded birds, whereas afterwards the survival rates of the remaining banded and non-banded birds were not significantly different (Table IV - 1 and Figure IV - 2). Importantly, those birds that died during the first period (banded or not) had a lower breeding success than those that survived (0.22 versus 0.30, P = 0.047) and the annual survival rate of banded penguins increased between the two periods (from 78% to 91%, Wilcoxon rank-sum test, P = 0.05). This suggests that banding has a stronger deleterious effect on low-quality birds and thus selects for high-quality individuals.

Table IV - 1*: Observed differences between life-history traits of banded and non-banded king penguins*

	Parameter	**Non-banded**	**Banded**	**P (banding)**
Early Group (EG)	**Arrival dates**	**21 November ± 2 days (189)**	**7 December ± 3 days (167)**	**< 0.001**
	Laying dates	**29 November ± 1day (160)**	**6 December ± 1day (122)**	**< 0.001**
	Breeding propensity	**0.95 (189)**	**0.87 (167)**	**0.04**
	Breeding success	**0.44 (160)**	**0.32 (122)**	**0.05**
	Foraging trips	**11.60 ± 0.20 day (512)**	**12.70 ± 0.20 day (344)**	**< 0.001**
All birds	**Overall survival on the decade**	**0.36**	**0.20**	**0.04**
	Overall / Annual survival on the first period (4 years and $^{1}/_{2}$)	**0.62 / 0.90**	**0.32 / 0.78**	**0.01**
	Overall and annual survival on the last period (5 years and $^{1}/_{2}$)	0.57/ 0.90	0.60 / 0.91	0.82

Significant results are indicated in bold. Data shows mean6s.e. The number of events (N) is shown in parentheses. Differences in N come from differences in studied stages (for example, not every bird arriving at the colony bred). Overall survival corresponds to the number of studied birds present at the colony at the end of the period divided by the number of studied birds present at the colony at the beginning of the period. Breeding propensity corresponds to the proportion of live birds that engaged in reproduction over the ten breeding seasons (that is, the number of reproduction events divided by the sum over the years of live birds). The early group is the group of birds that failed or did not engage in previous reproduction and were free to arrive early in the summer. This group is the one that most affects overall population reproductive success. For breeding analyses, P is the P value of the banding effect in the mixed model Y~banding + (1 | individual). For survival (investigated through schemes of presence/absence at the colony), P is the P value obtained from a Cox proportional hazards model with right censoring. Durations of foraging trips were standardized per period and then pooled together to run a single mixed-model analysis.

Second, we show that over the decade banded birds had significantly lower breeding propensity and success than non-banded birds (breeding probability of 0.87 versus 0.95 and breeding success of 0.32 versus 0.44; Table IV - 1 and Figure IV - 3). This could be explained by the significantly later arrival of banded birds to breed (average delay relative to non-banded birds was 16 days; Table IV - 1).

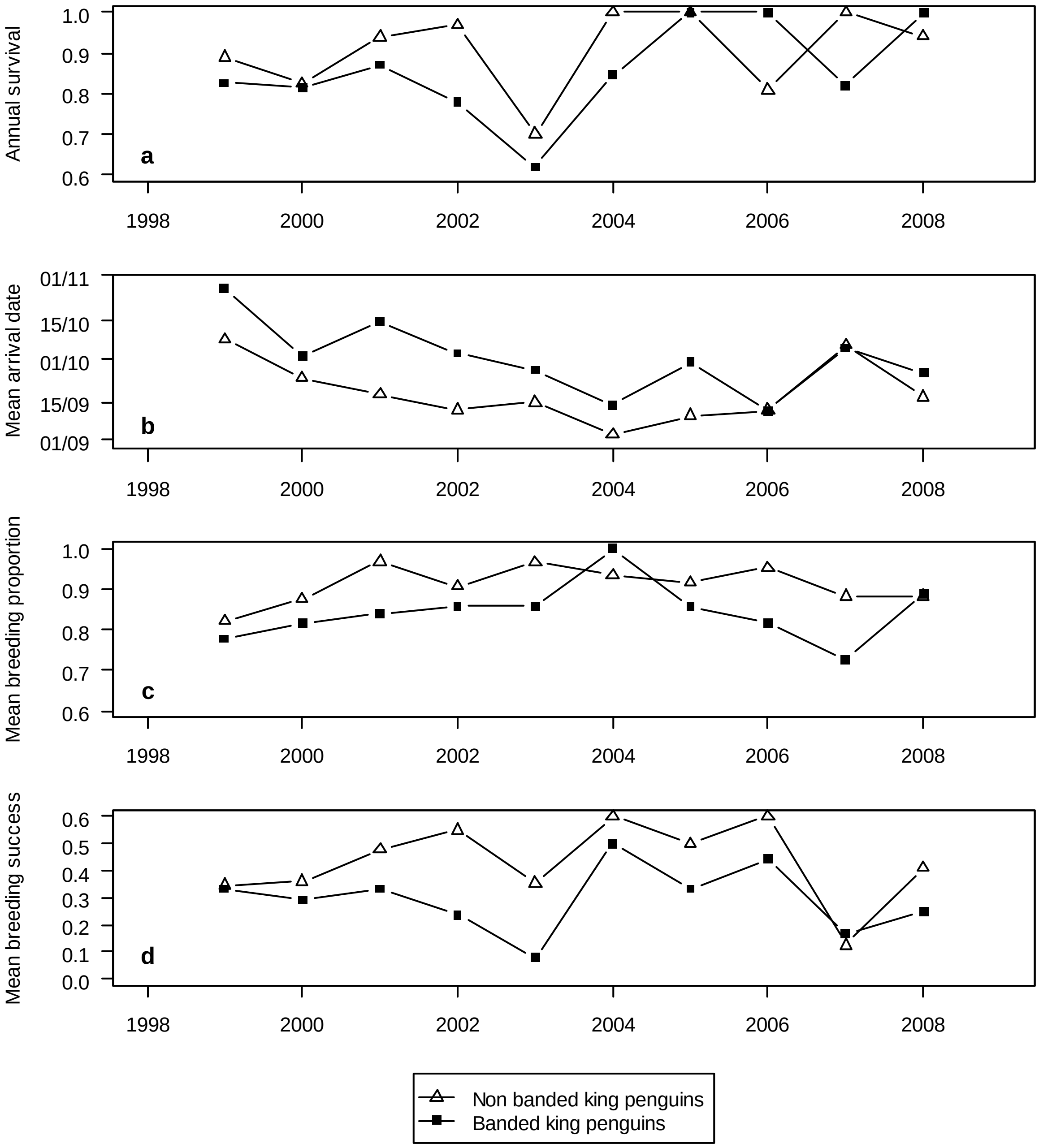

Figure IV - 3: *Differences between banded (■) and non-banded (Δ) penguins over the years in a, survival. b, arrival date. c, breeding proportion. d, breeding success*

Indeed, breeding propensity was negatively affected by arrival dates, meaning that those birds arriving later were less likely to engage in breeding attempts (model 9, P < 0.001; Table IV - 2). According to life-history trade-offs (Stearns 1992) between reproduction and survival for long-lived species, late-arriving birds may delay reproduction to the following year to avoid breeding costs that may jeopardize their own survival (Pfister 1998; Gaillard *et al.* 1998).

Table IV - 2 : *Results of fitting linear mixed models with binomial distribution to: a) the breeding decision of both timing group (FB and SB) of king penguins, and b) the breeding success of early breeders*

	N°	Models	Arrival or Laying Dates	Factor (group)	Interaction	AIC	ED
a) Breeding propensity							
FB	**9**	**Arrival**	**$-0.07 / 5.10^{-11}$**			**113.8**	**0.499**
	10	Arrival + group	$-0.07 / 7.10^{-11}$	-0.46 / 0.5		115.4	0.501
	11	Arrival * group	$-0.07 / 6.10^{-5}$	-1.69 / 0.6	0.01 / 0.6	117.1	0.502
SB	12	**Arrival**	**$-0.05 / 3.10^{-6}$**			**98.5**	**0.570**
	13	Arrival + group	$-0.05 / 3.10^{-6}$	-0.16 / 0.8		100.5	0.570
	14	Arrival * group	$-0.05 / 3.10^{-4}$	1.53 / 0.7	-0.01 / 0.7	102.3	0.571
b) Breeding success							
Early	**15**	**Arrival**	**$-0.060/7.10^{-8}$**			**349.8**	**0.10**
breeder	16	Arrival + group	$-0.059 / 3.10^{-7}$	-0.04 / 0.89		352.1	0.10
	17	Arrival * group	$-0.057 / 2.10^{-4}$	0.45 / 0.80	-0.006 / 0.79	353.8	0.10
	18	Laying	$-0.057 / 2.10^{-7}$			354.3	0.08
	19	Laying + group	$-0.055 / 7.10^{-7}$	-0.18 / 0.50		355.9	0.09
	20	Laying * group	$-0.057 / 10^{-4}$	-0.64 / 0.75	0.005 / 0.82	357.8	0.09

Best model is in bold. Estimates of the variable followed by Pvalues are written in the 3 columns. FB stands for failed breeders, *i.e.* birds which failed their previous reproduction and are thus free to breed early in the season. SB stands for successful breeders, *i.e.* birds which fledged a chick the previous year and due to the especially long breeding cycle of king penguins are late breeders this considered year.

Furthermore, in agreement with previous studies (Weimerskirch *et al.* 1992; Olsson 1996) we found that the later in the season king penguins arrived to breed, the lower was their breeding success (Figure IV - 4 and model 15, $P < 0.001$; Table IV - 2). This suggests an unfavourable timing in chick rearing, which then begins at the end of summer, when prey availability is much lower (Kozlov & Tarverdiyevma 1989). The reduced breeding success of banded birds could also be explained by the greater durations of their foraging trips at all summer stages of the breeding cycle (Table IV - 1 and Figure IV - 5). Indeed, a longer trip may either lead to breeding failure (that is, no longer being able to sustain the fasting period energetically, the partner abandons the egg before mate relief; Groscolas & Robin 2001) or directly jeopardize the survival of chicks waiting for food. Accordingly, birds failing in reproduction made significantly longer trips at sea than successful birds (21.8 versus 16.1 days, P < 0.001, for incubation birds and 11.5 versus 8.1 days, P < 0.001, for birds with chicks). Thus, the longer trip duration of the banded birds suggests that the detrimental effect of the bands can be explained by a reduced swimming and/or foraging efficiency resulting from the effect of flipper-band drag on the hydrodynamics of the bird, such as for Adélie penguins (Jackson & Wilson 2002).

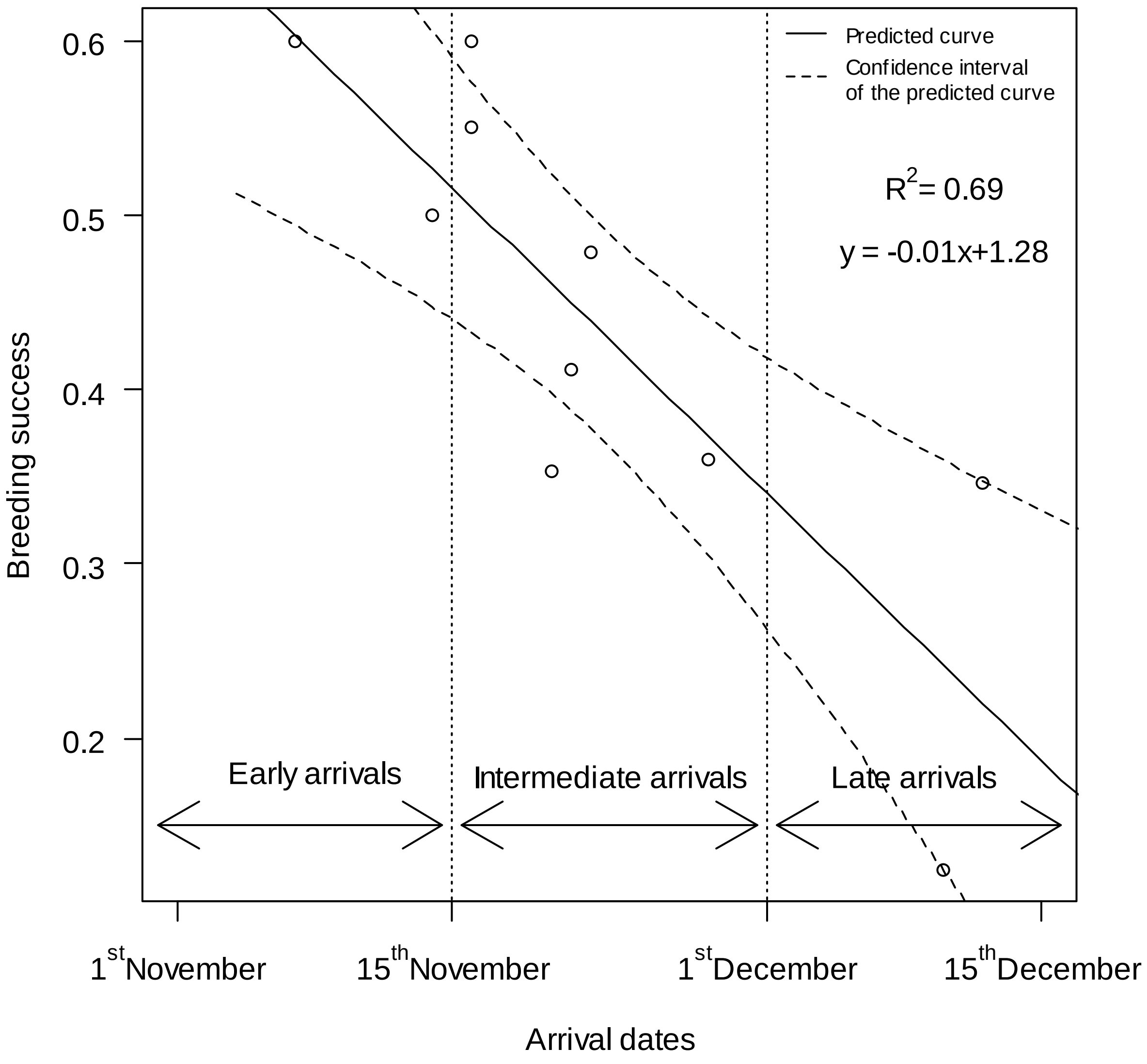

Figure IV - 4: *Mean annual breeding success depending on mean annual arrival dates at the colony to breed. Fitted linear model and confident intervals are indicated with lines. Statistics of this linear regression was: equation y ~ -0.01x + 1.28, R² = 0.69 and P < 0.001.*

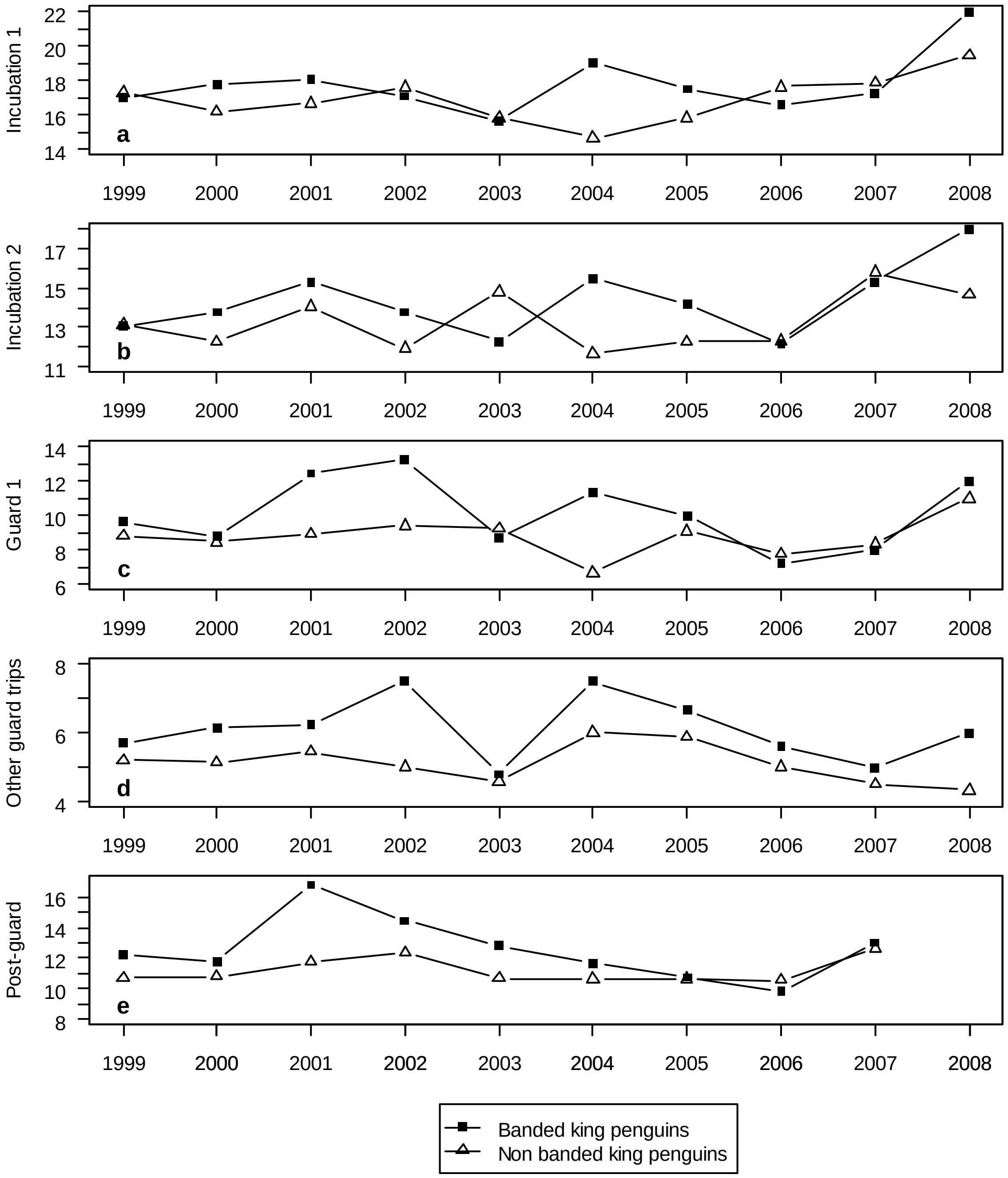

Figure IV - 5: *Foraging trip durations of banded (■) and non-banded (Δ) king penguins during incubation and brooding a, 1st incubation trip at sea. b, 2nd incubation trip at sea. c, 1st guard trip at sea. d, other guard trips at sea. e, post-guard trips at sea.*

Notably, our data clearly do not accord with the assumption that flipper bands have an impact essentially restricted to the first year after banding, which is the time suggested for birds to habituate to the handicap (Fallow *et al.* 2009; Barbraud & Weimerskirch 2001). Indeed, flipper bands also had a deleterious effect during the second half of our study (for example, P = 0.008 for arrival dates). These long-term effects indicate that there is no habituation to the handicap. We conclude that flipper bands lead to delayed breeding attempts, lower breeding propensities and longer foraging trips, which together explain the large drop observed in chick production between banded and non-banded birds during our study decade (80 versus 47 chicks produced; Figure IV - 3). Moreover, decreasing breeding success in seabirds increases their dispersal (Boulinier *et al.* 2008), and dispersal of penguins is still studied almost exclusively using flipper-banded birds. The question then arises about the significance of such data, as dispersal may not be representative of actual population dispersal in free-living penguins and may therefore constitute a serious bias.

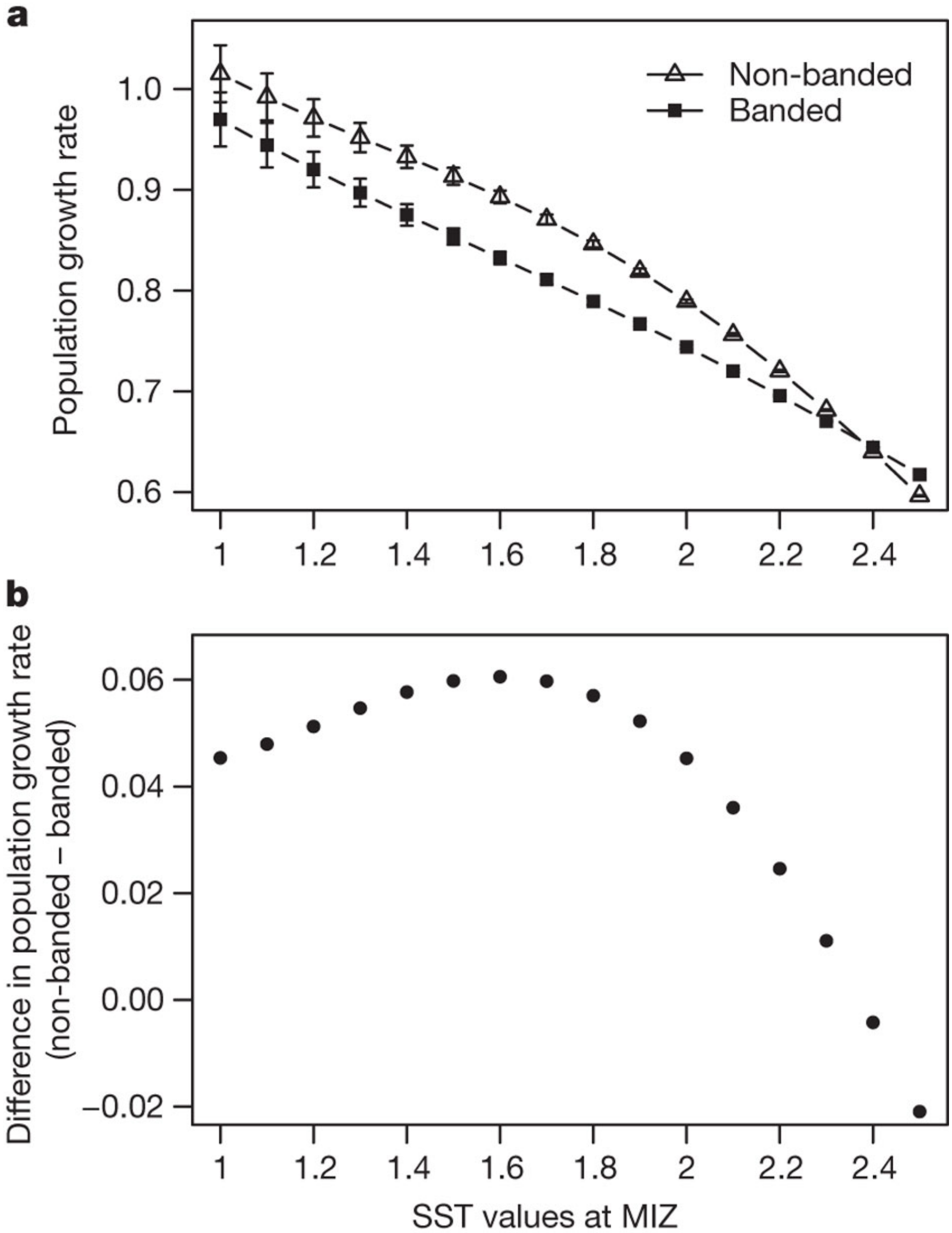

Figure IV - 6: *Simulated population growth rates of banded and non-banded penguins as functions of SST.*

a*, Growth rates of both populations according to SST at the marginal ice zone (MIZ). Error bars, s.e.m.* ***b****, Difference between the two growth rates. A quadratic relation well approximated the difference* ($\boldsymbol{Growth\ rate}\ \approx (\mathbf{0.27} \pm \mathbf{0.01})\boldsymbol{SST} - (\mathbf{0.09} \pm \mathbf{0.00})\boldsymbol{SST}^2$*, $P < 0.001$ for both SST and SST²).*

Finally, banded and non-banded penguins were differently affected by climate. Environmental conditions (Southern Oscillation index (SOI) and sea surface temperature (SST)) are known to affect penguins through changes in food availability (abundance or distribution), compelling individuals to forage for longer periods to reach sufficient body condition when conditions are warmer (Le Bohec *et al.* 2008a). In this regard, banded penguins arrived later to breed than did non-banded birds and even more so in years of lower SOI (that is, warmer phases of El Niño/Southern Oscillation; Deser & Wallace 1987; Table IV - 3; Figure IV - 7).

***Table IV - 3:** Results of fitting linear mixed models with Poisson distribution to the variation of dates of arrival of king penguins*

N°	**Climatic variables**		**'Group' banded/ non-banded**	**Interaction**		**AIC**	**ΔAIC**	**w_i**	**k**
1	**SST**	**SOI_t**	**'Group'**		**SOI * 'Group'**	**400.5**	**0**	**0.53**	**4**
2	SST	SOI_t	'Group'	SST * 'Group'	SOI * 'Group'	402.2	1.7	0.23	5
3	SST	SOI_t	'Group'			403.0	2.5	0.15	3
4	SST	SOI_t	'Group'	SST * 'Group'		404.7	3.7	0.08	4
5	SST	SOI_t				423.3	22.8	$< 10^{-2}$	2
6	[Chl*a*]	SOI_t				556.6	156.1	$< 10^{-2}$	2
7	SSTPF	SOI_t				590.5	190.0	$< 10^{-2}$	2
8	DistPF	SOI_t				1631	1230.5	$< 10^{-2}$	2

Best model is indicated in bold. N=356. SST is the mean of the SSTs around Crozet Archipelago 2 months before the arrival of the penguins, [Chl*a*] the mean concentration of chlorophyll centred on Crozet Archipelago two months before the arrival, SOI_t the annual value of the Southern Oscillation Index. DistPF is the distance between the Possession Island and the estimated Polar Front (calculated as the latitude at 4°C, by a linear regression between SST and latitude). SSTFP is the mean of mean SSTs over latitudes 46°S to 56°S, 2 months before arrival. k is the number of parameters in the model. ΔAIC is the difference of AIC compared to the best model. w_i corresponds to the AIC weight and represents the probability of model i being the best among the models presented.

Model 1 was more than twice as likely to be the best fitting model than the second best model and was the most parsimonious. It confirmed that with a 2-month time lag both banding and warm Sea Surface Temperature (SST) around Crozet contributed to late arrivals.

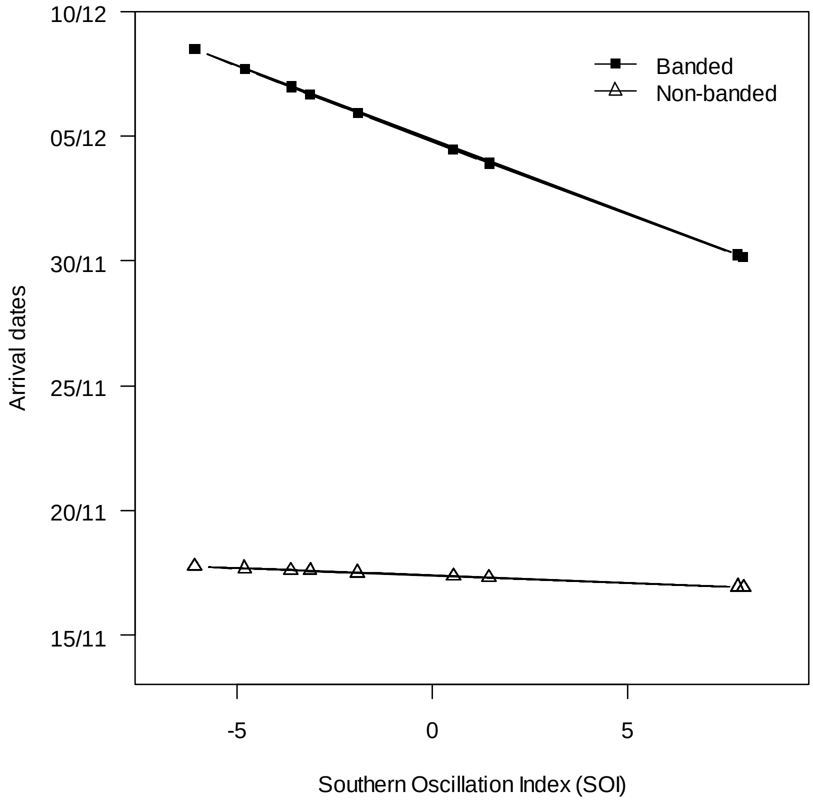

Figure IV - 7: *Arrival dates according to the Southern Oscillation Index (SOI) values for banded (■) and non-banded (Δ) penguins. The relations result from the value of the fixed effects issue of the mixed model 1 (Table S2).*

Additionally, when compared with that of non-banded penguins, the breeding success of banded birds was similar in years of late arrivals (difference of - 0.03, P = 0.52, N = 53 birds), lower (albeit not significantly) in years of early arrivals (difference of - 0.13, P = 0.32, N = 29) and much lower in years of intermediate arrivals (difference of - 0.19, P = 0.01, N = 70). Thus, over a single year, differences may not be apparent. Food availability at sea may be so poor in a given year that even non-handicapped birds fail in large numbers. For instance, in 2007 (a year of late arrivals) both banded and non-banded king penguins similarly failed to breed. In contrast, in years of very favourable environmental conditions, the environmental pressure on banded birds may be so weak that they may compensate for the extra cost inflicted by banding, which would explain the absence of (or weakness in) difference observed between banded and non-banded birds in favourable years such as 2004, 2005 and 2006. This accords with data on banded Adélie penguins, whose increase in foraging duration varied according to the year (Dugger *et al.* 2006), and on African penguins, which seem to be negatively affected by banding only during periods of reduced prey availability (Wolfaardt & Nel 2003). Similarly, we found that the population growth rates of banded and non-banded king penguins did not respond in the same way to variations in SST. Indeed, the relation between SST and the difference in population growth rates between the two groups was well approximated by a quadratic relationship, highlighting that this difference was most apparent in years of intermediate SST values (Figure IV - 6).

Thus, our decade-long monitoring demonstrates the detrimental effect of flipper banding and its interaction with climate on the major life-history traits of king penguins (Figure IV - 8). The effects of extensive banding schemes on penguin populations can on ethical grounds no longer be neglected, and studies considering population trajectories with regard to climate change seriously need to reconsider the biases inherent in studies using flipper-banded birds.

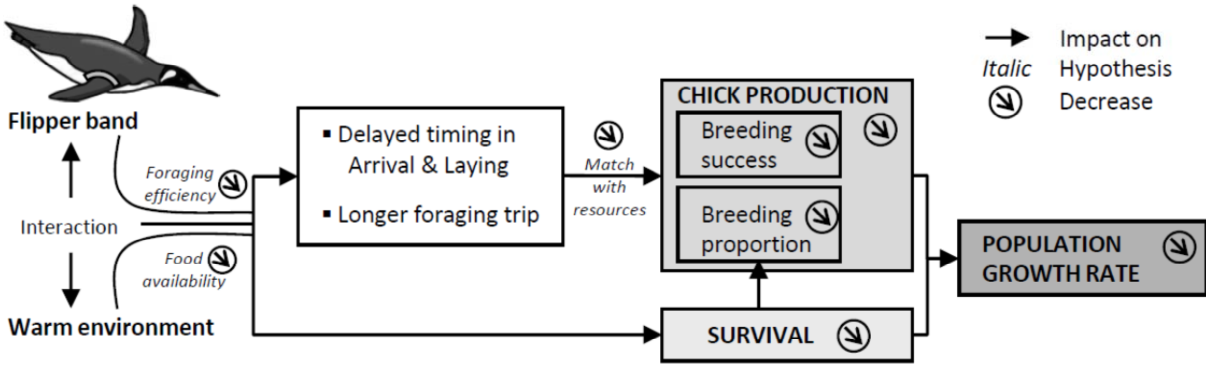

***Figure IV - 8:** Potential mechanisms involved in negative impacts of flipper bands on life-history traits and population dynamics in king penguins.*
Flipper bands and climate interact to affect chick production negatively, mostly through delayed timing, survival and, ultimately, population growth rate.

III. Consequences of this study

As one might imagine, such results motivated quite a debate in the penguin research world, as many long-term monitoring programs still rely on flipper-banding. The advantages and disadvantages of all three methods (flipper-bands, transponder tags and web tags) are further reviewed in Le Maho *et al.* 2011 (Appendix 2). Here, I would briefly like to comment on a few important points.

Our paper was not aimed at being a process of intent towards extensive banding schemes, rather we reported the worrying findings of long-term effects and emphasized that alternatives now exist. Some scientists advocate the importance of using bands to address questions such as dispersal. The first ethical question this raises is whether the ends justify the means (May 2004). Facing global change and threats to existing populations, we all agree: obtaining data is indisputably primordial. However, if one thinks that the benefits are overwhelming the costs, the proper question to ask is rather whether data acquired with banding will give us appropriate information. We have indeed shown that the impact of climate on penguins is different for banded and non-banded penguins, an issue which may translate to dispersal, as decreasing breeding success in seabirds may result in increasing dispersal rate (Boulinier *et al.* 2008). This explains why we concluded that scientists should reconsider the ethics of banding schemes.

We also suggest that data obtained from banded birds be considered with caution when making inferences on climate change. It is very important to note that we do not negate the effect of climate, quite the contrary (Le Bohec *et al.* 2008a). However, we do caution about biased inference on such a sensitive issue. Indeed, science ought to be rigorous, and if we do not want our conclusions on climate impacts to be criticized by climate skeptics, it is essential that deleterious effects be acknowledged when analyses are based on banded penguins, and these effects corrected for whenever possible.

Further, we did not question every result previously obtained through bands. Most of our actual knowledge is indeed ought to flipper-banding. As the negative effect of bands seems irremediably associated with the drag effect, our results do not contradict any studies carried out on land. Besides, no method is perfect and the only thing we can do as rightly stated by Rory Wilson is to "*strive to minimize the effects, quantifying them where possible so that we can put the resulting data into perspective*" (Wilson 2011). Transponder tags seem to minimize the effects of marking and seem a good option for penguin monitoring. However, we are completely aware that transponder tags also impair animals, as every research involving captures and handling of the animals. Thus, we need to seek further even less invasive methods. During the course of my PhD, a very interesting method based on biometrics and computer recognition of unique pattern configurations of the feathers has been developed. This would mean no capture of the bird and no marking whether external or internal. This technique seems very promising but for now it has been tested only on "spotted" African penguins with accuracy around 60% (Sherley *et al.* 2010). Besides it may be harder on other penguin species to differentiate the individual patterns. But one could think on other non-invasive techniques to develop. As an example, it could be interesting to study whether penguin footprints are individual and if this was the case to develop a computer-based recognition of their print using specific entry points to the colony, such as those used for Radio-Frequency-Identification (RFID).

IV. Three comparable automatic monitoring systems

During this PhD, we analyzed data coming from three comparable automatic monitoring systems, one in each location. Indeed, it seems very important in order to eventually compare the species and their response to climate to acquire data the same way. Birds were implanted with transponder tags under their skin, while antennas were placed on their passageways between the colony and the sea (Figure IV - 9). Each time a bird enters or leaves the colony, it crosses the antennas and is detected. Their way in or out is either determined by the order in which they cross 2 consecutive antennas (as in Figure IV - 9) or by an infrared detection for little penguins. The detection (date, time, number of the tag and way in or out) is then registered in a dataset. Most of the birds were tagged as chicks in order to know their age and their previous history (details are given in the methods of each study). A huge advantage of automatic monitoring system is that it allows for a continuous 24-hour monitoring (*i.e.* a constant recapture effort that is much more powerful than visual observations), resulting in a high reliability of survival estimates.

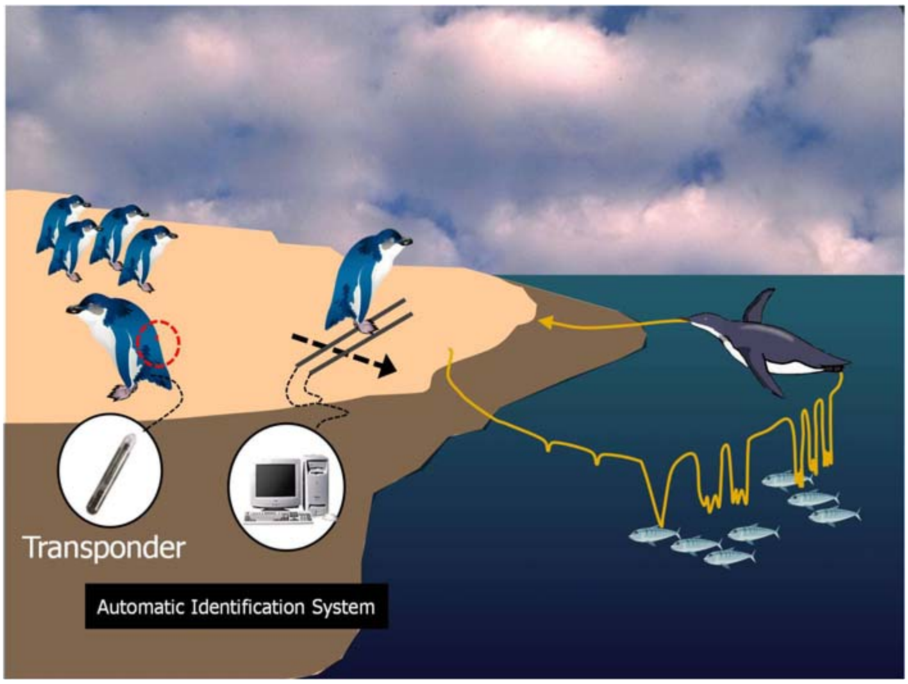

Figure IV - 9: *Schematic of an automatic monitoring system (adapted from Ropert-Coudert).*

The biggest transponder tags (for king and Adélie penguins) weigh 0.8 g (Figure IV - 1). They are passive and have thus no battery. Consequently, a single capture of the bird to implant the tag is required to monitor it all its life. The electromagnetic signal is emitted by the antennas and not the transponders, also avoiding the potential negative effects of constant electromagnetic fields on the birds. Transponders have no known adverse effects. They were shown not to affect survival of king penguins (Froget *et al.* 1998) nor breeding success, recruitment and survival in species as small as tits (Nicolaus *et al.* 2009).

Procedures of tagging differ slightly in between the three species. But animals are always handled carefully to minimize their stress (use of a hood, manipulation usually lasting between 5 and 10 minutes, *etc.*). Furthermore, concerns about infections should be minimal. For king and Adélie penguins, transponder tags are kept sealed sterile in iodine capsules (Betadine®) and are removed from the capsules only by the process of injecting them into the bird. Moreover, Vétédine® soap and alcoholic antiseptic solutions are used to disinfect the skin and the injecting needle before each insertion. Flesh wounds do not seem infected thereafter (personal observations on recaptured birds). Single use needles are used for little penguins with the transponder tag already sterily packaged inside the needle. In addition, the point of transponder entrance in the skin was sealed with vet use super glue, Vetbond ®. All the birds are measured and weighed at tagging. For king and Adélie penguins, genetic material is also sampled in order to sex them later in the lab (either blood sampling or sample of a feather, see details of the methods in the articles).

After an earlier pioneering study on an enclosed part of the colony and a single passage way for identification and weighing, the present system in Crozet has been installed in 1998. Its specificity lies in its buried antennas, so that there is no visible mark in the colony. About 1/3 of the pairs in the colony breeds in the monitored area, the so-called 'ANTAVIA' part (Figure IV - 10).

Figure IV - 10: *'ANTAVIA' part of the colony.*
The area is delimited in blue and the red arrows indicate the three passageways.

For Adélie and little penguins, the antennas are attached to a 'weighbridge' (Figure IV - 11; Figure IV - 12). Some periods of testing have shown that birds do not hesitate before crossing the bridge and this installation does not seem to delay them in any way. In Adélie Land, however, the way on top of the colony (*i.e.*, less used path) had to be canalized to be sure that the birds cross the bridge and do not go out on some other paths. Indeed, some penguins seemed hesitant at first and spent time to find their way out (the entry being no problem), but after some minor changes (moving of a few rocks, *etc.*) the way out was much more visible. Focal observations assured us that they then found their way out in no more than 5 minutes. The use of a bridge seems the only opportunity in Adélie land, where snow and ice is abundant forbidding the use of buried antennas.

Furthermore, in both Phillip Island and Adélie Land the bridge is not a simple transponder reader but a weighbridge, meaning that the system also has weighing scales, recording penguin body mass when they cross it (Figure IV - 12). This gives a unique database with body masses of the birds before and after each foraging trip (enabling us to get the body mass lost in the colony, gained at sea, given to the chicks, *etc.*). Corrections of potential drift are done every week by weighing objects of precise known weights and recalibration of the weighbridge in both locations.

***Figure IV - 11**: Phillip Island weighbridge.*
The weighbridge is situated between the sea and the colony on an obligate path of the penguins.

The system was installed in 1994 but it has been running continusously since 1999 in Phillip Island (Figure IV - 11), while it was set up in 2009 in Adélie Land. Because of the very short dataset obtained on Adélie penguins, the work will focus mainly on king and little penguins but some complementary results on Adélie penguins will be presented. The weighing system in Adélie Land is designed as a long platform composed by three scales in a row in order to get better precision for dynamic weighing (as the penguins usually do not stop on the bridge) and to be able to separate the body masses of different penguins crossing at the same time. Thus we obtain three dynamic curves of the mass per detection of a penguin instead of one body mass. At the moment, the necessary algorithm is still being tested and we had no access to the body mass of Adélie Penguins for this work.

Figure IV - 12: *Adélie penguin on the weighbridge.*
The bridge has to be snow-free to measure correct weights and is checked every day. The three scales in a row can be seen on this picture.

Figure IV - 13: *'ANTAVIA' colony on the Petrel Island.*
Due to its relief, the colony is accessible only by the bottom of the colony (from the sea-ice) or by its top (from where the picture has been taken). Three weighbridges have been installed, two on the bottom as it is the most used path.

Chapter V ○○○○●○○○○○

Effect of climate on juveniles

I. Climate effect of juvenile king penguins

Effects of individual pre-fledging traits and environmental conditions on return patterns in juvenile king penguins

(Article 3)

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Yvon Le Maho & Céline Le Bohec

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Despite the importance of early life stages in individuals' life history and population dynamics, very few studies have focused on the constraints to which these juvenile traits are subjected. Based on 10 years of automatic monitoring of over 2500 individuals, we present the first study on the effects of environmental conditions and individual pre-fledging traits on the post-fledging return of non-banded king penguins to their natal colony. Juvenile king penguins returned exclusively within one of the three austral summers following their departure. A key finding is that return rates (range 68-87%) were much higher than previously assumed for this species, importantly meaning that juvenile survival is very close to that of adults. Such high figures suggest little juvenile dispersal, and selection occurring mostly prior to fledging in king penguins. Pre-fledging conditions had a strong quadratic impact on juvenile return rates. As expected, cohorts reared under very unfavourable years (as inferred by the breeding success of the colony) exhibited low return rates but surprisingly, so did those fledged under very favourable conditions. Juvenile sojourns away from the colony were shorter under warm conditions and subsequent return rates higher, suggesting a positive effect of warming. The longer the post-fledging trip (1, 2 or 3 years), the earlier in the summer birds returned to their natal colony and the longer they stayed before leaving for the winter journey. The presence of juveniles in the colony was more than twice the duration required for moulting purposes, yet none attempted breeding in the year of their first return. Juvenile presence in the colony may be important for acquiring knowledge on the social and physical colonial environment and may play an important part in the learning process of mating behaviour. Further studies are required to investigate its potential implications on other life-history traits such as recruitment age.

Population growth rate is a function of several life-history variables (juvenile and adult survival, age at maturity, breeding success, *etc.*), and fluctuations in only one of those parameters may have effects on the rate at which populations are growing or declining. Explaining and predicting population trends under various climate scenarios thus requires a thorough knowledge of species' life-history traits, which result from complex trade-offs between specific reproduction, growth and survival rates under particular environmental conditions (Stearns 1989). Studies having considered these different life-history variables in an attempt to partition their contribution to population growth rate (Oli & Dobson 2003 and references therein), have reached varied conclusions depending on species. However, due to methodological limitations, life-history traits relating to early life stages have been largely overlooked. While a growing body of literature relates early life stages to later life-history traits (see Grüebler & Naef-Daenzer 2010 as an example), most calculations of population growth rate through matrix models are still based only on adult survival and breeding success. Nonetheless, early life parameters are major components of life-history strategies, and capital factors shaping population dynamics (*e.g.,* in *Marmota flaviventris,* Oli & Armitage 2004; in *Pygoscelis adeliae,* Wilson *et al.* 2001).

Recruitment into the breeding population has a critical impact on population turnover and population dynamics. In birds, however, the correlation between the number of young fledged by a population and that recruited into the same population is usually poor (median $R^2 = 0.25$ from studies summarized in Newton 1989). Thus, over the studied species, an average of as much as 75% of the variance in the number of recruits results from effects that occur between fledging and sexual maturity, and not from the number of fledglings produced. In seabirds, post-fledging return and survival are known to be affected by environmental conditions during the pre-fledging period (Hedgren 1981; Harris *et al.* 2007), notably through several biological aspects including brood size, hatching date, and fledging mass (Perrins *et al.* 1973; Jarvis 1974; Spear & Nur 1994; Cam *et al.* 2003; and references therein). A number of studies have documented the crucial role of environmental factors (such as climate variability) on breeding success and chick survival. However, it remains unclear whether and how these factors have consequences on future life stages. After fledging, juveniles lack crucial life skills (Marchetti & Price 1989) and are exposed to high rates of predation (Naef-Daenzer & Nuber 2001). Juveniles lack experience and exhibit a lower foraging efficiency compared to adults (reviewed in Marchetti & Price 1989; Wunderle 1991), as they undergo a learning period during which they acquire information on which feeding grounds are best and which hunting strategies are the most efficient. Their survival may accordingly be at stake (Lack 1954; Sullivan 1989; Grüebler & Naef-Daenzer 2010; and references therein). Juvenile quality at fledging, which should reflect pre-fledging conditions, may then play an important role in juvenile survival and consequently, have strong impacts on population dynamics.

Variability in early life parameters should thus not be neglected when studying the population dynamics of a species. In particular, special attention should be given to early life parameters of top predators, which are used more and more as key indicators of environmental stress in various ecosystems (seabirds reviewed in Durant *et al.* 2009). Upper-level predators indeed integrate the effects of climate forcing throughout the food chain (Boyd & Murray 2001), and thus constitute good models for assessing ecosystem health. In this regards, king penguins (*Aptenodytes patagonicus*) provide a useful means for studying the impact of climate change (Le Maho *et al.* 1993; Saraux *et al.* 2011a), and although the species has been well studied (Stonehouse 1960; Barrat 1976; Weimerskirch *et al.* 1992; Descamps *et al.* 2002), relatively little is known on the life-history traits of its early life stages. Juvenile penguins leave their colony as yearlings and become sexually mature at a minimum age of three or four years old but with an average age at first reproduction of six (Barrat 1976; Weimerskirch *et al.* 1992). While they still need to come ashore for moulting, they do not have to return as often or stay as long in the colony as adults, the latter which, because of breeding activities, are central place foragers. Although early studies have stated that immature king penguins are seen again in their natal colony after a few years (Barrat 1976; Weimerskirch *et al.* 1992), how immature birds budget their time away from the colony yet remained poorly understood. Furthermore, these studies relied on the monitoring of flipper-banded birds, and we know now the detrimental effects of flipper-bands on penguin fitness (Gauthier-Clerc *et al.* 20074; Saraux *et al.* 2011a).

Here, based on a 10-year automated transponder-based monitoring, we present the first study to consider the impacts of pre- and post-fledging environmental conditions, as well as the effect of individual parameters (*i.e.* sex, body condition and structural size) on the return rates of juvenile king penguins to their natal colony and lengths of their post-fledging trips away from the colony.

Materials and Methods

Permits and ethics statement

All animals in this study were handled only once (during their first moult) to first inject the transponder tag and two conduct morphological measurements. All procedures employed during this field work were approved by the Ethical Committee of the French Polar Institute (Institut Paul Emile Victor – IPEV) and conducted in accordance with its guidelines, also complying with French laws including those relating to conservation and welfare. Authorizations to enter the breeding site (permits n° 2005-191 issued on the 21st of November 2005) and handle birds (permits n° 99/346/AUT issued on the 30th of November 1999, 00/240/AUT issued on the 5th of September 2000, 01/315/AUT issued on the 4th of July 2001, 01/322/AUT issued on the 16th of August 2001, 2003-113 and 2003-114 issued on the 7th of October 2003, 2004-182 and 2004-183 issued on the 14th of December 2004, and 2005-203 issued on the 1st December 2005) were delivered first by the French "Ministère de l'Aménagement du Territoire et de l'Environnement" and then by the Terres Australes et Antarctiques Françaises (TAAF).

Handled animals were removed from the colony in order to minimize the disturbance to neighbouring birds and taken in a shelter a few meters away for manipulation. They were hooded to reduce their stress and manipulations lasted between 5 and 10 minutes. The transponder tags weigh 0.8 g and have no known adverse effects. They were shown not to affect survival of king penguins (Froget *et al.* 1998) or breeding success, recruitment or survival of tits (Nicolaus *et al.* 2009). Furthermore, concerns about infections should be minimal, as transponder tags were kept sealed sterile in iodine capsules (Betadine) and were removed from the capsules only by the process of injecting them into the bird. Moreover, Vétédine soap and alcoholic antiseptic solutions were used to disinfect the skin and the injecting needle before each insertion. Flesh wounds did not seem infected thereafter (personal observations on recaptured birds).

Penguin monitoring

Our study was conducted on Possession Island (46°25'S, 51°45'E, in 'La Grande Manchotière' colony) in the Crozet Archipelago. From 1999 to 2005, 2509 10-month old chicks were randomly sampled during their moult, a few weeks before fledging and were implanted with passive transponder tags under the skin of their leg, without any other external mark. Mean tagging dates varied over years (range 12th of November - 9th of December) due to annual differences in the timing of the moult period. A hundred birds were tagged later in the season in 2001 (January) and were thus discarded of the study to avoid the eventual bias of late fledging, leaving 2409 birds for the study. Each of our cohorts was considered representative of the year and was used to look at differences between years. The antennas buried under the usual and unique transit pathways in and out of the sub-colony allow for the continuous automatic collection of data on bird presence and movement. Although this automatic identification system (Gendner *et al.* 2005) presents the major advantage of not requiring recapture and avoiding disturbance of the animals, it only concerns a part of the colony (ANTAVIA sub-colony, between 8 and 10 thousand breeding pairs, *i.e.* about one third of the colony). Thus, to obtain a complementary view, we also controlled for the presence or absence of juveniles in the rest of the colony by weekly visual observations (based on age dimorphism, such as beak colouration) and estimated their number.

We analysed detection data over 10 years, *i.e.* from early November 1999 to the end of May 2009. Considering the first five cohorts tagged between 1999 and 2003, nearly all chicks (*i.e.* 99.9%) which were seen again in the colony during this decade came back within one of the three years following their fledging departure (*i.e.* before May n+3). We thus included chicks tagged in 2004 and 2005 in this study, and then disposed of 7 cohorts. Birds which were never detected after tagging were considered to have either died in the colony before fledging or encountered a dysfunction of their tag and were thus discarded from the study (34 animals discarded, leaving 2375 birds for the return behaviour study).

Survey

Tagging year was defined as the year of reference (*i.e.* year n). After tagging, as chicks tended to frequently transit in and out of the sub-colony before leaving, we considered as departure date the last date when the bird was automatically identified leaving the sub-colony during the austral summer of its tagging. Identically, we considered as return date the first date at which the bird was recorded back entering into the sub-colony. Duration on land before departure and trip duration were defined as the difference in days between departure date and tagging date, and between return date and departure date respectively. It is important to note that birds do not stay at sea during the whole post-fledging trip. Trip duration thus corresponds to the time spent away from the sub-colony and is composed of both time spent at sea and time spent on land outside the sub-colony. Finally, return rate was defined as the ratio of the number of birds detected again after their fledging (in one of the three following years) over the number of birds that left the colony.

Additionally, the automatic identification system allowed us to monitor the activities of the birds after their first return in order to determine the time spent in the natal sub-colony and see whether they attempted breeding. However, as birds need to frequently resume foraging trips to feed themselves, investigating their activity and use of the colony was only possible by considering the whole period during which they regularly visited the colony (frequency of visits > 1 per month), thus including periods of time when birds were physically present in the sub-colony and periods when they were out. The birds were considered as attempting to breed when at least two incubation shifts were observed, meaning that an egg was laid and incubation had started.

Individual traits: sex, structural size and body condition

Birds tagged after 2000 were blood-sampled at tagging and sexed using microsatellite DNA-analyses (adapted from Griffiths *et al.* 1998). In the absence of DNA-samples, *i.e.* for the first cohort, gender was determined by analysing the chronology of the sex-specific incubating shifts of their following breeding cycles (Stonehouse 1960; Descamps *et al.* 2002).

For each bird, flipper and beak lengths were measured at tagging (Stonehouse 1960). These two morphologic measurements are good descriptors of king penguin structural size and are highly repeatable measurements (Fahlman *et al.* 2006). As beak and flipper lengths were correlated (Spearman's rank correlation, $P<0.001$, $r=0.41$, $n=2509$), we used a principal component analysis to establish an index of structural size (SSI) as follows: $SSI = PC1 = 0.26 * Beak + 0.96 * Flipper$. The first principal component (PC1) between these two parameters explained 84% of the variation.

Body mass is highly variable in king penguins and can be associated with differences in nutritional status as well as structural size. Differences between body mass and structural size thus constitute a good index of nutritional state (Schulte-Hostedde *et al.* 2005). Body condition was then defined as the residuals of a regression of body mass on SSI (Schulte-Hostedde *et al.* 2005; $R^2=0.11$, $P<0.001$). As birds were tagged at a comparable moulting stage, BC at tagging was considered as a valid indicator of bird quality and was used without further correction.

As departure dates and BC were correlated (Spearman's rank correlation test; $r=-0.31$, $P<0.001$, $N=2473$), the impact of both variables on return rates or dates was studied using BC and the residuals of BC on departure dates as input variables in our models.

Environmental conditions

Environmental conditions have been shown to affect population dynamics at both local and global spatial scales (Stenseth *et al.* 2002). The use of 'weather packages' and large-scale climate indexes (global indices encompassing a combination of weather features, see Stenseth & Mysterud 2005), such as the Southern Oscillation Index (SOI), are good candidates for explaining the effects of environmental variability on top-predators of the Southern Ocean, such as the penguins (Le Bohec *et al.* 2008a). Negative SOI values indicate El-Niño events, whereas positive values indicate La Niña events (Deser & Wallace 1987). Monthly SOI (calculated from the monthly fluctuation in the air pressure difference between Tahiti and Darwin) were obtained from the Australian Bureau of Meteorology.

Since changes in Sea Surface Temperature (SST) have repercussions on the primary production and the food chain (Gregg *et al.* 2003), SST is frequently used as a local proxy of abundance and distribution of prey for king penguins (Le Bohec *et al.* 2008a). Daily SST values (in °C) were obtained from the National Ocean and Atmospheric Administration. However, little is known on the location of feeding grounds in sub-adult king penguins. They may exhibit a similar behaviour as the one of the adults, which forage around the Polar Front (PF) or the Marginal Ice Zone (MIZ) depending on the season (Charrassin & Bost 2001). However, unlike breeders, juveniles are not central place foragers. This could have strong impacts on the location of their feeding grounds. For instance, some sub-adult birds, probably originating from Macquarie Island, have been spotted in Australia or New-Zealand (Barrat 1976), which hints to the fact that they could well go as far up north as the subtropical area. We therefore tested for SST averaged on different areas to investigate the effect of temperature on post-fledging trips. A global area from the sub-tropical front to the MIZ (38-60°S, 46-56°E) was tested and divided in four small sub-areas surrounding notable oceanographic structures (38-42°S around the sub-tropical front, 42-46°S around the sub-Antarctic front, 48-52°S around the PF, 56-60°S around the MIZ). Oceanic fronts and areas associated with the seasonal sea ice retreat are indeed very productive regions (Moore & Abbott 2000) and important foraging grounds for top-predators (Bost *et al.* 2009).

Environmental conditions at sea were assessed over several periods. We considered mean values during the entire post-fledging trip, the first two months, the first year, or the first winter (May – September) spent outside the sub-colony, and finally during the two last months preceding their return at the colony.

The breeding success of the colony (Le Bohec *et al.* in prep.) was also used as a proxy for the conditions endured during the rearing period. Years of high breeding success (such as 2002 or 2004) could thus be viewed as more favourable years, compared to years of lower breeding success.

Statistics

All statistics were computed using R v. 2.9.0. and SPSS v. 17.0. statistical programs. Data were analysed using a maximum of likelihood generalized linear model approach. Generalized linear models were fitted with either Poisson distribution concerning trip duration or binomial distribution concerning return rate. Model selection was based on Akaike's Information Criterion (AIC) study, using both ΔAIC and AIC weights. In general, the model exhibiting the lowest AIC was selected, except when $\Delta AIC < 2$. In that specific case, AIC weights were examined as well as the number of parameters (models with smaller number of variables being favoured to avoid overparametrization, *i.e.* the most parsimonious models). The explained deviance of the model (in relation to the null model, *i.e.* the relative variability explained by the model compared to the entire variability in the dataset) and p-values were then used to conclude as to the effect of the parameters.

Some birds only returned to the colony after several years. Therefore, to explain the three-state categorical variable return year (distribution of birds in different yearly return groups), we computed ordinal logistic regressions, using the lrm function of the 'Design' package in R. Using Harrell's recommendation of graphical method, the parallel slopes' assumption was verified, validating the use of ordinal logistic regression (Harrell 2001). To investigate the effect of environmental conditions at sea on the proportion of birds within the three years of return, we also defined two different ratios for each cohort: i) *ratio1* corresponded to the number of birds coming back in year n+1 over the number of birds coming back at the colony overall years, and ii) *ratio2* corresponded to the number of birds coming back in year n+2 over the number of birds coming back on years n+2 and n+3. Then we used the SOI averaged on the first year at sea to explain the decision of coming back or not after this year (*ratio1*) and the SOI averaged on the two first years to explain the decision of coming back or not after two years (*ratio2*). We pooled *ratio1* and *ratio2* together in *ratio* after standardisation (to avoid an offset difference in between the two groups) and ran a single model with SOI as an explanative variable of *ratio*.

In order to compare different groups (*e.g.*, males versus females, or in between cohorts), we first checked for normality and homoscedasticity between groups, and non-parametric tests were used consequently (including Wilcoxon rank-sum test and Mood median test). Variables were considered significant for $P<0.05$ and Bonferroni's correction was applied whenever multiple comparisons were tested (differences were thus considered significant for $P < \frac{0.05}{n}$ with n the number of comparisons done).

Results

Summer of departure

The sex ratio of our sample was almost balanced between sexes (52% of males *vs.* 48% of females, P=0.13). Structural size indexes (SSI) were relatively similar between cohorts, with only two cohorts standing apart (cohorts 2000 and 2002, Figure V - 1a). Body condition (BC) on the other hand was highly different between cohorts (Figure V - 1b). Juvenile king penguins all fledged during austral summer. However, departures stretched over a long period (*i.e.* almost 5 months), extending from 9th of November until 22nd of March (Figure V - 1c).

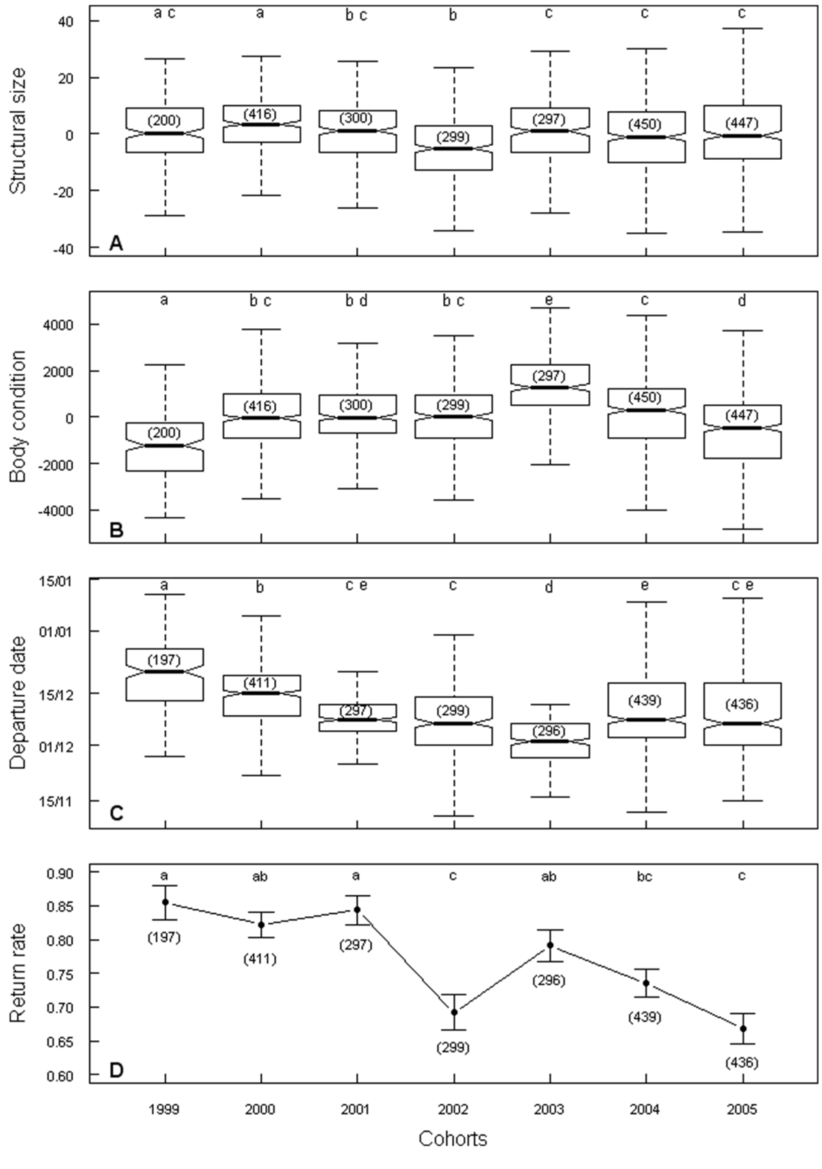

***Figure V - 1:** Inter-cohort differences in a) structural size (SSI), b) body condition (BC), c) departure date and d) return rate.*

Sample size is indicated in brackets. Panels a to c represent boxplots, while panel d shows means ± SE. Values not sharing a common letter are significantly different for $P < \frac{0.05}{21}$ *according to pairwise Bonferroni adjusted Mood tests.*

Sex, BC, SSI and cohort were used to explain differences in duration before departure. The model with all four variables was retained as best model by AIC selection (AIC=17662, Explained deviance=35%, ΔAIC = 119 with the closest model, *i.e.* model without sex) and all variables were significant (all $P<0.001$). However sex accounted for less than one percent in overall dispersal. Birds of better BC left earlier, whereas birds of greater size stayed longer.

Return rates

The global return rate obtained was of 77%, *i.e.* 1838 returned birds out of 2375 leaving the colony (all 7 cohorts over the whole period). Return rates varied significantly between cohorts ranging from 68% for the 2005 cohort, to 87% for the 1999 cohort (Figure V - 1d).

Plotting the return rates of these seven cohorts against population breeding success (BS), *i.e.* a proxy for the conditions endured during the rearing period, highlighted a potential quadratic effect of environmental conditions prior fledging on these return rates except for the 2005 cohort (Figure V - 2). There were no significant effects of either BS or BS^2, when running the model on all seven cohorts. However, excluding the 2005 data, we found an almost perfect fit between those variables (Return rate ~ BS + BS^2, $P=0.004$ and 0.003 respectively, $n=6$, $R^2=0.98$; Figure V - 2).

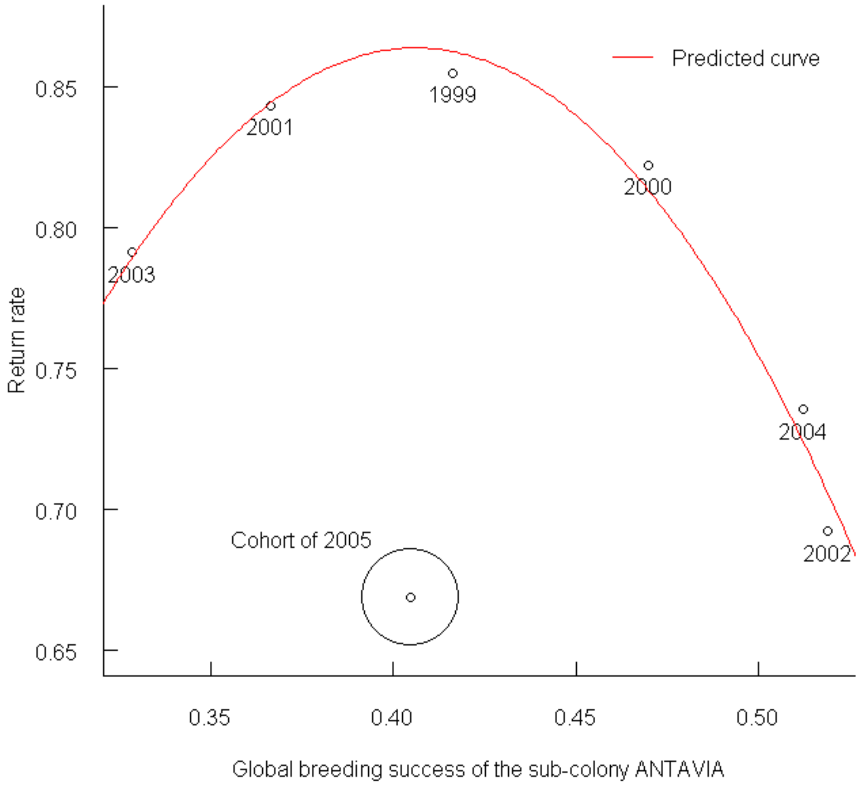

Figure V - 2: *Mean return rate per cohort related to the global breeding success of the colony. Fitted curve of the linear regression Return rate ~BS + BS^2 without the 2005 cohort is indicated in red.*

We also found an effect of climate at sea (of both SOI and SST whatever the area it was averaged on) on individual return probability. Model selection showed that SOI averaged on the whole trip and SST averaged on the whole trip and on the northern area (38-42°S, around the sub-tropical front) were the best explicative climatic variables (Table V - 1, models R1 to R10).

Adding biological variables, model R1.3 appeared as the minimal adequate model (Explained deviance=25%, AIC=1929, k=10, N=2375, Table V - 1, models R1 to R1.6), which predicted that return rate was affected by climate, BC, sex and year of fledging. Birds in better condition were more likely to return to the colony (P<0.001), while warmer conditions (higher SST and lower SOI) had a positive effect on the return rate of sub-adult king penguins (both P<0.001). On average, males presented a higher return rate than females (78% *vs.* 75%), but this varied substantially between years, from 15 percentage points more for males in 2005 (74% *vs.* 59%) to 7 percentage points more for females in 2003 (83% *vs.* 76%).

Table V - 1: *Model selection to explain individual return rate variability in juvenile king penguins*

N°	**Animal characteristics**	**Year**	**Depart**	**Climatic variables**	**AIC**	**ΔAIC**	**w_i**	**k**	**ED**
R1				**$SOI_w+SST_{w,z1}$**	**2119.6**	**0**	**1**	**2**	**17%**
R2				$SOI_w+SST_{w,z2}$	2258	138.4	<0.001	2	11%
R3				$SOI_w+SST_{w,z3}$	2345	225.4	<0.001	2	11%
R4				$SOI_w+SST_{w,z4}$	2315.8	196.2	<0.001	2	8%
R5				$SOI_w+SST_{w,tot}$	2260.6	141	<0.001	2	9%
R6				$SOI_w+SST_{2m,z1}$	2528	408.4	<0.001	2	<1%
R7				$SOI_w+SST_{y1,z1}$	2497.1	377.5	<0.001	2	<1%
R8				$SOI_w+SST_{wint1,z1}$	2528.6	409	<0.001	2	<1%
R9				SOI_w	2529.7	410.1	<0.001	1	<1%
R10				$SST_{w,z1}$	2405.5	285.9	<0.001	1	6%

R1				$SOI_w+SST_{w,z1}$	2119.6	191	<0.001	2	11%
R1.1	BC+SSI+SEX	Year	Depart	$SOI_w+SST_{w,z1}$	1929.9	1.3	0.22	12	25%
R1.2	BC+SSI+SEX	Year		$SOI_w+SST_{w,z1}$	1929.3	0.7	0.30	11	25%
R1.3	**BC+SEX**	**Year**		**$SOI_w+SST_{w z1}$**	**1928.6**	**0**	**0.43**	**10**	**25%**
R1.4	BC+SEX			$SOI_w+SST_{w,z1}$	2014.3	85.7	<0.001	4	21%
R1.5	BC	Year		$SOI_w+SST_{w,z1}$	1998.1	69.5	<0.001	9	22%
R1.6	SEX	Year		$SOI_w+SST_{w,z1}$	1933.4	4.8	0.04	9	25%

Best models are indicated in bold. ΔAIC is the difference of AIC compared to the best model. w_i corresponds to the AIC weight and represents the probability of this model being the best among the models presented. k is the number of parameters in the model. ED stands for explained deviance and has been calculated as the ratio of the deviance explained by the model (null deviance – residual deviance) on the null deviance.
BC and SSI are the body condition and structural size of the animal before departure. Depart is the residual of BC on the date of departure of the bird. SOI_w and SST_w are the Southern Oscillation Index and Sea Surface Temperature averaged on the whole trip for birds having returned and on the 3 years following the departure for those never seen again. SOI_{y1} was the average of SOI on the first year following departure. SST_{2m}, SST_{wint1}, SST_{y1} were averaged on the first 2 months, the first winter and the first year.
SST was averaged on different areas, z1 to z4 corresponding to areas surrounding the different fronts from north to south: z1, sub-tropical front; z2, sub-Antarctic front; z3, polar front; z4, marginal ice zone and tot being the whole area from north bounding of z1 to south bounding of z4.

Return dates

The first returns to the colony were observed occurring in three distinct periods during each of the three austral summers following juvenile fledging, regardless of the cohort (upper-right panel of Figure V - 3). Overall, the second return summer was far greater than the other two, *i.e.* 37% of the birds returned after a year, 54% after two, and only 8% after three. No birds were recorded returning during the austral winter. These results were confirmed by weekly observations of the whole colony during the 7-year study period (only one sub-adult was seen during winters of 2000 and 2001 in the whole colony). Other than during these three summers, we detected only three penguins returning to the colony, all of them arriving during the austral summer of year n+4.

Each summer was also composed of two return peaks. Hereafter, we refer to the three return years (n+1, n+2 or n+3) as ‘return year’, whereas the yearly peaks are referred to as ‘peak’. The more years sub-adults stayed away from their sub-colony, the earlier in the season they made their first returns to the sub-colony. Return year n+1 was indeed composed by two very similar peaks (46% in the first peak *vs.* 54% in the second peak), whereas return years n+2 and n+3 presented unbalanced ratios with 73% and 79% of returns in the first peak respectively. Moreover, peaks of year n+3 occurred earlier than peaks of year n+2, which themselves occurred earlier than peaks in year n+1 (Figure V - 3, median days of the two peaks 2nd of December / 27th of February *vs.* 16th of November / 25th of February *vs.* 8th of November / 21st of February for return year n+1, n+2, n+3, respectively).

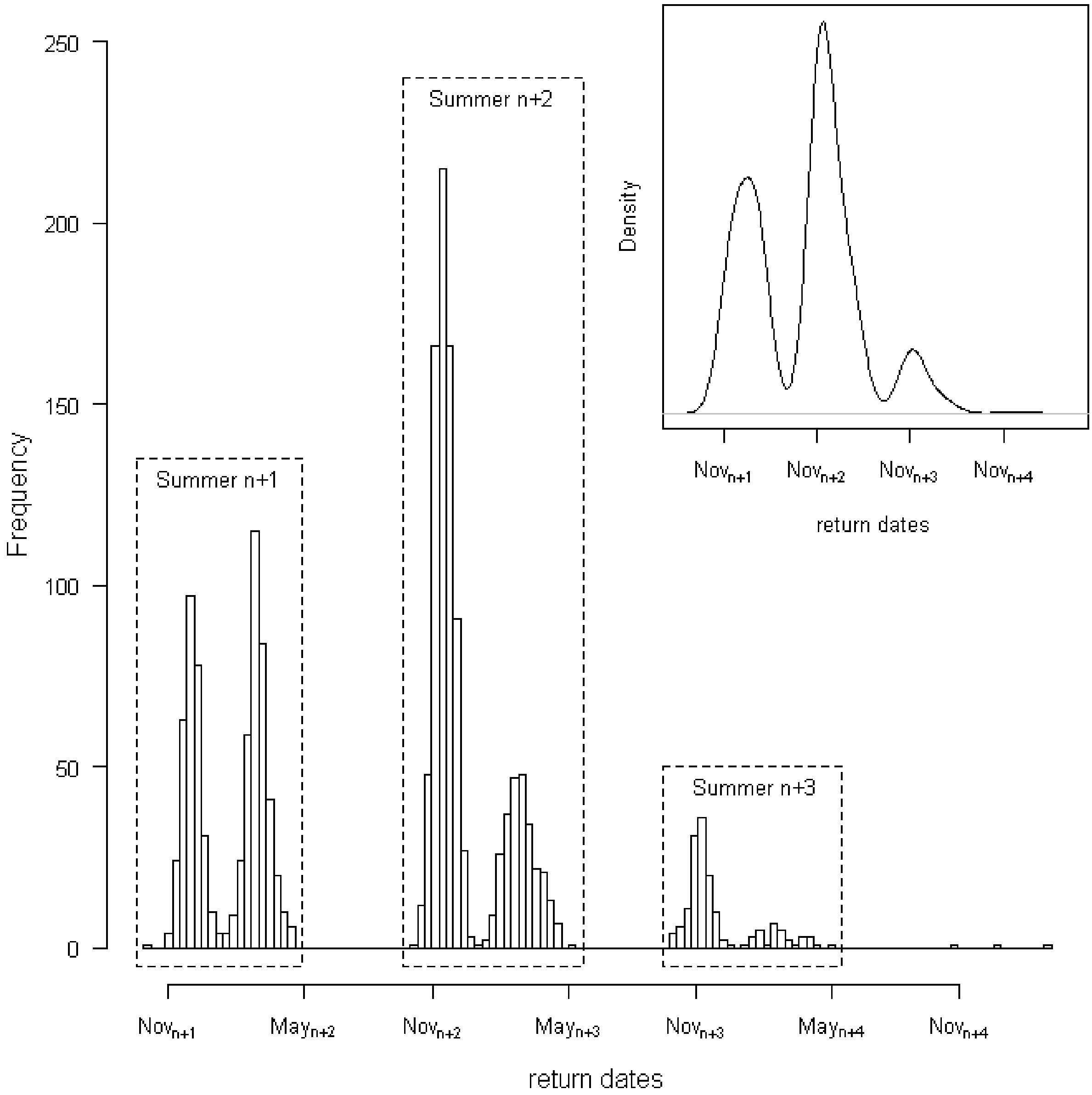

Figure V - 3: *Return date of post-fledging king penguins after their first trip out of the sub-colony (density and histogram).*

Sea trip duration

Trip duration of birds was significantly different between cohorts (Kruskal-wallis test, P<0.001). Birds of the 2005 cohort spent significantly more time away from their sub-colony than any other cohort (Pairwise Wilcoxon rank-sum tests adjusted with Bonferroni correction: P<0.001 for the 2005 cohort *vs.* every other cohort).

A difference in the mean trip duration between cohorts could be the consequence of two different situations: 1- the proportion of birds between the 3 years of return is different between cohorts (*ratio*) 2- the proportion is the same, but durations are not the same inside a single year of return. SOI negatively affected *ratio* (P=0.05), suggesting that in warmer conditions (low SOI), the proportion of birds coming back early increased. As for individual parameters, sex and BC had no effect on the probability to come back in one of the three years. The best selected ordinal logistic regression indicated that residuals of departure on BC had a positive effect on return year (P=0.005), *i.e.* that, independently of BC, those birds which left later the colony, spent a longer period away from their sub-colony. SSI had a negative effect indicating that smaller birds had a higher probability of coming back in years n+2 or n+3 than in year n+1 (P=0.05). Finally cohorts also had a significant effect (P<0.001) and differences between cohorts were asserted using Bonferroni corrected Wilcoxon rank-sum tests (see Figure V - 4).

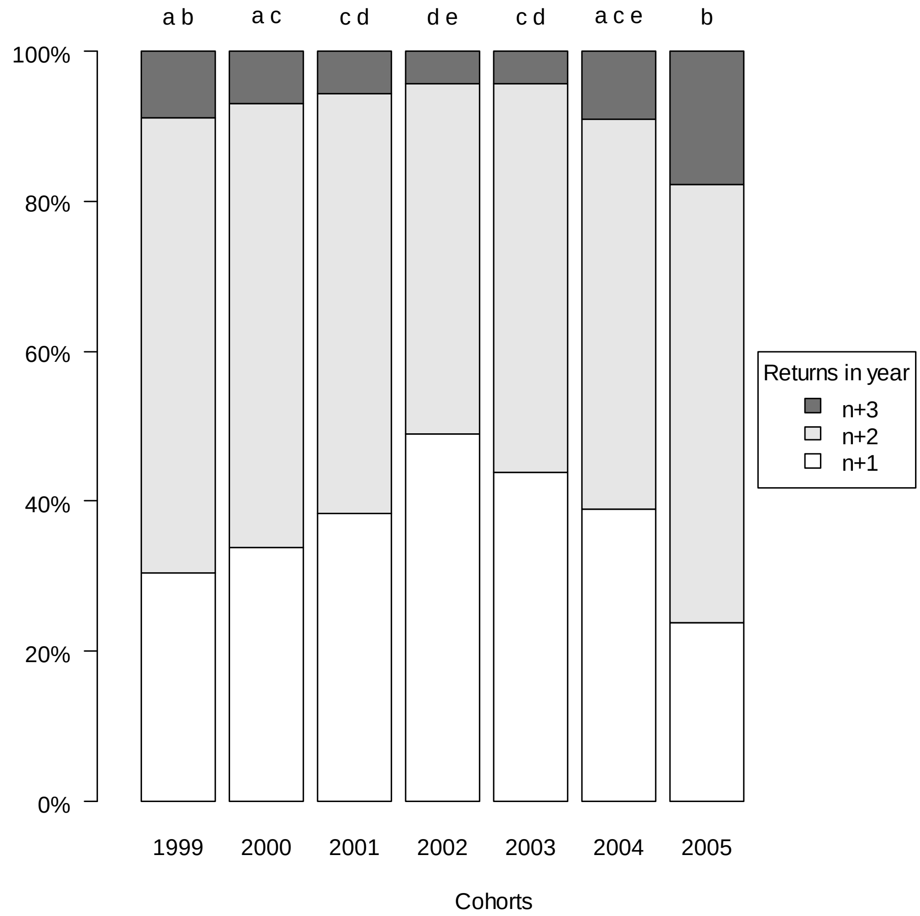

Figure V - 4: *Distribution of the returns of sub-adult king penguins among the 3 years of returns depending on cohorts. Values not sharing a common letter are significantly different.*

As for distribution in peaks inside return years, the best model (model P1.3, Explained deviance=96%, AIC=108.4, k=9, N=1902; Table V - 2) predicted that it was almost entirely explained by SOI averaged on the last year and the global area SST averaged on the last 2 months before return (both $P<0.001$). SOI had a positive effect and SST a negative effect, indicating that under warm conditions, birds returned earlier, *i.e.* in peak one instead of peak two. Birds of smaller SSI at fledging might tend to return later ($P=0.01$), even if size added only little information (ΔAIC=0.6).

Table V - 2*: Model explaining peak of return inside a 'return year'*

N°	**Animal specificity**	**Year**	**Depart**	**Climatic variables**	**AIC**	**ΔAIC**	**w_i**	**k**	**ED**
P1	BC + SSI + SEX	Year	Depart	$SOI_{yret} + SST_{2mret}$	113.9	5.5	0.03	12	0.96
P1.1	BC + SSI + SEX	Year		$SOI_{yret} + SST_{2mret}$	112.0	3.6	0.07	11	0.96
P1.2	BC + SSI	Year		$SOI_{yret} + SST_{2mret}$	109.9	1.5	0.19	10	0.96
P1.3	**SSI**	**Year**		**$SOI_{yret} + SST_{2mret}$**	**108.4**	**0**	**0.41**	**9**	**0.96**
P1.4		Year		$SOI_{yret} + SST_{2mret}$	109.0	0.6	0.30	8	0.96
P1.5				$SOI_{yret} + SST_{2mret}$	118.3	9.9	10^{-3}	2	0.95
P2	BC + SSI + SEX	Year	Depart	$SOI_{yret} + SST_{2mfirst}$	2456.8			12	0.03
P3	BC + SSI + SEX	Year	Depart	$SOI_{yret} + SST_{wintret}$	2468.9	2360	$<10^{-3}$	12	0.02

Best model is indicated in bold. ΔAIC is the difference of AIC compared to the best model. w_i corresponds to the AIC weight and represents the probability of this model of being the best among the models presented. k is the number of parameters in the model. ED stands for explained deviance and has been calculated as the ratio of the explicated deviance (null deviance – residual deviance) on the null deviance.

BC is the body condition of the animal before departure and SSI is its structural size. Depart is the residual of the regression of BC on the exact date of departure of the bird. SOI_{yret} is the average Southern Oscillation Index on their year of return, SST_{2mret} and $SST_{wintret}$ are the Sea Surface Temperature averaged on the last 2 months and the last winter preceding their return to the colony, respectively.

Post-return activity

Weekly observations of the whole colony all along the ten years of study allowed us to determine that the period of moult for the sub-adults extended from mid-November to the end of January. Upon their first return, juvenile birds continued to visit the colony for an average of 79 days (more than 2 ½ months), ranging from 0 to 255 days (about 8 ½ months). Independently of their year of return, the birds arriving at the beginning of the summer (*i.e.* in the first of the two peaks of each summer) visited the colony during a significantly longer period than the birds arriving late (median ± SE: 124 ± 2 days *vs.* 3 ± 1 days, P<0.001). In addition, the longer they stayed away from their sub-colony during their post-fledging trip, the more they attended the colony on their return (Figure V - 5). More than half of the birds coming back on the first year attended the colony for less than a week (*i.e.* 56%) compared to only 16% for birds first returning after two years, and 4% for birds first returning after three. Furthermore, almost all birds returning to the colony in one of the two first years returned again on the following summers, provided that they did not die (99.6 % from n+1 to n+2 and 99.3% from year n+2 to n+3). When coming back for the second time, birds spent more time at the colony than birds of the same age coming back for the first time (Figure V - 5). Identically, in year n+3, birds coming back for the third time at the colony spent significantly more time than birds coming back for the second time (Figure V - 5).

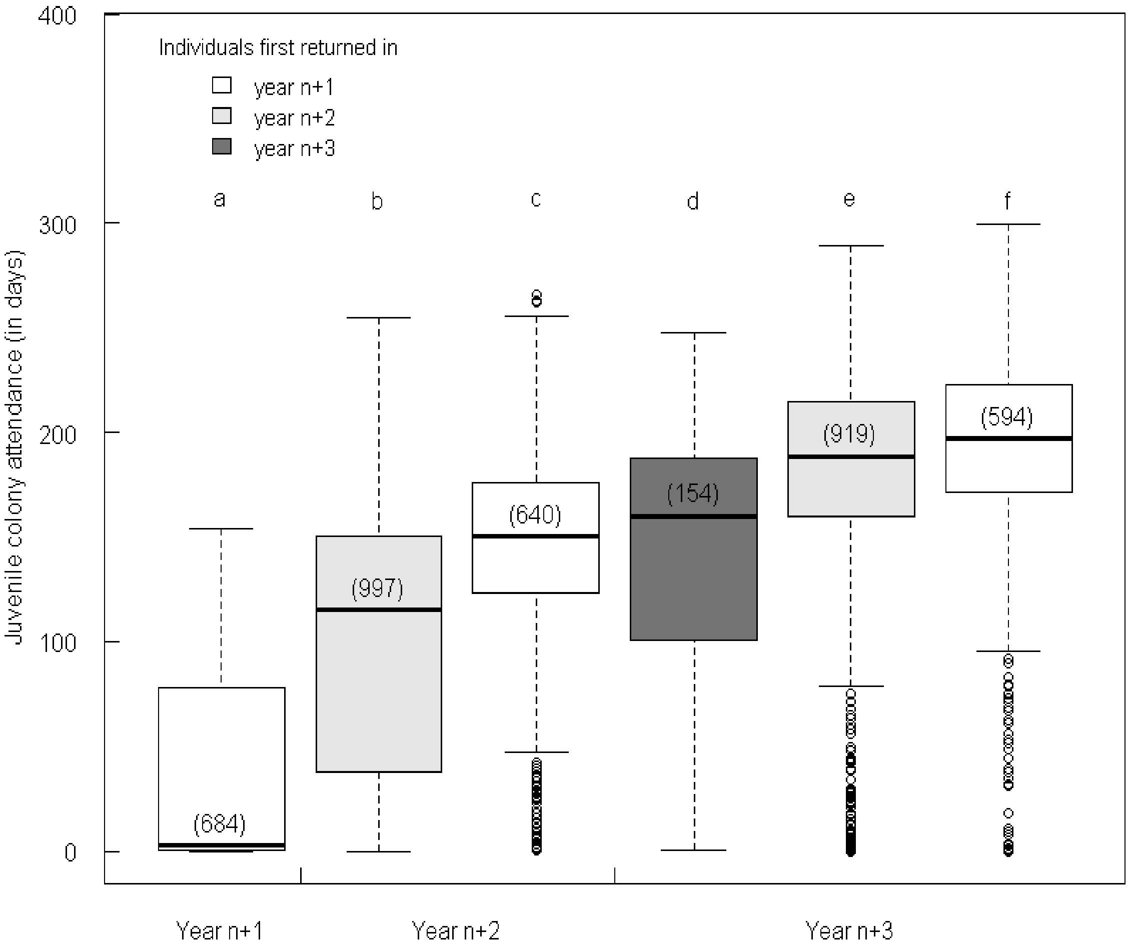

Figure V - 5: *Colony attendance (in days) upon return in the colony in the three years following their departure depending on the year of first return.*

Values not sharing a common letter are significantly different for $P < \frac{0.05}{21}$ *according to pairwise Bonferroni adjusted Mood tests. Median ± SE: 2 ± 2 days, 115 ± 2 days, and 160 ± 5 days spent upon return for birds first returning after 1, 2 and 3 years respectively.*

Although a few birds attempted to breed upon their first return to the colony (1.5%, *i.e.*, 28 over 1835 birds), all failed in fledging a chick. The proportion of breeders increased with age at first return (only 0.1% *vs.* 1.8% *vs.* 5.7%, for birds coming back in year n+ 1, n+2 and n+3 respectively). 61% of these birds trying to reproduce upon their first return to their natal sub-colony were females, in spite of the higher number of males studied (2.2% of females engaged in reproduction *vs.* 1.3% of males).

Discussion

Return rate, survival, emigration

In free-living non-banded king penguins, we found that more than ¾ of the fledglings return to their natal population after their first sojourn at sea. Over 7 consecutive years and for 2375 penguins, post-fledging return rates to the natal sub-colony ranged from 68% to 87% depending on cohort (average 77%). This proportion is far greater than has been previously found (*i.e.* 5.6 to 39%; Weimerskirch *et al.* 1992). Moreover, our return rates might even underestimate survival as some of those birds which were not detected again in the natal sub-colony, might have either emigrated or established themselves in another sub-colony of the same population. Emigration is usually thought to be very low in adult king penguins (94% of fidelity to breeding site; Barrat 1976). However, when compared to adults, the higher proportions of juveniles seen in other colonies (Barrat 1976; and 1.5% *vs.* 0.4% in Weimerskirch *et al.* 1992) suggest that juveniles might return on land outside of their natal colony more often than adults. Yet, our data suggest that juvenile dispersal might be small in this colony, and global return rate may be a good estimator of survival.

Survival is usually much lower for juveniles than for adults (Newton 1989; Martin 1995). Explanations are 1- the ‘constraint hypothesis’, suggesting a lack of experience among juveniles for different activities such as foraging, avoidance of predators, *etc.* (Martin 1995) and 2- the ‘selection hypothesis’, stating that birds with less adapted phenotypes disappear in early stages of life and thus that older population categories are only composed of good phenotypes (Newton 1989; Martin 1995). Unlike a lot of birds, king penguins exhibit a very low breeding success and fledglings have already overcome a strong selective pressure. Since we found here that more than 70% of the fledglings returned to their natal colony and were still alive three years after fledging, *i.e.* an average annual return rate of about 90%, we suggest that selective mechanisms for juvenile king penguins should mostly operate before fledging. Little is known regarding the ability to forage in king penguin juveniles. Yet, if there is an effect of age and experience on foraging (as in many birds (Wunderle 1991), and even other penguin species (Nisbet & Dann 2009)), lower juvenile foraging skills (Marchetti & Price 1989) might not be a strong limiting factor for survival in king penguins. Indeed, a lower efficiency of juveniles could be compensated for by longer periods of foraging since they are not subjected to the same constraints as breeding adults.

Body condition and structural size: departure and return

Chicks in poorer condition at fledging left the colony later, suggesting either that it took them longer to complete their moult (a very energetic process) or that, being too weak to leave, they were compelled to stay longer begging for food before departing. A minimal energy capital may then be required to depart at fledgling. Yet, chicks do not depart from the colony with a maximal body condition (BC), they rather go on fasting and lose weight before leaving, which probably improves their ability to perform prolonged immersion and deep diving (Corbel *et al.* 2009). Chicks of smaller structural size at fledging (SSI) left the colony earlier than bigger ones. According to allometric equations and surface to volume ratios, smaller birds should see their energy reserves depleted more rapidly than bigger ones (due to higher specific metabolic rates; Schmidt-Nielsen 1984) and may thus reach this optimal body condition after a shorter time of energy depletion.

BC at departure had a significant positive impact on return rate but no effect on trip duration. The opposite trend was observed for SSI, which did not affect return rate but had a negative effect on trip duration. BC is a good index of energetic reserves and can be critical for survival (Gaston 1997). A positive correlation between body mass and juvenile survival (directional selection; Linden *et al.* 1992) has indeed been highlighted in mammals (Clutton-Brock *et al.* 1987) as well as in birds (Tinbergen & Boerlijst 1990; Gaston 1997; Van der Jeugd & Larsson 1998; Naef-Daenzer & Nuber 2001; Schwagmeyer & Mock 2008). In king penguins, BC at departure presumably has a strong impact during the period spent to reach the first feeding grounds (and consequently survival at that time) but unlikely so on the duration of the entire trip (which lasts for more than a year, more time than needed to rebuild BC). Greater SSI however, could be an inherent advantage for juvenile survival in king penguins, as shown in other species (Van der Jeugd & Larsson 1998). Different explanations have been advanced, from inter-individual differences in anti-predator capacities (Sullivan 1989) or inter-individual competitive capacities (Tinbergen & Boerlijst 1990; Spear & Nur 1994), to differences in foraging efficiency (Beauplet & Guinet 2007). If the effect of SSI is not critical enough to negatively affect global return rate in juvenile king penguins, we suggest that birds with bigger flippers might be more efficient in swimming, diving and foraging (as has been found in seals, Beauplet & Guinet 2007), resulting in a shorter time to return to the colony. Larger body size may also confer the advantages of lower mass-specific metabolic rate according to allometric equations (Schmidt-Nielsen 1984). Such a lower metabolic rate may then increase efficiency at converting acquired resources into fat reserves (Festa-Bianchet *et al.* 1998). Larger birds would therefore be able to acquire earlier a sufficient body condition to return to the colony, where penguins endure obligate fasting.

Inter-annual variations and climate

The high variability observed in the global return rate and duration spent at sea between cohorts of juvenile king penguins may be a consequence of varying environmental conditions, either prior to fledging or during the post-fledging period spent at sea. Indeed, conditions experienced early in life may have important consequences on individual fitness (Lindström 1999). For instance, individuals born during years of low food availability will present low phenotypic quality, leading to high subsequent juvenile mortality. In this study, juveniles fledged under unfavourable conditions indeed exhibited low return rates. However, return rates did not increase linearly with favourable conditions, suggesting that an opposite mechanism occurred. Selection mechanisms happen at different life stages and the ‘selection hypothesis’ stating that birds with less adapted phenotypes would disappear in early stages of life could occur more or less early depending on the environment (Braasch *et al.* 2009). In common terns, under harsh conditions, most weak individuals are already eliminated prior to fledging, whereas in favourable years, many juveniles of lower quality survive the pre-fledging period but may die later when environmental constraints become critical (Braasch *et al.* 2009). Similarly, king penguin chicks fledged in years of very favourable conditions may be of highly heterogeneous quality as a result of low selection pressure in these years, and thus present lower return rates than birds fledged under ‘normal’ conditions. An alternative explanation could be a condition-dependent dispersal. Indeed, one can imagine that under favourable conditions, king penguin juveniles would have a higher ability to disperse. However, according to the concept of “voting with their feet”, we could expect the opposite, with higher dispersal when conditions are poor (decreasing breeding success has for instance been shown to increase dispersal rate in seabirds, Danchin *et al.* 1998; Boulinier *et al.* 2008).

Interestingly, those birds fledged in 2005 presented an especially low return rate, not attributable to delayed returns, as no birds were observed in the colony after the three usual return years. However, these birds were reared after the December 2004 tsunami, which greatly affected the studied colony despite being located some 6500 km away from the epicentre (Viera *et al.* 2006). Breeding success was not directly impacted by flooding within the studied sub-colony, as it is away from the shores. Nonetheless, chick-rearing was harsh for the breeders, due to high levels of stress and aggressiveness throughout the colony. In addition, physical disturbances such as tsunamis are considered to be important factors structuring marine (Sousa 1984) and biotic communities, physical habitats and nutrient distribution; and exploitable resources could thus be significantly disturbed (Krishnankutty 2006; Satheesh & Wesley 2009). As long-lived seabirds, king penguins are expected to invest a fixed amount in current reproduction and offspring therefore to support the whole cost of environmental conditions (Mauck & Grubb 1995). Consequently, chicks reared after the tsunami were presumably of low quality (this cohort indeed had a very low mean BC at fledging), explaining their poor post-fledging return rate. Further, prey distribution may still have been disturbed when chicks fledged, because of inertia in the ecosystem delaying the return to a new steady state. Survival right after fledging could thus have been strongly impacted.

Finally, under warmer conditions, juveniles survived better and returned earlier. According to adult survival trends (decreased survival with warm temperatures in their foraging grounds during winter; Le Bohec *et al.* 2008a), we would have expected the opposite result. However, juveniles and adults may display differences in foraging, related either to experience or different needs. For instance, nutritional requirements may be different, as juveniles may need higher levels of protein to finish their growth (Partridge & Green 1985) or conversely less energetic prey, as they only forage for themselves (Davies & Green 1976). Furthermore, juveniles may also forage at different locations since they do not have the constraints of central place foragers as breeding birds do. Unlike breeding adults, which mostly forage in two specific regions (Charrassin & Bost 2001), juveniles are thus free to go and forage wherever they need to. Barrat (1976) suggested that some juveniles could go as far up north as the subtropical area. In our study, we found as best explanatory climatic variable the SST averaged around the subtropical front, suggesting that this area may play a role for juvenile king penguins. The use of tracking methods (such as satellite tracking or GLS) or stable isotopes could then be valuable options to acquire knowledge on their feeding locations.

Benefits of early returns

Average age at first breeding in king penguins is reported to be 6 years old (Weimerskirch *et al.* 1992), however sexual maturity is probably reached earlier (around 3) as some birds have been seen to attempt breeding at 3 or 4 (Barrat 1976; personal observations). Importantly, we show here that birds are coming back in one of the three summers following their departure, *i.e.* between age 2 and 4, with as much as more than 90% coming back at 2 or 3. Moreover, all returns, without any exception, are recorded during the austral summer (from November to May). The return peaks of juvenile king penguins thus coincide with the breeding period, yet only a few of them attempted breeding. A possible explanation could be that juveniles need to return for moulting, which coincides with breeding. Based on weekly observations of the whole colony, their moult ranges between mid-November and the end of January. However, two different peaks of returns have been observed in each year, the second peak occurring at the end of February. Only birds returning in the first peak could thus have come for moulting purposes but they spent far more time than required for the moult. Therefore, young king penguins do not return to their natal colony exclusively for moulting purposes. We suggest that they engage in courting but are not selected as preferred mates by their conspecifics, thus failing to breed. Pairing is indeed highly competitive in king penguins and we may assume that young birds are at a disadvantage. In particular, older birds are known to present stronger secondary sexual characters, such as conspicuous ornamental colours of both beak and plumage (Nicolaus *et al.* 2007). In our study, older juveniles spent more time at the sub-colony, suggesting that the older they are when they arrive at the colony, the more they try to engage into breeding. Furthermore, birds coming back for the first time as very young individuals (*i.e.* at age two), later spend significantly more time in the sub-colony during the subsequent summers (at ages three and four) than other birds of the same age, *i.e.* three or four, coming back for the first time. If, as suggested by Barrat (1976), their presence at the colony is an important part of the establishment of reproductive behaviour, birds returning earlier in life would be able to gain more experience and better knowledge of their reproductive site (this includes best locations in the colony, avoidance of predators, or/and any social knowledge such as potential mates, brood neighbours, *etc.*). Since, however, few birds come back at age two; this strategy probably incurs other costs such as risks linked to the aggressive behaviour of breeders. Further studies relating breeding parameters such as recruitment age and age at first breeding success with age at first return to the natal group may help in answering this question.

II. Complementary results on Adélie penguins

A similar study has been conducted on Adélie penguins. As the sample size and the number of cohorts usable for the study is low, we could not address the question of the impact of climate in this study. Nonetheless, I still wanted to present the first results here, as they show differences from what have been published before in the literature.

Methods

Methods were similar to that used in the king penguin study. To avoid too many repetitions, here, we only point out the few differences.

Penguin monitoring

Our study was conducted in Dumont d'urville (66°40'S, 140°01'E), Adélie Land, Antarctica during 5 consecutive austral summers from 2006/2007 to 2010/2011. From the summer 2006/2007 to the summer 2009/2010, all chicks of the 'ANTAVIA sub-colony', which were still alive in February during their moult, a few days before fledging, were implanted with a passive transponder tag under the skin of their left leg, without any other external mark (*i.e.* 4 cohorts and 1055 chicks). In November 2006, 50 breeding adults were also fitted with a transponder tag. Transponder tags weigh 0.8g and have no known adverse effects (Froget *et al.* 1998, Nicolaus *et al.* 2009). Upon tagging, all birds were weighed with a precision scale (± 10 g). Except for the chicks tagged on the first year (February 2007), flipper and beak lengths of all other birds were measured. Birds were handled directly in the colony (a few meters away from the nests), the manipulation lasting less than 5 minutes on average.

Individual attendance was recorded continuously from early January 2009 to end of March 2011 (*i.e.* 3 consecutive seasons, the Adélie penguins being onland from October to March) using an automatic penguin monitoring system (APMS). Penguins marked with a transponder were detected when they crossed the APMS antennae on their way in and out of the colony, thus recording the transponder number, date, time and direction of each arriving and departing penguin. It should be noted that the APMS was not installed before the austral summer 2008/2009. Birds of the first cohort tagged in February 2007 could thus have returned to the colony in 2007/2008 without being detected. However, it seems very uncommon for birds to return after only one year (no bird of the three following cohorts returned after 1 year). Thus, we decided to consider our recapture effort constant over the whole study period.

Results

First Returns

Not a single bird was detected on the year following fledging (n = 854; Table V - 3). The first birds to return to the colony arrived two years after they fledged but some birds still returned for the first time at the age of 4 (Table V - 3).

Table V - 3: *Number of chicks returning each year for each cohort.*

	Nb of fledglings (~ 5-months old)	Nb of chicks first returning at 1-yr old	Nb of chicks first returning at 2-yr old	Nb of chicks first returning at 3-yr old	Nb of chicks first returning at 4-yr old
Cohort 2007	201	NA	111	24	11
Cohort 2008	268	0	95	71	NA
Cohort 2009	241	0	75	NA	NA
Cohort 2010	345	0	NA	NA	NA

NA stands for not applicable and corresponds either to data prior the installation of the APMS (Cohort 2007, 1-yr old) or to data not yet collected.

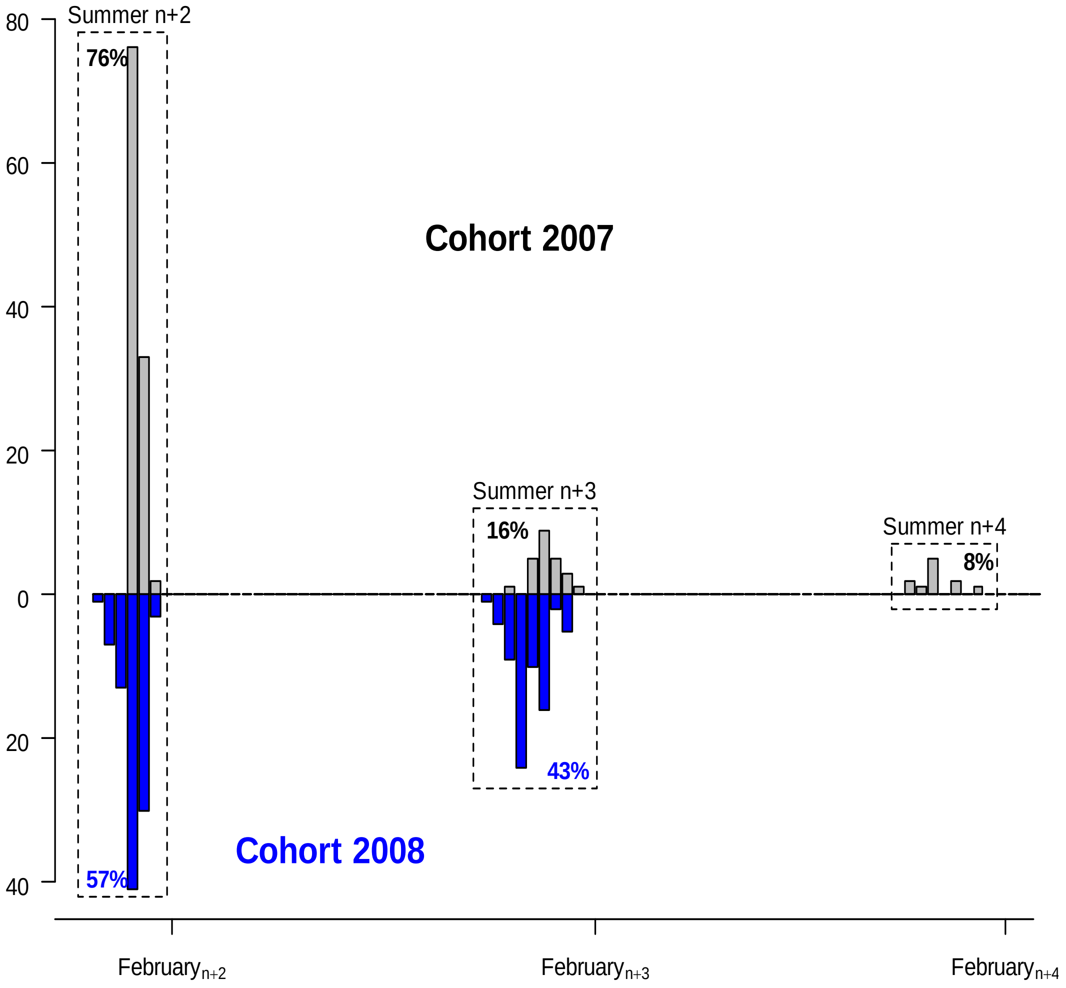

Figure V - 6: *Return date of post-fledging Adélie penguins after their first trip out of the colony.*

We could not determine return rates, as 5-year old birds may return to the colony for the first time in 2011/2012, thus increasing the actual number of birds returning. However, looking at the 1st cohort tagged in February 2007, we know that its return rate is at least of 73%, while at least 62% of the birds tagged in 2008 already returned after only 3 years.

Adélie penguins returned to the colony only during the summer time (Figure V - 6). Further, juveniles of the first cohort returned mostly 2 years after their fledging (76%, Figure V - 6), while the returns of the second cohort seemed more balanced between years 2 and 3 (57% *vs.* 43%; Figure V - 6).

Return dates and post-return duration in the colony

The older the individuals were at their first return, the earlier they arrived at the colony (Mean ± se: 5th January ± 1d. (n = 281) *vs.* 21st December ± 2d. (n = 95) *vs.* 9th December ± 2d. (n = 11); LM: $P < 0.001$; Figure V - 7) and the longer they visited the colony on that summer (31 ± 1d *vs.* 37 ± 2d *vs.* 49 ± 2d; LM: $P < 0.001$, n = 387; Figure V - 7).

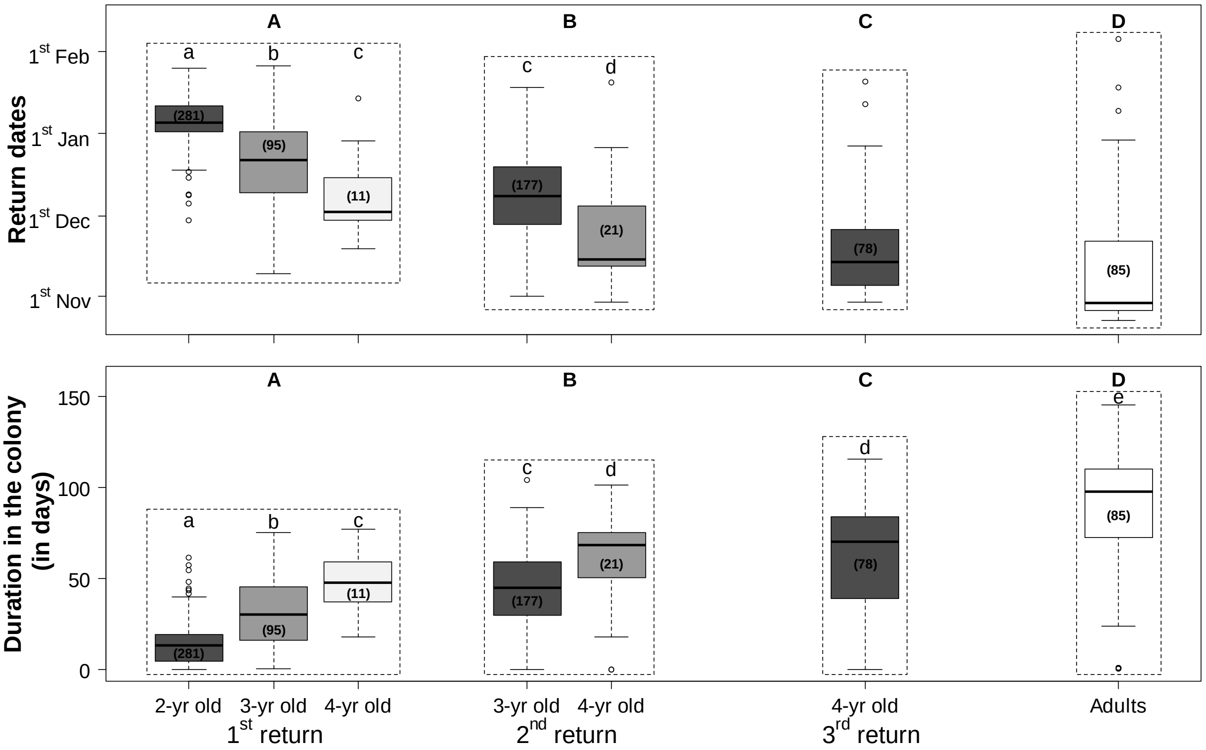

Figure V - 7: *Return dates depending on the age and the number of returns already performed by the individuals.*

The 1st, 2nd and 3rd returns correspond to individuals tagged as chicks (of the cohorts 2007 to 2009), while adult returns correspond to the returns of the 50 individuals tagged as breeding adults in 2006. Boxes not sharing a common superscript are significantly different (Wilcoxon test with Bonferroni adjustment). Capital letters give information on the significativity of differences between the stages all ages confounded (the dotted rectangles, i.e., 1st return vs. 2nd return vs. 3rd return vs. adults)

Further, birds arrived earlier and visited longer the colony on their third return than on their second return than on their first one (LMMs, $P < 0.001$, $n = 748$, $N = 302$; Figure V - 7). Breeding adults arrived earlier than juveniles whatever their age or the number of returns they already performed (0, 1 or 2; Wilcoxon tests, all $P < 0.001$; Figure V - 7).

The automatic monitoring system started on the 1st of January 2009, so that juveniles from the cohort 2007 returning after two years may have returned earlier without being detected and the return dates or duration of the first return at 2-yr old may be biased. However, we found similar results as the ones presented above when discarding these birds.

Influence of individual parameters on return

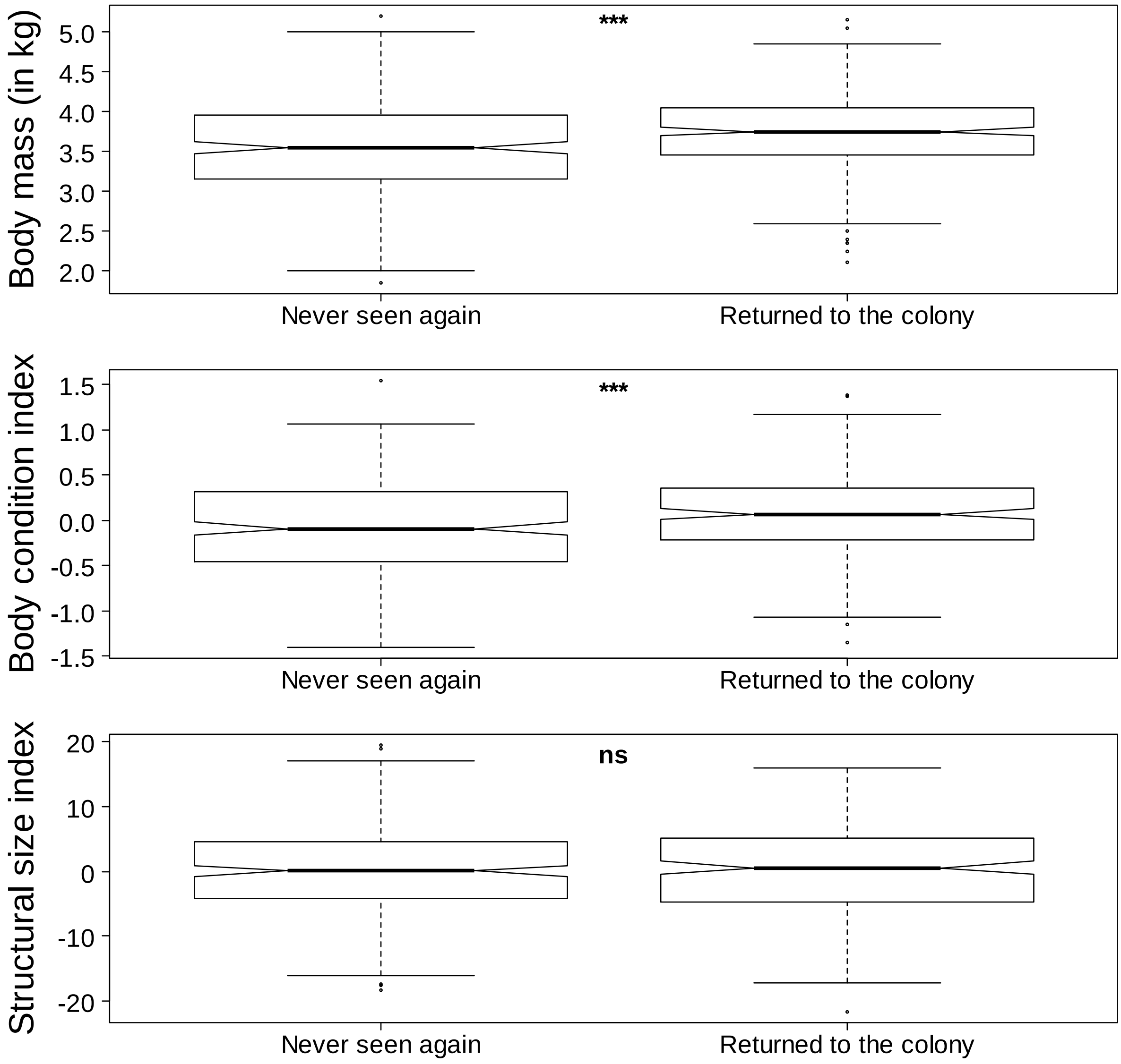

Figure V - 8: *Body mass, condition and structural size of individuals that returned to the colony and those never seen again.*
The cohort 2010 was not taken into account as none of these birds returned to the colony yet.

Birds that returned to the colony were heavier at fledging than birds that were never seen again (GLM: $P < 0.001$, $n = 706$; Figure V - 8). Studying only the 2007 cohort, the results were similar (GLMs; body mass: $P = 0.02$). Structural size index was calculated as a linear combination of beak and flipper length, PCA: SSI = 0.99*Flipper size + 0.12* Beak size, this first component explainin 90% of the variability. Note that birds of the 2007 cohort were not measured, so that structural size is available only in 2008 and thereafter. Structural size did not affect return rate ($GLM_{2007\text{-}2009}$: $P = 0.42$, $n = 515$; Figure V - 8). Body condition (residuals of the regression of body mass on body size index) influenced return rate (GLM: $P < 0.001$, $n = 515$; Figure V - 8).

Finally, the body mass of the individuals at fledging did not affect the number of years they spent out of the colony (LRs: Cohort 2007, $P = 0.87$, $n = 145$; Cohort 2008, $P = 0.79$, $n = 166$; Figure V - 9). Similarly structural size and body condition did not affect the number of years they spent out of the colony (LRs: Cohort 2008, $n = 166$, $P = 0.86$ for structural size and $P = 0.71$ for body condition).

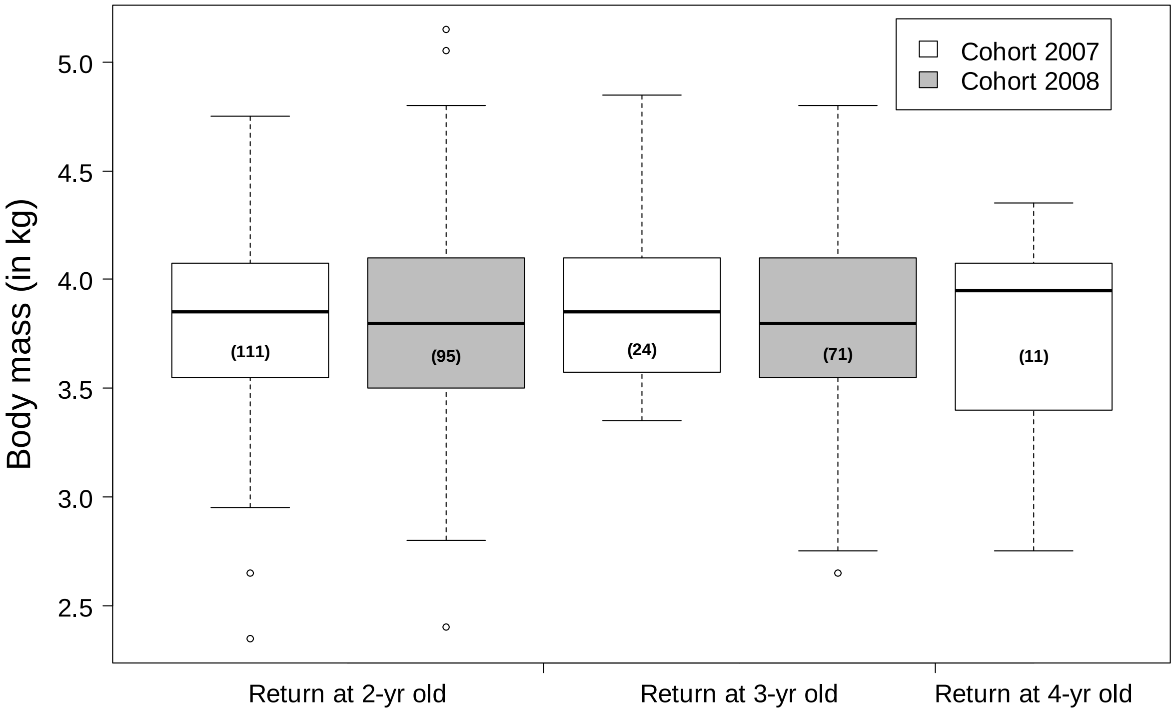

Figure V - 9 : *Body mass of fledglings later returning at 2-, 3- or 4-yr old*

Discussion

We could not determine return or survival rate in this study as the probability of resighting of the age-classes is unknown and penguins seem to still return for the first time at the colony even after 4 years. However, we found that 73% of the chicks fledged in 2007 returned to the colony in the 4 following years. Similarly, 62% of the chicks fledged in 2008 returned in the 3 following years. This shows that at least 73% and 62% of the fledglings survived until age 2. This number is especially high compared to the figures found in the literature. In his book devoted to Adélie penguins, Ainley (2002) presents age-specific survival for the two first age classes. Considering the non-banded population, survival from age 0 to 1 equals survival from age 1 to 2 and is 0.513. This means that survival from age 0 to 2 equals 0.263 (Ainley 2002), a figure less than half of what we found here. Such higher juvenile survival may have profound effects on population dynamics of Adélie penguins and especially on the population growth rate.

Further, the resighting probability at age 2 calculated in Ainley was of 0.215, knowing that the sighting probability of a bird that was in the colony was of 0.98. Altogether, this means that the probability of a bird to return at the colony at age 2 was of 0.219. Here, 44% of the fledglings had returned in the colony at age 2, indicating that birds return for the first time at earlier age than that estimated in Ainley (2002). Yet, these first returns seem to have important consequences on both age at first breeding and later breeding success (Ainley 2002). Indeed, Ainley shows that more than age, it is experience (in the colony and in breeding) that affects breeding performances. Here, we show that juveniles return later than adults but remain more and more in the colony as they become older or return for a second or third time. Birds returning early may thus gain experience and engage in reproduction earlier in life. It would be interesting to investigate the long-term effect of such decisions on future breeding attempts and survival and altogether on the lifetime reproductive success (LRS). Indeed, breeding earlier may increase experience and result on higher fecundity of the birds (Ainley 2002) but it could also be costly and result in higher mortality. For instance, females seem to reproduce earlier (Ainley 2002) but exhibit a higher rate of mortality than males.

The huge discrepancies in the figures we found compared to the ones in Ainley (2002) could result from different things. First, Adélie penguin populations have been shown to have very different trends according to their location (see review in Forcada & Trathan 2009), with population living under low latitudes (such as those in Adélie Land) decreasing, while those living under higher latitudes (such as those in Cape Crozier studied by Ainley) increased. This seems in opposition with our results though, the return rate being higher in our low latitude study colony. Yet, the population in Pointe Géologie Archipelago has been increasing constantly since the 80's (Jenouvrier *et al.* 2006), which may explain the increased return rates we observed. Additionally, data from Ainley has been collected in the 60's and 70's and great changes of the environment have occurred since. Adélie penguins have to face new conditions and may change to adapt to these conditions. For instance, a change in their breeding phenology (delay of laying dates) has been observed since 1950 in Adélie Land (Barbraud & Weimesrkirch 2006). Adélie penguins may try to shift their demographic strategy towards the r-strategy on the r-K gradient by starting to reproduce at a younger age. This would explain the increase in returns at age 2 between the two datasets. However, this is speculative and one would need to monitor the same population to observe such a change. Further, in other places, survival to first breeding has been shown to drop in the 80's (Trivelpiece *et al.* 2011) suggesting that return rates should be lower in our study than those studied by Ainley (2002).

Here, we could not study the effect of climate on return rate because of the limited dataset and will do that in the future. However, it is interesting to note that the two cohorts studied here presented strong differences. Return rates after 3 years differ from 0.67 for the 2007 cohort *vs.* 0.62 for the 2008 cohort. Regarding the timing of the return, most of the birds return in the second year for the 2007 cohort (82% / 18%), while the proportion is more balanced for the 2008 cohort (57% / 43%). It would be very interesting to study the effect of conditions both during early development (before fledging) and during the trip at sea on return rates and timing.

Finally, it is interesting to note how similar these complementary results on Adélie penguins appear to be to king penguin results presented above. Both studies yielded higher juvenile return rates than previously thought, potentially resulting from improvement in monitoring system and temporal or spatial variations. Also, body condition at fledging seems an important driver of survival during early ages but does not affect the time spent at sea before returning to the colony for the first time. If we have no explanation for the moment for the number of years spent at sea before returning, we suggest that it could affect the amount of experience gained by individuals and may influence later reproduction. The surprising result in comparing the two species concerns this duration at sea before returning for the first time. Adélie penguins present a higher turnover rate and are considered as a slightly faster species than king penguins in the slow-fast strategy continuum. Age at first reproduction in Adélie penguins is around 5 (Ainley 2002) versus 6 in king penguins, but at this age less than 40% have already attempted to breed (Weimerskirch *et al.* 1992). Thus, I expected Adélie penguins to return on land earlier to gain experience and be able to reproduce earlier than king penguins. Yet, we found quite the opposite with trips lasting at least 2 years and birds still returning for the first time after 4 years in Adélie penguins, while all trips lasted between 1 and 3 years in king penguins.

Chapter VI ○○○○○●○○○○

Reproductive strategies and climate

I. Parental effort in little penguins

Everybody needs somebody:
unequal parental effort in little penguins
(Article 4)

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According to life-history theory, individuals optimize their decisions in order to maximize their fitness. This raises a conflict between parents, which need to cooperate to ensure the propagation of their genes but at the same time need to minimize the associated costs. Trading-off between benefits and costs of a reproduction is one of the major forces driving demographic trends and has shaped several different parental care strategies. Using little penguins (*Eudyptula minor*) as a model, we investigated whether individuals of a pair provide equal parental effort when raising offspring and whether their behavior was consistent over 8 years of contrasting resource availability. Using an automated identification system, we found that 72% of little penguin pairs exhibited unforced (*i.e.*, that did not result from desertion of 1 parent) unequal partnership through the postguard stage. This proportion was lower in favorable years. Although being an equal pair appeared to be a better strategy, it was nonetheless the least often observed. Individuals that contributed less than their partner were not less experienced (measured by age), and gender did not explain differences between partners. Furthermore, birds that contributed little or that contributed a lot tended to be consistent in their level of contribution across years. We suggest that unequal effort during breeding may reflect differences in individual quality, and we encourage future studies on parental care to consider this consistent low and high contributor behaviour when investigating differences in pair investment into its offspring.

Maximizing individual fitness has driven evolution to shape mating systems and their strategies of parental care throughout the animal kingdom. From monoparental to biparental care or communal breeding (where several adults of a group take care of all the offspring), a diversity of partnerships can be found amongst animals. Birds are unique among vertebrates in that biparental care is the norm with more than 90% of the species (Lack 1968). In long-lived species that exhibit biparental care, there is a potential conflict between partners where both try to minimize cost of reproduction but must cooperate to breed at the same time (Trivers 1972; Maynard Smith 1977a; Houston *et al.* 2005). This conflict occurs because each parent will increase its fitness by investing in its offspring but may also risk its own survival at the same time and decrease its chance of breeding in the future (Clutton-Brock 1991). Each parent will thus benefit if the other does more of the work involved in raising the offspring.

Life-history theory suggests that in order to maximize its fitness, an individual will invest a specific amount of parental care resulting from the trade-off between benefits and costs associated with raising chicks (Stearns 1989). The solution of this conflict depends on the interactions between parents, the behavior of other animals in the population, and individual differences within sex (Webb *et al.* 1999; Barta *et al.* 2002).

Parental investment is defined as ‘‘any investment by the parent in an individual offspring that increases the offspring’s chance of surviving at the cost of the parent’s ability to invest in other offspring’’ (Trivers 1972), and in the case of birds for instance, includes nest building, incubating eggs, chick rearing, and nest defense. But for many bird species, the chick provisioning phase, that is, the period when chicks cannot feed by themselves and during which the parents deliver meals, is an energetically costly period when crucial decisions between costs and benefits have to be made (Drent & Daan 1980). Most studies on parental care have thus focussed their investigation to this crucial phase of the life cycle.

Parameters such as the age or sex of each partner in a pair could potentially affect parental investment share between parents. Age-related differences in foraging efficiency (*e.g.*, Daunt *et al.* 2007) could result in parental care differences and consequently in breeding success differences (Lack 1968). Many studies have indeed documented such a lower reproductive success for young birds (reviewed in Saether 1990; Clutton-Brock 1991, see also Komdeur 1996).

However, in most of the studies in which parental investment has been investigated, the division of that investment has been regarded as a ‘‘battle of the sexes’’ (Andersson 1994; Guerra & Drummond 1995; Aho *et al.* 1997; Weimerskirch *et al.* 2000; Barlow & Croxall 2002; Lewis *et al.* 2002, 2005; Velando & Alonso-Alvarez 2003; Markman *et al.* 2004; Quillfeldt *et al.* 2004; Hamer *et al.* 2006). Parental differences in offspring provisioning have been recorded in a number of sexually sizedimorphic species (Aho *et al.* 1997; Weimerskirch *et al.* 2000; Velando & Alonso-Alvarez 2003; Lewis *et al.* 2005) and are usually attributed to the influence of parents’ body size on foraging efficiency and competitive ability (Andersson 1994; Markman *et al.* 2004). However, differences between males and females in provisioning behavior may also occur in the absence of sexual size dimorphism (in northern gannets, *Sula bassanus*, Lewis *et al.* 2002; in Manx shearwaters, *Puffinus puffinus*, Quillfeldt *et al.* 2004; Hamer *et al.* 2006). Additionally, whereas males may provide more parental care in some species (*e.g.*, the wandering albatrosses, *Diomedea exulans*, Weimerskirch *et al.* 2000; or the lesser spotted woodpecker, *Picoides minor*, Witkander *et al.* 2000), females may be the ones to invest more into offspring in others (such as the willie wagtail, *Rhipidura* *leucophrys*, Goodey & Lill 1993; the blue-footed booby, *S. nebouxii*, Guerra & Drummond 1995; or the macaroni penguin, *Eudyptes chrysolophus*, Barlow & Croxall 2002).

However, differences in parental care might not solely be explained by a sexual bias, and some species have been shown to equally share parental duties between sexes (sandwich tern, *Thalasseus sandvicensis*, Fasola & Saino 1995). Equal sharing at the species level does not necessarily mean that both parents equally share in each pair but rather that depending on the pairs, it may be either the male or the female that compensate for its partner. Yet, to date, few studies have considered alternatives to sexual bias in order to explain differences in investment into parental care. Because breeding costs are probably not the same nor have the same impact on survival or further breeding attempts in different birds, parental care may be dependent of individual quality. In house sparrows, *Passer domesticus*, for instance, Schwagmeyer & Mock (2003) showed that good parents exhibit consistency in provisioning behavior across breeding events. These authors suggested that variation in parental care could be attributed to differences in individual quality (the so-called ‘‘parental quality differences’’ hypothesis, Schwagmeyer & Mock 2003).

A substantial number of studies on parental care have been experimental, that is, where 1 partner was handicapped, and the performances of the 2 members of the pair were evaluated (cf. Beaulieu *et al.* 2009b and references therein). Furthermore, most of these studies were conducted on a yearly time basis, and very few studies have been carried out on multiple breeding seasons (only 4 studies on the 16 previously cited). Except for Schwagmeyer & Mock (2003), none of them investigated how parental care might change over years. Yet, such information is necessary to understand how the environment may influence parental decisions, as well as to test for the parental quality differences’ hypothesis. Environmental variability and seasonal fluctuations might lead to different breeding costs endured by the parents and thus to different parental care strategies depending on the breeding season.

In this study, we investigated parental investment (parental effort and costs of this effort) through differences between partners (without limiting our study to a sex effect) in little penguins, *Eudyptula minor*, over multiple breeding seasons and in natural conditions. Little penguins are long-lived seabirds, showing small sexual size dimorphism (Arnould *et al.* 2004). Their foraging ability is probably more constrained during the breeding season than most other seabirds, as they have one of the shortest foraging ranges (<20 km during chick rearing, Collins *et al.* 1999), and forage in an environment with very unpredictable food supply (Gales & Pemberton 1990; Chiaradia *et al.* 2010). These features make them a useful model to study differences in individual quality at critical times when they are raising their offspring. During the postguard phase, chicks are left unattended by their parents, and both parents are foraging at sea. Parents attendance and investment thus become independent of each other (Daniel *et al.* 2007), unlike their attendance pattern at other stages (Chiaradia & Kerry 1999). Therefore, foraging differences should be more apparent at individual level.

Here, parental effort was investigated during postguard by examining if individual contribution in parental care was more, less, or equal to its partner. We measured both the frequency of visits and meal size brought back to the chicks. Using long-term continuous data, we further examined whether this behavior was consistent over 8 years of contrasting environmental conditions, that is, whether there is any intrinsic individual quality associated with differential parental investment. We also investigated at the population level how parental strategies were determined by resource availability (*i.e.*, in different years, as inferred by breeding success, Chiaradia & Nisbet 2006) and the success of previous breeding stages. We finally examined benefits of the different parental strategies through the reproductive outcomes (fledging success and chick growth) and their costs (impacts on return rates and local survival).

Materials and Methods

Monitoring and field protocol

Little penguins were studied at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (lat 38°15'S, long 143°30'E), where about 14 000 pairs of little penguins nest (Cullen *et al.* 2009). This study was conducted during 8 breeding seasons from 2001 to 2008, where 2001 refers, for instance, to the breeding season 2001–2002. The study site (see details in Chiaradia & Kerry 1999) is a part of a colony containing 100 artificial burrows (wooden nest boxes) of which 50– 86 boxes were occupied in each year (see Table VI - 1). All adults nesting in these burrows for more than 2 years were included in the study. They had been previously marked with electronic transponder tags (Allflex Australia Pty Ltd, Capalaba, Queensland, Australia), subcutaneously implanted between the scapulae, mostly as chicks, and sexed by bill measurements in subsequent years, when first found in the colony as adults. The bill-size discriminant has been calibrated for birds of Phillip Island with an accuracy of 91% (see Arnould *et al.* 2004). Furthermore, as we investigated pairs, sex ID was double checked by male–female association, meaning that any chance of error would occur at a probability of less than 1%. About 35 % of individuals were marked as adults and had their age estimated by adding 3 years at the marking date (Daniel *et al.* 2007), based on the average age of first breeding of 2–3 year olds (Nisbet & Dann 2009). Because little penguins show a high site fidelity (Bull 2000), this adult age correction should not have underestimated their ages as nesting site was checked for unmarked birds at regular intervals since 1978 (Dann & Cullen 1990). To make sure this method did not introduce a bias, whenever we investigated for an eventual effect of age, we ran our models over 2 datasets including either all birds or only those marked as chicks. Our analyses yielded similar results and only those on all birds are presented below.

Table VI - 1: *Summary of annual data on breeding success and mean body of little penguins from 2001 to 2008 at Phillip Island*

	Nb of pairs observed	**Mean fledgling number per pair**	**Male body mass**	**Female body mass**
2001	58	0.52 ± 0.07	1085 ± 7 g	969 ± 6 g
2002	50	1.58 ± 0.07	1119 ± 5 g	1034 ± 4 g
2003	50	1.18 ± 0.08	1149 ± 4 g	1050 ± 4 g
2004	66	0.71 ± 0.06	1094 ± 5 g	993 ± 5 g
2005	75	1.03 ± 0.07	1146 ± 6 g	1028 ± 5 g
2006	63	0.82 ± 0.08	1125 ± 7 g	1012 ± 7 g
2007	52	1.23 ± 0.09	1127 ± 6 g	1026 ± 5 g
2008	86	0.52 ± 0.06	1137 ± 5 g	999 ± 4 g

Individual attendance was recorded continuously using an automatic penguin monitoring system (APMS) designed by the Australian Antarctic Division (Kerry *et al.* 1993). Penguins marked with a transponder, that is all penguins in the study site, were detected when they crossed the APMS platform on their way in and out the colony. The APMS automatically recorded the transponder number, body mass (to the nearest gram), date, time, and direction of each arriving and departing penguin (see details in Robinson *et al.* 2005).

Nests were checked 3 times a week using a purpose-built transponder reader. This allowed us to determine the exact breeding timing (laying, hatching, and fledging dates as well as end of chick guard stage). Chicks were weighted 3 times a week to the nearest 1 g (in a bucket on a digital weighing scale) during postguard stage, when both parents were foraging during the day and therefore absent from the nest. Body mass was used to examine chick growth using peak growth mass and fledging mass as variables (Chiaradia & Nisbet 2006).

Breeding success

Overall, breeding success was measured as the number of chicks fledged (chicks which were fully feathered—ages 45 days—when last encountered were considered fledged) per female, hatching success as the number of eggs hatched per eggs laid, guard success as the number of chicks reaching postguard stage per eggs hatched, and postguard success as the number of fledged chicks per chicks beginning postguard. We also used an index of success before postguard, as a combination of hatching and guard success: Number of chicks reaching postguard on number of eggs laid, hereafter referred to as hatching/guard success index. Both postguard success and hatching/guard success index were divided into 3 categories: low (success < 0.6), average (0.6 ≤ success <0.8), and high success (success ≥ 0.8).

Adult body mass and meal size

We concentrated our analyses of body masses on the first 40 days of postguard (the mean duration of postguard was 43 days) because the number of mass records dropped thereafter by almost 50% as the birds reduced progressively their returning to the colony. Meal size in this study is defined as the amount of food (in grams) brought ashore by an adult to its chicks. We used the body mass difference between a bird entering and leaving the colony to calculate meal size. As parents always arrive after sunset and depart before sunrise, staying only a few hours at night in the colony to feed the chicks during postguard (Daniel *et al.* 2007), mass difference was a reasonable proxy of the amount of food brought to chicks. In fact, meal sizes found in this study (mean 258 g) were consistent with previous findings measured by directly weighing chicks before and after meals (see Figure 4 in Chiaradia & Nisbet 2006).

Number of foraging trips in the pairs

Arrival and departure data from the APMS were also used to calculate the number and duration (in days) of foraging trips during the postguard stage. The number of foraging trips was used as a proxy of parental effort. We calculated the number of foraging trips during the postguard for each breeding individual from 2001 to 2008. For each pair, we defined 2 types of partnerships: 1) equal pairs, that is, pairs that made equal number of trips during postguard. 2) unequal pairs, that is, parents that made unequal number of trips, that is, 1 parent made 3 or more trips than its partner (a difference of 3 trips representing on average 14% more trips by 1 partner). This 3-trip cutoff has been selected as a result of the distribution of the difference in number of trips. In each unequal pair, we then examined which parent made more or fewer trips than its partner. To simplify, we refer to them here as high and low contributors, respectively. To investigate if an unequal partnership was due to desertion of either one of the partners at one stage of postguard, we tested whether the difference in the number of trips achieved by the 2 partners was constant over postguard. Therefore, we divided postguard into 10-days period and computed a mixed model with period as explanatory variable.

It is important to note as well that we could not study whether differences between partners resulted from an individual contributing a lot or from its partner contributing much less. Environmental conditions vary both from year to year and within a season. Thus, the absolute number of trips a bird performed could neither be compared from 1 year to another nor with the number of trips of other birds. Only partners would endure similar conditions and be comparable.

Statistics

All statistics were computed using R 2.8.0 statistical program (R Development Core Team 2008). Data were longitudinal because individual penguins were recorded over multiple breeding seasons. Data were modeled using a maximum of likelihood mixed model approach (lme4 package, Bates & Maechler 2009). Generalized linear mixed models were computed with the individual or the pair, that is, the individual and the partner (when looking at data originating from the pair and not the individual, such as breeding success) as random effects, enabling us to account for repeated measures, because birds were tracked over multiple breeding seasons. Whenever no effect of the years was investigated, year was added as a random effect. Fitted models were generalized linear ones with either Poisson distribution for body mass and chick growth analyses or binomial distribution for breeding success.

Models were used for 2 different purposes:

1. To investigate the influence of different parameters (*e.g.,* age, sex) on a variable, such as the number of trips or the meal size. Fitted models were thus selected through a stepwise procedure by using Akaike's Information Criterion (AIC). The explained deviance of the model (in relation to the null model, that is, the relative variability explained by the model compared with the entire variability in the dataset) and P values were then used to conclude as to the effect of the parameters.
2. In order to assess differences between groups (*e.g.,* equal pairs *vs.* unequal pairs or high *vs.* low contributors). Mixed models were then computed, and P values alone were used to conclude if there were significant differences between groups.

For cross-sectional data (1 data per bird, comparison in between seasons or comparisons of means over all years studied), independence of the data was not violated and so nonparametric tests could be used. When homoscedasticity between groups was ascertained (but not normality), Wilcoxon's rank summed test was used. Variables were considered significant for $P < 0.05$, and Bonferroni's correction was applied whenever multiple comparisons were tested (differences were thus considered significant for $P < \frac{0.05}{n}$ with n the number of comparisons done).

Results

Equal versus unequal number of foraging trips between partners

We grouped 8 years of foraging trips to examine whether there were differences in the number of trips completed between partners during postguard stage in relation to sex, age, and pair bond. Overall, 72 % of pairs exhibited an unequal partnership, and we found that 1 parent made on average 7 more trips than its partner (standard error = 0.2, n = 570 pairs * years), that is, as much as around 30% trips more. These percentage and mean number of trips were not affected by brood size at the beginning of postguard (mean difference in number of trips between partners, 6.4 ± 0.3 *vs.* 6.5 ± 0.6 for 1 and 2 chicks, respectively). Unequal number of trips was not related to sex (22 ± 1 trips in average for females and 23±1 for males, n = 340 for each group, mixed model: degrees of freedom df = 466, n = 680 trips for 212 individuals, Z = 20.14, P = 0.89). Importantly, there was no difference in the total number of trips between equal and unequal pairs (P = 0.51; Table VI - 2), but postguard stage lasted longer (4 days on average) for unequal pairs than it did for equal pairs (P < 0.001; Table VI - 2).

Table VI - 2 : *Parameters used to measure differences between equal and unequal pairs of little penguins over 8 years.*

	Equal Pairs	Unequal pairs	DF	Z-values	P-values
Proportions	28% (169)	72% (433)	-	-	-
Number of PG trips	44 ± 2 (170)	45 ± 1 (432)	202	0.7	P=0.51
PG duration	**41 ± 1 (134)**	**45 ± 1 (194)**	**25**	**-4.1**	**P<0.001**
Age	8.3 ± 0.3 (169)	8.5 ± 0.2 (424)	395	-1.3	P=0.20
Breeding success	1.18 ± 0.07 (169)	1.27 ± 0.03 (432)	98	-0.6	P=0.32
Chick peak mass	**1141 ± 12 (96)**	**1093 ± 9 (265)**	**359**	**12.2**	**P<0.001**
Chick fledging mass	**986 ± 19 (94)**	**942 ± 10 (265)**	**357**	**12.1**	**P<0.001**

Values are mean ± SE. Sample size into brackets. DF stands for degree of freedom of the mixed model. Significant results are in bold. PG stands for Postguard

Between years, the proportion of unequal pairs was highly variable (ranging from 54% in 2002 to 88% in 2006; Table VI - 3), as was the mean difference in number of trips (ranging from 4.8 to 8.8). The mean difference in number of trips and the proportion of unequal pairs were highly correlated ($P = 0.003$, $rho = 0.90$), and we thus only present results on proportion. We separated years into 3 categories of low ($prop \leq 0.6$), average ($0.6 < prop \leq 0.7$), and high ($prop > 0.7$) proportions of unequal pairs. These proportions were correlated to what happened both before postguard (hatching/guard success index) and during postguard (postguard success): The proportion of unequal pairs was low when both measurements of success (postguard and hatching/guard success index) were high (year 2002, Table VI - 3), whereas high levels of unequal pairs appeared when either postguard or hatching/guard success indexes were low, except in 2008 (Table VI - 3). We thus investigated how the minimum of these 2 measures of success affected the proportion of equal and unequal pairs, so that a low level from one of the successes would be taken into account. This minimum explained partly the proportion of equal and unequal pairs (linear regression: adjusted $R^2 = 0.39$, $df = 7$, $t = 22.3$, $P = 0.05$). The year 2008 presented a much higher Cook's distance (more than twice the following one) and was thus considered as an outlier. The same regression was thus computed excluding 2008, and the minimum explained 79% of the variation in the proportion (adjusted $R^2 = 0.79$, $df = 6$, $t = 24.9$, $P = 0.004$).

Table VI - 3: *Proportion of unequal pairs in little penguins depending on hatching/guard success index and post-guard success.*

	Hatching/ guard success index	**Post-guard success**	**Proportion of unequal pairs**
2001	High (0.84)	Low (0.42)	High (0.80)
2002	High (1)	High (0.86)	Low (0.54)
2003	High (0.90)	Average (0.73)	Average (0.67)
2004	Average (0.77)	Low (0.53)	High (0.71)
2005	Low (0.57)	High (0.93)	High (0.76)
2006	Low (0.46)	High (1)	High (0.88)
2007	High (0.98)	Average (0.68)	High (0.71)
2008	Average (0.69)	Low (0.38)	Average (0.67)

In addition, the difference in the number of trips achieved by partners was constant over the whole postguard. The model with period as explanatory variable was not better than the null model ($\Delta AIC < 2$ and less than 1% of the deviance was explained). Finally, there was no age difference between individuals of equal and unequal pairs (mean of 8 years for both groups, $P = 0.20$; Table VI - 2).

Unequal parental care: a consistent behavior at the individual level

Unequal pairs were when one individual (the high contributor) made more foraging trips during postguard than its partner (the low contributor). The age difference between the 2 partners did not explain the high or low contributor status of the birds: high contributing birds could be either younger or older than their low contributing partner (mixed model: df= 350, n = 542 for 192 birds, Z = 21.24, P = 0.21). Furthermore, high and low contributors exhibited similar return rates after 1 year (*i.e.*, resighted in the following season, 0.81 6 0.03 *vs.* 0.79 6 0.02 for high and low contributors, respectively; mixed model: df = 281, n = 462 for 180 birds, Z = 0.47, P = 0.64) and similar local survival (which is the probability that a particular individual occupying a site during one breeding season survives and settles in the same site during one of the next breeding seasons, *i.e.*, resighted in any season after, 0.87 ± 0.02 *vs.* 0.84 ± 0.02 for high and low contributors, respectively; mixed model: df = 281, n = 462 for 180 birds, Z = 0.83, P = 0.41).

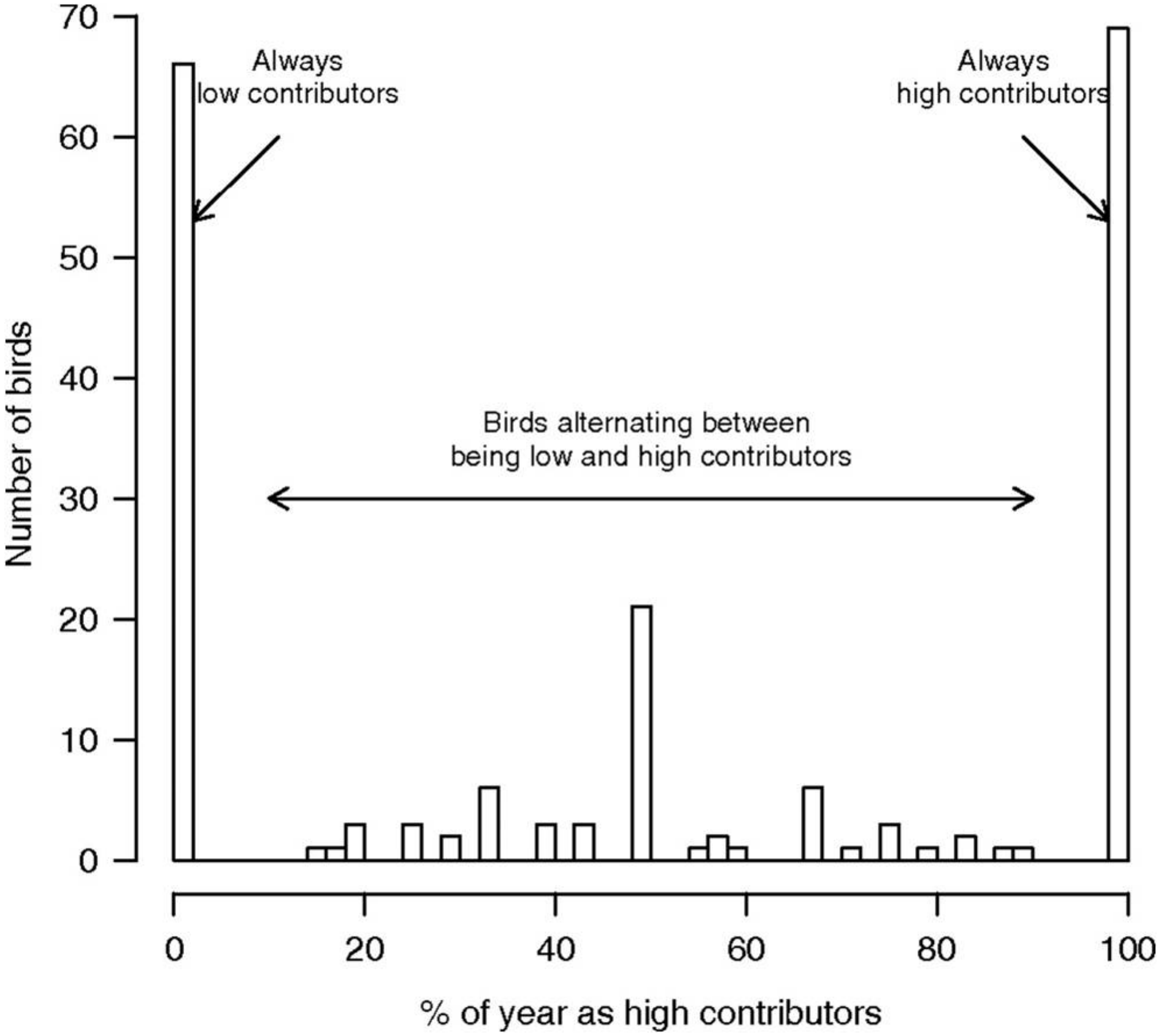


Figure VI - 1: *Number of little penguins displaying low or high contribution to their partnership.*

A total of 69% of little penguins (135 of 197 birds) in unequal partnership group were consistently high and low contributors over the years, either always making more trips than their partners or always making fewer trips than their partners (Figure VI - 1). The remaining 31% (62 birds) alternated between being high and low contributing partners over the years. Within the alternating parent group, a total of 21 of 62 were recorded with an equal number of years as high and low contributor. Altogether these 62 birds changed 108 times from being low to high contributors, or vice versa, and in approximately 50% of these changes (53 cases of 108), they stayed with the same partner. When examining whether penguins divorced or reunited with previous partners, there was no difference in pair bond between alternating birds and consistent ones (Wilcoxon test P = 0.92, Table 4). There were also no differences of breeding success between penguins that alternated between being low and high contributor and consistent penguins (one chick fledged per pair in average, P = 0.37; Table VI - 4). However, when alternating birds were analyzed separately, they exhibited a much higher breeding success during a year when they changed from high to low or vice versa, than when they kept the same pattern over 2 or more consecutive years (1.33 after a change *vs.* 0.97 after no change, mixed model: df = 282, n = 345 for 62 birds, Z = 2.95, P = 0.003). Finally, alternating and consistent birds exhibited similar mean differences in the number of trips between partners (6.6 *vs.* 6.3 trips for consistent and alternating birds, respectively; mixed model: df = 401, n = 599 for 197 birds, Z = 0.57, P = 0.56).

Table VI - 4*: Summary of the breeding activities between little penguins that were displaying consistent and alternating behaviour at high or low parental contribution (see text for definition).*

	Consistent birds	**Alternating birds**	**DF**	**Test statistics**	**P-values**
Proportions	69% (135)	31% (62)	-	-	-
Divorce rate	0.38 ± 0.04 (99)	0.35 ± 0.04 (61)	-	W=2992.5*	P=0.92
Breeding success	0.94 ± 0.04 (135)	1.00 ± 0.05 (62)	195	t=0.90**	P=0.37

** Wilcoxon test. ** Student t test. Values are means ± SE. Sample size into brackets. DF is the degree of freedom from mixed models.*

Meal size

Overall, females brought 9% less food to the chicks than males (meal size = 250 ± 2 g *vs.* 276 ± 3 g, mixed model: df = 6622, n = 6784 for 161 individuals, Z = 2.71, P = 0.007; Figure VI - 2A). However, regardless of sex, high contributors brought back 4% more food than low contributors (meal size = 264 ± 2 g *vs.* 253 ± 3 g, mixed model: df = 5349, n = 5496 for 146 individuals, Z = 14.8, P < 0.001; Figure VI - 2B). There were no significant differences in the meal size between high contributing females and their low contributing partners (255 ± 3 g for high contributing females and 267 ± 4 g for low contributing males, mixed model: df = 2603, n = 2701 for 97 individuals, Z = 1.53, P = 0.13, Figure VI - 2C). But high contributing males brought 15% more food than their partner (meal size = 284 ± 3 g *vs.* 242 ± 3 g, mixed model: df = 2690, n = 2795 for 104 individuals, Z = 4.4, P < 0.001, Figure VI - 2D). Finally, meal size was affected by brood size (192.7 ± 8.1 g *vs.* 219.6 ± 3.4 g, for 1 and 2 chicks, respectively, P < 0.001).

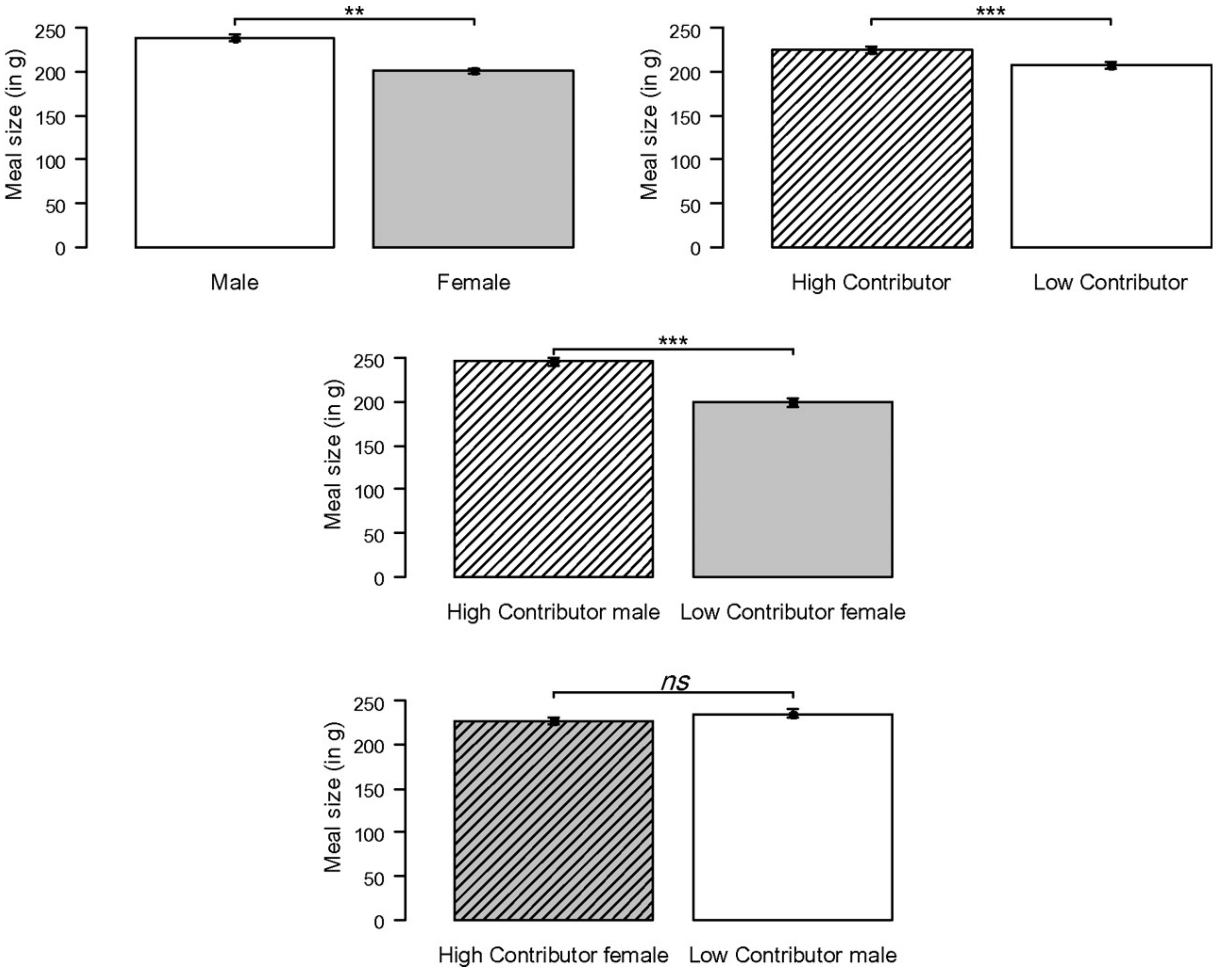


Figure VI - 2 : *Meal size delivered to chicks inferred from the adult body mass difference between arrival (in) and departure (out) to and from the little penguin breeding colony during the postguard stage.*

Equal versus unequal parents

Equal and unequal pairs had similar postguard success (P = 0.32, mixed model with year as a random factor to take into account the fact that the number of equal pairs increased in favorable years, Table VI - 2), and the difference in number of trips between partners had no effect on their success (mixed model: df =69, n = 270 for 105 birds and 95 partners, Z = 0.084, P = 0.93). However, equal pairs fledged heavier chicks than unequal pairs (45 g difference at fledging and 50 g, *i.e.,* about 5% of their total body mass at peak growth, both P < 0.001, Table VI - 2). Furthermore, equal and unequal pairs exhibited similar return rates (resighted in the following year, 0.76 *vs.* 0.78, respectively, P = 0.66) and similar local survivals (resighted in any year, 0.82 *vs.* 0.85, P = 0.71).

In unequal partnerships, there were no differences of postguard success in high contributing male pairs versus low contributing male pairs (mixed model: df = 80, n = 280 for 103 birds and 96 partners, P = 0.95). However, pairs with high contributing males fledged chicks on average 10 g heavier than pairs with high contributing females (model: df = 334, n = 336, Z = 22.71, P = 0.007).

Discussion

Understanding parental investment is fundamental for discussion on sexual selection and the evolution of mating systems. Here, we examined one important aspect of parental effort, that is, unequal parental care in chick provisioning in a typical biparental care species, the little penguin. Most pairs (72% throughout the whole study) exhibited unequal parental effort, meaning that one individual of the pair contributed more than the other one (7 more trips on average) and that independently of brood size. Such unequal parental care in the chick provisioning period could result either from differences in provisioning effort all along the period or from desertions of one of the 2 partners. According to the parental investment theory, female desertions are not frequent in species where success varies only with postcopulatory investment, a typical situation in birds (Wade & Shuster 2002). Desertions in males occur when the fitness gain, which might accrue to a male from his caring for existing young and incrementing their viability, is much smaller than that obtained from additional mating (Maynard Smith 1977b). Nest desertion nest desertion in little penguins can occur at incubation and during chick guarding, but usually results in early breeding failure, as sharing parental care is necessary until the end of the postguard stage (parents alternate during these periods; Chiaradia & Kerry 1999; Numata *et al.* 2000). Successful parents thus cannot desert their chicks too early in the reproduction. For this reason, we only examined parents with chicks during the postguard stage. A desertion during postguard would usually not allow enough time to additional mating, which very rarely occurs this late in the breeding cycle

(Saraux C, Chiaradia A, Ropert-Coudert Y, *personal observations*) as it would not result into fitness gain. Therefore, desertions were not expected in that stage unless the survival of one parent was at risk. This was confirmed by our data, as no desertions were observed during postguard along our 8 years of study.

Furthermore, meal size is another sensitive parameter to measure parental effort along with the frequency of feeding. Thus, we controlled for this parameter to confirm that penguins which appeared to be high contributors (*i.e.*, higher frequency of visits than its partner) were not doing so at the expense of meal size and indeed contributed more to chick rearing. In general, males fed larger meals to the chicks than females during our 8 years of study. Sex-biased meal size may result from differences in diving behavior as males are able to dive deeper and longer than females (Bethge *et al.* 1997; Yorke *et al.* 2004). To avoid the confounding effect of sex and high/low contributor status, we analyzed separately pairs with mothers as the high contributors and pairs with fathers as the high contributors. Pairs with high contributing fathers exhibited a much greater difference between the 2 partners than the basal difference between males and females alone. High contributing males fed meals, which were 15% heavier than their partners, whereas pairs with high contributing females did not exhibit any differences in meal size within the pair. This shows that not only did high contributing males provision their chicks more frequently but also carried more food than did their partners. High contributing females fed their chicks a similar meal size as their mate but did come ashore to feed the chicks more frequently.

Differences in provisioning of offspring are usually attributed to sex dimorphism, foraging efficiency, and intraspecific competition (Andersson 1994; Markman *et al.* 2004). In little penguins, males are larger than females (Arnould *et al.* 2004) and breeding and foraging successes change with experience and age (Nisbet & Dann 2009; Zimmer *et al.* 2011). In this study, however, these patterns did not emerge in relation to unequal care, which was not related to sex as either the male or the female could be the high contributor in the pair (*i.e.*, the parent feeding the chicks more frequently than its partner). Unequal care was not related to age either. Furthermore, not only did individuals show unequal parental effort within a season but further maintained this behavior consistently during subsequent seasons. Because our data encompassed 8 years, parents thus retained their behavior over at least half of their life (Sidhu *et al.* 2007), suggesting that one individual, regardless of its sex, always tended to make substantially greater effort than its partner toward raising its offspring.

High contributor behavior was not related to an increase in age and breeding experience, rather from an individual specific characteristic, which does not change over the years. This supports the hypothesis of parental quality differences of Schwagmeyer & Mock (2003), which states that variation in parental care could be attributed to quality differences among individuals. It should be noted that there were exceptions when birds were not consistent on their parental investment over time. Some birds were observed to alternate between being a high and a low contributor across years. These birds did not exhibit a higher divorce rate than consistent birds, which suggests that changes in their investment status were not due to finding of a better partnership. Furthermore, in half of the cases of alternating investment status, birds shifted from high to low contributors without changing partners. These birds could be individuals of similar quality, for which parental care strategies could result from a punctual decision, possibly due to actual body condition at any time during the breeding season (such as in king penguins, Gauthier-Clerc *et al.* 2001).

Differences in individual quality have been used to explain variation among individuals in different traits (Vaupel *et al.* 1979; Cam & Monnat 2000). Despite of the widespread interest in this heterogeneity between individuals; ‘‘individual quality remains a somewhat elusive concept within ecology’’ according to Wilson & Nussey (2010) likely due to the complexity of measuring it. Fitness is often perceived as a proxy to individual quality and confusion between the 2 terms frequently occurs. Here, because low contributors are always paired with high contributors and the outcome of a reproduction is the same for both partners of a pair, breeding success of high and low contributors will be the same. Fitness would thus only differ through differences in longevity, which was beyond the scope of this study. However, we showed that there were no differences in return rates and local survival between high and low contributors. If as we suggest here, high contributors are of better quality, we would expect them to be able to sustain higher reproductive costs without affecting their survival and return rates. Thus, our findings suggest that the amount of parental effort is a reflection of parent quality and the amount of energy it could allocate to reproduction without jeopardizing its future breeding prospective. Further, in the context of parental investment theory, birds investing more energy in reproduction should endure higher associated costs and exhibit lower return rates. Here, we found no differences in costs associated to higher parental effort and suggest that the unequal parental care observed results from a difference in parental effort (by-product of individual quality) but not from a difference in parental investment. Yet, consequences of this disproportional investment on parents’ longevity require further investigations. Indeed, costs of one single reproduction could well be not visible immediately on survival but significantly affect longevity when added on multiple reproductive years. In order to test whether unequal parental care is a by-product of individual quality, individual quality should not be measured by fitness directly but as a result of differences in phenotype (Wilson & Nussey 2010). Further studies may for instance consider investigating individual quality through other parameters which can provide a better index of quality which does not rely on life-history traits. For instance, the initial length and shortening rate of telomeres have been shown to affect some of the fitness components in different species (Monaghan & Haussmann 2006; Bize *et al.* 2009).

Strategies of chick provisioning result from the balance between benefits of raising chicks and associated costs (Stearns 1989). We therefore investigated how different strategies between equal and unequal pairs would impact breeding success and ultimately individual fitness. Equal and unequal pairs made the same total number of trips, when both partners were analyzed together. Postguard success was neither affected by the behavior of the pairs (*i.e.,* equal or unequal) nor by the difference in the number of trips achieved by parents, which is similar to findings of Takahashi *et al.* (2003b) on Adélie penguins *Pygoscelis adeliae*. However, breeding success is not the only important parameter to be considered. About 75% of the variance in the number of recruits in breeding bird populations is not accounted for by differences in number of fledglings and results from the period between fledging and sexual maturity (median $r^2 = 0.25$ for studies reviewed in Newton 1989). Environmental pressures experienced during the growth period may affect individual phenotypes and future survival expectancies (especially first-year survival). Some fledging traits such as body size or condition have indeed been found to be correlated with postfledging survival (Korpimäki & Lagerström 1988; Owen & Black 1989; Harris *et al.* 1991; Schmutz 1993). Although breeding success is a composite of several confounding factors such as incubation failure and predation, chick growth and fledging quality could thus be a finer measurement of parental care differences. In little penguins, fledging body mass has been shown to be an important factor of survival of fledglings during their first year after leaving the colony (Dann 1988). In our study, equal pairs fledged heavier chicks than unequal pairs. Chicks from equal pairs would have a more regular food intake, which could positively affect their growth. Although equal parental care seems a better strategy in terms of benefits in raising chicks, it was the least observed amongst little penguins. As long lived species, seabirds are expected to favor their survival at the expense of the current breeding attempt (Stearns 1989; Mauck & Grubb 1995, ‘‘the prudent parent’’ Drent & Daan 1980). They will thus choose the best strategy in terms of reproduction only when associated costs are not too high, that is, when their survival is not at stake. In years of good conditions, such as 2002, the costs associated with breeding were probably lower, and both partners could maintain the same level of parental investment resulting in a larger number of equal pairs. Conversely, in years of unfavorable breeding conditions, individuals may try to minimize reproductive costs, in particularly in long-lived species (*e.g.*, Weimerskirch *et al.* 1997a), leading to more apparent within pair differences. This long-term strategy to reduce breeding costs within the partnership seems relevant as unequal pairs exhibited similar return rate and local survival to those of equal pairs. Besides, higher reproductive costs could be the result of unfavorable environmental conditions occurring during only one part of the breeding season, for example, a short-term decrease in resource availability that would take place either before or during postguard. We detected that by comparing the number of foraging trips. The proportion of unequal pairs and average difference in number of trips was negatively correlated with an index summarizing the hatching and guard success, and with the postguard success. Years of poor hatching or guard success would result in high expected costs and as adults base offspring allocation decisions on expected levels of resource availability (Lalonde 1991), in a high level of unequal investment. However, years with high hatching/guard success could also become poor years, when postguard conditions turned up to be unfavorable (2001, 2004, and 2007). Thus, parental investment strategies do not seem to be set at the beginning of the breeding season but can change dynamically depending on environmental changes during postguard itself.

Our findings suggest that differences in parental care were related to differences in individual quality regardless of age and gender. Such a result may shift the focus of parental investment studies from looking at differences between males and females to considering the inherent individual quality, elusive as it may be (Bergeron *et al.* 2010; Wilson & Nussey 2010), which can play a crucial role in parental investment in biparental system.

II. Impact of climate on little penguin breeding

Which time-scale to use to study the impact of climate on breeding success in little penguins?

(Article 5)

Claire Saraux, André Chiaradia

In preparation

Climate change is now unequivocal and should continue in the following centuries (IPCC 2007). Every living organism is thus facing new selective pressures from its environment. We already know that an important number of biological systems are affected by perturbations resulting from environmental changes (Hughes 2000; McCarty 2001; Walther *et al.* 2002; Parmesan & Yohe 2003). At the dawn of the 6th extinction crisis, it is thus indisputably necessary to increase our understanding of ecosystems and their responses to climate. It has appeared in the last two decades that large-scale climate indices are very good predictors of ecological variation (Post & Stenseth 1998; Post & Forchhammer 2002; Stenseth *et al.* 2002; Stenseth *et al.* 2003). The North Atlantic Oscillation (NAO) and the El-Niño Southern Oscillation (ENSO) are probably the two best-known large-scale climate phenomena and have both been demonstrated to strongly affect ecological processes. The use of global indices or 'weather packages' (as named in Stenseth *et al.* 2003) presents several advantages, the main ones being to integrate variations of several climate factors (temperature, wind, or rain changes are often coupled and driven by a single large scale phenomenon) into a simple and single measure (Stenseth *et al.* 2003). Most surprisingly, the use of these global indices even often outperformed the use of local weather variables when it comes to explain changes in life-history traits or population trends (Post & Stenseth 1998; Post & Forchhammer 2002; Hallett *et al.* 2004; Stenseth & Mysterud 2005). Using the Soay sheep, *Ovis aries*, as an example, Hallett and colleagues (2004) demonstrated why NAO index could better explain ecological changes than local weather parameters. They showed that high rainfall, high winds or low temperatures could severely affect survival at any time during the entire winter (Hallett *et al.* 2004). Thus, previous studies that used monthly values only, the most common time scale used (Weladji *et al.* 2002) failed to capture the association between climate and sheep survival. In contrast, NAO is indexed for the entire winter (December to March), which enables to span over the whole period of risk for sheep. The temporal scale at which the effect of climate is investigated is thus crucial and may explain why global indices such as the NAO may work better than local variables. Yet, it remains difficult to mechanistically link climate change and observed upheavals in many ecosystems (Kearney & Porter 2009) and strong performances of weather packages are even more difficult to link with the proximal processes that underpin them (Clutton-Brock & Coulson 2002). Further, local weather has also been shown to correctly predict ecological changes in some species (*e.g.* Keller & van Noordwijk 1994; Gaillard *et al.* 1997).

Ecosystems are difficult to encompass in their entirety due to their complexity (Ciannelli *et al.* 2005) and climate effects on ecosystems are often investigated through a few key species considered representative of the whole ecosystems and relatively easy to monitor. At the top of food-webs, top-predators represent good candidates for such representative species and are increasingly used as indicators of ecosystem health (Verity *et al.* 2002). Indeed, the effect of climate on lower levels of food webs should be integrated at the top of the chain (Croxall *et al.* 1988; Le Maho *et al.* 1993; Boyd & Murray 2001; Boyd *et al.* 2006; in case of bottom-up control). Climate could thus act at different levels on top-predators affecting them both directly through physiology for instance and indirectly through the food web. Climate effects may thus not be visible immediately and appear only after a lag of several months or years (Thompson & Grosbois 2002). Therefore, the effect of climate on top-predators is usually investigated at a large temporal scale.

Oceans cover more than 70% of the Earth surface and contribute to most of the world biological production (Mann & Lazier 1991). However, mainly due to methodological problems, knowledge on the effect of climate in marine ecosystems is scarce (Richardson & Poloczanska 2008). As a response, top-predators such as seabirds have been used increasingly in the past recent years as indicators of climate change (see reviews: Bost & Le Maho 1993; Piatt *et al.* 2007; Durant *et al.* 2009).

Here, we investigate whether large scale variables are relevant to examine the effect of climate on a marine top-predator: the little penguin. Monthly sea surface temperature (SST) 6 months prior to breeding has been shown to be correlated with breeding output in little penguins (Cullen *et al.* 2009). However, SST explained only 22% of the variance in number of chicks fledged per pair before 2000 (Cullen *et al.* 2009). Further monthly SST during breeding was not correlated with breeding success (Cullen *et al.* 2009). Here, we examine the effect of climatic parameters during the breeding period on little penguin success over 30 years using published data (1980 to 1994: Mickelson *et al.* 1991; Nisbet & Dann 2009; Cullen *et al.* 2009) and this study (1995 to 2010). Further, we used several penguin variables at a finer scale over 10 years to examine at which time scale penguins may respond to changes on climatic variables during breeding.

Methods

Our study was conducted on little penguins at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (38°15’ S, 143°30’ E), where ~14 000 breeding pairs of little penguins nest (Cullen *et al.* 2009). This study was conducted during eleven breeding seasons 1995, 1996 and from 2000 to 2009, where 1995 refers to the breeding season in the austral summer of 1995 – 1996. The study site used for these analyses (see details in Chiaradia & Kerry 1999) is a part of a colony containing 100 artificial burrows (wooden nest boxes), of which 48–76 were occupied in each year. All nesting adults were tagged mostly as chicks (or as adults in few cases) using passive transponder tags (Allflex, Capalaba, Australia), which were then implanted subcutaneously between the scapulae.

Breeding success and the different phase of breeding

Breeding success was determined as the number of chicks fledged per pair (cpp) based on the proportion of eggs laid that resulted in fledged chicks (*i.e.,* chicks which were fully feathered and of age >40 days when last encountered, were considered fledged). Data were standardized as relative values in relation to the long-term mean in the analysis (Chiaradia *et al.* 2010). For the 30 year breeding success versus SST analysis, we used published breeding success data from 1981 to 1995 (1981 to 1994: Mickelson *et al.* 1991; Nisbet & Dann 2009; Cullen *et al.* 2009; see also Chiaradia *et al.* 2010) and this study (1995 to 2010).

Breeding in little penguins is divided in three separate consecutive phases, namely the incubation that ends by egg hatching, the guard that ends when the chicks are left alone in the colony and the post-guard that ends by fledging of the chicks. Hatching success was defined as the numbers of eggs laid that hatched. Guard success was defined as the number of chicks at hatching that reached post-guard. Finally, post-guard success was defined as the number of chicks fledged per chicks reaching postguard.

From 2000 to 2009, all nests were checked three times a week, when presence of penguins inside the nest was detected by a portable transponder reader. This allowed us to determine the number of chicks fledged and the exact phenology of breeding events: laying, hatching, and fledging dates, as well as the end of the guard stage for each pair. Chicks were weighed three times a week to the nearest gram during post-guard (*i.e.,* the period from the first date on which neither adult was present in the nest, to fledging of the last chick). Fledging body mass was thus considered as the mass recorded at the last encounter prior to fledging (see details in Chiaradia & Nisbet 2006).

Chick reserves

In 1995 and 1996, all nests were inspected daily starting right after hatching. The exact hatching date enabled us to know the age of the monitored chicks. From the first day of postguard, 78 chicks were weighed twice a day to the nearest gram using a digital balance until they died or fledged. Chicks were weighed first in the morning at about 08:00 and in the evening between 18:00 and 20:00 Eastern Standard Time. During post-guard, chicks are left alone in the colony during the day and parents return to the colony to feed their chicks only at night time (around 1 to 4 hours later the evening weighing). Between the two daily weighings, chicks were thus fasting and losing body mass. We used the difference in chick body mass between morning and evening of a same day to investigate body mass loss of the chicks at the beginning of fasting (period corresponding to about 10 to 21h of fasting). As chicks were monitored through the whole post-guard and thus at very different body masses, we investigated specific body mass loss, *i.e.* the ratio of the difference in body mass divided by the time of this difference and the mass of the individual ($\frac{dm}{mdt}$). Further, in some cases parents did not return to feed their chicks at night, so that the chicks were observed fasting for a longer period. In these cases, we also calculated specific body mass loss between the evening weighing and the next morning weighing and between morning and evening of the second day, and so on.

Chick growth

For chicks from 2000 to 2009, we investigated chick growth (*i.e.* chick body mass change) according to calendar weeks. However, chick growth in little penguins is not linear (Chiaradia & Nisbet 2006) and differences observed between weeks could well result from chick age rather than from differences in foraging conditions. Here, using chick body masses collected over the 10 breeding seasons, we observed a positive-negative Gompertz curve (Huin & Prince 2000; Figure VI - *3*), first increasing almost linearly and then decreasing. We modeled chick growth using a general additive model (green line; Figure VI - *3*A). Then, to take into account this relationship, we investigated chick body mass change through residuals of this model. A positive residual corresponds to a body mass that will be situated above the average curve and thus to a higher than average growth, while a negative residual represents a smaller than average growth. As growth curve vary according to years and condition, either by different peak values or different peak timings for instance (see Chiaradia & Nisbet 2006; Figure VI - *3* B), we computed one general additive model per year and used the residuals of these 10 models. This enabled us to investigate changes in chick growth between weeks within years.

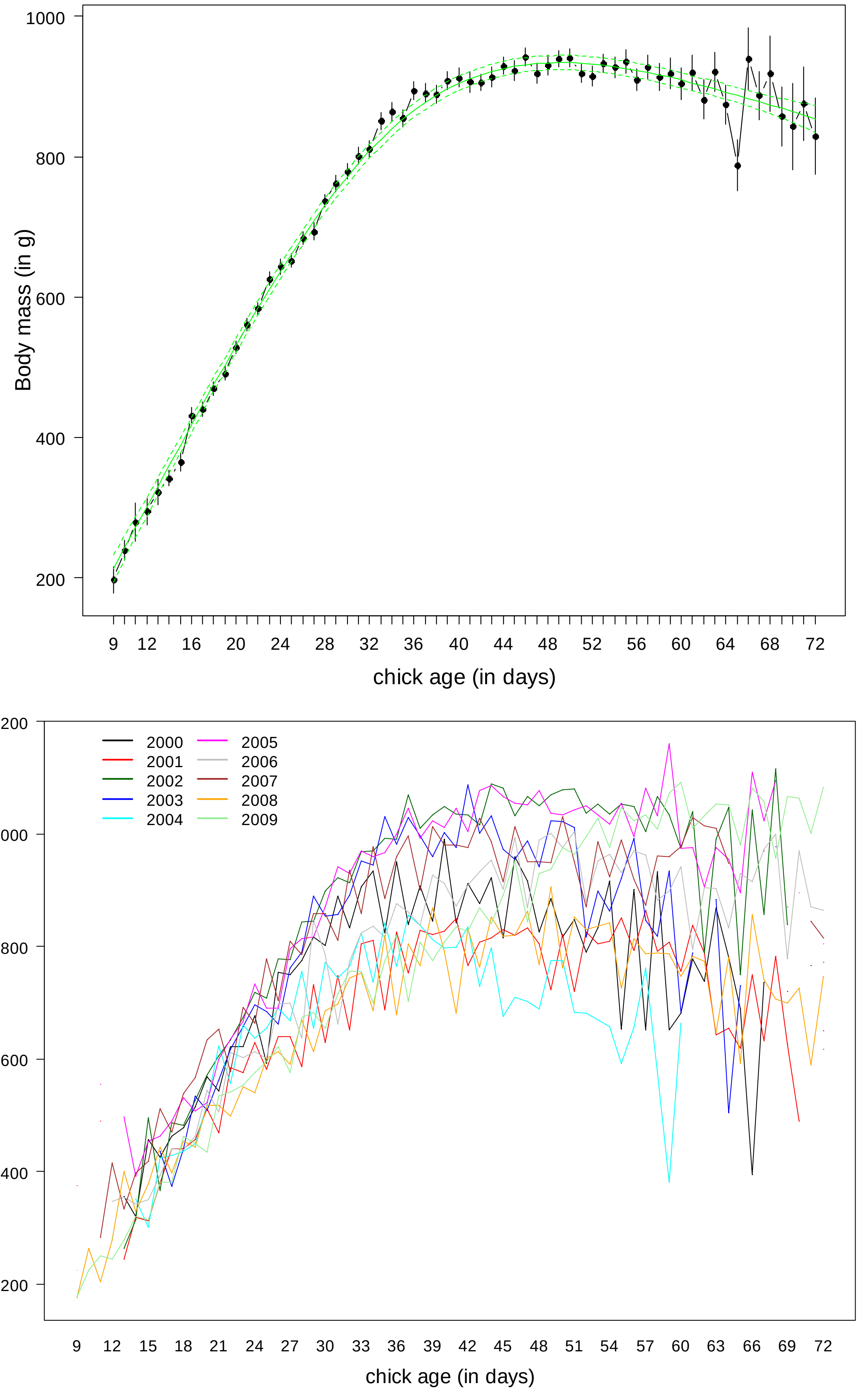


Figure VI - 3: *Chick growth in little penguins. A) average over the years, bars indicate standard errors and green line the general additive model fitted. B) growth for each year of the study.*

Sea Surface Temperature

Sea surface temperature was obtained from the US National Oceanic & Atmospheric Administration website (http://www.esrl.noaa.gov). The data are derivate from optimum interpolation analysis (NOAA OI SST V2) which uses in situ and satellite SST's plus SST's simulated by sea-ice cover (Reynolds *et al.* 2002). Data were produced monthly on a one-degree grid and averaged for an area between 38° and 40° S and 143° and 145° E (see details in Cullen *et al.* 2009).

Stats

All statistics were computed using R 2.9.0 statistical program (R Development Core Team 2009). When data were longitudinal because individual penguins were recorded over multiple times (for instance for chick growth or chick reserves), data were modeled using a maximum of likelihood mixed model approach (lme4 package, Bates & Maechler 2009). Generalized linear mixed models (GLMM) were computed with the chicks as random effects, enabling us to account for repeated measures. To investigate the influence of different parameters (*e.g.,* age of the chicks) on a variable, such as body mass or specific body mass loss, fitted models were selected through a stepwise procedure by using Akaike's Information Criterion (AIC). To assess the significance of each factor and the interactions within the best models we examine p-values calculated using analysis of variance chi-square tests to compare models with and without the factor.

When using means over several individuals, we used linear model (LM) or generalized linear model (GLM) to assess the relationship between parameters. In these cases, P-values and adjusted R^2 are given as indication of both the significance of the parameter and the deviance explained by the model. Correlation tests were also used to check correlations between different parameters.

In order to determine whether the distribution of dead chicks per week was uniform, we calculated P-values bootstrapped over 1000 simulations, *i.e.* we drew n (n corresponding to the number of weeks) integers following a Poisson distribution of mean equal to the mean number of dead per week 1000 times. Then we calculated P-value as the probability of the standard error associated with our real distribution to be higher than this of simulated distributions.

Finally, we investigated autocorrelation within time-series of weekly chick growth by using the acf function in R. Correlation between values that appeared significant in the graph were then assessed with correlation tests.

Results

Effect of SST/SOI on BS

Breeding success index was affected by SST averaged on the usual breeding period (*i.e.* from September to January) (LM: $P = 0.003$; $R^2 = 0.25$, $n = 30$ years; Figure VI - 4). SOI during the breeding period did not influence breeding success (LM: $P = 0.28$, $n = 30$ years).

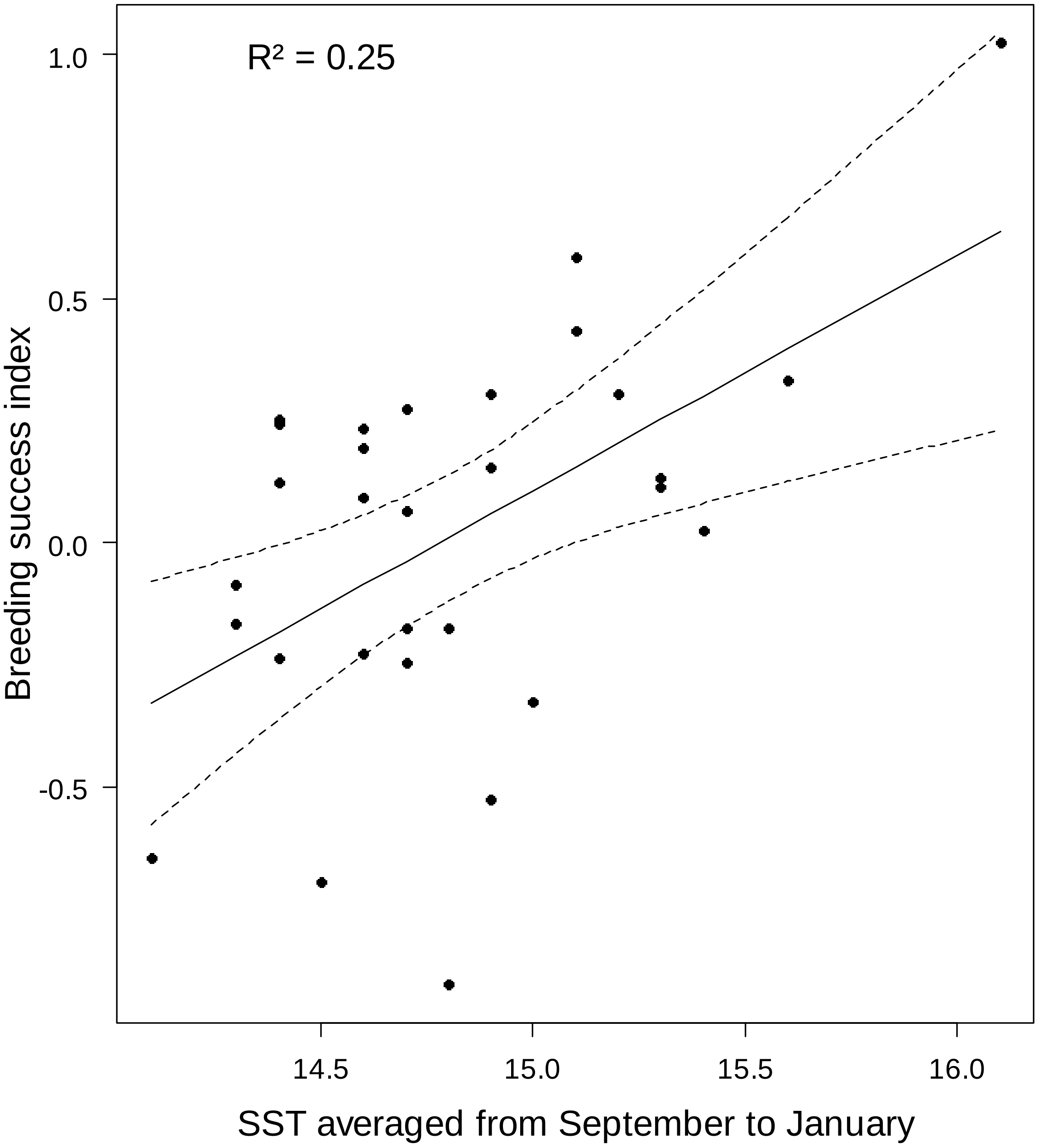


Figure VI - 4: *Breeding success index according to Sea Surface Temperature averaged on the breeding season for 1981-2010.*

Decomposition of Breeding in three stages

Breeding success varied according to years (GLMM: χ^2-test compared to null model: χ^2 = 143.3, P < 0.001; Figure VI - 5). All three stage successes (hatching, guard and post-guard success) also varied according to years (GLMM: χ^2-tests compared to null model: all P < 0.001; Figure VI - 5). Additionally, the success of each of these three phases were independent from each other (correlation tests: hatching and guard success: P = 0.07 and post-guard success with hatching and guard success: P = 0.66 and P = 0.81 respectively). Both hatching and post-guard success affected breeding success (GLM: P = 0.003 and P = 0.002 respectively). Guard success however did not affect significantly breeding success (P = 0.14).

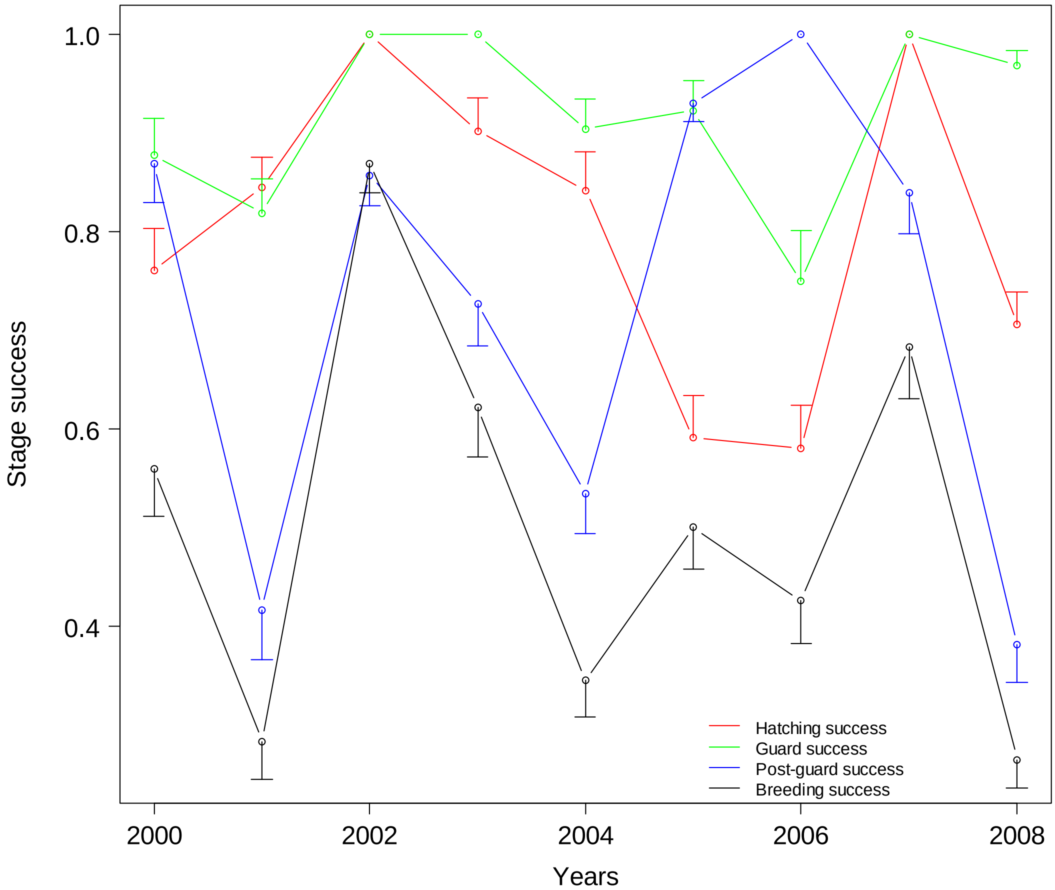


***Figure VI - 5:** Breeding success and the success of the three breeding stages according to years. Bars represent standard errors.*

Chick reserves

Chicks of 1995 and 1996, weighed twice a day, have been used to study how reserves got depleted. Chicks lost an average of 0.57% of their mass per hour during the day following a feeding event (range: [0.02%; 2.02%], n = 1910, N = 78). This rate was independent from the year (LMM: χ^2 test with null model: P = 0.62, n = 1910, N = 78) and increased linearly with chick age (LMM: χ^2 test with null model: P < 0.001, n = 1910, N = 78; the means per age are represented Figure VI - 6 along with the curves corresponding to a GLM computed on means: both P < 0.001, $R^2 = 0.69$). Older chicks thus lost less body mass per hour relatively to their body mass.

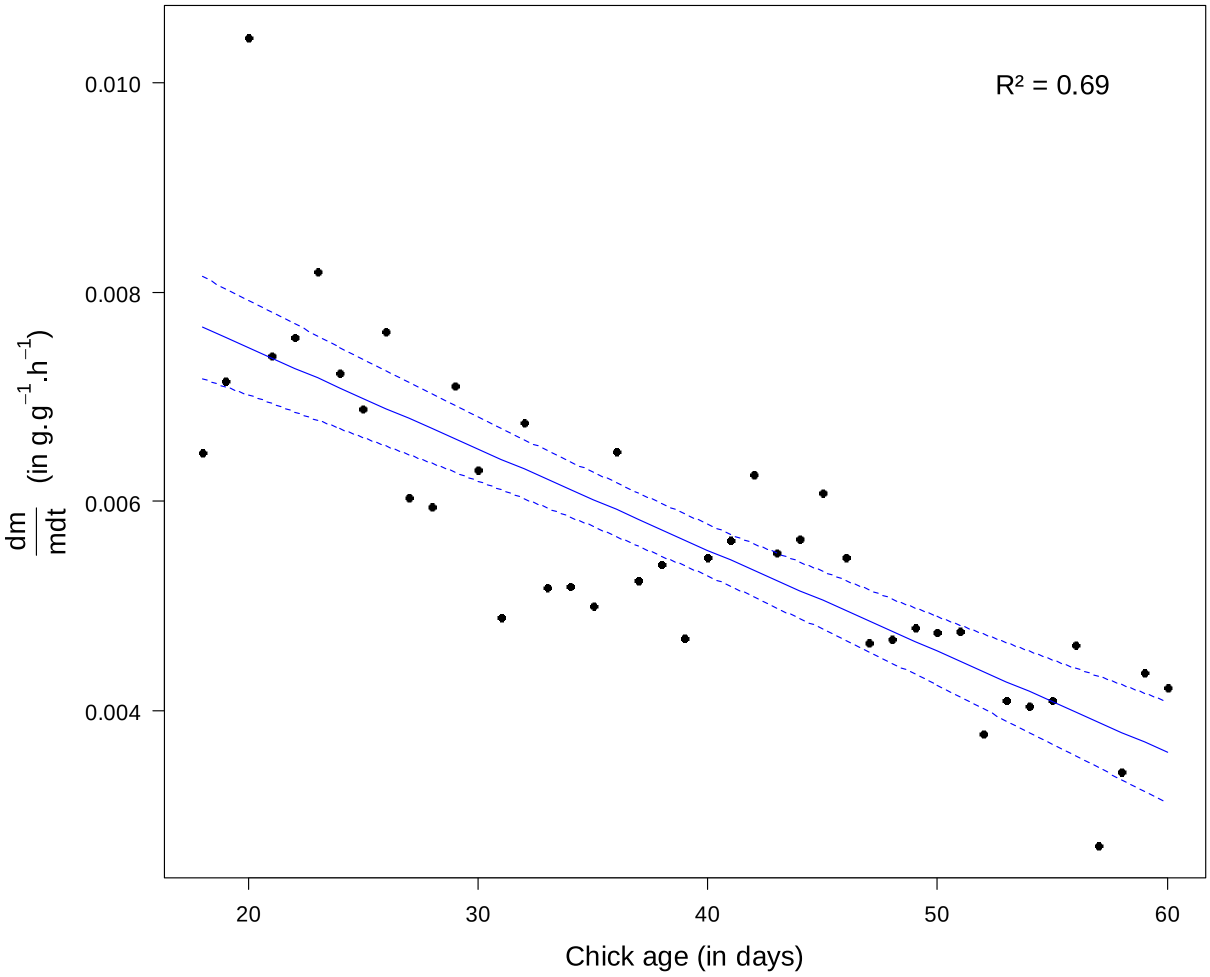


Figure VI - 6: *Specific body mass loss per hour of chicks according to their age.*
This body mass loss was estimated using two measurements one in the morning and one in the evening separated by 11 hours, given that the chick was fed the night before, some 10 hours before the first weighing.

Further, focusing on birds that fasted for a few days, specific body mass loss depended on a day/night variable (Figure VI - 7), chicks losing more mass at night (GLMM: χ^2 test with null model: P < 0.001, n = 39, N = 20). Additionally, we found a significant decrease in the specific body mass loss between the first day and the following ones (Wilcoxon tests: all P < 0.001) and a stabilization of specific body mass loss after (Figure VI - 7, Wilcoxon tests: all P > 0.09). Similarly, we found a decrease in night-time specific body mass loss between night 2 and the following ones (Wilcoxon tests: all P < 0.001) and a stabilization after night two (Wilcoxon test: P = 0.37; Figure VI - 7).

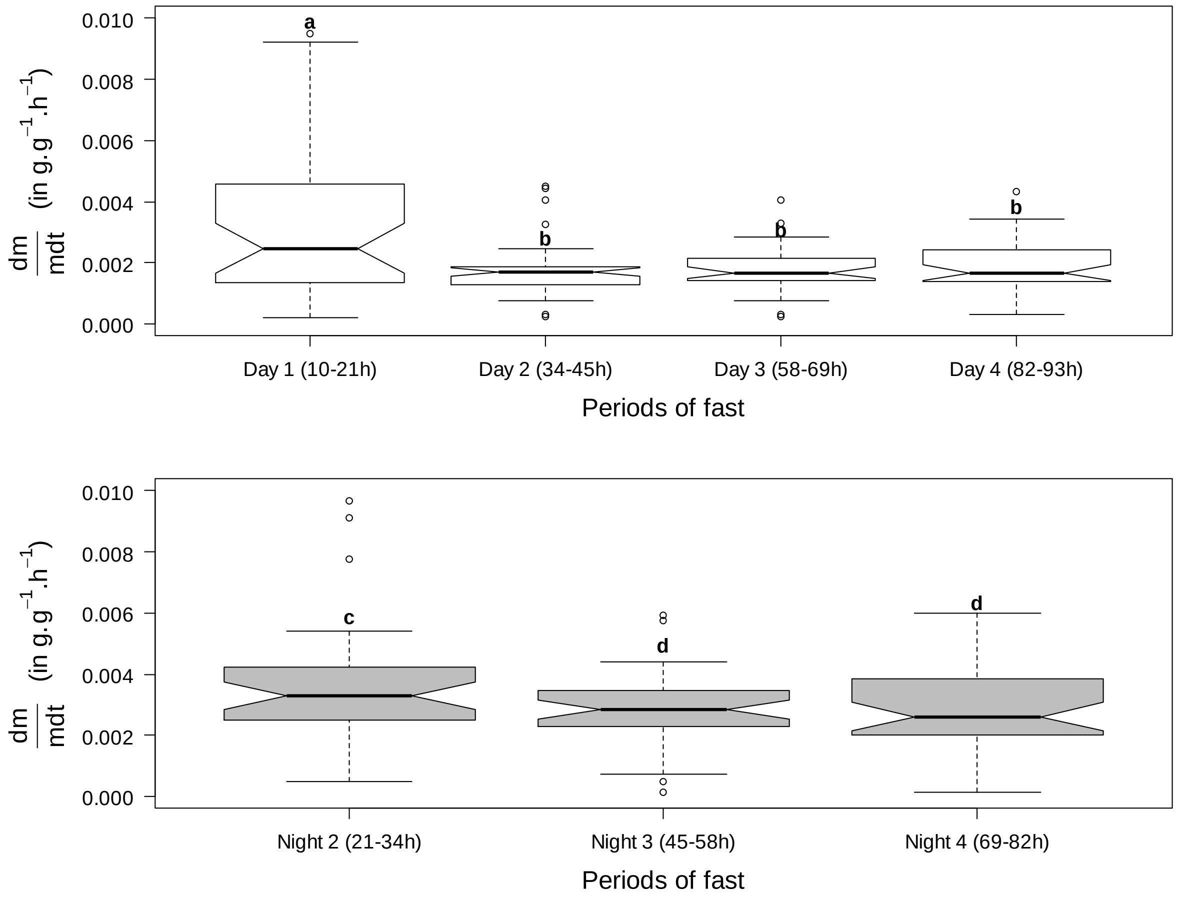


***Figure VI - 7:** Specific body mass loss of little penguin chicks along fasting.*
Boxes not sharing superscript letters are significantly different. In grey are represented nights, while we represented day-time in white. Chicks were fed during night 1, some 10 hours before the beginning of day 1.

Chick growth and mortality in post-guard

The standard error associated with the number of dead chicks per week was especially high, meaning that chick mortality was concentrated on particular weeks (bootstrap on standard errors over 1000 simulations of a Poisson distribution along 177 weeks with a mean equal to 1.42, *i.e.* the mean number of dead chicks per week along the whole study period: $P < 0.001$; Figure VI - 8). Indeed, we can observe in Figure VI - 8 several weeks without any dead chicks but also some weeks on which more than 10 chicks died (range: 0-19 dead chicks per week). This concentration of mortality held true for most of the years when investigated separately except for 3 years in which chick mortality did not go over 3 chicks per week (2003, 2005, 2006; see stats from bootstraps on Figure VI - 8).

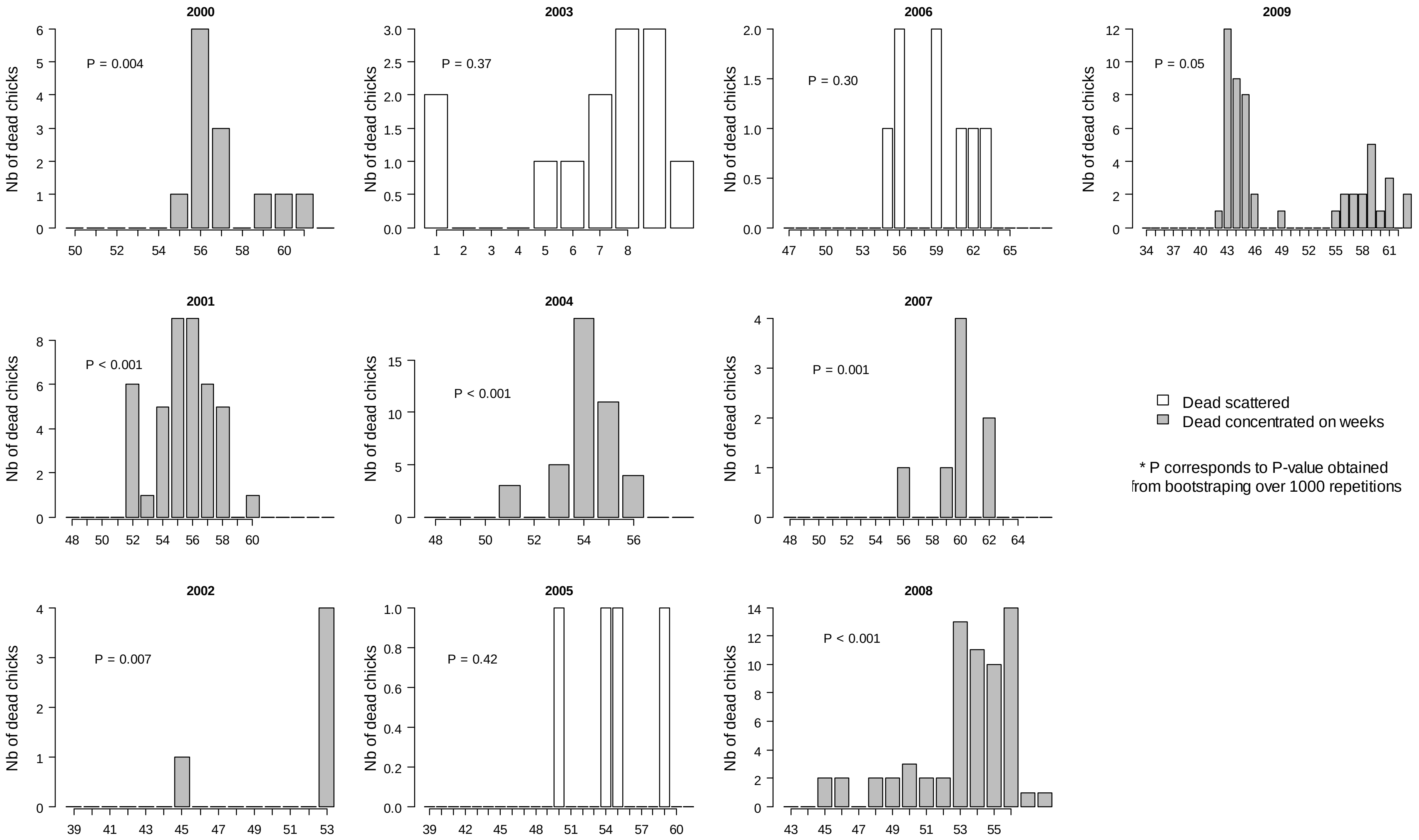
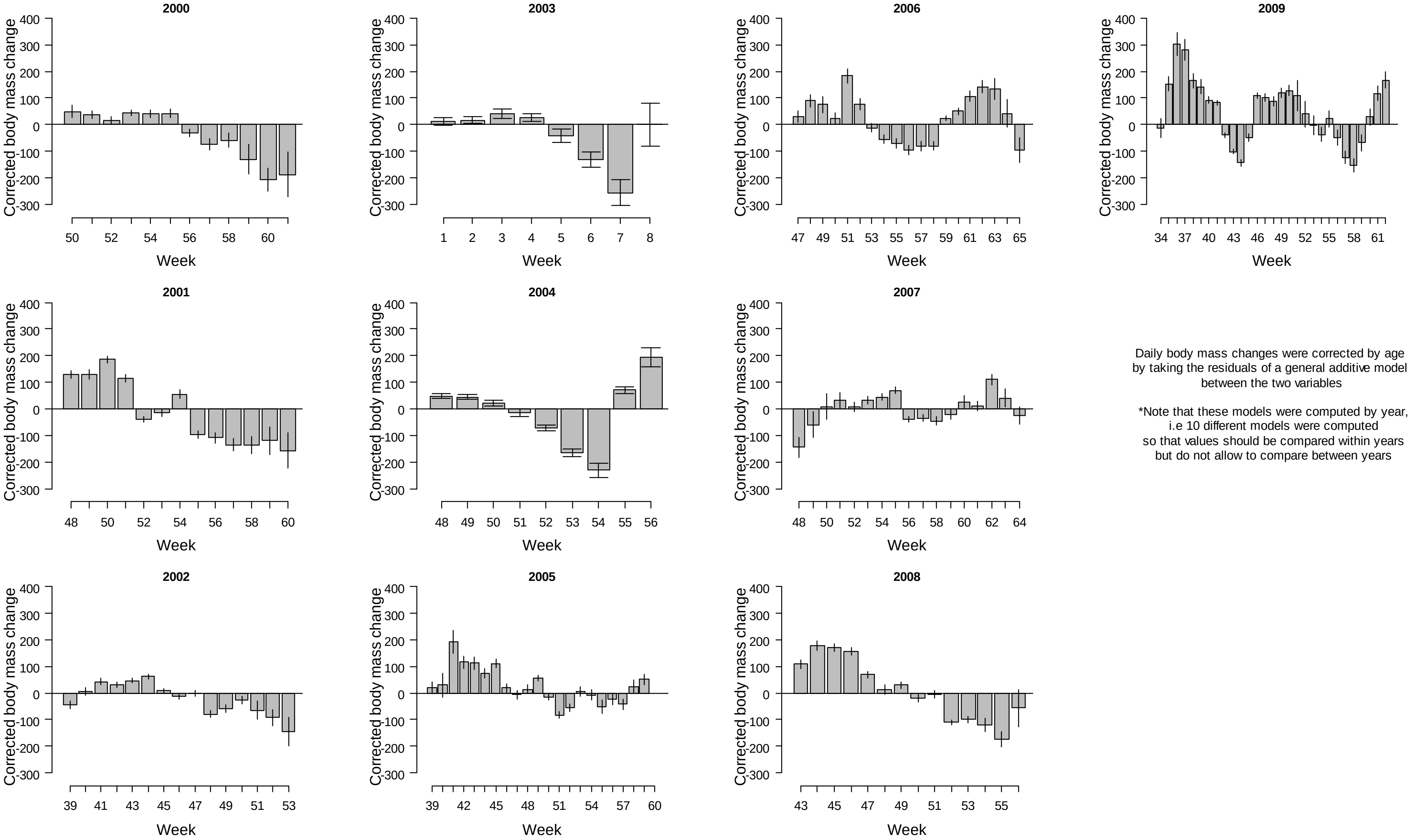


Figure VI - 8: *Number of chicks dead per week for each year of the study.*



Daily body mass changes were corrected by age
by taking the residuals of a general additive model
between the two variables

*Note that these models were computed by year,
i.e 10 different models were computed
so that values should be compared within years
but do not allow to compare between years

Figure VI - 9: *Corrected body mass changes per week for each of the study years.*

As chick growth (body mass) is not linear, we investigated mean chick growth per calendar week corrected by chick age (see Methods). Positive values correspond to weeks, in which body mass gain is above average for that chick age. Conversely, negative values correspond to weeks during which body mass gain was below average (note that this does not mean that chicks lost body mass). Corrected chick growth varied between positive and negative values during the 10 years of study (Figure VI - 9). Yet, it did not vary completely randomly, as corrected chick growth was autocorrelated with both lags 1 and 2 that were significant (autocorrelation function: Lag 1: $\rho = 0.72$, $P < 0.001$; Lag 2: $\rho = 0.40$, $P < 0.001$); *i.e.* the growth in a given week was correlated with growth the 2 weeks before. The autocorrelation function was different according to years: in three years growth was not autocorrelated at all (2003, 2004, 2007), in four others, only the correlation with a lag of 1 week was significant (2001, 2002, 2006, 2009) and in the three last years, we observed a significant correlation with both lags of 1 and 2 weeks (2000, 2005, 2008).

Weekly chick survival (ratio of dead chicks over number of chicks existing in this week) was significantly affected by weekly growth rates (LM: $P < 0.001$, $R^2 = 0.21$, $n = 177$ weeks). It was also significantly affected by previous weekly growth rates (lag = 1 week: LM: $P < 0.001$, $R^2 = 0.15$, $n = 176$, lag = 2 weeks: LM: $P < 0.001$, $R^2 = 0.09$, $n = 175$). However, weekly growth rates were auto-correlated. In order to remove this correlation, we used the residuals of weekly growth rates with a lag on weekly growth rates. Weekly survival was not explained by these residuals (LMs: 1-week lag: $P = 0.39$, $n = 176$; 2-week lag: $P = 0.13$, $n = 175$).

Finally, the average age at death of the monitored chicks was 50 days (range [8d - 84d]). Focusing on chicks that died older than 50 days (more than half of the chicks studied), we observed that they exhibited lower body mass all along the growth period than chicks that later fledged (Figure VI - 10; GLMM: $P < 0.001$, $n = 9156$, $N = 650$).

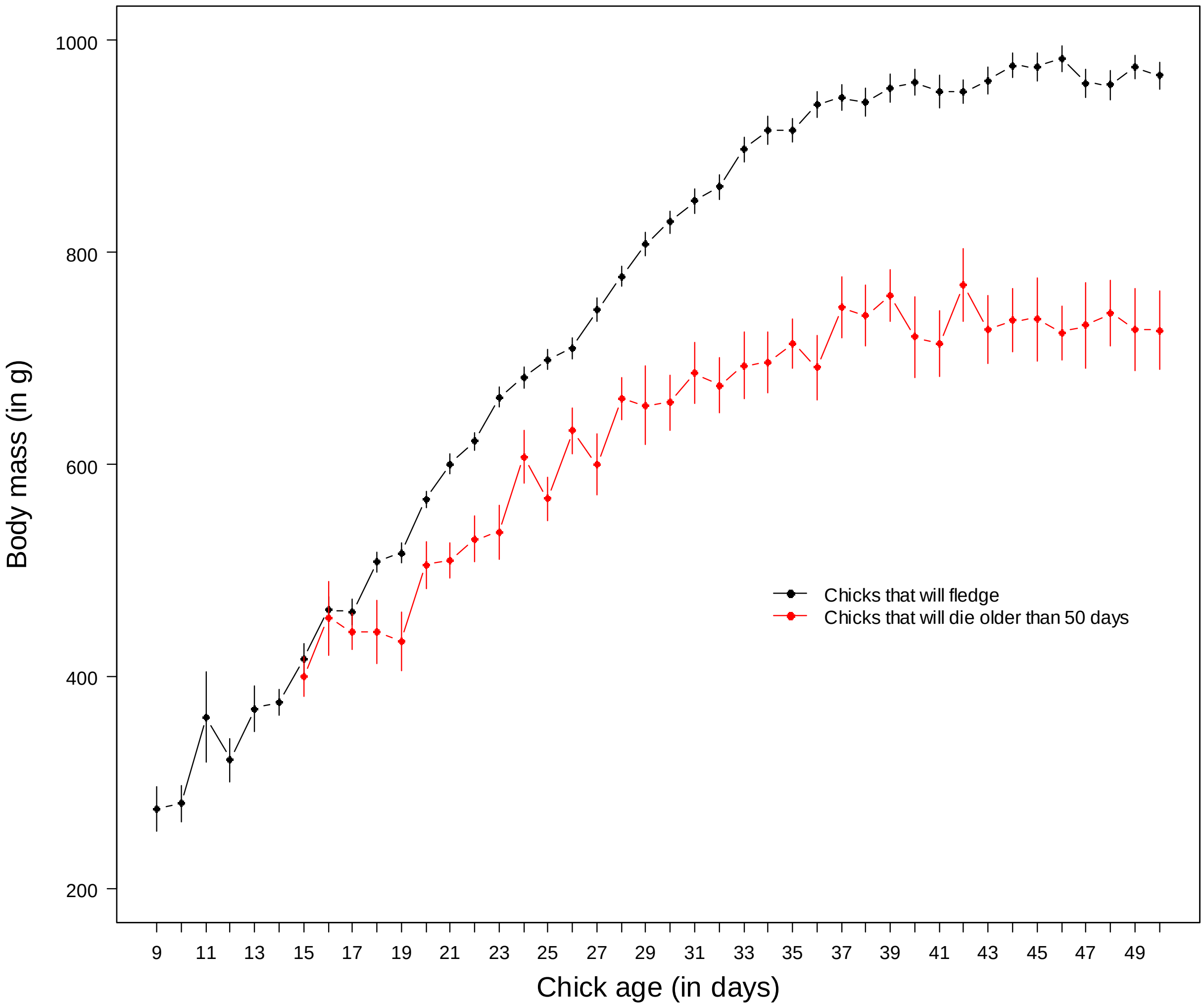


Figure VI - 10: *Chick growth (inferred by mean body mass according to age) for chicks that will fledge (in black) and chicks that will die older than 50 days (in red).*

Means are presented for age at which more than 10 measurements were taken. Bars represent standard errors.

Discussion

Over a 30-year period, breeding success in little penguins was significantly correlated with a composite of seasonal mean of Sea Surface Temperature (SST). This could appear surprising in the light of previous results, which showed no correlation between monthly SST and breeding success during the months of breeding on slightly longer time series (Cullen *et al.* 2009). Breeding in little penguins may be divided in three consecutive stages of incubation, guard and post-guard and breeding success is thus a combination of the successes of each of these stages. Here we found that these three successes were not correlated between each other, meaning that a year of high hatching success may well turn into a nightmare for breeding little penguins. Therefore, we suggest that monthly values are not representative of the whole breeding period conditions and are inappropriate to investigate the effect of climate on breeding in little penguins. Similarly to Hallett and colleagues' findings (Hallett *et al.* 2004), our results highlight the need to study climate effect using parameters encompassing the whole ecological period. However, this does usually not allow to understand the underlying mechanisms through which climate acts. Therefore, we focused our study on a very fine temporal scale (the week) to see which climate parameters could be relevant according to the ecology of the species. Our results showed that breeding success was more sensitive to hatching and post-guard success than guard success, the latter which did not significantly affect breeding success along our 10 years. Guard corresponds to the shortest period (about 2-3 weeks, Chiaradia & Nisbet 2006) of the cycle and is usually associated with a low mortality of the chicks. During this period, one parent stays with its chicks while the other goes out at sea to forage for less than a day. Longer trips are rarely observed in this period, which ensures frequent food for the chicks. Incubation and post-guard are associated with longer and more variable foraging trip duration (Kato *et al.* 2008, Saraux *et al.* 2011d), so that the effect of environmental conditions on chicks should be more apparent on these two periods. Yet, as egg death is hard to determine in little penguins (eggs can be deserted for up to 7 days and still be viable if incubation resumes, Chiaradia 1999), we focused on the post-guard period, for which we could obtain exact dates of death. In this period, we found that chick deaths were concentrated on some weeks rather than being equally distributed between the different weeks of the period. This indicates that post-guard success results from a combination of good and bad weeks. For instance in 2004, 19 chicks died in the same week, 30 if you consider the two consecutive weeks, transforming the relatively good post-guard success until then of 0.91 into a poor post-guard success of 0.58 in only two weeks. This suggests that investigating the effect of environmental conditions on different breeding stages separately may not even be a small enough scale. Such mortality and dependency to punctual environmental conditions could be explained by the lack of chick reserves. As long-lived species, little penguins exhibit a slow growth (Stearns 1976). Yet, this species is relatively small and metabolic rate should therefore be relatively important (Schmidt-Nielsen 1984). This is especially true for young chicks as we observed in this study: due to their lower size, they exhibit a higher specific body mass loss than older chicks. Young chicks should thus be able to fast for shorter periods than older chicks and be more sensitive to punctual changes in the environment. But even for older chicks, reserves can be depleted very rapidly. Here, specific body mass loss of fasting chicks showed a significant decrease during the second night of the fast (21-34h of fasting) and then became stable. Specific body mass loss is often used as a proxy to determine the three fasting phases (*e.g.* Cherel & Le Maho 1985; Cherel *et al.* 1987). Briefly, phase I is a short period characterized by high specific body mass loss that rapidly decreases until they reach a low value that will keep constant during phase II. Finally, the critical phase III is reached when lipids are depleted and the animal has to switch towards protein utilization to fuel its metabolism resulting in an increase of specific body mass loss. Our results thus indicate that the beginning of phase II for little penguin chicks occurs after only about 1 day of fasting. We could not determine entry in phase III here, though investigating the data per fasting event; we detected increases of specific body mass loss at the end of our monitoring (*i.e.* after 4 days) in 8 cases out of 39, which could possibly signal for a transition towards the critical phase III. Further studies on chick fasting based on specific body mass loss but also metabolite concentration such as uric acid, would help to understand the average duration of phase II (Le Maho *et al.* 1981; Cherel *et al.* 1988). Yet, our purpose here was not to fully understand fasting mechanisms in little penguins but rather to get the general idea of how long the reserves could allow chicks not to be fed before entering a critical phase. Our results suggest that little penguin chick condition could strongly vary in only a few days. This seems to be confirmed by the correlation between weekly survival and weekly body mass changes (after correction by age). We expected weeks of high number of death to occur after weeks of negative body mass changes. Yet, surprisingly, we found a correlation between these two variables without any lag, suggesting that harsh conditions affect chicks so rapidly that they could die in a week time. An interesting result is that chicks that died had a lower body mass than chicks that then fledged (once controlled for age) not only right before their death but all along the whole post-guard. Altogether, we suggest that unfavourable conditions may result in chick death rapidly through depleted reserves and that this should happen mostly in the case of chicks of already lower quality.

Our results show that breeding success results on a combination of several factors that could each be modified by changes occurring at very small temporal scale. A single week could be fatal to post-guard success for instance. Therefore, we suggest that the effect of climate on breeding parameters should be investigated at the smallest resolution possible and not through average conditions on the whole breeding cycle. Here, we also found that average chick growth per week was strongly autocorrelated, with both lags 1 and 2 significant. This indicates either that environmental conditions change on a time scale longer than the week (rather a couple of weeks or 3 weeks) or that consequences of environmental conditions are buffered along a few weeks. Foraging efficiency and consequently breeding success have been shown to be affected by the stratification of water and the seasonal presence of thermoclines in foraging zone of little penguins (Ropert-Coudert *et al.* 2009). This study showed that in a year of strong winds and stormy conditions, water was mixed which resulted on the disappearance of the thermocline. In years when water is not stratified penguin prey may disperse widely while thermal stratification seems to create physical barriers that the prey cannot cross, easing penguin purchase. Further study at a finer scale showed that thermocline can be present but disperse within weeks which also affected foraging efficiency (Pelletier *et al.* submitted). In case of extreme event such as storms, water stratification could be mixed very rapidly, which could well explain our differences in weekly chick growth and survival within years.

Acknowledgments

This study was based on data collected over several years, we are very grateful for all field assistance from several volunteers and students, in particular J. Yorke, T. Daniel, P. Fallow, M. Salton, P. Wasiak and R. Long and the staff of the Phillip Island Nature Park: in particular P. Dann, L. Renwick and all field rangers. The Automated Penguin Monitoring System was kindly provided by the Australian Antarctic Division, with particular thanks to Knowles Kerry and Kym Newbery as well as all engineers involved in the R&D of this system. We are also thankful for grants received from BHP-Billiton, Penguin Foundation and the Australian Academy of Science. NOAA_OI_SST_V2 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/

III. Breeding in Adélie penguins

Inter-annual variability in breeding success and fledgling quality of Adélie penguins: a result of sea-ice extent?

(Box 1)

Claire Saraux, Yvon Le Maho

Unpublished work

Adélie penguins breed during the austral summer: from October to March, between the retreat of the sea-ice and the next sea freeze-up. The timing of sea-ice retreat is supposed to affect phytoplankton bloom intensity and timing (Moline *et al.* 2008) and consequently through cascade effects the rest of the food chain. In a recent study conducted on the same pairs in two seasons with contrasting sea-ice timing, Beaulieu and colleagues (2009a) showed that body mass, nutritional stress and reproductive success of Adélie penguins did not change between these two seasons, though foraging trip duration and metabolite levels varied. Based on stable isotope analyses, the authors suggest that Adélie penguins manage to switch towards different prey species depending on the timing of sea-ice retreat and that the advancement in sea-ice retreat observed around Antarctica should not be a threat to Adélie penguins. Yet, breeding success of a population also results from the number of breeders in the population. Further, breeding success is not the only parameter to be considered. About 75% of the variance in the number of recruits in breeding bird populations is not accounted for by differences in number of fledglings and results from the period between fledging and sexual maturity (median $r^2 = 0.25$ for studies reviewed in Newton 1989). Some fledging traits such as body size or condition have indeed been found to be correlated with postfledging survival (Dann 1988; Korpimäki & Lagerström 1988; Owen & Black 1989; Harris *et al.* 1991; Schmutz 1993). Here, we investigate over five consecutive seasons the number of breeders, of fledglings and fledging quality (as inferred by body size and mass) in Adélie penguins.

Methods

Penguin monitoring

Our study was conducted in Dumont d'urville (66°40'S, 140°01'E), Adélie Land, Antarctica during five consecutive austral summers from 2006/2007 to 2010/2011. Monitoring of the whole ANTAVIA sub-colony was done through counts of adults and chicks on pictures taken from similar spots and at similar dates each year. The number of breeding pairs was thus assessed by counts of incubating males in their first shift in November.

From summer 2006/2007 to summer 2010/2011, all the chicks of the 'ANTAVIA sub-colony', which were still alive in February during their moult, a few days before fledging, were implanted with a passive transponder tag under the skin of their left leg, without any other external mark (*i.e.* 5 cohorts and 1255 chicks). In November 2006, 50 breeding adults were also fitted with a transponder tag. Transponder tags weigh 0.8 g and have no known adverse effects (Froget *et al.* 1998, Nicolaus *et al.* 2009). Upon tagging, all birds were weighed with a precision scale (± 10 g). Except for the chicks tagged on the first year (February 2007), flipper and beak lengths of all other birds were measured. Birds were handled directly in the colony (a few meters away from the nests), the manipulation lasting less than five minutes on average.

The number of chicks per pair (cpp) was calculated as the number of fledglings divided by the number of breeding pairs at the beginning of the season.

Structural size and body condition indices

We constructed a structural size index for all birds whose beak and flipper had been measured (*i.e.* birds of cohorts 2008-2011). As beak and flipper lengths were correlated (Spearman's rank correlation, $P<0.001$, $r=0.33$, $n=1060$), we used a principal component analysis to establish an index of structural size (SSI) as follows: SSI = PC1 = 0.14 * Beak + 0.99 * Flipper. The first principal component (PC1) between these two parameters explained 90% of the variation.

Body mass can be associated with differences in nutritional status as well as structural size. Differences between body mass and structural size thus constitute a good index of nutritional state (Schulte-Hostedde *et al.* 2005). Body condition was then defined as the residuals of a regression of body mass on SSI (Schulte-Hostedde *et al.* 2005; $R^2=0.18$, $P<0.001$).

Sea-ice extent and distance to open water

Distance to open water was calculated as the shortest straight-line distance between the colony and the nearest open water on cloud-free satellite images (resolution: 1 km; see Beaulieu *et al.* 2009a). These distances were calculated by Météo France several times a month (the number of times depending on the actual changes in sea-ice observed on these images). We used these distances averaged on the whole breeding season, *i.e.* from early October to late March each year. In the five years considered in the present study, open water always reached the colony before the end of the breeding season (in January at maximum). The average distance over the breeding cycle was very highly correlated to the timing of sea-ice retreat (as inferred by the first date of open water reaching the colony; $P = 0.01$, $r = 0.94$) and consequently probably mostly driven by this phenomenon. But it also accounts for differences in sea-ice extent when sea-ice retreated at similar times.

Results

Breeding pairs

The number of breeders did almost not vary according to years except for 2007-2008 (263 pairs in November 2007 *vs.* 307 pairs in November 2010, *i.e.* a 17% increase; Figure VI - 11).

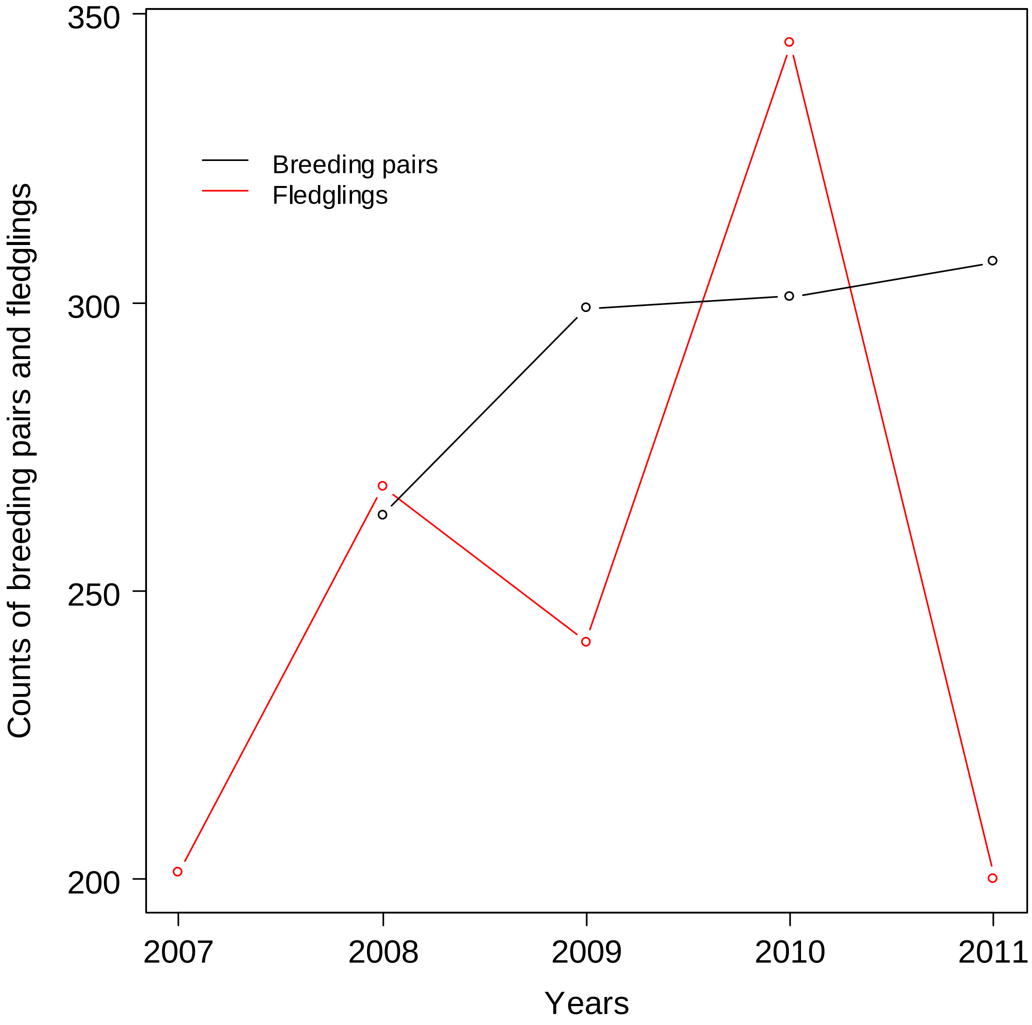


Figure VI - 11: *Number of breeding pairs and fledglings according to year.*
Note that Year 2007 corresponds to the breeding season 2006-2007,

Fledged chicks

The number of fledglings in the studied sub-colony varied from 200 in 2010 to 345 in 2009 (Figure VI - 11), *i.e.* a difference of 43% between the two consecutive seasons. The number of fledglings was not explained by the number of breeders (LM: t = -0.20; P = 0.86).

Structural size of fledged chicks did not vary according to year (Wilcoxon tests: all P > 0.26; Figure VI - 12). This held true when looking at flipper size only (Wilcoxon tests: all P

> 0.50). Beak size however did slightly vary in between years (from 30.0 ± 0.2 in 2009 and 2010 to 32.1 ± 0.1 in 2008; F-test between model with years and null model: P < 0.001).

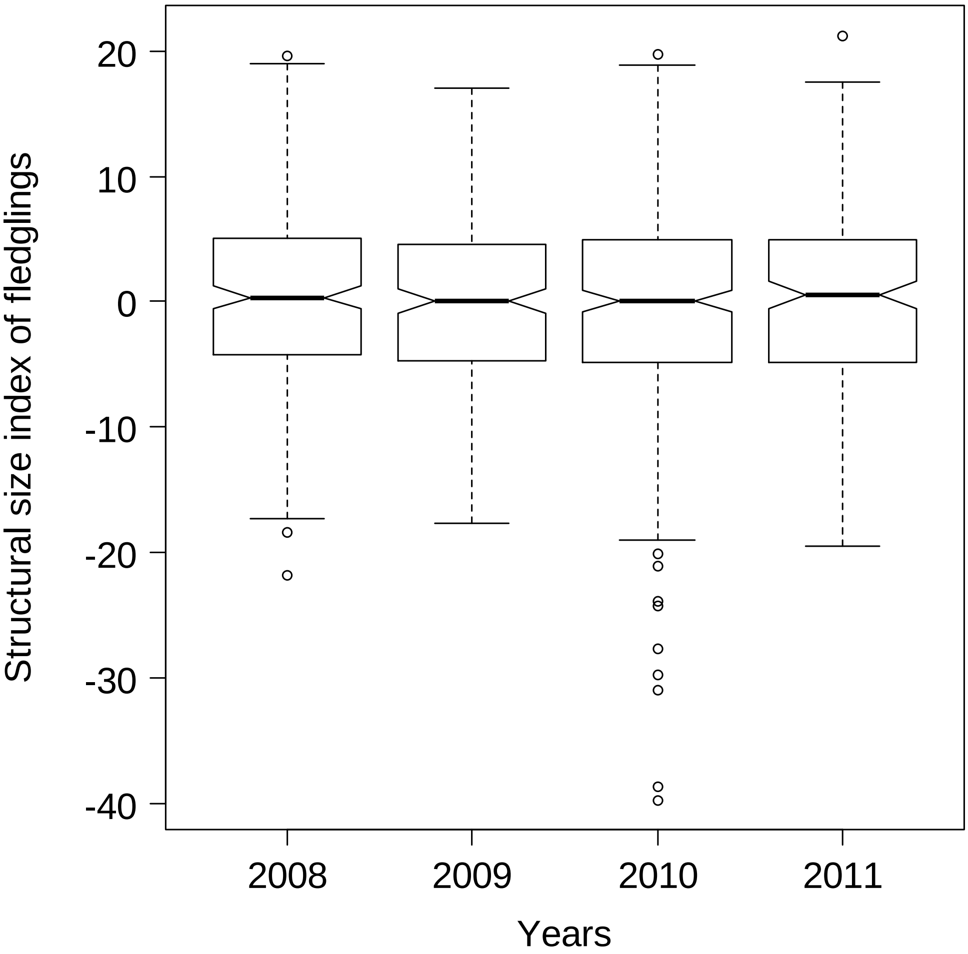


Figure VI - 12: *Structural size of chicks fledged in 4 different years.*

Body mass and body condition of fledglings varied according to year (both F-tests with null model: P< 0.001; Figure VI - 13). However, average body mass of fledglings was not correlated with the yearly number of chicks fledged (correlation test: P =0.44; Figure VI - 13). Body size was not correlated with the number of chicks fledged either (correlation test: P = 0.80). Finally, body condition and body size were not correlated to the number of chicks per pair (*i.e.,* number of fledglings divided by number of breeding pairs at the beginning of the season: correlation tests: both P > 0.50).

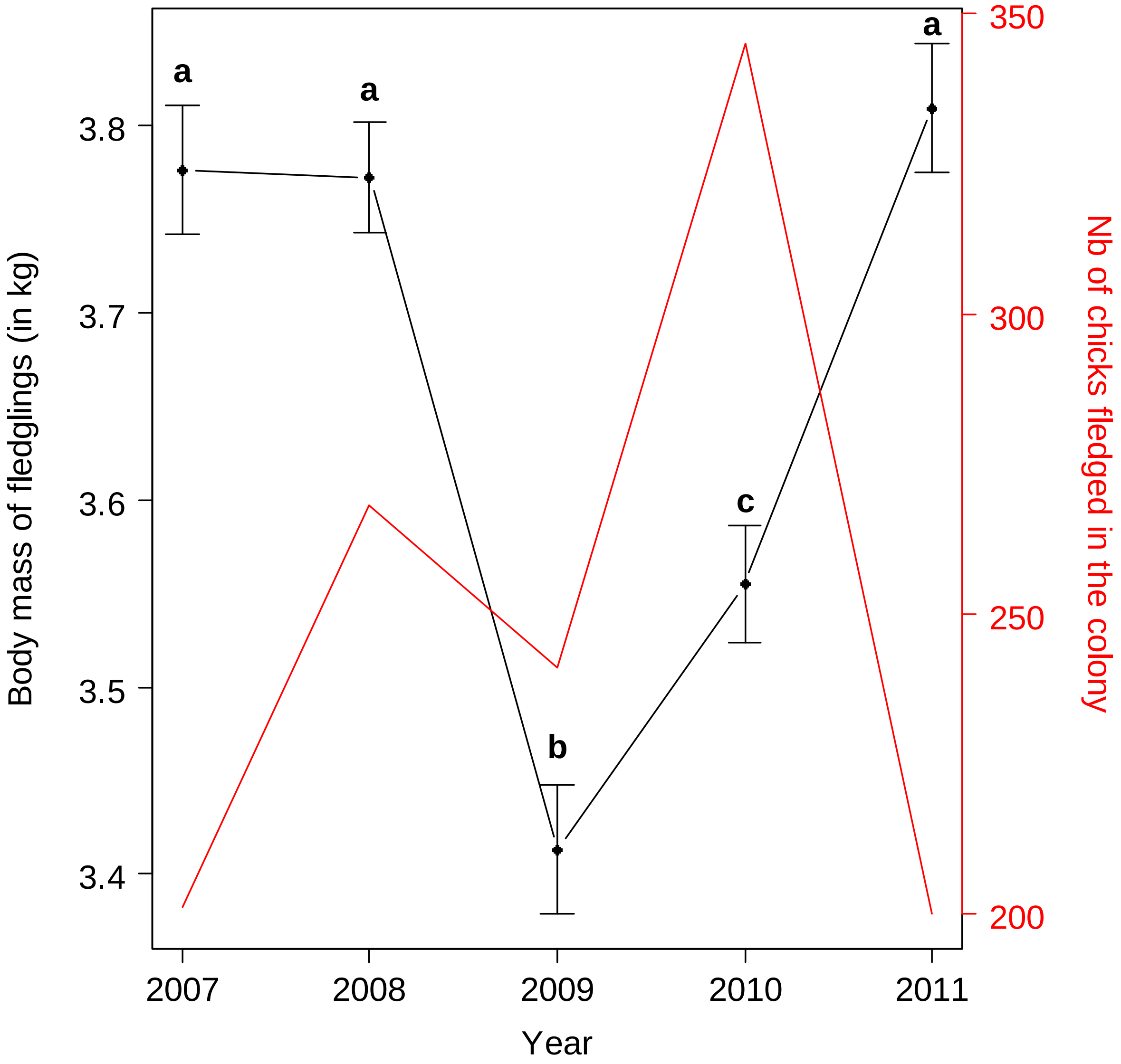


Figure VI - 13: *Body mass of fledglings and number of chicks fledged per year.*
Bars indicate standard errors. Average body masses sharing no superscript are significantly different (Wilcoxon test with Bonferroni adjustment).

Sea-ice extent

The number of fledglings in the colony was positively affected by the average distance to open water (LM: t = 4.80, P = 0.02, R^2 = 0.85; Figure VI - 14), *i.e.* the further away open water was, the higher was the number of chicks that fledged. Average distance to open water did not affect structural size and body condition of fledglings (LMs: P > 0.30).

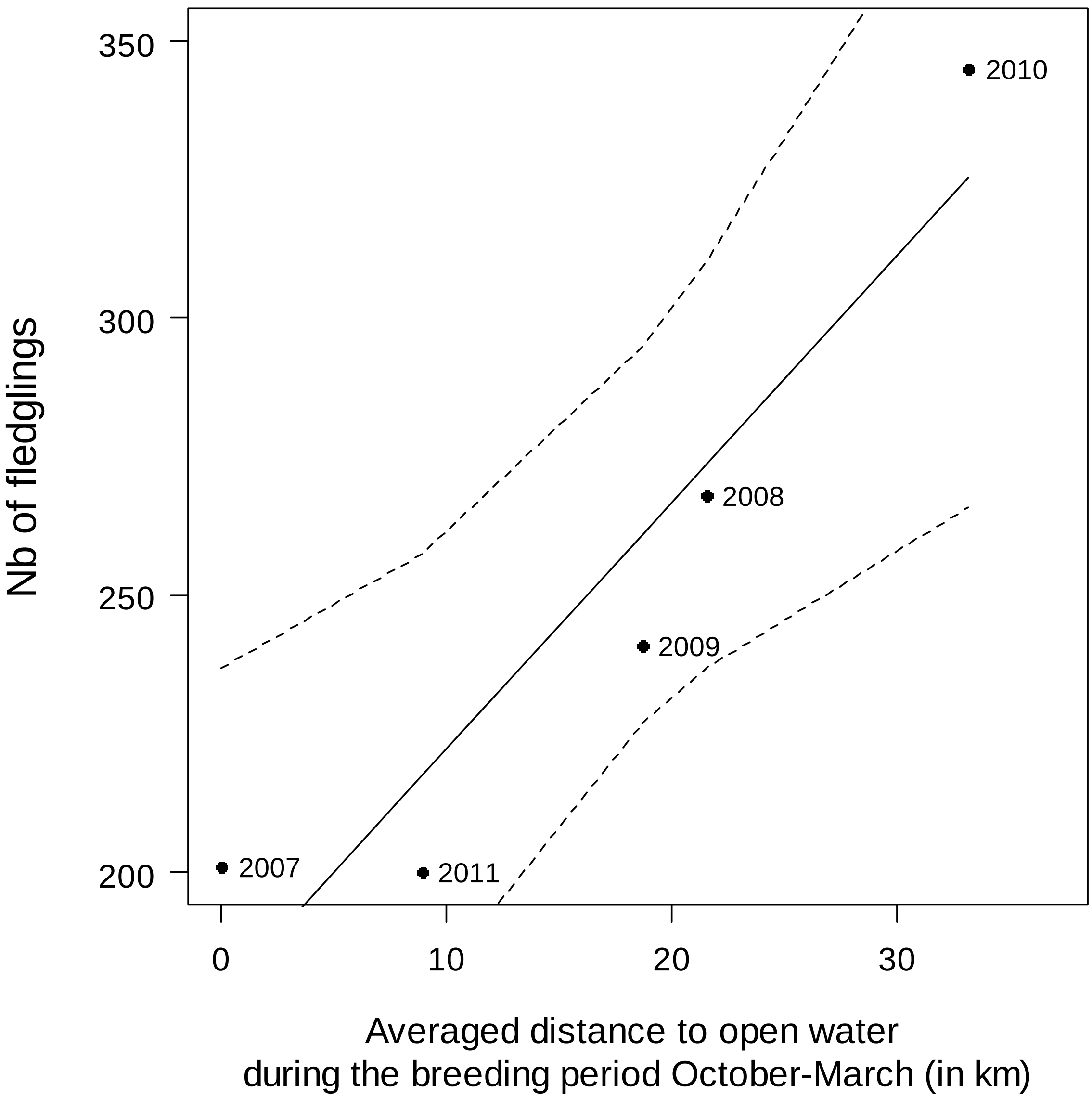


Figure VI - 14: *Number of fledglings in the colony according to the average distance to open water during the breeding period.*

Discussion

Here, we showed an important inter-annual variability in the number of chicks fledged in the colony (from 200 to 345). Yet, this variability did not result from changes in the number of breeding pairs at the beginning of the season, which were relatively small. Therefore, we suggest that the number of fledglings in a colony depends mostly on the actual capacity of the parents to raise their chicks. Additionally, we found no difference in structural size of fledglings between the four years of our study but significant differences of body mass and body condition. This interesting result suggests that chicks may devote a different part of their energy to growth depending on the year in order to compensate for different provisioning rates from their parents and to reach similar body size at fledging (*i.e.* the constraints on size may be so high that investment into growth is incompressible). As energy is limited, individuals have to compromise between their different biological functions (Stearns 1989, Stearns 1992) and differences in investment into growth should result in differences in energetic reserves and body condition.

Secondly, we showed that sea-ice extent had an effect on the number of chicks fledged in the colony. Interestingly, Beaulieu and colleagues (2009a) showed that an early sea-ice retreat did not affect the plankton bloom timing but increased the primary production (higher Chlorophyll concentration). However, an early sea-ice retreat had previously been shown to be associated with the dominance of small pico-nanophytoplankton on large microphytoplankton (Montes-Hugo *et al.* 2008) and as the grazing efficiency of krill decreases with the size of plankton (Moline *et al.* 2004), the authors suggest that an early sea-ice retreat could lead to a lower krill recruitment despite a higher abundance of plankton. This seemed to be confirmed by a lower proportion of krill in their diet in the year of early sea-ice retreat (Beaulieu *et al.* 2009a). Surprisingly this had no consequences on nutritional stress and breeding success of the parents. The authors advocate that penguins were able to switch towards other prey species, mainly fish. Here, we found a significant decrease of the number of fledglings in years of average low distances between the colony and open water, *i.e.* in years of early sea-ice retreat. Yet, both studies were conducted on the same island and in similar years. Our study encompassed five years versus two for the study of Beaulieu and colleagues (2009a) but these two years (2006-2007 and 2007-2008) were included in our study and resulted in a 33% increase of fledglings in between the two years. Rather than contradicting results of this previous study, we think that our results complement them interestingly. Beaulieu and colleagues showed that individuals could switch towards other prey in years of early sea-ice retreat without important consequences (despite a significant decrease of metabolite indicating a less energetic input of this modified diet). Yet, this was conducted only on 22 individuals chosen through selective sampling since only birds that were present the two years and remained in a stable pair were included in the study. Selected birds may then have been the most competitive ones that were able to respond to different levels of food availability. Here, we suggest that inter-individual variation could play an important role in the ability to respond to different foraging conditions so that the effect of sea-ice retreat would be visible only on less competitive birds. At the scale of the colony the breeding success consequently decreases but at the pair scale, breeding success could well be maintained. This may also explain why we found no relation between body mass and the number of fledglings in the colony. Indeed, in years of unfavourable conditions, parents that manage to fledge their chicks should be the most competitive ones, which were able to adapt their foraging so that chick provisioning should not be too much affected. By opposition, in years of favourable conditions, most parents (competitive or not) manage to produce chicks so that chicks of variable quality should be produced. Further, late sea-ice retreat led to longer foraging trips (Beaulieu *et al.* 2009a) so that feeding frequency should be smaller in years of late sea-ice retreat, which could also affect fledgling body mass.

Sea-ice retreat thus seems to importantly affect breeding success of Adélie penguins through krill recruitment (Trivelpiece *et al.* 2011). But it is important to note that some individuals (probably the most competitive ones) are able to adapt to these variable conditions (Beaulieu *et al.* 2009), suggesting that phenotypic plasticity may help Adélie penguins to face future sea-ice extent changes.

Acknowledgements:

We are very grateful to Météo France for data on distances between the colony and open water. We thank Michaël Beaulieu for his advice and suggestions on these analyses and Manuelle Cottin for her explanations on sea-ice data. We also thank David Lazin, Anne-Mathilde Thierry, François Cathy, Marion Debin, Françoise Amelineau for their help in field work. This work was supported by the French Polar Institute (Institut Paul-Emile Victor), the Centre National de la Recherche Scientifique through the program ‘‘Zone Atelier des recherches sur l’Environnement Antarctique et Subantarctique.’’

IV. Variability of sex-ratio in king penguins

Inter-annual variability of sex-ratio in king penguins: a result of climate?

(Article 6)

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Magali Beaugey, Yvon Le Maho, Céline Le Bohec

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[*] Both authors contributed in equal part to the work

In preparation

Optimal sex allocation depends on the species under consideration and of its mating system. For instance, it is expected that in a monogamous species, the optimal sex allocation of parents should be equal towards males and females. However, sex ratio at a given time results not only from parental sex allocation but also from sex-specific mortality. In this study, we monitored the sex ratio at fledging in a monogamous colonial species, the king penguin, over 10 consecutive years, and investigated the potential causes of its variations. Over more than 4000 penguins, we found the overall sex ratio at fledging to be slightly biased towards males (51.6%), which might be the result of higher benefits to produce males owing to potentially higher adult male survival. This bias was however not observed in every year and the inter-annual variability in the sex ratio at fledging was important (from 44.4% of males in 2000 to 58.3% in 2002). These variations were correlated to local oceanographic conditions (Sea Surface Temperature *SST*, and distance between the colony and the Polar Front, an important feeding ground for king penguins), as an increase in both parameters led to an increase in sex-ratio bias (deviation from the balanced sex ratio: 50%). Additionally, we found the sex ratio of fledglings to be highly correlated to the difference in body condition between the two sexes, suggesting that it might be less costly to produce females (smaller sex) when environmental conditions are limiting. In contrast, neither changes in the social environment (population density in the colony) nor timing in the breeding season appeared to affect the sex ratio at fledging. Finally, investigating sex-ratio changes through early life-history stages, sex ratio tended to return to equilibrium at the first breeding attempt compared to the sex ratio at chick-fledging and to the sex ratio upon first return to their natal colony. In the context of ocean warming, an increase in sex-ratio bias, which consequently might lead to a deviation from the optimal operational sex ratio[21] (OSR), may importantly affect population dynamics and viability.

Because it directly affects the proportion of individuals that may reproduce (Keyfitz & Flieger 1971; Caswell 2001) within a population, adult sex ratio[22] (ASR) is a key factor in population dynamics. If the consequences of ASR have become a central issue in the demographic study of human populations (with growing concerns about the

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[21] OPERATIONAL SEX RATIO: sex ratio of the reproductive population (Mayr 1939)

[22] ADULT SEX RATIO: proportion of males and females that composed the population in breeding age

highly male-biased ASR in India or China; Tuljapurkar *et al.* 1995), it remains commonly accepted by ecologists that fluctuations in ASR should be strongly regulated around an optimum in wild populations (Petterson *et al.* 2004). However, fluctuation in sex-dependent mortality (especially juvenile mortality) before recruitment into the breeding population, or variations in parental sexual allocation before and after birth may strongly affect ASR, and consequently Operational Sex Ratio (OSR), *i.e.* the sex ratio of the breeding population (Mayr 1939).

According to the life-history theory, individuals should be selected as to maximise the propagation of their genes (Stearns 1992). Parental allocation could therefore depend on the sex of the offspring if the two sexes exhibit different benefits in future propagation of the genes. Sexual allocation (reviewed in great extent in Frank 1990) should thus differ according to mating systems and parental investment strategies (reviewed in Hasselquist & Kempenaers 2002). For instance, in polygynous species, males are at a greater reproductive advantage than females, as they typically mate with several partners and produce more offspring than females on average (*e.g.* one male Weddel seal, *Leptonychotes weddellii*, fertilizes 5 females on average, Cornet & Jouventin 1980). The overproduction of one sex with high fitness benefits may then be favoured and selected in some species (Emlen *et al.* 1986; Lessels & Avery 1987). On the contrary, the reproductive potential of a population should be maximal when ASR is balanced (Fisher 1930; Nunney 1999). Fisher (1930) showed that an equal number of males and females is the only stable equilibrium and that sex allocation should thus be equal between the sexes. Indeed, if a bias is introduced in the ASR, benefits associated with the production of the outnumbered sex would be higher, which would tend to bring it back to equilibrium (‘frequency-dependent selection hypothesis’, Allen & Clarke 1984). Further, in order to maximize its fitness, a monogamous population should have as many breeders as possible in balanced proportions (otherwise one sex may be limiting, and part of the population would not participate to its overall growth).

However, individuals should maximize their lifetime reproductive success and not the success of a single reproductive event (Pilz *et al.* 2003). Sex allocation thus does not only result from the immediate benefits associated with the propagation of their genes but rather from the trade-off between these benefits and the costs associated with raising offspring, which could affect future breeding events (Williams 1966; Stearns 1989). If benefits are equal between sexes such as in monogamous species, the sex ratio should be biased towards the less costly sex. For instance, in dimorphic species, one sex is bigger than the other and costs associated with the production of this sex should be high, resulting in a bias towards the smaller sex.

Biased sex ratio could then be adaptive (Hamilton 1967; Trivers & Willard 1973; Charnov 1982). This might also result from the fact that benefits of producing males or females on inclusive fitness (sum of direct fitness through its own offspring and indirect fitness through kin) could be different. For instance, kin cooperation and competition often occur between individuals of the same sex (*e.g.* Viblanc *et al.* 2010) resulting in a biased sex ratio towards the sex in which competition is lower or cooperation higher (Hamilton 1967). Similarly, the resource competition model (Clark 1978; generalisation of Hamilton's model) highlights an additional cost of producing offspring for mothers, which will then have to compete with them to feed (or to find mates or reproductive sites). Consequently, mothers should favour the sex that disperses most.

In the light of the above theories, sex allocation should be affected by any parameter able to modify benefits or costs of producing male or female offspring. First, sex ratio may depend on exogenous parameters and the environment in which parents live. Social environment may affect secondary sex ratio[23]. For instance, an increase in population density tends to decrease male production in red deers, *Cervus elaphus*, due to nutritional stress during pregnancy that may affect foetal loss (Kruuk *et al.* 1999). Sex ratio can also vary according to breeding timing, as has for instance been shown in some bird species, where it is affected by laying dates (*e.g.* in great tit, *Parus major*, Lessels *et al.* 1996; and in collared flycatcher, *Ficedula albicollis*, Rosivall *et al.* 2004). Likewise, in the painted turtle (*Chrysemys picta*), early clutches are composed essentially by males, and late clutches by females (while at similar temperatures), which seems to be the result of different steroid quantities allocated in egg yolk depending on the breeding period (Bowden *et al.* 2000). Finally, climate can also influence secondary sex ratio. In the pond slider, *Trachemys scripta*, sex is highly correlated with temperatures that impact steroid quantities in egg yolk (Crews 1996). In addition, changes in atmospheric and oceanographic conditions (and the associated nutritional stress) have been shown to affect breeding females in elephant seals, *Mirounga angustirostris* (Crocker *et al.* 2006), and the current warming trend of the North Pacific is associated with a bias towards males in this species. The latter result might be explained by intra-sexual competition for resources, as males and females forage in separate areas (Lee &

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[23] SECONDARY SEX-RATIO : sex ratio at birth or hatching in birds

Sydeman 2009). Thus under unfavourable conditions, females would tend to produce males that will not compete with them later (Lee & Sydeman 2009). Similarly, Hewison & Gaillard (1996) gave support to the resource competition model by showing a male-biased sex ratio under unfavourable conditions in roe deer that might be explained by a higher dispersal of juvenile males than females.

Finally, other mechanisms can act on sex-ratio at the individual level. Given that parental investment affects offspring reproductive performances, Trivers & Willard's hypothesis (1973) states that, in polygamous species, mothers of good quality or in good condition at a given reproduction should invest more in the sex exhibiting the most variable breeding success. Indeed, under this assumption, an individual of the sex of most variable breeding success raised by good quality parents should exhibit high reproductive performances compared to other individuals of its sex, while an individual of the least variable sex (even if of greater quality than average) should have similar reproductive performances than other individuals of its sex. Ungulates are ideal models to test such an hypothesis because of their polygyny and dimorphism.Yet, though some evidences have been presented to support it, the Trivers & Willard's hypothesis remains equivocal (see Hewison & Gaillard 1999 for a review). For instance, in some less dimorphic species, such as roe deer *Capreolus capreolus*, mothers in good condition have been observed to actively discriminate in favour of females (Hewison *et al.* 2005). Thus, sex ratio may depend on parents' quality, condition, age or experience. For instance, in mountain goats, *Oreamnos americanus*, older females produce more sons (Côté & Festa-Bianchet 2001). This is in accordance with Trivers & Willard's hypothesis, given that older females are of better 'quality' through increased experience and social rank.

In this study, we investigate sex-ratio variability in a colonial yearly monogamous species, the king penguin, *Aptenodytes patagonicus*. In the context of the current climate change and the effects of warming on king penguin life-history traits (Le Bohec *et al.* 2008a), investigations of sex-ratio variability in this species is crucial to understand how and to which extent sex ratio biases might affect population breeding success and its dynamics over time. Sex-dependent mortality between hatching and fledging has been observed in a variety of species (reviewed in Clutton-Brock 1986). King penguins take more than a year to fledge their single chick (Barrat 1976) and breeding is associated with a high energetic cost mainly due to central-place forager constraints. Yet, as long-lived species, king penguins should favour their own survival rather than their reproduction, and the conflict between these two functions should be especially strong under harsh environmental conditions. Thus, environmental conditions during chick rearing should play an important role in chick survival and sex ratio may change between hatching and fledging. As a consequence, our study mostly focused on sex ratio at fledging and investigated its inter-annual variability during 10 consecutive years over more than 4000 king penguins.

Methods

Sampling and sex determination

Our study was conducted in the king penguin colony of ‘La Grande Manchotière’, on Possession Island, Crozet Archipelago (46°25’S, 51°45’E). As chick sex determination is difficult through visual cues in this species, sex was determined through genetic analysis on DNA obtained from blood samples (method adapted from Griffiths *et al.* 1998). Briefly, this technique relies on polymerase chain reaction (PCR) amplification of one intron from the sex chromosome CHD1 gene, which in birds differs in size between the Z and W chromosomes (Griffiths *et al.* 1998, Fridolfsson & Ellegren 1999). Females were characterized by displaying both a W-specific fragment and a Z-specific fragment, while males showed only the shorter Z-fragment.

From 2000 to 2009, 3787 10-month old chicks from the long-term monitored sub-colony ‘ANTAVIA’ were randomly captured in three different sub-areas during their moult, a few weeks before fledging, and implanted with passive transponder tags under the skin of their leg, without any other external mark. At that time, birds were also measured (flipper and beak), weighed and blood sampled before release.

The king penguin breeding cycle lasts more than 1 year (about 14 months on Crozet Archipelago; Barrat 1976; Weimerskirch *et al.* 1992; Descamps *et al.* 2002). Bird arrival at the colony therefore depends on the success and timing of the previous year’s breeding attempt and the laying period of king penguins extends for over four months, with two peak periods (Stonehouse 1960; Barrat 1976): one for ‘early breeders’ (before 1 January) and another one for ‘late breeders’ (after 1 January). In that context, in order to investigate a potential effect of laying period, 400 individuals divided in two equal groups of 200 early and 200 late chicks were captured as early as possible after hatching (between 1-week and 1-month old) every year since 2007. As mortality is very high during chick rearing, chicks were first marked temporarily with small external plastic pin tags (Floytag®) and surviving chicks were later transponded with passive tags according to the same protocol as the one above (tagging, blood sampling, morphological measurements and weighing). During these four years, a total of 626 penguins survived until fledging. However, sample sizes are strongly biased towards chicks hatched early as the success in late breeding is very low (Weimerskirch *et al.* 1992). The effect of laying period was also investigated between years, using the mean annual laying date of early breeders.

Finally, in the last year (2010), blood sampling was taken at the first capture (when marked with pin tags) in order to determine the sex ratio as close to hatching as possible and to monitor changes between sex ratio at hatching and at fledging. To limit the disturbance, only a few drops were laid on a filter paper (Whatman® 113g). Also, 35 additional chicks were sampled in 2009 right after hatching (as part of establishing the new protocol with filter paper).

Sex-ratio was defined as the proportion of males in the population (and is always given as %). Sex ratio bias was defined as the deviation from the balanced sex-ratio (*i.e.* 50%) and was thus calculated as the absolute difference between the proportion of males and 50%.

Structural size and body condition

For each bird, flipper and beak lengths were measured (Stonehouse 1960) at tagging. These two morphologic measurements are good descriptors of king penguin structural size and are highly repeatable measurements (Fahlman *et al.* 2006). As beak and flipper lengths were correlated (Spearman's rank correlation $_{n=4012}$, $P < 0.001$, $r = 0.31$), we used a principal component analysis to establish an index of structural size (SSI) as follows: SSI = PC1 = 0.26 * Beak + 0.97 * Flipper. The first principal component (PC1) between these two parameters explained 79% of the variation.

Body mass is highly variable in king penguins and can be associated with differences in nutritional status as well as structural size. Differences between body mass and structural size thus constitute a good index of nutritional state (Schulte-Hostedde *et al.* 2005). Body condition was then defined as the residuals of a regression of body mass on SSI (Schulte-Hostedde *et al.* 2005; $R^2 = 0.09$, $P < 0.001$).

King penguins exhibit a sexual size dimorphism, males being larger than females on average, though the two distributions intersect (Barrat 1976). This dimorphism was also observed in this study for beak length (+ 2.2%, $P < 0.001$), flipper length (+2.1%, $P < 0.001$) and body mass (+3.2%, $P < 0.001$).

Life-history of microtagged birds

The antennas buried under the usual and unique transit pathways in and out of the sub-colony allow for the continuous automatic collection of data on bird presence and movement (see Gendner *et al.* 2005). Such data gives information on individuals' life after fledging, especially on first returns to the colony (Saraux *et al.* 2011b), reproduction (Descamps *et al.* 2002) and age-specific survival and breeding performances (Le Bohec *et al.* in prep.). By monitoring the individuals from fledging, we are able to assess potential changes in sex ratio through different life stages. As king penguins mature slowly and attempt to breed for the first time at an average age of 6 years (Weimerskirch *et al.* 1992) and reproduce successfully for the first time at an even older age, we were able to investigate changes in sex ratio only between 3 different stages: fledging, first return to the colony and first reproductive attempt. Further, only the first 6 cohorts were used as penguins were too young in the others to have already attempted to breed.

Environmental descriptors

Environmental conditions have been shown to affect population dynamics at both local and global spatial scales (Stenseth *et al.* 2002). The use of 'weather packages' and large-scale climate indexes (see Stenseth & Mysterud 2005), such as the Southern Oscillation Index (SOI), are good candidates for explaining the effects of environmental variability on top-predators of the Southern Ocean, such as penguins (Le Bohec *et al.* 2008a). Negative SOI values indicate El-Niño events and are usually associated with warm temperatures in our study area, whereas positive values indicate La Niña events (Deser & Wallace 1987). Monthly SOI (calculated from the monthly fluctuation in the air pressure difference between Tahiti and Darwin) were obtained from the Australian Bureau of Meteorology.

Since changes in Sea Surface Temperature (SST) might impact the primary production and the food chain (Gregg *et al.* 2003), SST is frequently used as a local proxy of abundance and distribution of prey for king penguins (Le Bohec *et al.* 2008a; Saraux *et al.* 2001b). Monthly SST values (in °C) were obtained from the National Ocean and Atmospheric Administration. Data were averaged on a global area (46-60°S, 46-56°E) encompassing feeding areas both during summer (Polar Front, PF) and winter (Marginal Ice Zone, MIZ; Charassin & Bost 2001). The distance between the PF and the Possession Island was also estimated from SST data, as the PF is situated at the latitude at which SST reaches 4°C during summer (Park *et al.* 1993). These three environmental variables were averaged on two different periods. Indeed, conditions before the onset of breeding may affect parental body condition (McNamara & Houston 1996), and thus parental investment. Then, conditions during breeding should affect parents' foraging efficiency that, in turn, might impact chick growth and survival, and may consequently be a source of changes in sex ratio. Exact periods on which the parameters were averaged are specified for each result.

The breeding success of the colony (Le Bohec *et al.* in prep.) was also used as a proxy for the conditions endured during the rearing period. Years of high breeding success (such as 2002 or 2004) could thus be viewed as more favourable years, compared to years of lower breeding success.

Finally, social environment may also affect sex ratio through population density in some species. King penguins breed in dense colonies of thousands of pairs. Further, density varies according to the period (sharp increase from November to January) and may affect physiological state of parents (Viblanc *et al. in prep*). Thus, we built yearly density index of the colony to investigate its potential effect. We assessed density from counting of individuals on pictures taken in December (peak density of the breeding season) since 2007. We also built a second index based on the presence of the microtagged individuals, as the proportion of birds breeding in a given year among birds alive and in breeding age.

Statistics

All statistics were computed using R - 2.13.0. statistical environments (R development Core Team 2011). Data were analysed using a maximum of likelihood generalized linear model approach. Generalized linear models (GLM) were fitted with binomial distribution to explain sex ratio by environmental factors or laying period. The most appropriate model was selected using the Akaike information criterion (AIC). Linear models (LM) were also computed when only annual means were considered. Adjusted R^2 are indicated along with P-values.

In order to compare between years, we first checked for normality (Shapiro-wilk) and homoscedasticity between groups, and parametric (Student test) or non-parametric tests (Wilcoxon rank-sum test) were consequently used. Finally, to compare sex ratio between the three different life stages, we used a binomial test of proportion (prop.test). Variables were considered significant for $P<0.05$ and Bonferroni's correction was applied whenever multiple comparisons were tested (differences were thus considered significant for $P < \frac{0.05}{n}$ with n the number of comparisons done).

Results

Sex ratio at fledging and inter-annual variability

Over the 10-year study period, overall sex ratio at fledging was slightly biased towards males, *i.e.* a higher number of males fledge compared to females (1941 females *vs.* 2071 males; *i.e.* 48.38% *vs.* 51.62%; GLM $_{n=4012}$: z = 2.05, P = 0.04; upper-right panel on Figure VI - 15).

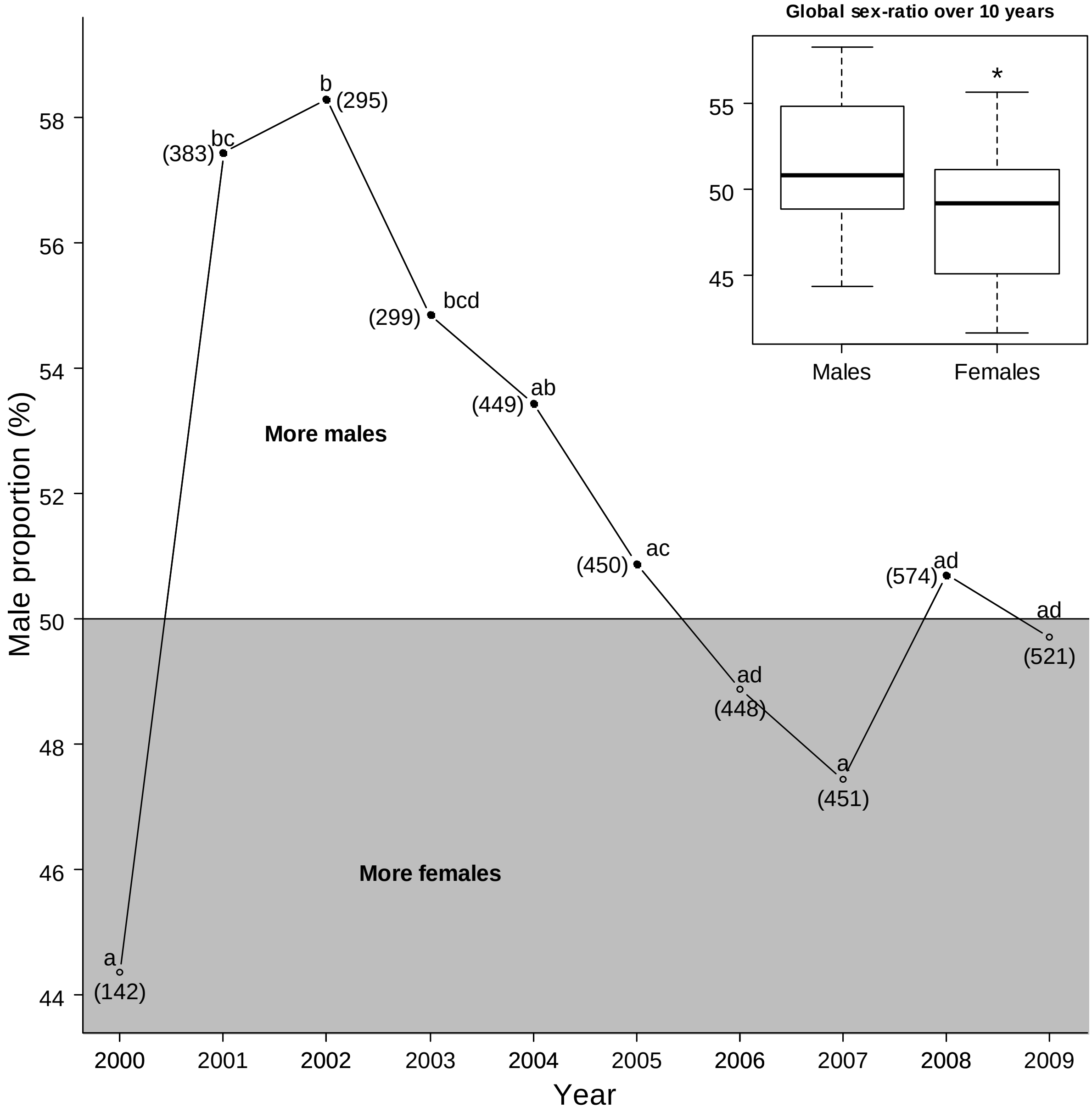

Figure VI - 15: *Overall sex ratio (i.e. proportion of fledging males) obtained over the period (upper-right panel) and per year.*

*The grey part (i.e. proportion of fledging males below 50%) corresponds to a sex ratio biased towards females, while the white part corresponds to a male biased sex ratio. * indicates a significant difference (i.e P < 0.05). Points sharing no common superscript are significantly different.*

Yet, sex ratio at fledging varied according to years (Pairwise tests given in Figure VI - 15), and the bias towards males was observed in 6 of the 10 study years. From 2000 to 2002, the proportion of males fledging increased significantly (from 44.37% to 58.31%; $GLM_{2000\text{-}2002,\ n = 437}$: z = 2.72, P = 0.006). Then this proportion of males decreased continuously from 2002 to 2007 (from 58.31% to 47.45%; $LM_{2002\text{-}2007,\ n = 6\ (2392\ \text{birds})}$: t = -15.76, P < 0.001; R^2 = 0.98). Finally, sex ratio at fledging was stable during the last 3 years from 2007 to 2009.

Effect of the timing in the breeding season: early vs. late breeders

At hatching, when pooling all individuals from 2009 (some 35 birds not represented Figure VI - 16) and 2010, we found no difference in sex ratio between early and late chicks ($GLM_{2009\text{-}2010,\ n = 454}$: z = -1.37; P = 0.17). When focusing specifically on year 2010, the proportion of males at hatching tended to be higher, though not significantly, in early chicks than in late chicks (57.95% *vs.* 48.66%; $GLM_{2010,\ n=419}$: z = -1.90, P = 0.06; Figure VI - 16).

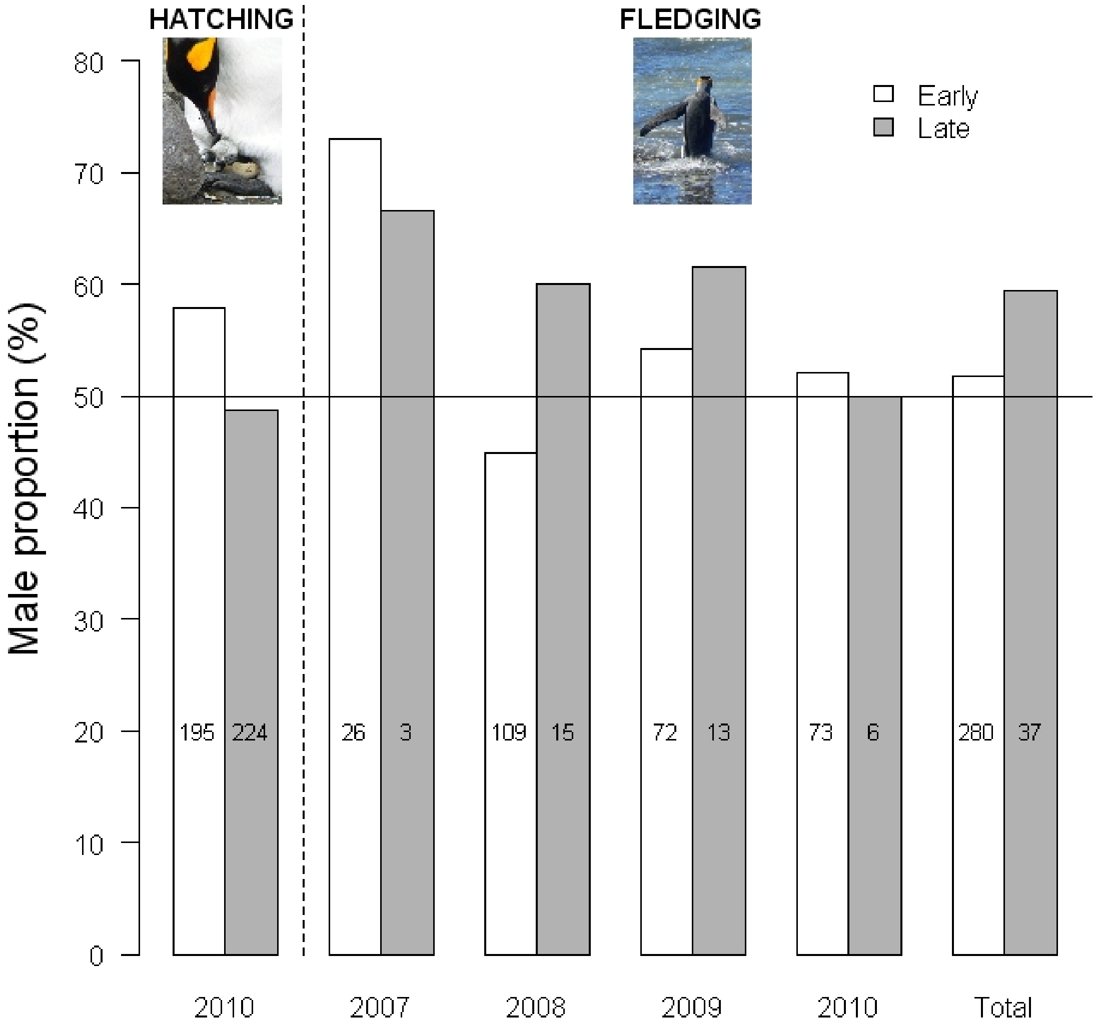

Figure VI - 16: *Sex ratio of chicks laid early (in white) and late (in grey) at hatching (for 2010) and at fledging for 2007-2010. Sample sizes are specified in the bars.*

From hatching to fledging, several chicks died and we investigated whether sex ratio could be modified. Sex ratio for early and late chicks did not vary between hatching and fledging when considering 2009 and 2010 chicks together (Proportion $\text{test}_{2009\text{-}2010,\ n = 214/79}$: P = 0.16 for early chicks; Proportion $\text{test}_{2009\text{-}2010,\ n = 240/13}$: P = 0.26 for late chicks), nor when considering 2010 chicks alone (decrease of 5.90% but Proportion $\text{test}_{2010,\ n = 195/73}$: P = 0.47 for early chicks; increase of 1.34% but Proportion $\text{test}_{2010,\ n = 224/6}$: P = 1 for late chicks; Figure VI - 16). However, due to very low breeding success of late breeders, our sample size at fledging for late breeders was very small.

Sex ratio at fledging of chicks hatched early or late in the season was determined from 2007 to 2010 (Figure VI - 16). Overall, the proportion of males seemed higher in late chicks than in early chicks (except for 2007 where only 3 late chicks succeeded in fledging), though this difference was not significant ($\text{GLM}_{2007\text{-}2010,\ n = 317}$: z = 0.88, P = 0.38). No difference was highlighted per year either ($\text{GLM}_{2007,\ n = 29}$: z = 0.23, P = 0.81; $\text{GLM}_{2008,\ n = 124}$: z = 1.08, P = 0.28; $\text{GLM}_{2009,\ n = 85}$: z = 0.49, P = 0.62; $\text{GLM}_{2010,\ n = 79}$: z = -0.097, P = 0.92).

Finally, mean annual laying date of the colony did not affect annual sex ratio at fledging ($\text{LM}_{2004\text{-}2009,\ n = 6}$: t = -0.20, P = 0.85).

Effect of climatic parameters

The Sea Surface Temperature (SST) did not affect directly the proportion of males fledged whatever the period on which it was averaged (LMs: P > 0.08). However, as shown in Figure VI - 17, the sex ratio at fledging seemed balanced at low SST (upper panel), while the bias increased at higher SST. The bias in sex ratio (deviation from the balanced sex ratio: 50%) at fledging increased with SST whatever the period considered, *i.e.* before laying ($\text{LM}_{\text{-6months}}$: t = 3.59, P = 0.007, R^2 = 0.57) or during the whole breeding cycle ($\text{LM}_{\text{breeding}}$: t = 5.90, P < 0.001, R^2 = 0.79).

Similar results were obtained when considering the distance to the Polar Front. PF distance did not affect sex ratio (LMs: P > 0.43), but positively affected sex-ratio bias ($\text{LM}_{\text{summer}}$: t = 4.30, P = 0.003, R^2 = 0.66).

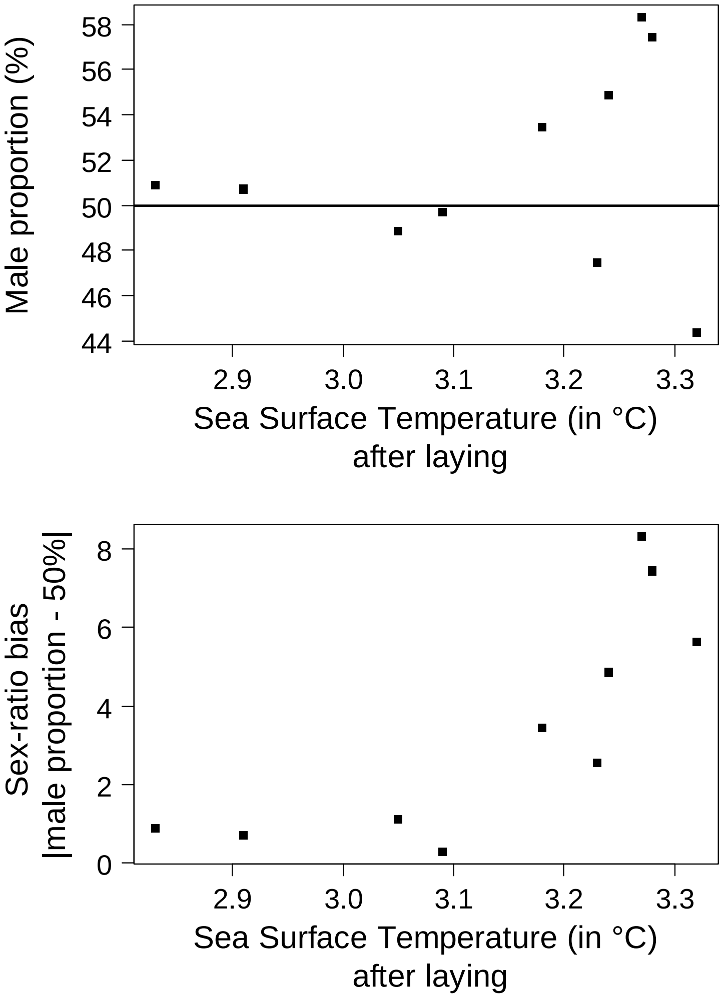

Figure VI - 17: *Sex ratio (upper panel) and sex ratio bias (lower panel) at fledging according to Sea Surface Temperature after laying.*

SOI did not affect sex ratio at fledging (LMs: P > 0.25) nor did it affect sex-ratio bias (LMs: P > 0.37). However, the period of decreasing in sex ratio at fledging (2002-2007) coincided with negative values of SOI (except for 2006; Figure VI - 18).

Finally, sex ratio and bias in sex ratio at fledging were not correlated to the overall breeding success of the colony, used here as an indicator of the environmental conditions during chick rearing (Pearson correlations: r = 0.10, P = 0.77 and r = 0.18, P = 0.61, respectively).

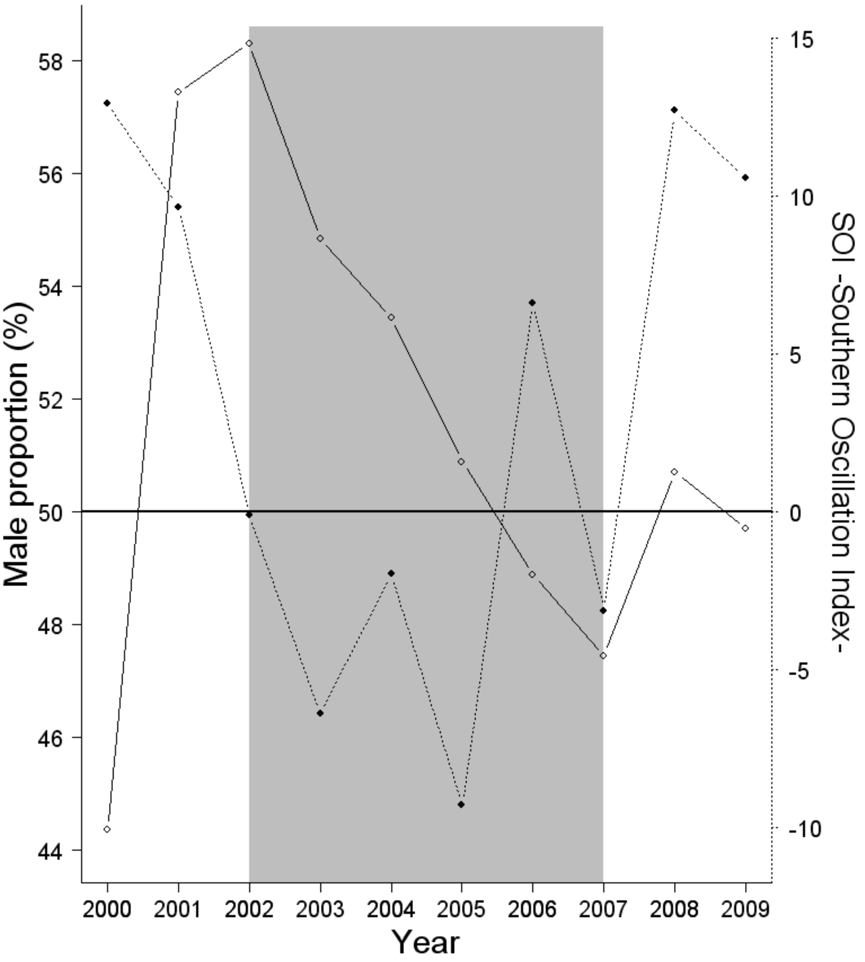

Figure VI - 18: *Sex ratio at fledging (solid line, open circle) and Southern Oscillation Index (dotted line, full circle, averaged on the period after laying) per year.*
The grey part corresponds to the period of decreasing male proportion and negative SOI (apart from 2006).

Effect of social environment

Colony density did not appear to affect sex ratio at fledging ($LM_{2004\text{-}2009}$: t = 0.87, P = 0.43). The other colony index, calculated through counting of individuals breeding in the colony, gave the same result ($LM_{2007\text{-}2009}$: t = 1.89, P = 0.31).

Chicks were randomly captured in three sub-areas, but we did not find any spatial effect on the sex ratio at fledging (P > 0.18 for each pairwise comparison, and ΔAIC < 2 compared to null model).

Dimorphism and body condition

A sexual dimorphism was present both in size and mass; males being larger and heavier than females (see Methods). However, when looking at body condition, *i.e.* residuals of body mass regressed on structural size, we observed that the difference between males and females was not constantly in favour of males (Figure VI - 19). Males had a significantly higher body condition than females only in 2004 (Wilcoxon $_{n=449}$: W = 29005, P = 0.004).

The mean annual difference in body condition between males and females was correlated with sex ratio at fledging (Pearson correlation: r = 0.68, P = 0.03; Figure VI - 19). Thus, high proportions of males occurred concomitantly with better body conditions of males compared to females.

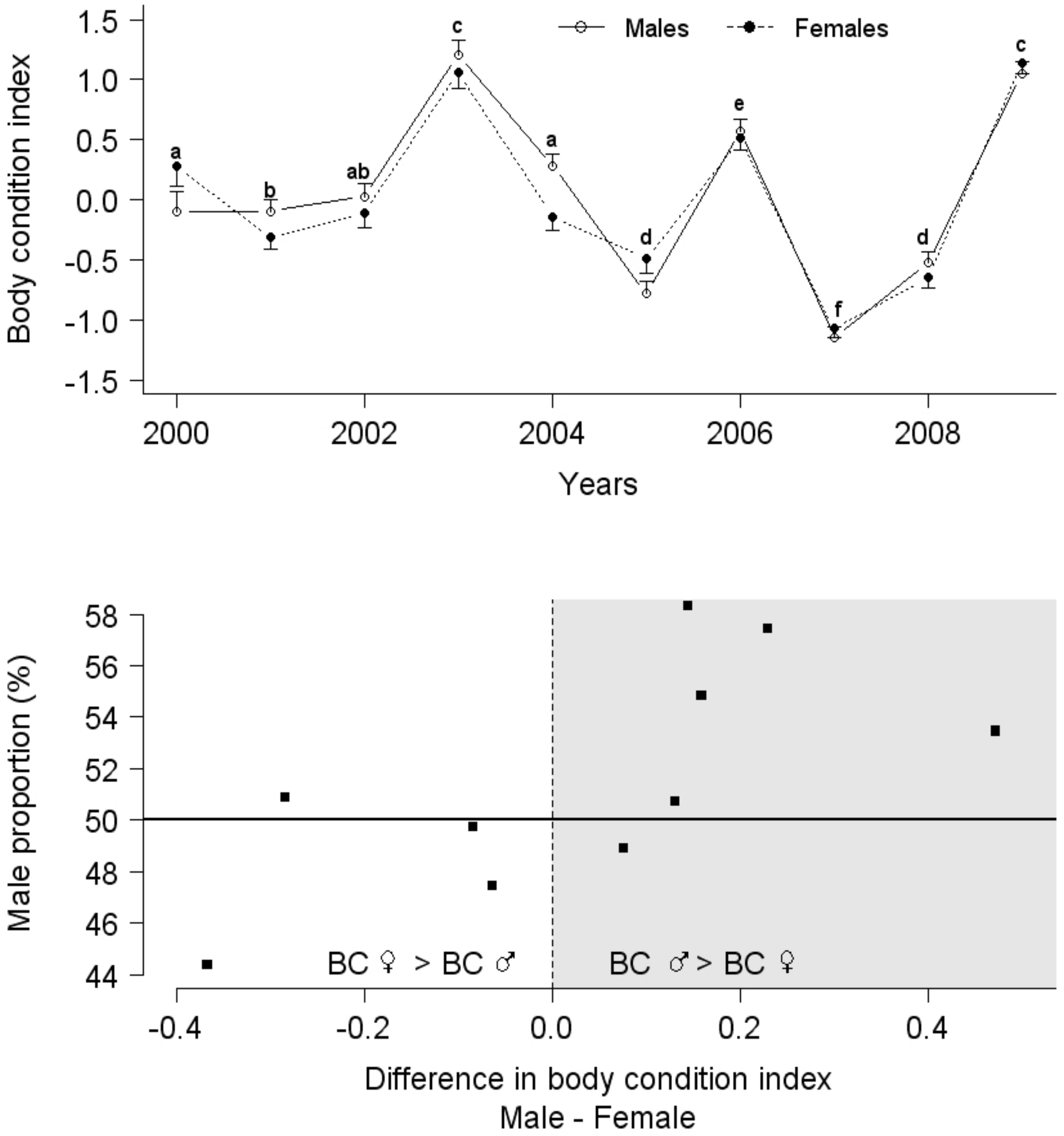

Figure VI - 19: *Body condition of males (solid line, open circle) and females (dotted line, full circle) according to year (upper panel), and sex ratio at fledging according to the difference between body condition of males and females (lower panel).*

Letters in superscript indicate differences between years in the average (male and female) body condition. The grey part corresponds to the years when males exhibit a higher body condition than females, while the white part corresponds to the opposite. Note that the horizontal solid line indicates the balanced sex ratio at fledging; every point situated above corresponds to a higher proportion of males, while below corresponds to a higher proportion of females.

Sex-ratio variation according to life stages

Sex ratio at first breeding attempt obtained on the first 6 cohorts was more balanced than at fledging (51.26% *vs.* 54.12%, Proportion test $_{n = 1990/1497}$: P = 0.001) or at first returns (51.26% *vs.* 55.24%, Proportion test $_{n = 1497/792}$: P = 0.042; Figure VI - 20).

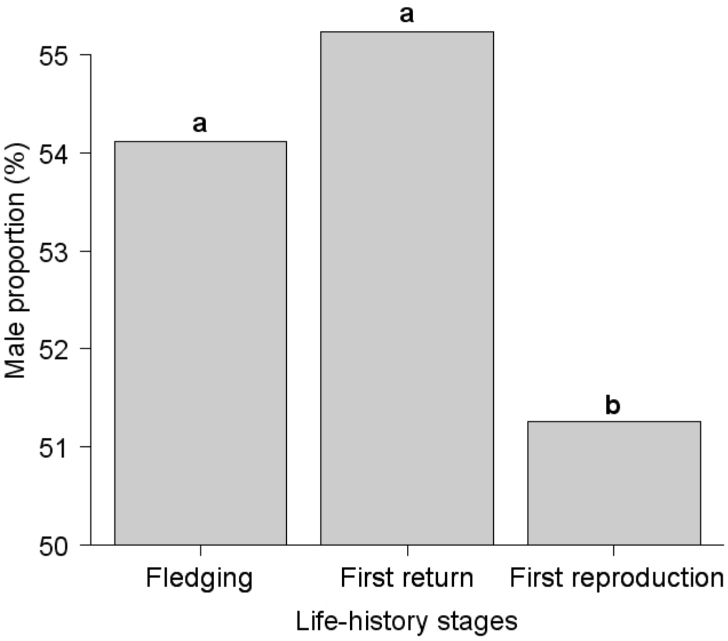

Figure VI - 20: *Sex ratio according to life-history stages.*
Bars sharing no common superscript are significantly different.

Discussion

King penguins are monogamous at the scale of a breeding season (*i.e.* they have a single partner during the season but exhibit a high inter-annual divorce rates; Olsson *et al.* 2001). Therefore, according to sex allocation theory, parental investment should be equal towards both sexes and sex ratio should be balanced (Fisher 1930, Hamilton 1967). A recent study in king penguin focusing on parental investment (through the number of feeding events) at the end of the breeding season indeed showed an equal parental investment towards male and female chicks (Corbel 2008). Yet, parental allocation results from trade-offs between benefits and costs associated with raising offspring (Stearns 1989), and thus differences in the balance of benefits and costs in raising males or females may lead to differential sex allocation and a potential bias in the sex ratio. King penguins exhibit a slight sexual dimorphism in favour of males. Costs associated with raising males should therefore be higher. Further, as the species is monogamous and displays obliged bi-parental care, breeding success of males and females should be similar. However, breeding success of one sex depends both on its actual success in raising a chick but also on the proportion of individuals engaged in the reproduction at a given year. Global breeding success could thus be different between males and females. Indeed, king penguin males appear to take more sabbaticals than females (Le Bohec *et al.* 2007), probably due to the long breeding cycle of the species and the fact that males may finish raising chicks later than females (Corbel 2008). Therefore, males should have a lower global breeding success than females, and benefits of raising males should be lower. The balance between benefits and costs then seems in favour of females in king penguins, and we thus expected a sex ratio biased towards females. Nevertheless, we found a higher proportion of males than females that fledged during our 10-year study. This bias towards males had already been found in adult sex ratio of our studied colony (Le Bohec *et al.* 2007), but also on another king penguin colony settled in South Georgia (Olsson & Van der Jeugd 2002). How to explain these results, which at first glance appear contradictory? In long-lived species, individuals should maximize their lifetime reproductive success (LRS) rather than breeding success on a given year. In that context, LRS results both from punctual breeding success and the number of past and future breeding events (Stearns 1992), the latter depending on the individual survival. We suggested that punctual breeding success might be in favour of females. Nonetheless, LRS could exhibit the reversed trend due to survival. According to a previous study in South Georgia (Olsson & Van der Jeugd 2002), survival of males and females is similar in favourable conditions. However, when conditions get unfavourable males survive better. Similarly, survival rate of males in our colony was estimated at 94.2%, while female survival was only 90.7% (survival rates estimated on 407 individuals marked as breeding adults between 1999 and 2010; unpublished results) though the difference was not significant (Cox survival model: $P = 0.18$). Benefits to raise males could then be higher and might explain the slightly biased sex ratio observed in this population. Males might thus be slightly more costly (due to dimorphism) have lower annual breeding success as a group (due to more sabbaticals) but also higher lifetime reproductive success (due to enhanced survival). The resulting balance is difficult to determine and overall optimal sex ratio should be close to equilibrium. Here we observed a slight bias towards males over the 10-year period but sampling on different years we could have found the opposite. King penguins seem thus to maintain sex-ratio as close to equilibrium as possible over a long-term period.

Our data showed that sex ratio at fledging was highly variable depending on the year (from 44 to 58% of males), and if it was globally biased towards males on the whole study period, it was not the case every year. Sex ratio at fledging depends on both sex allocation prior to laying, which may affect the secondary sex ratio (*i.e.* sex ratio at hatching), and sex-specific mortality from hatching to fledging. Unfortunately, we could investigate changes in sex ratio from hatching to fledging on a single year (2010) for now. Nonetheless, focusing on early chicks (as very few late chicks survived until fledging), we found a reduction, though not significant, of about 6% in the proportion of males between hatching and fledging, suggesting that mortality during the rearing period may play an important role on the population sex ratio. Therefore, we investigated the impact of environmental conditions prior to breeding that might reflect the effect of the condition of the mother on sex allocation, but also during chick rearing. We found an effect of Sea Surface Temperature (SST) both prior to breeding and during chick rearing and of the distance to the Polar Front (PF) on sex ratio at fledging. SST is known to be a good environmental descriptor of prey availability (Gregg *et al.* 2003) and may thus affect foraging behaviour of parents and ultimately chick provisioning. SST has indeed been shown to affect breeding success in king penguins (Le Bohec *et al.* 2008a). In addition, changes in the latitude of the PF may also have strong effects on chick rearing. The PF is an important feeding ground for king penguins during summer time (Charrassin & Bost 2001), and the further the front moves away from the colony, the greater are foraging trips (in terms of distance and duration). Breeding is associated with high energetic constraints in king penguins, and longer foraging trips during the incubation or brooding periods, for instance, may lead to the abandon of the reproduction by the partner waiting on land to be relieved (Groscolas & Robin 2001). Here, we show that the bias in sex ratio at fledging increased with SST and the distance to the PF. However, this relationship was not directional, high SST leading to a sex ratio biased either in favour of males or females. The global index (Southern Oscillation Index *SOI*) had no impact on the sex ratio at fledging during our study period. However, previous studies have shown that SOI may affect biological parameters only above a certain intensity threshold (see for instance the effect of SOI on population trends in Vargas *et al.* 2007). In our 10-year study period, SOI varied between -9.2 and 13 (means on the 6 months following hatching), which cannot be considered as extreme values. By comparison, SOI varied between -33.3 (1983) and 31.6 (1973) in the last 50 years. Thus, we suggest that the absence of relationship between SOI and the sex ratio at fledging may result from a lack of intense La Niña / El-Niño events during our study period.

Finally, we also investigated a potential effect of social environment on the sex ratio at fledging through colony density, which might incur different energetic costs for king penguin parents (Viblanc *et al. in prep*). However, colony density, as well as location in the colony, did not appear to affect sex ratio of the chicks at fledging. Yet, chicks were all captured in a relatively small part of the colony, and it would be interesting to investigate further the potential role of habitat quality on sex ratio. Indeed, environmental constraints, such as parasite infestation, predation pressure, may vary according to the location within a colony (Mangin *et al.* 2003, Descamps *et al.* 2005) and if associated costs are higher for one of the two sexes, sex ratio could change across the colony.

Parents are also expected to adjust offspring sex ratio according to the difference in costs of rearing sons or daughters, and the potential consequences of these costs on future reproductions and survival. If producing a male is associated with higher benefits in terms of fitness than a female, but more costly because of larger size, we expect more males to be produced when conditions are favourable. Indeed, in years of unfavourable conditions, mothers may prefer to produce a less costly sex, either because reproduction is likely to fail or because it could impair their future breeding success ('cost of reproduction hypothesis'; Cockburn *et al.* 2002). Numerous studies revealed greater reproductive costs endured by females depending on the sex of the offspring (see Cockburn *et al.* 2002). Additionally, males being larger than females in king penguins, they could be more vulnerable to food shortage (Nager *et al.* 2000). The reproductive value of males might thus be lower during harsh environmental conditions and parents might gain more profits to produce females. For instance, lesser black-backed gulls, *Larus fuscus fuscus*, have been shown to increase the number of females as their condition was decreased experimentally (Nager *et al.* 1999). Similarly, in blue-footed boobies, the sex-ratio appears as a response to the disadvantage daughters (*i.e.* the bigger sex) face from being reared under unfavourable conditions (Velando 2001). We found no correlation between sex ratio at fledging and the breeding success of the colony (a parameter that may be used as indicator of breeding conditions; Chiaradia & Nisbet 2006). Nonetheless, this sex ratio appeared to be highly correlated with the difference in offspring body condition between the two sexes (*i.e.* when male-biased sex ratio was observed; males exhibited a higher body condition at fledging than females). Chick body condition at fledging can be considered as an index of chick 'quality', as body condition affects post-fledging survival (Saraux *et al.* 2011b). Our results thus accord with our predictions that females would be less costly to produce and the sex ratio should be consequently biased towards them under strong climatic constraints. Moreover, males produced those unfavourable years should be of lower 'quality' and/or condition. Conversely, under favourable environmental conditions, sex ratio at fledging should be biased towards males that should be of good ‘quality’.

In several bird species, reproductive outcome depends on the period at which individuals start to breed. For instance, in chinstrap penguins, *Pygoscelis Antarctica*, chicks raised later in the season are smaller and of lower body condition than chicks raised early in the season (Moreno *et al.* 1997). Sex ratio at hatching has also been shown to change according to the season in the painted turtle (Bowden *et al.* 2000). Timing of breeding is very important in king penguins, as they are an asynchronous species. Late breeders have very low or almost null breeding success (Barrat 1976; Olsson 1996), as late chicks face higher constraints, especially in terms of building reserves before the winter fast (Weimerskirch *et al.* 1992). Yet, we found no difference in sex ratio at fledging between early and late breeders. However, these results need to be interpreted with caution, as our sample sizes of late chicks at fledging were small (3/15/9/6 according to the year). Results on sex ratio at hatching should thus be more indicative. Unfortunately, these results were obtained on a single year for now and need to be confirmed. The proportion of males hatching early tended to be higher than that of males hatching late (58 *vs.* 49%), though this result was not significant (P = 0.06).

If the understanding of mechanisms through which parents can manipulate sex ratio of their offspring and how environmental conditions can affect these mechanisms is fundamental, the parameter that affects population dynamics is the operational sex ratio. Therefore, we investigated changes in sex ratio across life-history stages. Sex ratio in king penguins tended to return to equilibrium at recruitment (*i.e.* at the first breeding attempt), as predicted by the optimal sex-ratio theory (Fisher 1930). However, we observed that adult survival of males and females could differ, so that sex ratio would be biased in an aging population. In Adélie penguins, *Pygoscelis adeliae*, Ainley & DeMaster (1980) found that mortality rate was higher in females, and aging population has been consequently found to be biased towards males. Therefore, it would be interesting in the near future to investigate sex ratio in later life-history stages of king penguins to assess the role of sex ratio in population dynamics of this species (Veran & Beissinger 2009).

Whereas many species exhibit deviations from an equal sex ratio, these deviations have been mostly inconsistent (Kruuk *et al.* 1999). The authors suggest that the sex ratio might be affected by several mechanisms acting simultaneously, each of them depending on environmental conditions. In this study, king penguin sex ratio at fledging was highly variable between years. Yet, the overall sex ratio at fledging averaged on the 10-year study period was only slightly biased towards males, maintaining the population sex ratio close to equilibrium, *i.e.* the optimal sex ratio for a monogamous species such as the king penguin. However, we also highlighted the effect of environmental factors on sex ratio at fledging, such as the Sea Surface Temperature or the distance between the breeding colony and their feeding ground, factors that also affect breeding success of the species (Le Bohec *et al.* 2008a). The increase in warm episodes predicted by the Intergovernmental Panel on Climate Change (IPCC 2007) may then increase the probability to deviate from the balanced optimal OSR. Such a modification could have important consequences on population dynamics (Veran & Beissinger 2009) and contribute to a decrease of the population (Vargas *et al.* 2007). Also, it could affect other life-history traits such as dispersal, by increasing the benefits of emigration for the supernumerary sex. In conclusion, our study suggests that climatic perturbations may play an important role on shaping the sex-ratio of long-lived seabird populations, and further studies are warranted to assess its effect on population persistence over time. In this regards, long-term data sets will provide powerful tools for future investigations.

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Chapter VII ○○○○○○●○○○

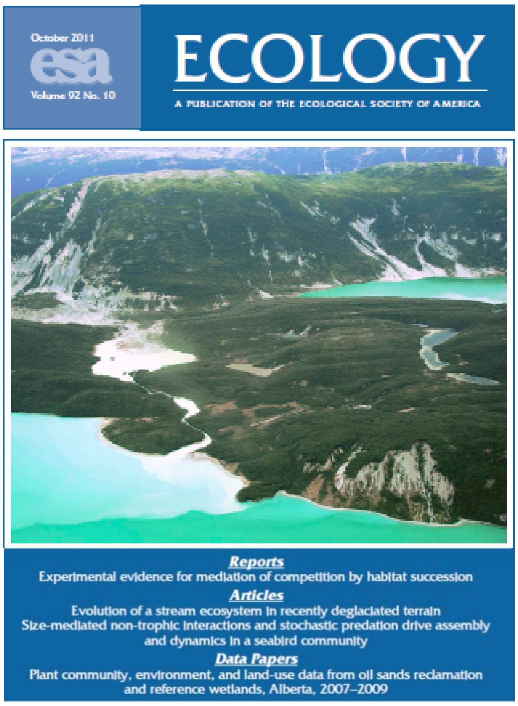
Flexibility and plasticity of foraging strategies

I. Foraging strategies in inshore little penguins

Flexibility in foraging strategies of inshore birds: *how little penguins maintain their body reserves while feeding their chicks*

(Article 7)

Claire Saraux, Sarah Robinson-Laverick, Yan Ropert-Coudert,
Yvon Le Maho & André Chiaradia



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Breeding animals face important time and energy constraints when caring for themselves and their offspring. For long-lived species, life-history theory predicts that parents should favor survival over current reproductive attempts, thus investing more into their own maintenance than the provisioning of their young. In seabirds, provisioning strategies may additionally be influenced by the distance between breeding sites and foraging areas, and offshore and inshore species should thus exhibit different strategies. Here, we examine the provisioning strategies of an inshore seabird using a long-term data set on more than 200 Little Penguins, Eudyptula minor. They alternated between two consecutive long and several short foraging trips all along chick rearing, a strategy almost never observed for inshore animals. Short trips allowed for regular provisioning of the chicks (high feeding frequency and larger meals), whereas long trips were performed when parent body mass was low and enabled them to rebuild their reserves, suggesting that adult body condition may be a key factor in initiating long trips. Inshore seabirds do use dual strategies of alternating short and long trips, but from our data, on a simpler and less flexible way than for offshore birds.

When breeding, animals face important time and energy trade-offs between caring for themselves and for their young (Trivers 1974), and the outcomes of this parent–offspring conflict largely influence overall reproductive success (Nur 1988). Life-history theory predicts that to maximize its lifetime reproductive success, an individual will invest a specific amount in reproduction resulting from the trade-off between the benefits and costs associated with raising chicks (Stearns 1989). In this context, long-lived birds are expected to favor their survival at the expense of the current breeding attempt (Stearns 1989; Mauck & Grubb 1995; and see the ‘‘prudent parent’’ in Drent & Daan 1980), and should minimize risks when investing in their offspring (Goodman 1974). Parental investment, defined as ‘‘any investment by the parent in an individual offspring that increases the offspring chances of surviving at the cost of the parent ability to invest in other offspring’’ (Trivers 1972), includes features in birds such as nest building, egg incubation, chick rearing, nest defense, and foraging. Yet, for many bird species, the chick-provisioning phase is the critical period of investment due to high energetic costs (Drent & Daan 1980), as during chick rearing, parents must decide whether and how to allocate the energy they gather between themselves and their offspring. However, nutritional and energetic requirements often differ between adults and their offspring (Murphy 1996) and food may come from different patches when parents are self-catering or caring for their young (Markman *et al.* 2004). Central-place foragers, such as seabirds, are faced with the additional constraint of returning to a central breeding site on land (or ice) to feed their offspring (Costa 1991), which limits the range of suitable foraging areas. Decisions regarding foraging grounds and hunted prey are then to be considered in the light of such trade-offs.

For seabirds to compromise between offspring provisioning and body maintenance, it has been suggested that parents may alternate between short coastal trips to provision their offspring, and long trips to more remote feeding grounds to restore and maintain their body condition (Weimerskirch *et al.* 1994; 1997a; Weimerskirch 1998). However, factors triggering a parent's choice to undertake a long or short foraging trip may differ between species. For instance, if Sooty Shearwaters, *Puffinus griseus*, seem to respond to a threshold in their body condition below which they will always initiate a long foraging trip (Weimerskirch 1998), other species seem able to alter the length of foraging trips in response to the body condition of the chicks (Weimerskirch *et al.* 2000). Although trips of bimodal durations have been widely reported in procellariiforms (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994; 1997a; 1998; Granadeiro *et al.* 1998; Booth *et al.* 2000; Congdon *et al.* 2005), the indication of dual feeding is very limited outside this taxon, with a few alcids as exceptions, such as Thick-billed Murres, *Uria lomvia* (note that both short and long trips have been reported for that species, but not for the same individuals; Benvenuti *et al.* 1998) and Little Auks, *Alle alle* (Welcker *et al.* 2009). Aside from Little Auks, all these species are offshore birds, foraging at great distances from their colonies. Yet, the provisioning strategy of seabirds often depends on the distance birds have to travel to reach their foraging grounds, and provisioning strategies are thus expected to be drastically different between offshore and inshore species.

Inshore species such as the Black-browed Albatross, *Diomedea melanophris*, the Shy Albatross, *Thalassarche cauta*, or the Gentoo Penguin, *Pygoscelis papua*, perform short-lasting trips both during incubation and chick rearing (Weimerskirch *et al.* 1986; Williams & Rothery 1990; Hedd 1998). As these birds do not rely on distant food resources, their foraging trips are much shorter (ranging from six hours to a couple of days, depending on the species) and far more frequent than offshore species (Weimerskirch *et al.* 1997b). However, to support the annual requirements of an inshore species, food must be adequately predictable and abundant in inshore areas (Hedd 1998). Variable food and environmental conditions across breeding seasons would entail different energetic costs for parents. Yet, when food supply changes within the foraging range, virtually nothing is known on whether and how inshore seabirds adapt their foraging strategies to continue provisioning food both for themselves and their offspring. A recent study on breeding Adélie Penguins, *Pygoscelis Adeliae*, showed that changes in environmental conditions (such as ice cover or presence of icebergs) affected their foraging behavior, with less food brought back to the chicks, longer foraging trips, and higher body mass loss for the parents along the season (Ballard *et al.* 2010). However, no concomitant change in the foraging strategy was observed (Ballard *et al.* 2010), and Adélie Penguins seemed unable to respond to these changes.

Here we examined the provisioning strategies of an inshore seabird species, the Little Penguin, *Eudyptula minor*. Little Penguins are visual hunters that only feed at sea during the daytime (Cannell & Cullen 1998; Collins *et al.* 1999; Ropert-Coudert *et al.* 2006) and return ashore to nest only after sunset (Klomp & Wooller 1991; Chiaradia & Nisbet 2006). They have one of the shortest foraging ranges among seabirds (<20 km; Collins *et al.* 1999), and therefore they can be good models of inshore species, which constitute the majority of seabirds. Little Penguins have also occasionally been observed to make longer (several days) trips during chick rearing (Collins *et al.* 1999; Weavers 1992), and previous studies have reported their use of bimodal-trip strategies during incubation to optimize both reproduction and survival, potentially using longer trips to target more profitable distant prey patches (Kato *et al.* 2008). Such characteristics thus make Little Penguins ideal models to examine a possible plasticity in foraging strategies of inshore seabirds. Here, using data collected over eight years of continuous monitoring of more than 200 birds, we investigated whether changes in foraging strategies may be used by these inshore foragers to improve chick provisioning, and which parameters (*e.g.,* sex, year, and so on) may be key determinants underlying provisioning decisions. As one-day trips are the rule during chick guard (Chiaradia & Kerry 1999), we investigated provisioning strategies only during postguard, a period when parents are not dependent on the attendance of their partner (Daniel *et al.* 2007), and when chicks are left unattended in the colony. We also addressed the question of whether the length of foraging trips was a response to depleted adult body mass in years of variable food supply.

Methods

Monitoring and field protocols

Our study was conducted on Little Penguins at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (38°15’ S, 143°30’ E), where ~14 000 breeding pairs of Little Penguins nest (Cullen *et al.* 2009). This study was conducted during eight breeding seasons from 2001 to 2008, where 2001 refers to the breeding season in the austral summer of 2001– 2002. The study site used for these analyses (see details in Chiaradia & Kerry 1999) is a part of a colony containing 100 artificial burrows (wooden nest boxes), of which 48–76 were occupied in each year. All nesting adults were tagged mostly as chicks (or as adults in few cases) using passive transponder tags (Allflex, Capalaba, Australia), which were then implanted subcutaneously between the scapulae. Birds were later sexed by bill measurements (Arnould *et al.* 2004), when first found in the colony as adults in subsequent years.

All nests were checked three times a week using a portable transponder reader. This allowed us to determine the number of chicks fledged and the exact phenology of breeding events: laying, hatching, and fledging dates, as well as the end of the guard stage for each pair. Post-guard (*i.e.,* the period from the first date on which neither adult was present in the nest, to fledging of the last chick) success was defined as the number of chicks fledged (*i.e.,* chicks which were fully feathered and of age >40 days when last encountered, were considered fledged) per chicks reaching postguard.

Chicks were weighed three times a week to the nearest gram during post-guard. Fledging body mass was thus considered as the mass recorded at the last encounter prior to fledging (see details in Chiaradia & Nisbet 2006).

Foraging trips

Foraging trips were recorded using an automatic penguin monitoring system (APMS) designed by the Australian Antarctic Division (Kerry *et al.* 1993). The APMS was located on the main colony entrance between the beach and the colony and consisted of a weighing platform to determine the body mass of the penguins, a transponder reader to record the identity of the individual and two infra-red beams to detect the direction of movement of the birds (Kerry *et al.* 1993). The system automatically recorded the transponder number, date and time, and direction of each arriving and departing penguin (see details in Robinson *et al.* 2005). Foraging-trip durations were analyzed through the recorded detections. As Little Penguins depart to sea before sunrise and return after sunset, duration in hours can be dependent on the year period (Chiaradia & Kerry 1999). To avoid this bias, we looked at foraging duration at one-day intervals and duration of every foraging trip was rounded in days. Foraging trips were separated into two categories of short (≤ 2 days) and long trips (≥ 3 days) according to the distribution of trip duration (Figure VII - 1). Short trips lasted 1.2 ± 0.0 days (mean ± SE), while long ones lasted 4.3 ± 0.1 days.

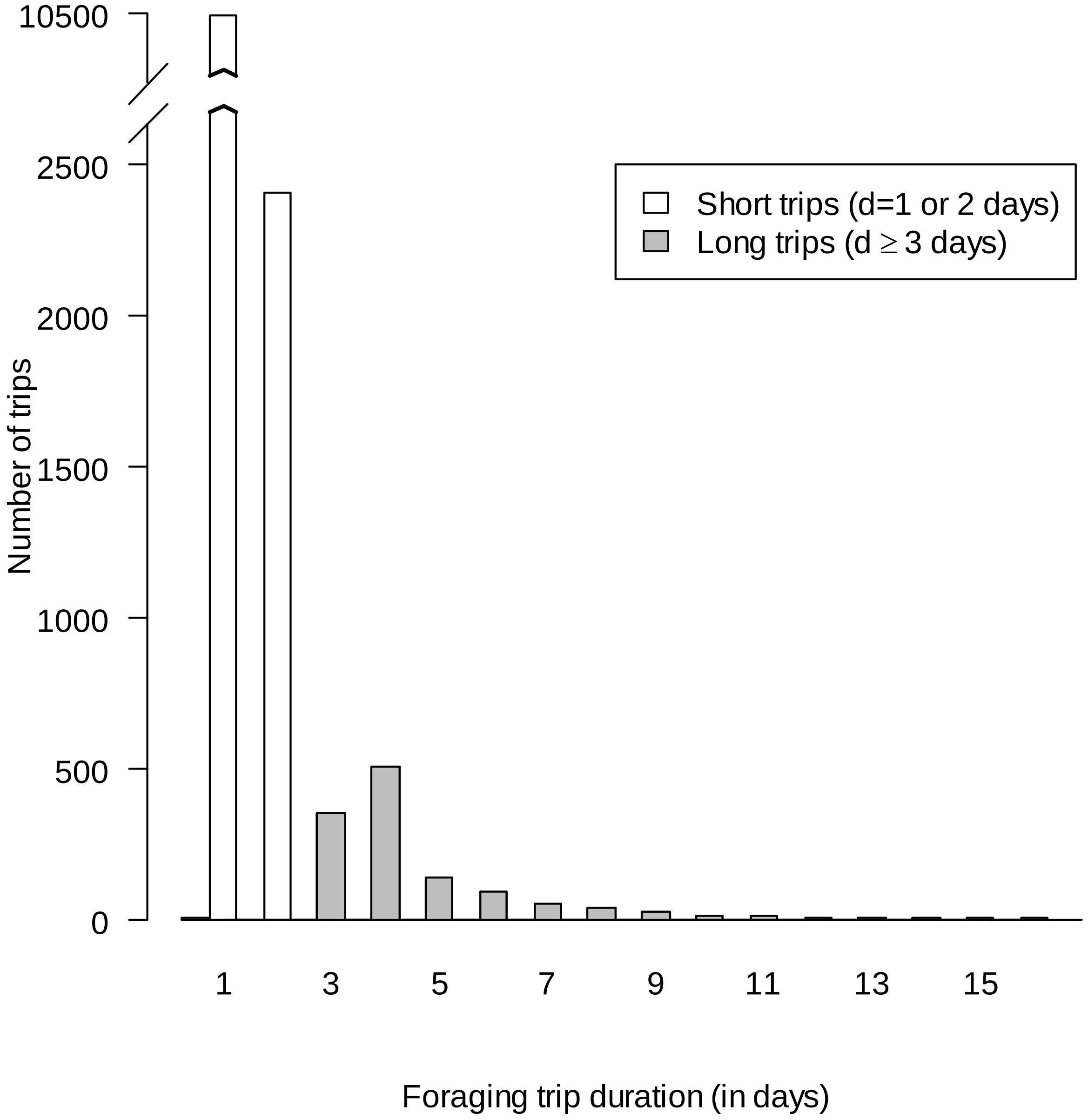

Figure VII - 1 : *Histogram of foraging trip duration*

Adult body masses and meal size

We focused our analyses of body masses on the first 40 days of post-guard (the average duration of postguard was 43 days) since the number of records dropped thereafter by almost 50%, as the birds progressively reduced their returning rate to the colony. Furthermore, raw data from the APMS were adjusted to account for tare drift and error of the system as described in Robinson *et al.* (2005). Meal size is defined hereafter as the amount of food (in grams) given by an adult to its chicks. During post-guard, as parents stayed for only a few hours at a time in the colony to feed the chicks (Daniel *et al.* 2007), we used the difference in body mass between a bird entering and then leaving the colony to estimate meal size. Meal sizes found in this study (mean 258 ± 1 g) were consistent with previous findings measured by directly weighing chicks before and after meals (see Fig. 4 in Chiaradia & Nisbet 2006). Three different adult body masses were examined in the following for a given foraging trip: the ‘‘departure mass,’’ which is the mass of the bird leaving the colony at sunrise, the ‘‘return mass,’’ which is the mass of the bird returning to the colony at sunset, and finally, the ‘‘post-feeding mass,’’ which is the mass of the bird going out to sea once more after having fed the chicks. The ‘‘return mass’’ thus equals ‘‘post-feeding mass’’ plus meal size.

Statistics

All statistics were computed using R 2.8.0 statistical program (R Development Core Team 2008). Data were longitudinal as individual penguins performed several trips in a single post-guard stage and were, moreover, recorded over multiple breeding seasons. Data were modeled using a maximum likelihood mixed-model approach (lme4 package; Bates & Maechler 2009). Mixed models were computed with the individual (bird) as a random effect, enabling us to account for repeated measures. Fitted models were usually generalized linear ones with Poisson distribution for foraging-trip duration or meal size. However, when looking at body masses, a normal distribution was fitted, as the numbers were high enough to assimilate a Poisson distribution to a normal one. Linear models were also computed to compare annual means. Variables were considered significant for $P < 0.05$. Results are given as means ± standard error (SE).

Results

Foraging trips

Over the eight years that were analyzed, we recorded a total of 14 116 foraging trips (n) for 212 different individuals (N). Little Penguins mostly performed short daily foraging trips, but were also observed to undertake longer trips lasting several days (mean ± SE = 1.4 ± 0.0 days, range = 1–16 days, 74% of one-day trips; Figure VII - 1). Gender did not influence foraging-trip duration (1.4 ± 0.0 days for both sexes; generalized linear mixed model [GLMM]; P = 0.59, n = 14 116, N = 212 birds).

Succession of foraging trips

Looking over all years together, birds almost exclusively began the post-guard period by undertaking long foraging trips (*i.e.,* in 91% of the cases, 416 out of 459). The proportion of first trips undertaken as long trips was not influenced by the individuals' age (GLMM; P = 0.66, n = 454, N = 189). However, we found that females began the post-guard period by undertaking long foraging trips more often than did males (94% ± 2% *vs.* 87% ± 2%; GLMM; P = 0.02, n = 459 [226/233], N = 192 [102/90]). The percentage of post-guard events starting with a long trip varied in between years from 78% in 2001 to 100% in 2002, 2003, and 2005. In years during which the guard period lasted longer, the proportion of birds undertaking long foraging trips at the onset of post-guard was higher (linear model [LM]; $t_7 = 2.99$, P = 0.02, $R^2 = 0.60$).

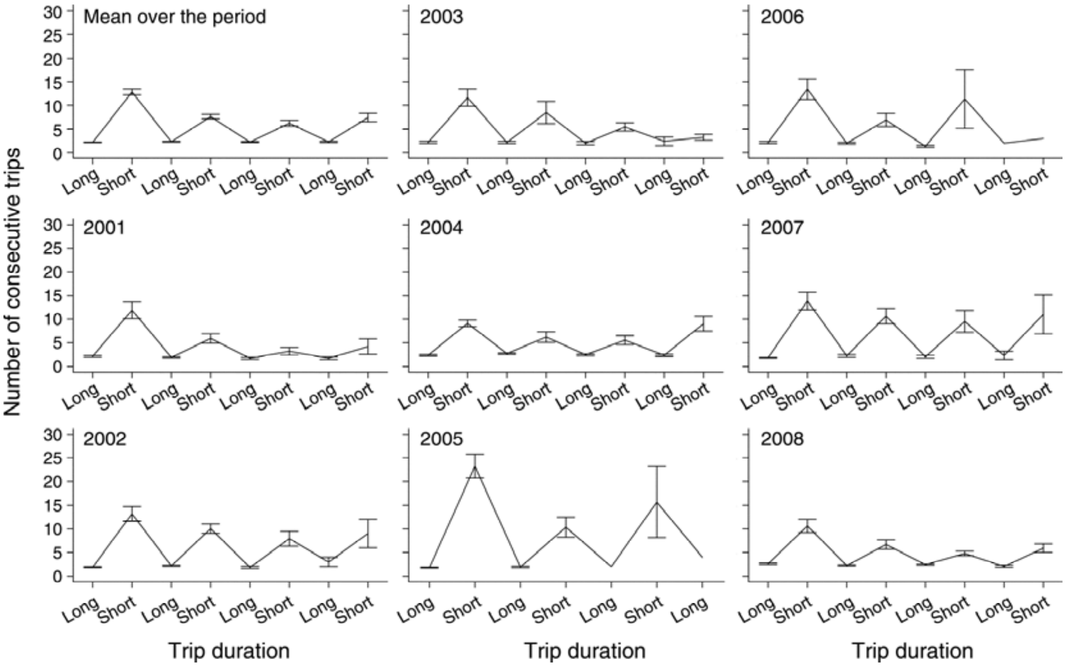

Figure VII - 2: *Pattern of alternation between long and short trips during the post-guard period. Averages ± s.e. are given over the whole study period (i.e. 8 years) and for each year separately.*

In general, birds alternated between long and short foraging trips in a similar pattern. They usually performed two long trips followed by several short ones (overall mean of 10.0 ± 0.4 short trips), resuming two long trips afterwards, and continued this pattern until their chicks fledged (Figure VII - 2). This pattern of alternation between long and short trips was present regardless of sex, age, or year (Figure VII - 2); however, we observed differences in the frequency of this pattern. While the number of consecutive long trips was constant (independent of the rank of the event, *i.e.*, whether it is the first, second, or n^{th} time they perform long trips, the sex and the year GLMMs; P = 0.20, P = 0.45, and P = 0.054, respectively; n = 944, N = 188), the number of consecutive short trips decreased with the rank of the event and varied between years from 7.5 in 2004 to 20.3 in 2005 on average (GLMM; P < 0.001, n = 875, N = 185; Figure VII - 2).

Body mass and foraging trip duration

Importantly, the body masses of birds departing to sea for long trips were significantly smaller than the body masses of birds departing for short trips (1050 ± 5 g *vs.* 1073 ± 1 g; linear mixed model [LMM]; P < 0.001, n = 8213, N = 164; Figure VII - *3*A).

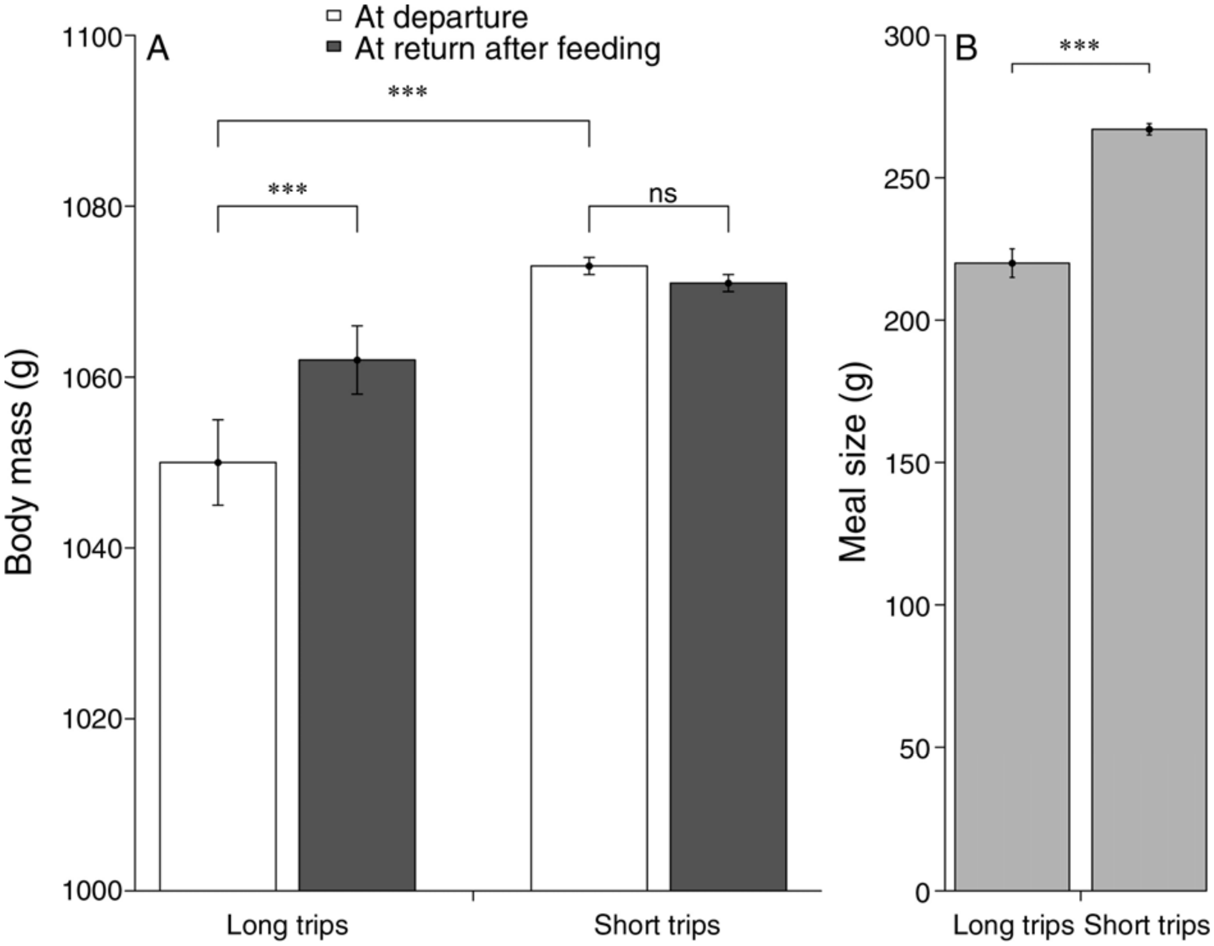

Figure VII - 3: *A) Changes in parents' body mass before and after short vs. long foraging trips. Post-foraging body mass (dark grey) corresponds to parents' body mass after feeding the chicks. B) Meal size given to the chicks after short vs. long trips.* $^{n.s.}$ *non significant,* *** *P < 0.001.*

When returning from their foraging trips, birds had put on mass, and their mass gain (return mass-departure mass) was significantly higher after short trips than after long ones (265 ± 2 g for a short trip *vs.* 232 ± 6 g for a long one; GLMM; P < 0.001, n = 4366, N = 153). When returning from short trips, birds delivered more food to the chicks than when returning from long trips, as indicated by their body mass loss during the few hours they spent in the colony feeding the chicks (267 ± 2 g *vs.* 220 ± 5 g; GLMM; P < 0.001, n = 4366, N = 153; Figure VII

- *3*B). When considering parents' body masses after having fed the chicks, birds had not gained mass when they returned from a short trip (average of 2 ± 1 g lost, but not significantly different from 0; GLMM; P = 0.8, n = 4014, N = 149; Figure VII - *3*A), whereas, on the contrary, birds returning from a long trip had gained 12 ± 4 g on average (GLMM; P = 0.02, n = 352, N = 121; Figure VII - *3*A). This pattern was further confirmed by analyses of body mass after a set of consecutive trips. At the end of a set of long trips, a bird gained 19.9 ± 10.9 g, while at the end of a set of short trips, a bird had lost 22.6 ± 8.4 g (GLMM; P < 0.001, n = 1171, N = 84).

Impact on chick-rearing

The percentage of long trips did not affect the length of the post-guard stage (GLMM; P = 0.57, n = 318, N = 160). However, it significantly influenced chick development both through post-guard success (*i.e.,* chick survival; GLMM; P < 0.001, n = 426, N = 176) and chick mass at fledging (GLMM; P = 0.01, n = 315, N = 154).

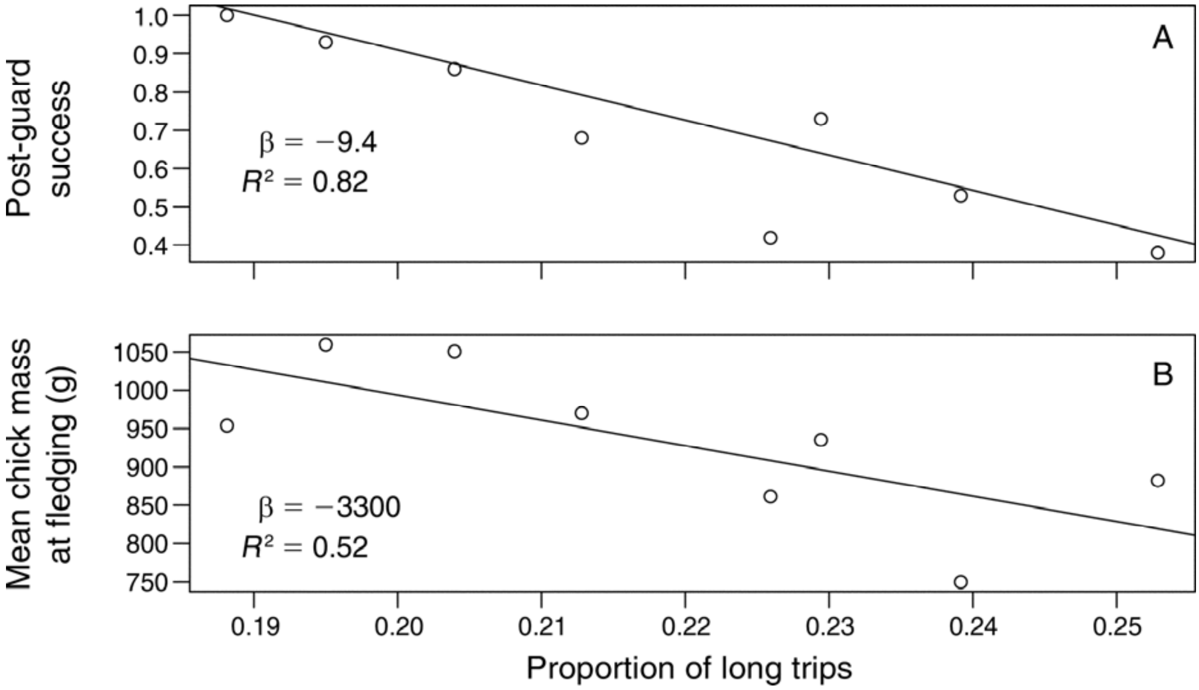

Figure VII - 4: *Impact of foraging trip duration on A) post-guard success, B) fledgling body mass. Regression lines and statistics (R^2 and regression coefficients) are indicated.*

Indeed, an increase of 1% in the percentage of the long trip lead to an almost 10% decrease in post-guard success (LM on annual means; slope = -9.4, t_7 = -5.24, P = 0.002; Figure VII - 4), and resulted in a drop of 33 ± 12 g in chick mass at fledging (LM on annual means; slope = -3300, t_7 = -2.567, P = 0.042; Figure VII - 4).

Discussion

Little Penguins alternated long and short foraging trips during late chick rearing, a strategy well known in offshore seabirds, but virtually never observed in inshore species. Inshore seabirds do not rely on distant food resources and usually perform short foraging trips to coastal areas close to their breeding sites, as, for instance, in Black-browed and Shy Albatrosses, or Adélie penguins (Weimerskirch *et al.* 1986; Hedd 1998; Ballard *et al.* 2010). Some inshore species also exhibit a dual pattern of short and long trips either in duration or distance (see murres in Benvenuti *et al.* 1998 and gentoo penguins in Lescroël & Bost 2005). However, this dual pattern resulted from a mutually exclusive behavior, *i.e.,* some birds conducted short trips, while others conducted long ones (depending on sex, breeding site location, and so on). Here, it is important to note that alternations of short and long trips were observed on the same individuals, refuting the hypothesis of specialization of inshore birds to rigid travelling mode. In little penguins, individuals typically conducted a majority of short trips. However, parents appeared to exhibit plasticity in behavioral foraging strategies, as they regularly alternated short trips with longer foraging bouts to compromise between providing both for their chicks' needs and their own. At first glance, the pattern exhibited by foraging parents (subsequently alternating between several short trips and two long trips) may seem relatively constant. This result may suggest that foraging strategies are not as diverse in Little Penguins as that observed in offshore seabirds, and thus, lack flexibility to environmental conditions. However, while it is true that there is only small variation in the number of long trips performed in a row (*i.e.*, adults always leave for two long foraging trips in a row), there is much greater variation in the number of short trips achieved in between long trips (Figure VII - 2). Such plasticity in trip frequency could be an adaptation to respond to fluctuating resources availability.

Short trips are used to provide food regularly to the chicks, whereas long trips seem to meet parent needs. Short trips were indeed associated with no reserve gains for the adults, but significantly bigger meals for the chicks, and thus, a guarantee of more frequent food supply for growing offspring. This is especially important in inshore species, whose chicks cannot sustain long periods of starvation (Chiaradia & Nisbet 2006), unlike offshore birds (Cherel & Le Maho 1985; Schultz & Klomp 2000). Short trips thus appeared at least as beneficial for little penguin chicks as they are reported to be for the chicks of offshore species (Weimerskirch 1998). This was further confirmed by our findings of a negative impact of increased proportion of long trips on chick survival and fledgling masses. However, after a number of successive (chick-provisioning) short trips, adults faced depleted reserves, and ultimately jeopardized their survival. Thus, when the breeding parent reached a low threshold in its body mass, it typically seemed to shift to long trips to improve its body condition. Therefore, we suggest that adult body condition triggers the choice between short and long trips in Little Penguins, as in the Blue Petrel, where it has been suggested that adults may regulate their foraging strategies so that their body mass does not go below a certain mass threshold (Chaurand & Weimerskirch 1994). According to life-history theory (Stearns 1989; Mauck & Grubb 1995) and the resulting prudent parent hypothesis (Drent & Daan 1980), long-lived animals such as Little Penguins should mostly focus on maintaining their own condition, rather than that of their offspring. Accordingly, in our study, parents appeared to invest into chick provisioning (performing short foraging trips) for as long as they were able to maintain a certain body condition. When body condition dropped, long trips became mandatory. This was confirmed by the fact that after the guard phase (a phase constituted of short trips solely), almost all birds shifted to long trips, the only exceptions being when a shorter than usual guard period enabled parents to maintain a sufficient body condition, for them to perform some extra short trips.

Long trips are usually associated with foraging in more distant areas. In colonial species, various studies have shown that prey availability is generally lower close to the colonies than further away, resulting either from intraspecific competition or prey depletion (Lewis *et al.* 2001; Ainley *et al.* 2003b; 2004). Distant trips may then reduce competition (Birkhead & Furness 1985), as when adults depart from a single location, the density of birds will decrease with increasing distance from that location. This was, for instance, suggested for the Blue Petrel (Chaurand & Weimerskirch 1994). In Little Penguins, trip duration and distance traveled are highly correlated, at least for trips lasting less than 10 days (see Fig. 3 in Collins *et al.* 1999), which represent the vast majority of the trips. Long journeys during chick rearing could thus be explained by the targeting of more distant and profitable prey patches, as previously suggested by Kato *et al.* (2008) during incubation. However, we found that the total mass gain (*i.e.,* the mass of prey foraged) was higher after short foraging trips than after long ones. One may then find this in contradiction with the hypothesis that birds target greater prey patches further away from the colony. Yet, this may be explained by the fact that food may be entirely processed when parents return from long trips, whereas it may be only partially digested in the birds' stomach when they return from short trips (Wilson *et al.* 1989b). Additionally, differences in strategies when foraging for themselves or for the chicks may result from different nutritional requirements, such as higher levels of proteins needed for chick growth (Partridge & Green 1985). For instance, in king penguins, the winter diet of the chicks appears to rely mostly upon cephalopods caught over the continental shelf, whereas parents hunting for themselves do so much further away from the island on a combination of cephalopods and high-protein myctophids (Cherel *et al.* 1993b). Parents may thus target different locations to forage on different prey depending on whether food is to be allocated to the chicks or themselves. Stable-isotope analysis, a method used to determine diet segregation, showed that the diet of adults and chicks exhibited different $\delta^{13}C$ and $\delta^{15}N$ signatures in Little Penguins, suggesting that they do not rely on the same resources and that their foraging zones are different (Chiaradia *et al.* 2010). Finally, long trips could also result from longer time spent foraging, but in the same areas as the ones used for short trips, as suggested by Ropert-Coudert *et al.* 2004a. Spending longer in the same foraging areas, birds may be less opportunistic and encounter higher quality items (classic central place foraging, sensu Orians & Pearson 1979).

Thus, it seems that inshore seabirds (such as little penguins) may exhibit some plasticity in their foraging strategies, though for those species, strategies appear less flexible than those of offshore seabirds. It is interesting to note that this plasticity was not observed in another inshore penguin, the Adélie penguin (Ballard *et al.* 2010), perhaps due to the smaller and inflexible time window to breed at the Antarctic continent. Explanations for bimodal strategies in inshore species thus warrant further investigations, and using data-loggers to investigate potential differences in foraging areas and/or diving behavior between short and long trips, should provide valuable insight on behavioral adaptations to a fluctuating environment.

II. Foraging strategies in offshore king penguins

Foraging strategies in chick-rearing king penguins
(Box 2)

Claire Saraux, Benjamin Friess, Yvon Le Maho, Céline Le Bohec

In preparation

A recent study reported the negative effect of Sea Surface Temperature warming on breeding success in king penguins (Le Bohec *et al.* 2008a). King penguins have a very unusual breeding cycle lasting more than a year so that breeding success should be dependent on environmental conditions over the entire year. Here, we studied the number of feeding visits achieved by parents all along the chick-rearing period and investigated the biotic parameters that might affect it, as well as its inter-annual variability. The king penguin breeding cycle has been extensively studied but mostly through monitoring of a few banded individuals (Stonehouse 1960; Barrat 1976; Weimerskirch *et al.* 1992). The use of an automatic monitoring system enabled us to investigate parents' return to the colony to care for their chicks over a large number of individuals (N = 801) and across several years (2003-2009), removing potential biases due to the negative effect of flipper-bands.

Materials and methods

Penguin monitoring

Our study was conducted on Possession Island (46°25'S, 51°45'E, in 'La Grande Manchotière' colony) in the Crozet Archipelago. Since 1998, 10-month old chicks have been randomly sampled each year during their moult, a few weeks before fledging and have been fitted with subcutaneous passive transponder tags without any other external mark. Transponder tags weigh 0.8 g and have no known adverse effects. They were shown not to affect survival in king penguins (Froget *et al.* 1998) nor breeding success, recruitment and survival in great tits (Nicolaus *et al.* 2009). The antennas buried under the usual and unique transit pathways in and out of the sub-colony allow for the continuous automatic collection of data on bird movements. This automatic identification system (Gendner *et al.* 2005) presents the major advantage of not requiring recapture thus avoiding disturbance of the animals, and produces a unique dataset on non-banded king penguins (see bias introduced by flipper-bands in Gauthier-Clerc *et al.* 2004; Saraux *et al.* 2011a).

Upon tagging, both flipper and beak lengths were measured (except for the first cohort tagged in 1998). These two morphologic measurements are good descriptors of king penguin structural size and are highly repeatable measurements (Fahlman *et al.* 2006). Flipper and beak measurements were correlated ($P < 0.001$, $r = 0.40$). A principal analysis component showed that the first component explained 83% of the variance in these two variables.

Therefore we used this first component as a structural size index SSI (SSI = 0.96 * Flipper + 0.26 * Beak). Birds tagged after 2000 were also blood sampled at tagging and sexed using microsatellite DNA-analyses (adapted from Griffiths *et al.* 1998). In the absence of DNA-samples, *i.e.* for the two first cohorts, gender was determined by analyzing the chronology of the sex-specific incubating shifts of their following breeding cycles (Stonehouse 1960, Descamps *et al.* 2002).

King penguins become sexually mature at a minimum age of three or four year old but with an average age at first reproduction of six (Barrat 1976, Weimerskirch *et al.* 1992). In order to have a sufficient sample size of breeding king penguins, we analyzed breeding data from 2003 to 2009. The breeding cycles and parameters of the known-aged 801 birds concerned (*i.e.,* birds of the 8 cohorts tagged as 10-month old chicks between 1998 and 2005 that did reproduce long enough for eggs to hatch between 2003 and 2009) were established by interpreting the movements of the birds between the breeding area and the sea (see Descamps *et al.* 2002; Le Bohec *et al.* 2007 for details). As mentioned above, king penguins exhibit a unique breeding cycle in that it lasts more than a year. Successful birds would thus be late for the next reproduction, leading to two different peaks of laying within a given breeding season (Barrat 1976). Breeders laying before the 1st of January are considered as early breeders, while the ones breeding after new year's eve are the so-called late breeders.

Number of chick feeding visits

Detections by the underground antennas enabled us to determine for each transponded bird transits in and out of the colony. As breeding king penguins come back on land to care for their chick, we investigated the number of entries in the colony as a proxy of parental feeding events. However, once the chicks have thermally emancipated and become more venturous, parents do not continuously remain with the chicks when returning to feed. Thus, it is more than frequent that parents wander around the colony, go for a bath in the bay and pass over the antennas several times a day. In order to avoid overestimation due to this problem, we only considered entries that were preceded by a trip out of the colony of at least 3 days. Hereafter, we refer to such events as feeding visits (Figure VII - 5).

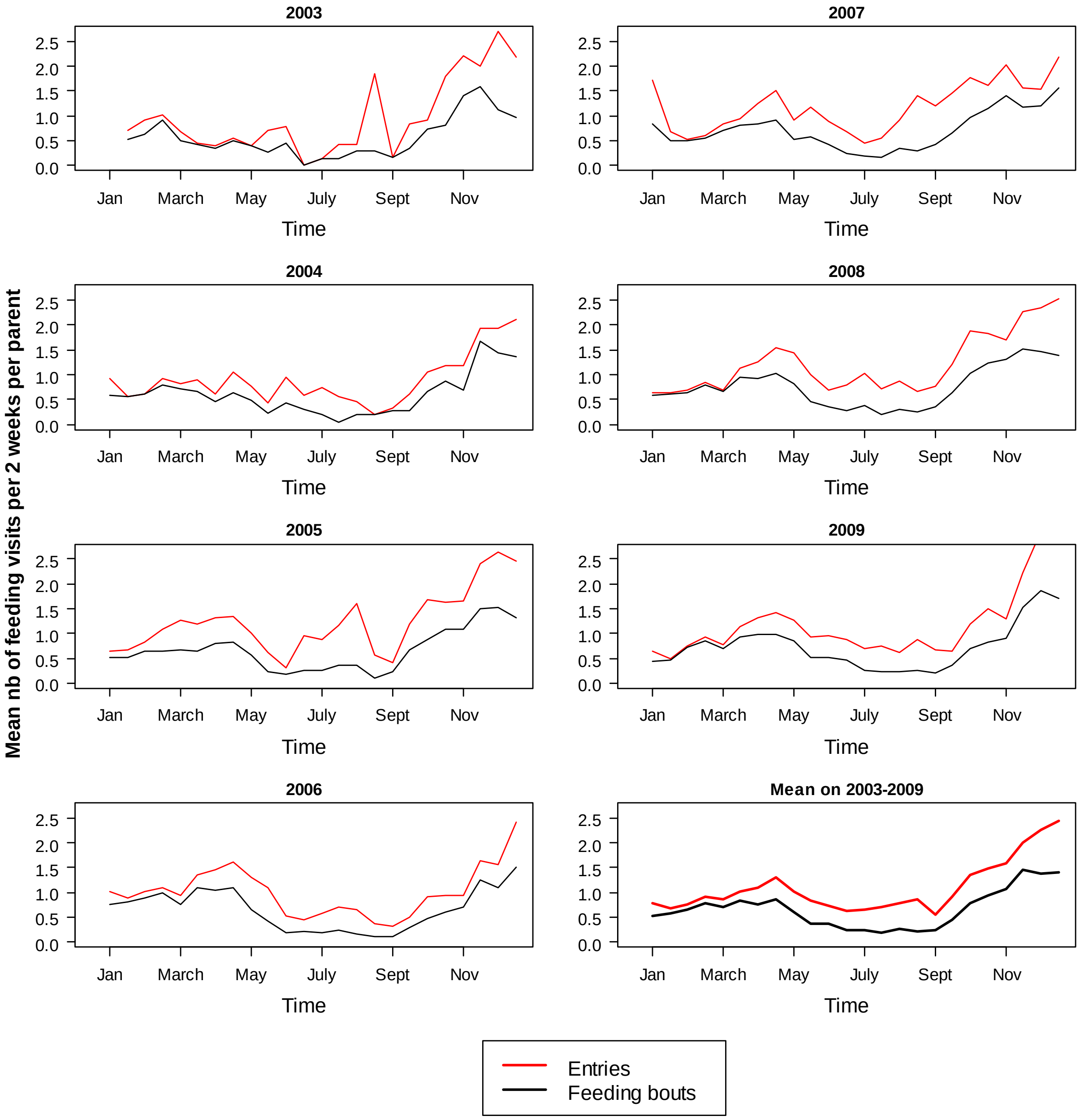

Figure VII - 5: *Mean number of returns to the colony per 2 weeks per parent for each study year. The red line corresponds to the exact number of entries in the colony, the black line corresponds to entries after an absence of at least 3 days.*

Additionally, newly-hatched chicks cannot thermoregulate by themselves, so that parents have to brood them under the incubation patch. This means that after returning to the colony, parents will remain there several days (average duration from 6 to 9 days according to the brooding shift; Descamps *et al.* 2002) and the number of returns may thus not be a good indicator of feeding frequency. This brooding period lasts for about 31 days (Weimerskirch *et al.* 1992). Therefore, we separated brooders (considered here as 31-day period after the exact egg-laying) and parents raising emancipated chicks (Figure VII - 6). This figure confirms the very low feeding rate estimated with our method in brooding birds. In the following, results are presented only for individuals rearing emancipated chicks.

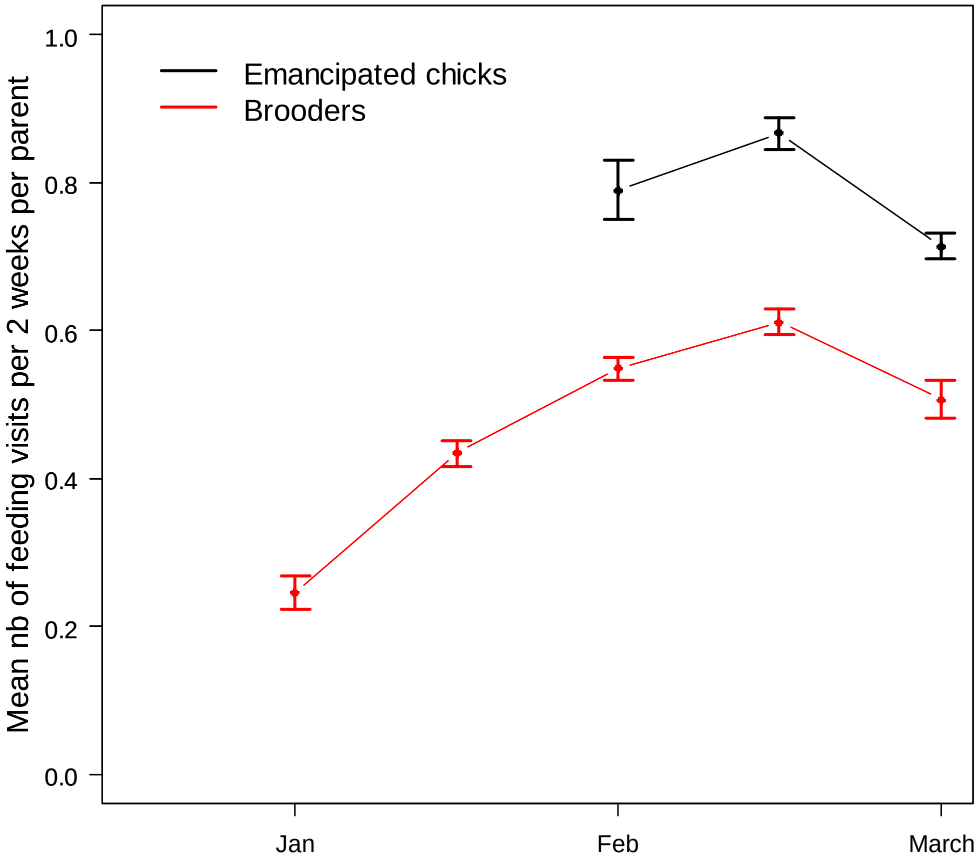

Figure VII - 6: *Mean number of feeding visits per 2 weeks per parent for brooding parents and parents raising emancipated chicks.*

Environmental descriptors

Changes in Sea Surface Temperature (SST) have repercussions on the primary production and the food chain (Gregg *et al.* 2003), and consequently SST is frequently used as a local proxy of abundance and distribution of preys for king penguins (Le Bohec *et al.* 2008a). Monthly SST values (in °C) were obtained from the National Ocean and Atmospheric Administration. SST was averaged over 2 different areas: 1) at the Polar Front (48-52°S, 46-56°E), at which king penguins forage during summer (Charrassin & Bost 2001); 2) over the whole area from Crozet to the southernmost foraging area of king penguins, *i.e.* the Marginal Ice Zone (46-60°S, 46-56°E).

Statistics

All statistics were computed using R v. 2.9.0. Data were analyzed using a maximum of likelihood generalized linear mixed model approach. Generalized linear mixed models were computed with individuals as random terms enabling us to account for repeated measures. Models were fitted with Poisson distribution. Model selection was based on AIC method, using both ΔAIC and AIC weights starting with the complex model and eliminating step by step terms that are not contributing. In order to compare different groups (*e.g.,* age categories and years), we first checked for normality and homoscedasticity between groups, and non-parametric tests were used consequently (including Wilcoxon rank-sum test). Variables were considered significant for $P<0.05$ and Bonferroni's correction was applied whenever multiple comparisons were tested (differences were thus considered significant for $P < \frac{0.05}{n}$ with n the number of comparisons done).

Results

Description of chick rearing in terms of feeding visits

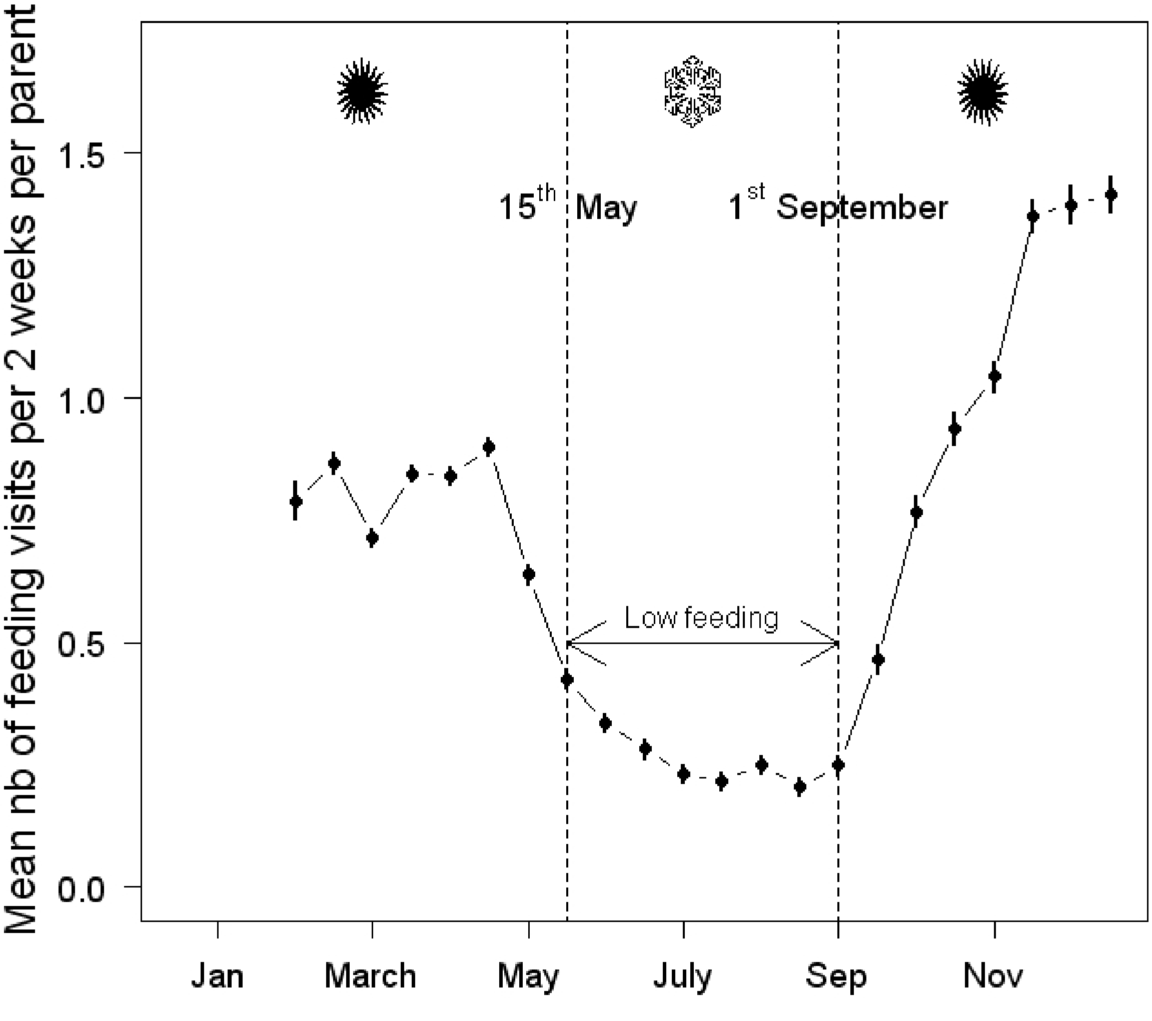

Figure VII - 7: *Mean number of feeding visits per 2 weeks per parent along the chick-rearing period. Bars represent standard errors. Points were represented for N > 200 individuals. Vertical dashed lines indicate the separation between the 3 periods and were obtained by breakpoint analyses.*

The mean number of feeding visits changed along the chick-rearing period, which can be divided into three periods (Figure VII - 7). According to a breakpoint analysis, the winter low feeding period lasted from mid May to early September. In the first period (February to mid-May), the number of returns to feed their chicks was relatively stable until mid-March, when it dropped (mean over the period: 0.80 ± 0.01 feeding visit per 2 weeks per parent). From mid-May to beginning of September the number of feeding visits was low (mean over the period: 0.28 ± 0.01 feeding per 2 weeks per parent), while it increased significantly thereafter to reach the highest value at the end of November (mean over the period: 1.03 ± 0.01 feeding per 2 weeks per parent). During the winter period, each parent returned on average 1.73 ± 0.05 times to the colony (range 0-7). Chicks should therefore have received an average of 3.5 visits during this period. Additionally, 16% of the parents that were still rearing chicks in winter (*i.e.* in 132, N = 120 individuals, out of 808 cases, N = 492 individuals) never returned to the colony during this period.

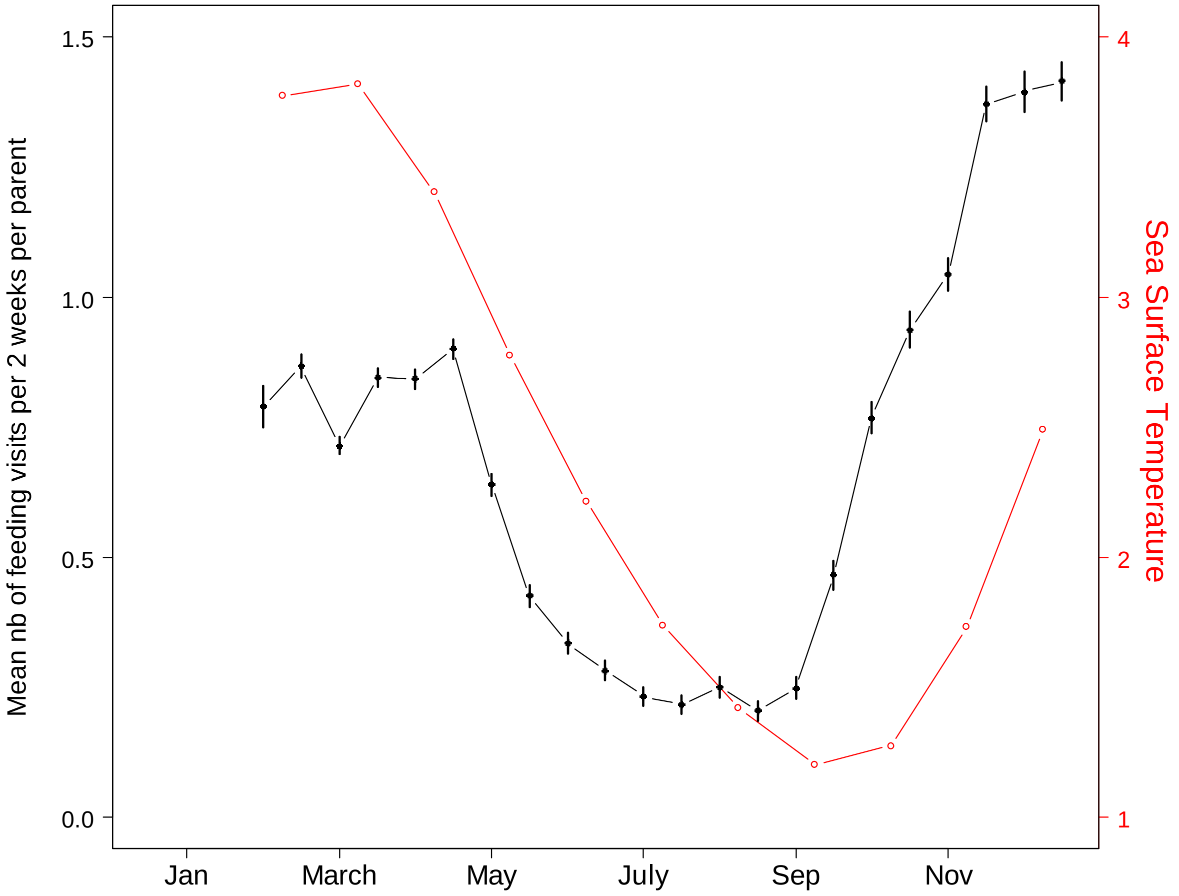

Figure VII - 8: *Mean number of feeding visits per 2 weeks per parent along the chick-rearing period (in black) and Sea Surface Temperature (SST) at the Polar Front (in red).*

This pattern was not correlated to the sea surface temperature at the Polar Front, whatever the time lag considered (Correlation $\text{test}_{\text{no lag}}$: P = 0.45; Correlation $\text{test}_{\text{lag = 1 month}}$: P = 0.82; Correlation $\text{test}_{\text{lag = -1 month}}$: P = 0.12; Correlation $\text{test}_{\text{lag = -2 months}}$: P = 0.07; Figure VII - 8).

Parameters influencing the number of feeding visits

Overall, males returned slightly more often to the colony than females (0.65 ± 0.01 *vs.* 0.69 ± 0.01 for females and males, respectively; GLMM: P = 0.006, n = 14461, N = 696; Figure VII - 9A). Yet, males and females performed a similar number of returns during the first period (*i.e.* before the 15th of May; 0.80 ± 0.01 *vs.* 0.81 ± 0.01 for females and males, respectively; GLMM: P = 0.59, n = 6321, N = 696; Figure VII - 9 A) and the third period (*i.e.* after the 1st of September; 1.02 ± 0.02 *vs.* 1.04 ± 0.02 for females and males, respectively; GLMM: P = 0.59, n = 2857, N = 331; Figure VII - 9 A). During the winter period, males returned more frequently to the colony than females (GLMM: P < 0.001, n = 4869, N = 482; 0.24 ± 0.01 *vs.* 0.35 ± 0.01 for females and males, respectively; Figure VII - 9 A).

Late breeders returned significantly less times to the colony than early breeders (0.42 ± 0.03 *vs.* 0.68 ± 0.01; GLMM: P < 0.001, n = 14616, N = 714; Figure VII - 9 B). This result held true in both the first and third period (GLMMs: P < 0.001; Figure VII - 9 B) but the number of returns was not significantly different during winter for early and late breeders (GLMM: P = 0.11, n = 4919, N = 492; Figure VII - 9 B).

The number of feeding visits significantly increased with adult age (GLMM: P < 0.001, n = 14616, N = 714; Figure VII - 9 C and Figure VII - 10). This held true when investigating age differences over the three periods separately (GLMMs: all P < 0.001; Figure VII - 9 C).

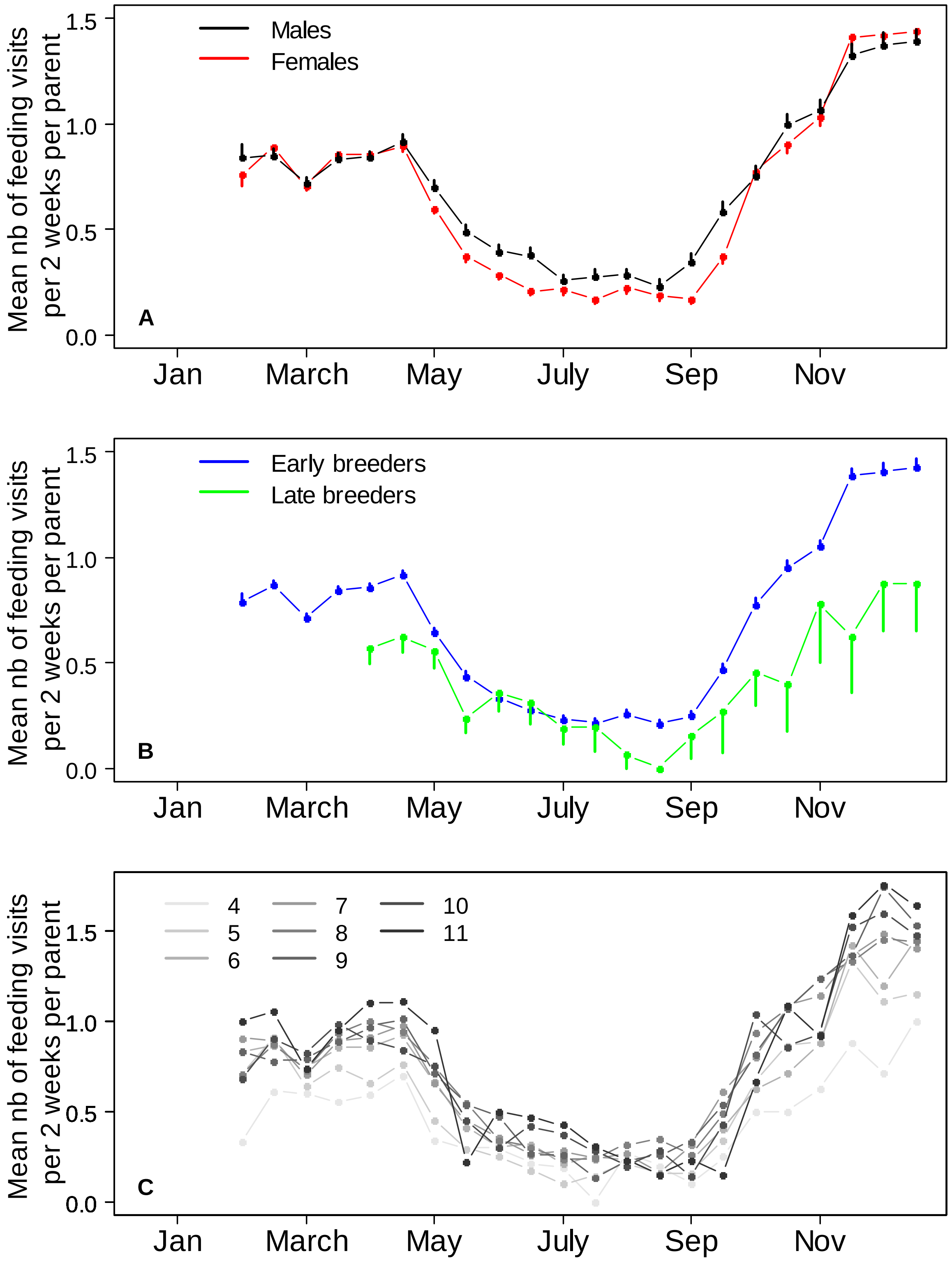

Figure VII - 9: *Mean number of feeding visits per adult per 2 weeks per parent along the breeding season according to* ***(A)*** *Sex,* ***(B)*** *Breeding Timing,* ***(C)*** *Age.*
Standard errors are indicated on (A) and (B), but not on (C) for visualization purposes. On (C), grey intensity increases with age, i.e. the darker the line, the older the birds.

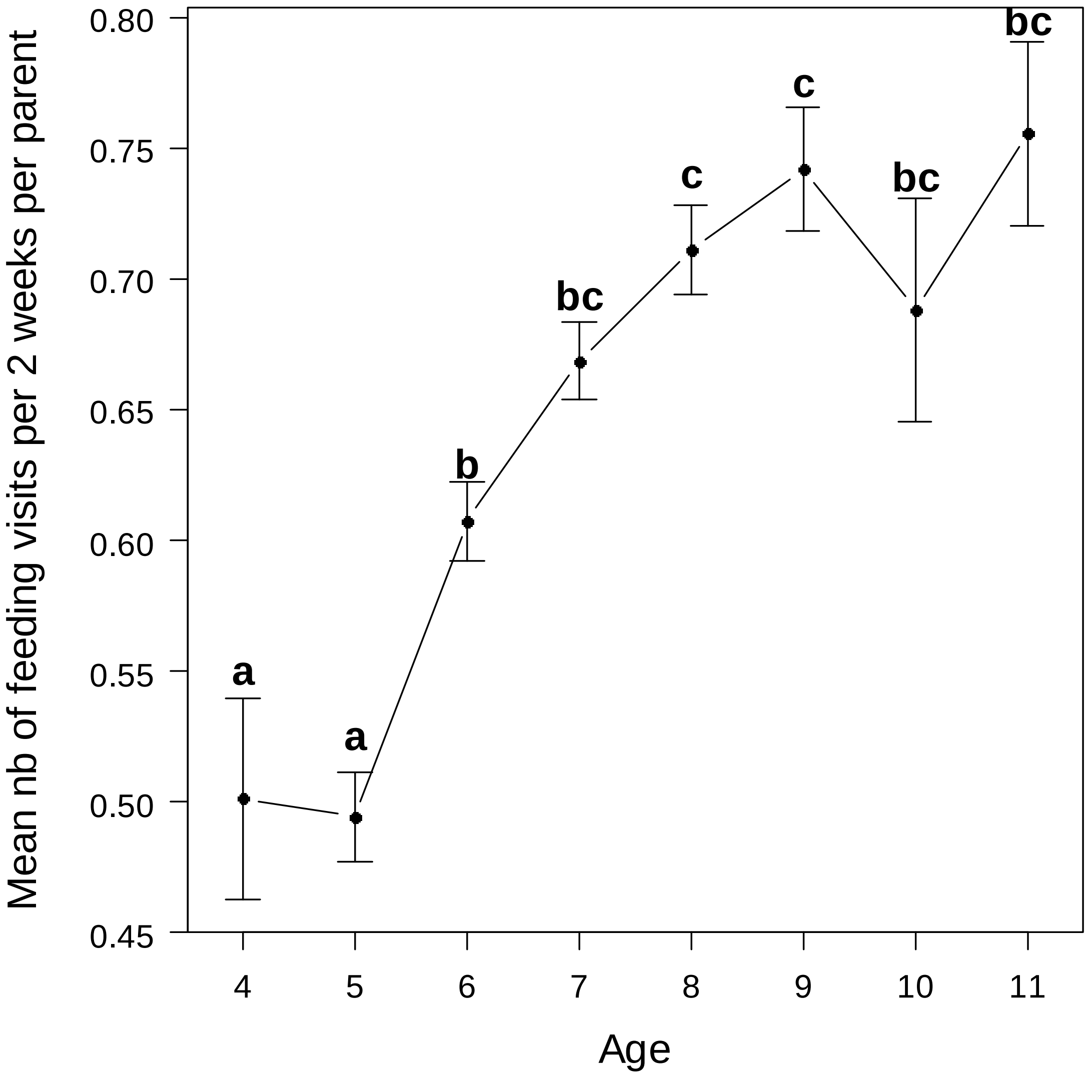

Figure VII - 10: *Average number of feeding visits per 2 weeks per parent according to the age of the individual.*

Finally, the number of feeding visits was significantly affected by structural size (GLMM: P = 0.007, n = 12699, N = 661), *i.e.* larger birds returned more to the colony to feed their chick.

Inter-annual variability

The timing of winter (as inferred by breakpoint analysis) varied slightly across years, beginning between the 15th and 30th of May and ending between the 15th of August and 15th of September (Figure VII - 11). SST averaged on the first period did not affect the timing of the onset of winter period (LM: P = 0.83). Similarly, SST during winter did not affect the timing of its end (LM: P = 0.36).

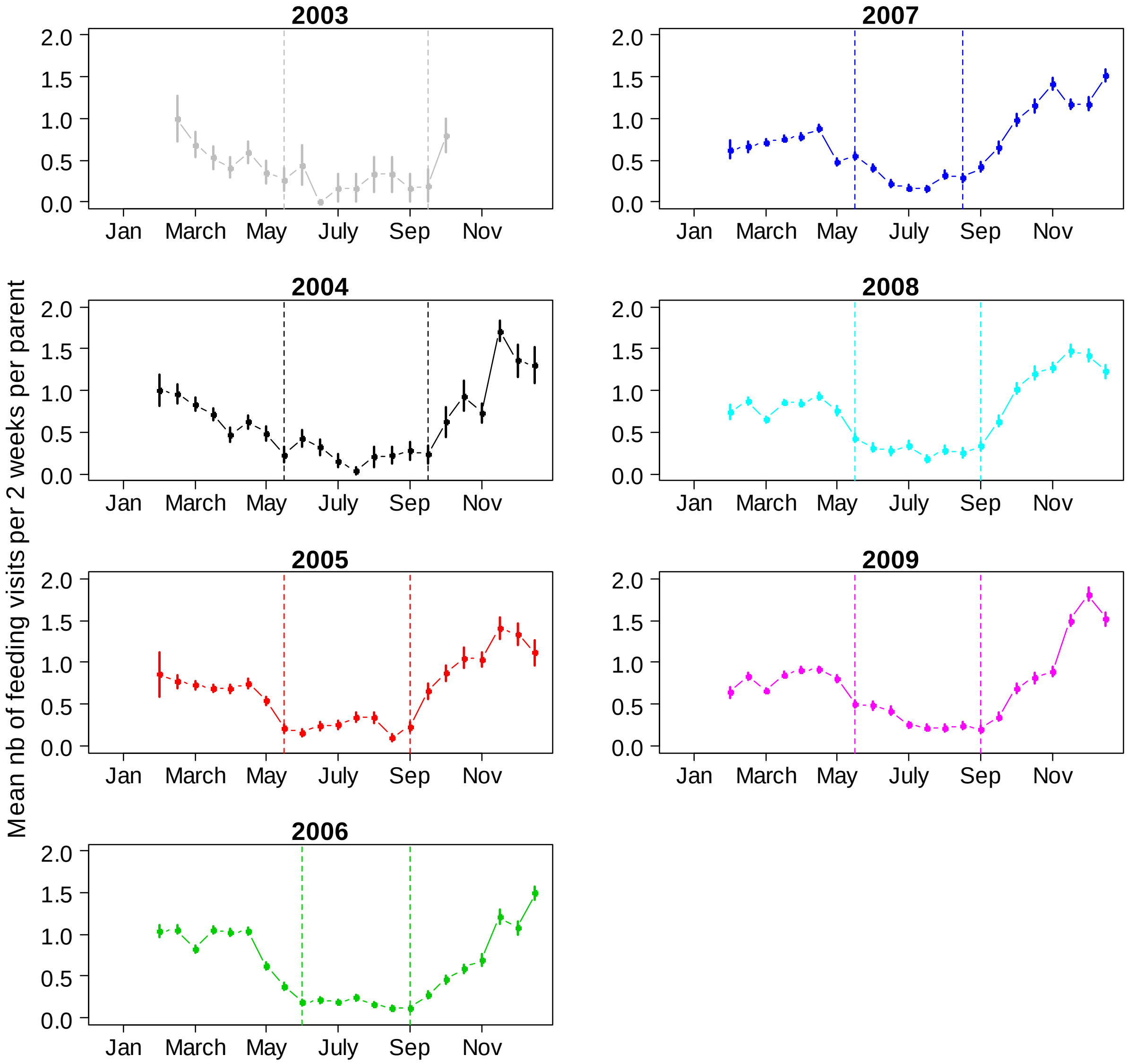

Figure VII - 11: *Mean number of feeding visits per 2 weeks per parent along the breeding season for each year. Bars represent standard errors and dotted lines indicate the winter period, obtained by breakpoint analysis.*

The number of feeding visits per 2 weeks per parent varied according to the year (χ^2-test with null model: $P < 0.001$, $n = 14616$, $N = 714$; Figure VII - 12). Differences between years were observed in each of the three periods but were not the same, *e.g.* in 2006, the number of feeding visits was higher than in 2005 during the first period, similar during the winter period and lower during the third period. These differences were not explained by SST averaged on the period considered (LMs: $P = 0.54$, $P = 0.29$, $P = 0.92$, $P = 0.66$ on the whole chick-rearing period, the 1st, 2nd and 3rd periods, respectively).

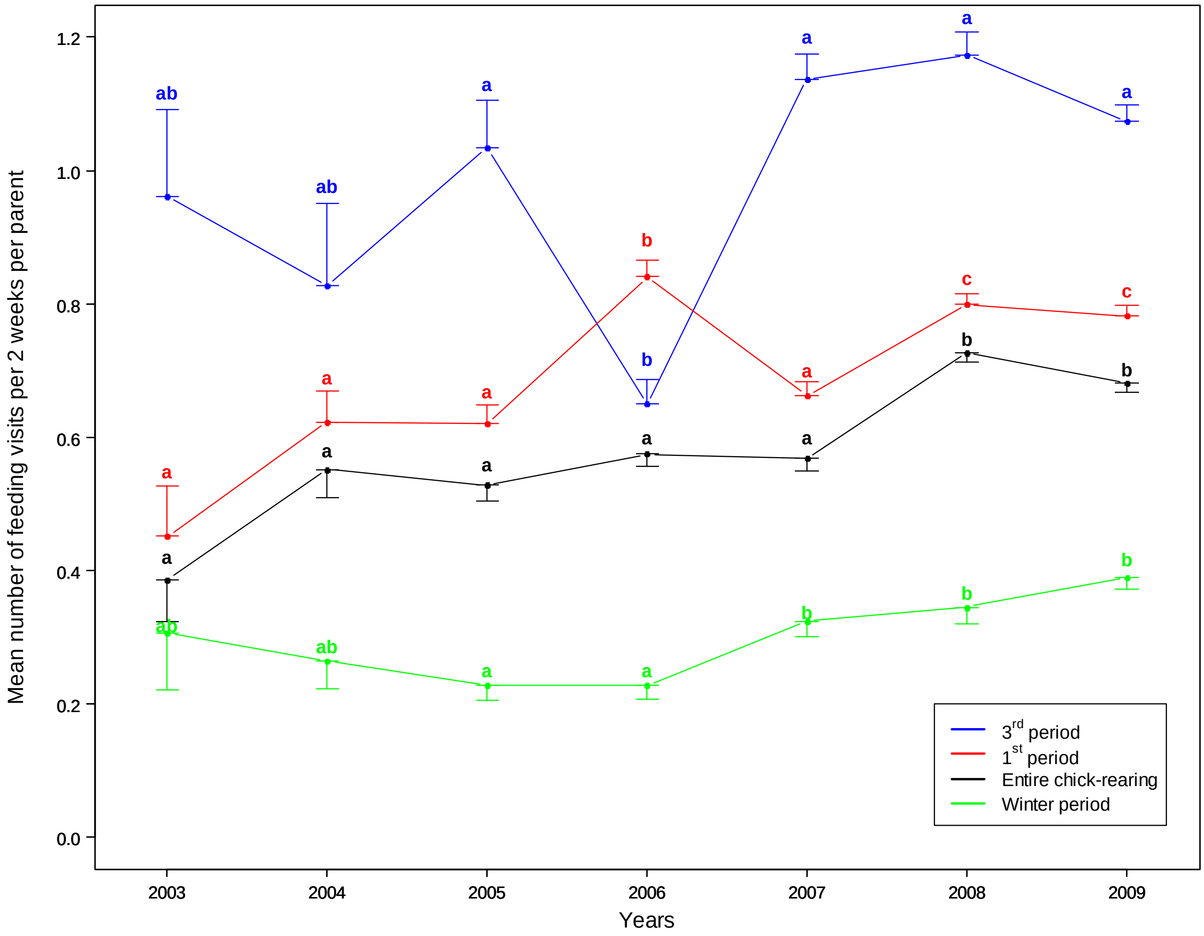

Figure VII - 12: *Mean number of feeding visits per 2 weeks per parent averaged on the season (black line), the first period (red line), the winter period (green line) and the third period (blue line) according to years.*
Years sharing no common superscript are significantly different.

Winter strategies

During winter, breeders appeared to display 4 different strategies. The first strategy (thereafter named '*absence'*) corresponded to parents that returned less than twice during the whole winter period and were absent for a very long time (*i.e.* at least 2 months, range: 61-158 days, mean = 104 days). Second, we observed birds that resumed long foraging trips in between which they stayed a few days (less than a week) in the colony (named '*foraging trips'* thereafter). Third, some birds were observed to combine both strategies by either resuming foraging trips at the beginning of winter followed by a long absence or by absenting for a long period followed by foraging trips (absence: 45-97 days, mean = 68 days, strategy called '*foraging trips with one long absence'*). Finally, the last strategy observed was the one we called '*blocks*', as birds alternated between one very long trip (26-85 days, mean = 52 days), a long sojourn on land (10-59 days, mean = 25 days) finished by another long trip (9-123 days, mean = 56 days). This last strategy was distinguished from long foraging trips or absence due to the long period spent on land at their return to the colony. During that time, parents did not stay continuously in the ANTAVIA sub-colony and went in and out of the sub-colony with trips out of the sub-colony lasting less than 3 days. The most common strategy was the achievement of '*blocks*', while the least observed was that of long '*foraging trips*' (Figure VII - 13 A).

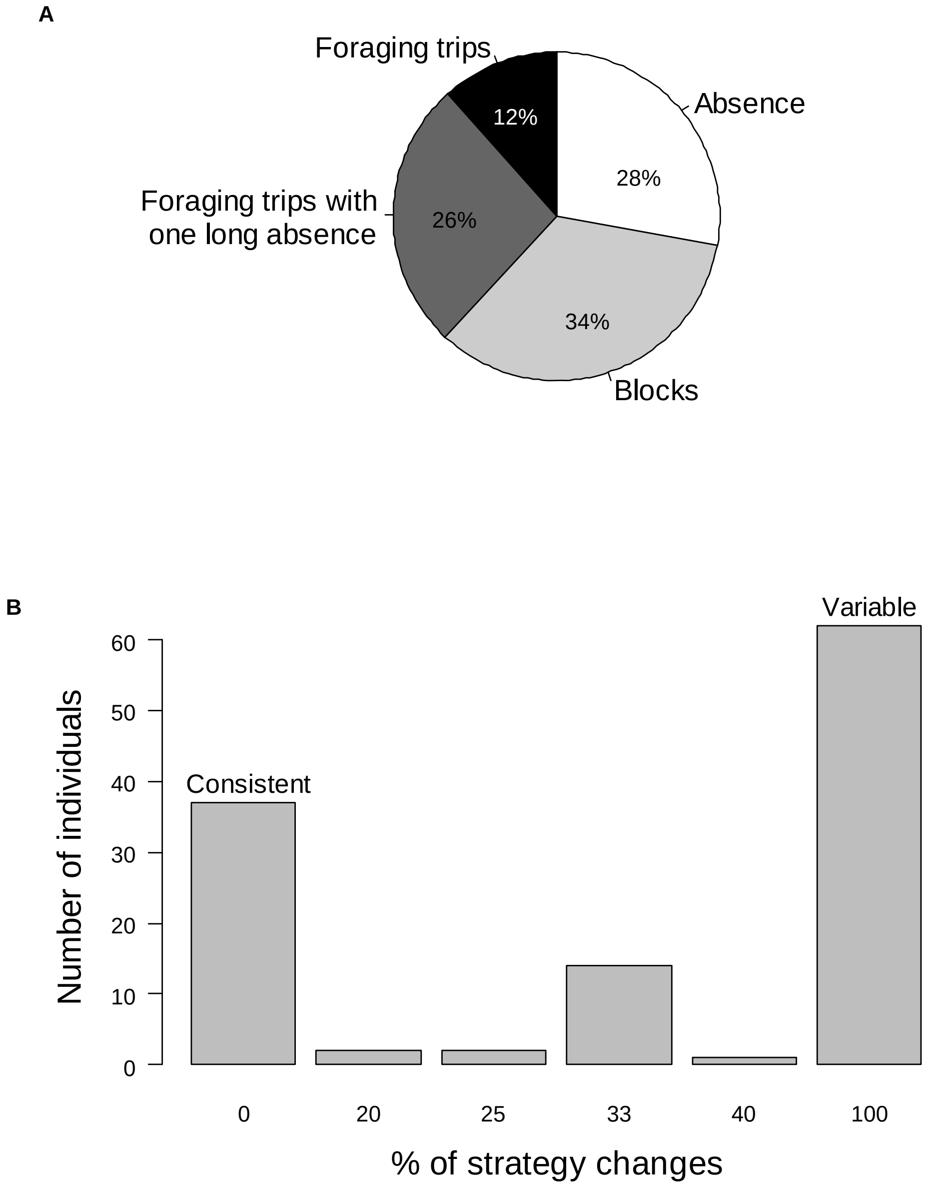

Figure VII - 13:*Winter strategies.* ***A)*** *Repartition of these strategies on 521 winter events (N = 369).*
B) *Consistency in strategies for the 118 individuals monitored more than twice.*
This is represented by the percentage of changes of each individual (i.e., % = 100 means that the individual changes of strategy each winter).

These strategies were not explained by individuals' age but did vary according to sex (χ^2 contingency test: $P < 0.001$). In proportion, females achieved more '*blocks*' and were more '*absent*' compared to males, while males achieved long '*foraging trips*' (with an absence or not) more often than females. Birds achieving '*foraging trips*' were of bigger structural size than birds achieving '*blocks*' or being '*absent*' (pairwise Wilcoxon tests: P = 0.006). Yet, these differences were not apparent when investigating birds of the two sexes separately. Further, focusing on birds monitored over at least two breeding seasons, we observed that most of them changed their strategies between breeding seasons at least once, however some 31% kept the same strategy (Figure VII - 13 B). The strategies used varied according to years (pairwise χ^2 contingency tests: 2006 differed from all other years but no other significant differences were observed; Figure VII - 14).

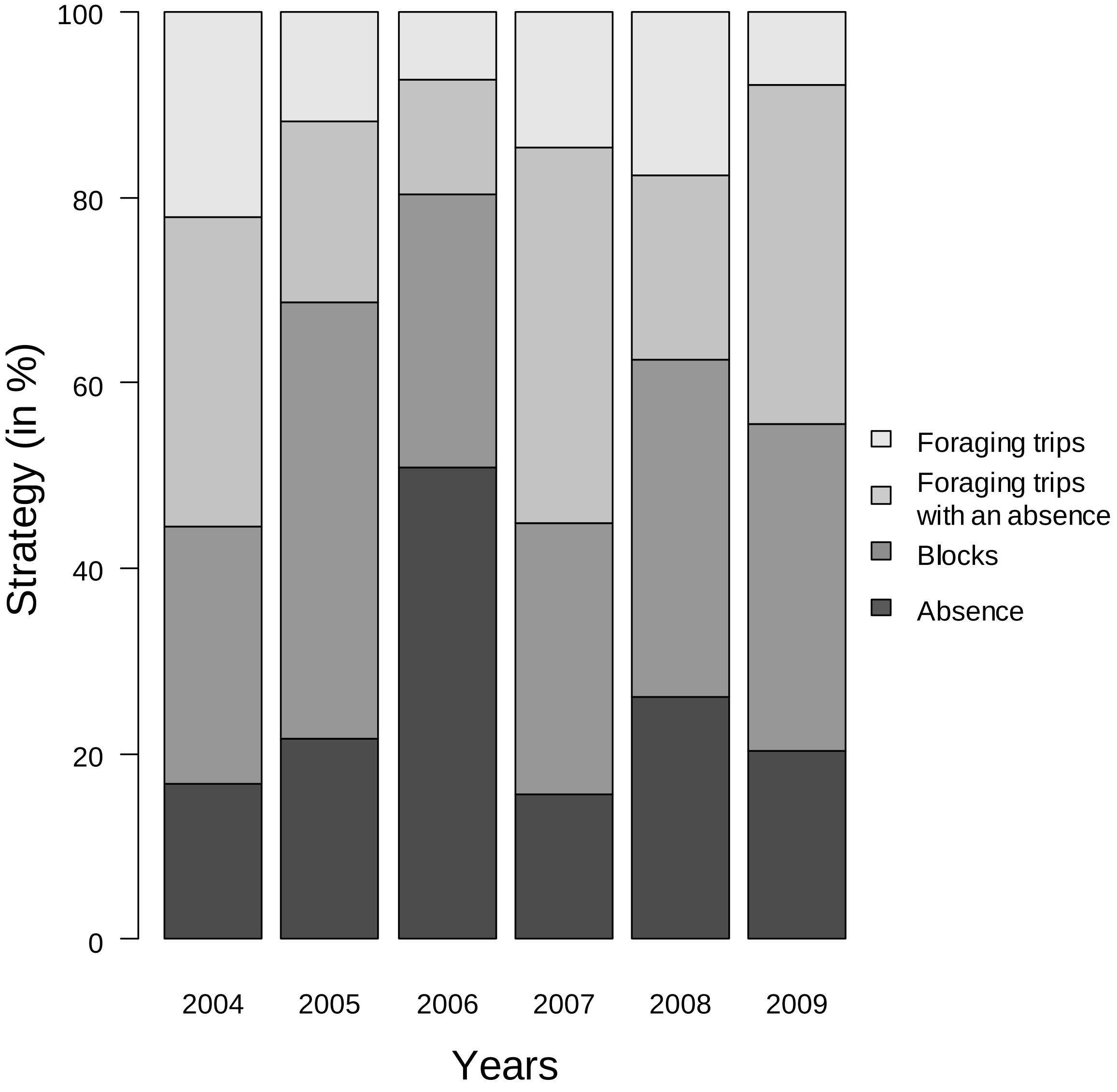

Figure VII - 14: *Winter strategies used depending on the year.*

Breeding success was affected by these strategies ('*absence*': 0.65 ± 0.04, '*Foraging trips*': 0.72 ± 0.06, '*Blocks*': 0.76 ± 0.03, '*Foraging trips with an absence*': 0.86 ± 0.03; GLMM: χ^2 test with null model: $P < 0.001$, n = 521, N = 369).

Discussion

In this study, we highlighted three different periods of chick rearing based on the feeding behaviour of parents. Our results support previous studies, showing that after thermal emancipation of the chicks, parents return regularly to feed them until winter, then parental feeding visits decreased (Barrat 1976; Weimerskirch *et al.* 1992 Descamps *et al.* 2002), resulting in a fasting period for chicks (Barrat 1976; Cherel *et al.* 1987; Weimerskirch *et al.* 1992; Descamps *et al.* 2002). Our results here confirm those of Descamps and colleagues (2002) conducted on 50 birds showing that parents returned more often to the colony during winter than previously thought. The automatic monitoring system yields a high recapture probability and may explain these results. Further, we found that 16% of the monitored individuals did not return between the 15th of May and the 1st of September. The probability for a chick to fast for the whole winter period, *i.e.* that neither of its two parents return, is thus lower than 16% (equal 2% if parents are independent). This is much lower than the 48% of fasting chicks observed in Weimerskirch and colleagues' study (1992). An interesting result when focusing on these fasting events is the fact that they were distributed over a wide range of individuals rather than concentrated on a few, suggesting that it is not related to an intrisic parental strategy or a parent low intrinsic quality but rather depends on the punctual condition of the parents. Focusing on this winter period, poorly studied until now, we highlighted the existence of 4 different parental strategies from an almost complete absence of the parent to regular foraging trips (though of longer duration than those performed in the first and third chick-rearing periods). While age did not affect these strategies, we found that males conducted more '*foraging trips'* (with or without an absence) strategy than females, which were more likely to use the '*absence*' or '*block*' strategies. In this latter most-observed strategy (34%), parents left the colony for more than a month and a half, long enough to reach the productive Marginal Ice Zone (birds monitored to go there by TDR in a previous study conducted 2-month trips on average and spent between 14 to 43 days in the MIZ; Charrassin & Bost 2001) before returning to, and staying for a relatively long period of time in the colony. On average parents stayed almost a month in the colony during this period, leaving the monitored sub-colony for less than 3 days at a time. During this period, parents probably rely on food reserves accumulated during the previous long sojourn at sea but may also feed opportunistically in the bay or close to the colony. This could be beneficial for the chicks ensuring them of food intake for almost a month, as parents are thought to forage for their chicks close to the colony (Cherel *et al.* 1993b; Bost *et al.* 2004). After this period, parents return at sea for a long trip of almost two months probably to rebuild their body reserves (see Saraux *et al.* 2011d). The strategies used during winter affected the resulting breeding success. Birds which were mostly '*absent*' during winter exhibited a lower breeding success. Yet, interestingly their success was far from inexistent (BS = 0.65 ± 0.04 of success for birds reaching winter and using the '*absence*' strategy), suggesting that either the partner compensated for this absence or that the chick hold the fast. The proportion of these strategies slightly varied in between years with only one year significantly differing from the other (2006).

Following winter, parents resume feeding activity and exhibit the highest rate of feeding allowing chicks to complete their growth and fledge. Our continuous monitoring of more than 800 individuals provided us with an accurate timing of the winter low-feeding period that appears shorter than in previous studies (mid-May to early September compared to mid/end April to September/October in Barrat 1976 based on 3 chicks and Weimerskirch *et al.* 1992 on 41 chicks). The inter-annual variability in this timing was low as if the winter period was fixed. Additionally, the pattern of feeding visits along the chick-rearing period and timing of the three periods seemed very consistent, as it did not change according to parent sex, age or breeding timing. Age is often associated with increasing foraging efficiency (*e.g.* Zimmer *et al.* 2011) and increasing breeding experience (*e.g.* Nisbet & Dann 2009), so that older parents may have tried to delay the first winter trip in order to provide their chick with higher amounts of reserves to hold the subsequent fast. Similarly, chicks of late breeders would be younger than and not as developed as early chicks when reaching the winter period. Late breeders may thus have attempted to delay the first winter trip to increase their chances of breeding success. Yet, king penguins are a long-lived species and as such are expected to favour their survival over their breeding success (Stearns 1989). This may explain the prudent strategy observed and the absence of delayed entry in winter (prudent parent: Drent & Daan 1980). Interestingly the winter period timing was not related to seasonal changes in Sea Surface Temperature. Indeed, the decrease in the feeding visit rate at the onset of winter occurred before the decrease in SST (about a month before). King penguins forage at the Polar Front during summer but travel much further during winter even crossing the northern limit of the ice pack (Charrassin & Bost 2001; Bost *et al.* 2004). This change in foraging areas has been suggested to be driven by the seasonal vertical migration of the main prey of king penguins, *i.e.* myctophids, which dive to 200-400 meters during winter (Kozlov *et al.* 1991). According to Kozlov and colleagues (1991), myctophid abundance at accessible depth declines as early as April, explaining the decrease in feeding visits we observed between April and May, as parents may begin to achieve longer trips to more distant areas. Similarly, in spring myctophid abundance is still relatively low but their distribution span over a high vertical extent suggesting that penguins could forage again on myctophids. Again, the increase of parental feeding visits at the end of the breeding cycle occurs before SST increases (about 2 months before). This example shows that SST is not a good predictor of prey availability at a small temporal scale and that it cannot be used to explain king penguin feeding visits at such a small scale.

The average number of feeding visits in each period did vary according to a wide set of factors. Males returned more than females to feed the chick during winter. Conversely, early breeders exhibited a higher number of feeding visits than late breeders, both during the first and third periods but not during the winter period. Our results show that late breeders were not able to compensate for their late start by increasing the rate of feeding visits or by delaying the beginning of the fast. Therefore, late chicks may accumulate smaller reserves before the winter fast, explaining the very high mortality rate observed in late chicks (Weimerskirch *et al.* 1992). Finally, the number of feeding visits significantly increased with parents' age irrespectively to the period considered. More precisely, the number of feeding visits increased between age 4 and 8 before levelling-off with no apparent differences between age 8 and 11. The increase in foraging efficiency with age (Wunderle 1991; Zimmer *et al.* 2011) is usually explained by a lack of experience in young individuals (Wunderle 1991) explaining why differences disappeared after a while.

Finally, the average numbers of feeding visits of the different periods were not correlated. This suggests that a high feeding visit rate during the first period does not guarantee a high rate all along chick rearing (see for instance in 2006).

In conclusion, the flexibility in foraging strategies appeared very small in chick-rearing king penguins, which presented a very consistent pattern, in terms of feeding visit rate along chick-rearing, regardless of their sex, age and breeding timing but also of the years. Only the average amount of returns to the colony to feed the chicks varied, probably in response to different environmental conditions. Yet, SST averaged on each of the three periods did not explain the variations observed in the number of feeding visits. In the winter period, parents use four different strategies with a preference for two of them in females ('*absence*' and '*blocks*') and for the 2 others in males ('*foraging trips*' and '*foraging trips with an absence*'). Individuals appeared to change strategies often according to the breeding season. However, the proportion of the different strategies varied only slightly, so that they could be the response of individual state at that time rather than a general response of breeding individuals to environmental conditions.

Acknowledgements

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Chapter VIII ○○○○○○○●○○

Response to climate changes and population models:

Synthesis & Discussion

I. Summary of the main results

The overall object of this thesis was to investigate the plasticity of penguin responses to environmental changes. By considering 3 species overcompassing latitudes from polar to temperate environments, our aim was to obtain a representative assessment of the effects of climate and environmental change throughout the Southern Ocean ecosystems. The approach (*i.e.* RFID) used in our studies was unique, as it enabled to monitor penguins with minimal interference on their behaviour and activities (though a critical view of the technique is discussed below) in their natural environment, and as such provided powerful insight into the impact of environmental variables on their life-history traits. In the following table (see Table VIII - 1), I summarize the main results of our studies before moving on to a discussion on what insights those results bring to our current knowledge about the effects of climate change on penguins, and more generally on marine ecosystems.

Table VIII - 1 : *Summary of the main results of this work*

Species	Traits	Results
Little penguins 	Reproduction	• Unequal parental effort within most pairs, independent of sex and age but consistent through years ➔ a mirror of parental quality (Saraux *et al.* 2011 c) • Breeding success only slightly affected by average SST (Saraux *et al. in prep.)* • Breeding = combination of good and bad weeks, on which chick mortality is concentrated (Saraux *et al. in prep.)*
	Foraging strategies (Saraux *et al.* 2011 d)	• Existence of a dual strategy: alternation of short and long trips • Decision between short and long trips triggered by adult body condition • Short trips beneficial to the chicks / Long trips beneficial to the adults
King penguins 	Penguin Monitoring (Saraux *et al.* 2011 a)	• Long-term effect of flipper-bands on both survival and breeding • Interaction between climate and bands: banded penguins do not react the same way to climate as non-banded ones
	Juveniles (Saraux *et al.* 2011 b)	• High return rates • Returns in the 3 summers following fledging • Positive effect of SST on return rate • Quadratic effect of conditions during raising on return rates
	Reproduction (Saraux *et al. in prep.*)	• Important inter-annual variability of sex ratio at fledging • Fledging sex ratio bias increases with SST
	Foraging strategies (Saraux *et al. in prep.*)	• Changes in feeding visits of breeding adults along chick-rearing: 3 periods • Timing of low feeding (*i.e.* winter): mid-May to end of August, no differences ♂/♀, early/late and between years. Timing not affected by SST • 4 strategies during winter
Adélie penguins 	Juveniles (Saraux *unpublished*)	• High return rates • Differences in return timing according to cohorts
	Reproduction (Saraux *unpublished*)	• Inter-annual variability in number of fledglings in the colony independent of number of breeding pairs but explained by sea-ice conditions • Inter-annual variability in body mass but not in body size of fledglings

II. Effects of climate depend on the life-history traits & the species

As indicated in the above Table VIII - 1, **contrasted results were observed concerning the effect of climate on the three penguin species studied**. Warming trends either affected penguins positively (juvenile survival in king penguins, Article 3: Saraux *et al.* 2011b), negatively (breeding success and adult survival in king penguins Le Bohec *et al.* 2008a; breeding success in Adélie penguins, Box 1), or both positively and negatively according to studies (*e.g.* reproduction in little penguins, see Cullen *et al.* 2009; Article 5: Saraux *et al. in prep*). While contrasted results on the effect of climate on Southern Ocean top-predators have been reported in the literature between species or between populations of a same species (Forcada *et al.* 2006; Barbraud *et al.* 2011b), most of these results concerned population trends. Here, we focused our analyses on different life-history traits providing us with a better understanding of the mechanisms resulting in these contrasted results.

1) Difference between life-history traits within a species

The first notable contrasted finding concerns differences in response of juveniles and adults of a same population of king penguins to climatic variables. Most of the differences reported in the literature have been explained by differences between species biology or between climate changes occurring at different locations. Here, we showed that juvenile king penguins had higher return rates when SST was warmer (Article 3: Saraux *et al.* 2011b). This result opposes to the negative effect demonstrated on breeding success and adult survival (Le Bohec *et al.* 2008a). The effect of SST on king penguins is supposed to be mostly indirect, acting through a change in prey availability and distribution. However, little is known on juvenile whereabouts and their preferred prey. For instance, juvenile king penguins may exhibit different nutritional needs than those of adults in order to complete their growth (Partridge & Green 1985). A lack of experience may also force juveniles to be less specialized than adults, opportunistically changing the type of prey on which they forage. Foraging only for themselves, less energetic prey may be sufficient to their maintenance (Davies & Green 1976). In addition, juveniles are under fewer constraints than adults as they do not have to return frequently or in a given time space on land to breed. Juveniles are thus free to go and forage wherever it is more favourable. Barrat (1976) suggested that juveniles could go as far up north as the subtropical area. Our data also suggest that such an area could play a role for juveniles. Adult survival was shown to be negatively affected by warming in their winter foraging place (Le Bohec *et al.* 2008a). But, juveniles may spend the winter in completely different areas than adults, thus modifying the effect of climate and warming of the oceans on their foraging. This result shows that **a change in the environment can be integrated differently in individuals of a same species depending on their constraints** (here, central-place forager or not). Knowledge on juvenile feeding locations or even on non-breeding adult responses to climate would be valuable inputs for a better understanding of those results (see Chapter X).

2) Difference across species: *king and little penguin reproduction*

Previous studies have shown that latitudes could have an important role to play in the impact of climate on species (Hoegh-Guldberg & Bruno 2010). For instance, a recent study of Barbraud and colleagues (2011b) conducted on three seabird species of the Southern Ocean reported that the northernmost distributed species was predicted to be little affected by future warming, while strong declines are expected for the two more southerly species due to SST warming and decrease in sea-ice extent. Similarly, we found here that little penguin reproduction was slightly correlated with SST during breeding (Article 5, note that no correlation was found before with monthly values of SST), while SST is known to importantly affect breeding success of king penguins (Le Bohec *et al.* 2008a). Yet, SST has increased similarly in the last 100 years in areas around Phillip Island and Crozet ($\text{increase}_{1900\text{-}2000}$ in Phillip Island = 1.25 ± 0.14°C *vs.* increase in Crozet = 1.15 ± 0.09°C). Two hypotheses can explain these different responses facing a similar change. A first one could be that little penguins are now less sensitive to changes in SST due to the delay observed in their breeding phenology (Chambers 2004b; Cullen *et al.* 2009). This would explain why SST was a better predictor of breeding success in the past that nowadays (Cullen *et al.* 2009). Yet, this would be in contradiction with Cullen and colleagues (2009) predictions as SST warming is expected to lead to earlier breeding. Another point which seems important to highlight in this case comes from the breeding biology of the species. The breeding cycle of king penguin is long (more than a year) compared to that of little penguins (2/3 months) and frequency of feeding events is very different in the two species (Table VIII - 2). Little penguins are much smaller and both adults and their chicks cannot fast for as long as king penguin adults and chicks. Breeding success in little penguins is thus dependent on conditions every week during the 3 months of the breeding cycle and a good breeding season can deteriorate to a catastrophic one in a matter of weeks (Article 5). In contrast, king penguin chicks can fast for much longer (up to 5 months, Cherel & Le Maho 1985; Cherel *et al.* 1987) and their success depends on the average conditions along the season. Unfavourable conditions for a short time can be compensated by favourable conditions before or afterwards. Conversely, the average SST along the season should not be very meaningful for little penguins if the variability in environmental conditions (and more specifically oceanographic conditions) is important. Ropert-Coudert and colleagues (2009) showed that little penguin foraging was dependent on the presence of thermoclines that act as physical barriers for their prey. Thermoclines and water stratification are highly dependent upon wind condition and storms, which vary rapidly. Oceanographic conditions might thus change rapidly and affect breeding success much more than average SST.

Table VIII - 2: *Summary of relevant differences in breeding biology of king and little penguins*

	King penguins	**Little penguins**
Breeding cycle length	> 1 yr	~ 2/3 months
Feeding events	Not frequent (1 or 2 per 2 weeks and less during winter, Box 2)	Very frequent (mostly every day)
Chick reserves	Can fast for up to 5 months (Cherel & Le Maho 1985)	Entry in phase two after only 1 or 2 days (Article 5)
Temporal scale for climate	Integration on the whole season	Week by week

Depending on the biology of the species, the temporal scale at which we should look at the effect of climate can be very different, as illustrated here with differences in little and king penguins. Average trends can be less relevant than variability. Climate change has mostly been viewed as the overall average warming trend of our planet. However, there is growing evidence supporting that climate change should not only be visible in average trends but also translate in an increase of climate variability (see references in Morris *et al.* 2008). Ecologists have similarly paid more attention to the effect of changes in climate average than in climate variability (*e.g.* Easterling *et al.* 2000; Parmesan & Yohe 2003; Thomas *et al.* 2004). Yet, environmental variability might well cause vital rate variability and affect population growth rate (Morris *et al.* 2008). Stochastic demography theory predicts that an increase in variation of vital rates will negatively affect population growth and fitness (Lewontin & Cohen 1969; Pfister 1998). However, these predictions are not always verified mostly because vital rates affect differently population growth rate and because the equations established do not account for correlations between vital rates (Morris *et al.* 2008). An increase in variability may thus lead to decreased, increased or stable population growth rate depending on the shape of the functional relationship between the population growth rate and the environmental parameter considered (whether it is concave, convex or linear; Drake 2005). Studying the effect of environmental variability on vital rates is thus a critical issue for more accurate predictions of the effects of future climate change. Long-lived species seem to be less affected by environmental variability as their life-history traits could buffer against this variability (Morris *et al.* 2008). A study of several long-lived top predators (seabirds and marine mammals) of Antarctica recently showed that except for Antarctic fur seals, all the other species have been able to buffer their main vital rates against the effects of recent climate changes (Forcada *et al.* 2008). Fitness was optimized by keeping a low inter-annual variance in adult survival and propensity to breed, the two vital rates most affecting the population growth rate variability (Forcada *et al.* 2008). The longevity of penguins may thus help them in coping with climate change. Nonetheless, Forcada and colleagues (2008) warn about an increase in the climate fluctuations potentially leading to stronger repercussions on life-histories, especially for species exhibiting less flexible life histories in regard to their environment.

III. From individual strategies to population trajectories

Once the effects of climate on life-history traits are assessed, it is possible to combine them in order to obtain population trends under different climate scenarios. Population models presented in chapter I enable to summarize all the information in a single variable, the asymptotic long-term population growth rate λ. Future trends of the population can then be predicted and help in defining conservation measures, for instance.

1) Age structured models

As explained in chapter I, population models enable to translate results obtained on the individual to a population level in order to infer population trends. These models rely on partitioning the population on different groups of individuals, in which each individual is assumed to behave in a similar fashion. Partitioning of the population is usually conducted according to the life-cycle of the species and often relies on size, reproduction mode or age. In the particular case of age, the population is divided in age classes and population matrices are based on age-specific survival and breeding success, corresponding to Leslie matrices (Leslie 1945; Leslie 1948). This is a good model if age is the major driver of changes in survival and breeding success. The effect of age on life-history traits has been described in several species. In long-lived or slow species, sexual maturity is delayed for several years, so that it is important to distinguish between young individuals not contributing to the breeding success of the population and older ones. Additionally, survival and breeding success often increase with age (Wooller *et al.* 1990; Hamer & Furness 1991; Weimerskirch 1992), at least in the first years of life before peaking at middle age (Nisbet & Dann 2009; Zimmer *et al.* 2011). This could be due to increased experience (Marchetti & Price 1989; Wunderle 1991) but also to increased reproductive effort as the value of reproduction increases with age (Williams 1966). The reversed effect is also observed at the end of life, when breeding performances or survival decrease with age due to senescence[24] processes for instance (Ericsson *et al.* 2001; Reid *et al.* 2003 for reproduction; Loison *et al.* 1999; Ericsson & Wallin 2001; Cameron & Siniff 2004; see also Jones *et al.* 2008 for a more complete review on senescence in vertebrates). These two opposed processes result in a quadratic effect of age on breeding performances or survival (Hamer & Furness 1991). In penguins, age also seems to be an important factor explaining the vital rates of a population. For instance, foraging trip duration and consequently breeding success increase with age in king penguins (Le Vaillant *et al.* unpublished). In little penguins, breeding and foraging success have been shown to increase before levelling of around 8 yr-old (Nisbet & Dann 2009, Zimmer *et al.* 2011). A quadratic effect has also been found in most of breeding performance indicators in this species (Saraux *et al. in prep*). Therefore, we used age-class matrices to predict population trends in king penguins.

2) Population dynamics and previsions according to future climatic scenarios

A previous study in 2008 showed that both adult survival and breeding success were negatively affected by SST warming (Le Bohec *et al.* 2008a). However, this study was conducted on adult birds of unknown age. Thus, we conducted new analyses with

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[24] SENESCENCE: Decline in physiological functioning with age that results in a decrease in reproductive rate, increase in mortality rate or both (Ricklefs 1998).

demographic models based on age-class matrices to have a more robust analysis of the risks for the population facing climate change. Not surprisingly, warming was showed to negatively affect population growth rate in the same colony. What is more disturbing, if not alarming, was the quasi-extinction[25] risk predicted for this population before the end of the 21st century (Le Bohec *et al. in prep,* see box below and appendix 3). Every scenario (and associated SST increase), except the completely utopian case of no warming at all, led to quasi-extinction before 2096.

King penguins on the verge of extinction? (see Appendix 3 for the complete version)

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Using data available for non-banded king penguins of known age, we built annual stage-structured matrices from 1999 to 2007 (Caswell 2001) to assess the population changes of the past decade in relation to climate variability. Elasticity analyses show that population growth rate is mostly sensitive to changes in temperature-dependent survival and breeding success of adults but also in post-fledging survival. Further, simulated population trajectories under environmental stochasticity coupled with environmental change scenarios indicate that the studied population should reach quasi-extinction before the end of the 21st century (between 2055 and 2096 depending on the warming scenario; Figure VIII - 1).

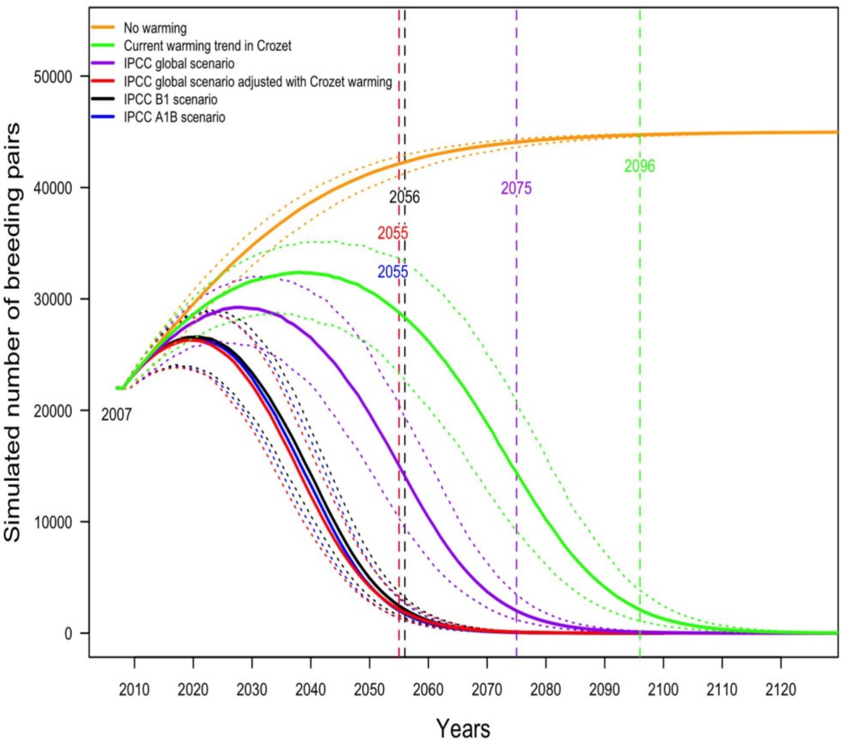

Figure VIII - 1: *Simulated Markov chain population trajectories (1000 runs) of the studied king penguin population under environmental stochasticity coupled with climatic scenarios.*

Growth rates were obtained from population matrices where adult breeding success and survival were dependent from SST. Global change was represented by linear trends in SST with a slope issue from 6 different scenarios, in which stochasticity was added based on variance of SST of the last century

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[25] QUASI-EXTINCTION: decline of 90% of the initial population size

3) Could non-included parameters change such previsions?

As for any predictive model, the population trends predicted above are based on assumptions and simplifications, which may all introduce errors on the predictions. Here I attempt to review the simplifications made in light of our findings, and see whether they may significantly change the dramatic results we found on future population trends for the emblematic king penguin.

> *« Le simple est toujours faux. Ce qui ne l'est pas est inutilisable. »* ***Paul Valéry***
> *(The simple is always false. What is not is unusable).*

The matrix used for such calculations was the following one:

$$
A_t = \begin{pmatrix}
0 & 0 & 0 & OBS_4 & OBS_5 & OBS_6 & OBS_7 & OBS_8 & OBS_{Ads} \sim SSTcro \\
S_{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_{23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & S_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_{45} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & S_{56} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & S_{67} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & S_{78} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{89} & S_{Ads} \sim SSTmiz
\end{pmatrix}
$$

Age classes were used, which seems pertinent for penguins, as explained above. However, all adults older than 8 year old were pooled together into a single age class. Breeding success and survival stopped increasing and appeared to level off around this age, explaining the use of separate classes for younger ages but not afterwards. Yet, this does not allow for an eventual decrease of the performances after a certain age. King penguins are long-lived seabirds, which could live for more than 20 years. Thus, senescence presumably appears very late in their life time (Jones *et al.* 2008), which has prevented us to study it for now (*i.e.* not enough known-aged old birds). The model then considers that old birds contribute the same to the population breeding success and survival. However, this simplification is an optimistic one overestimating population growth rate, meaning that reality could be even worse.

Further, the basis of age-class population models is the assumption that all individuals of one class behave the same way and here respond the same way to climate. Yet, each individual is different and if the heterogeneity is high in an age class, such a model should mask the possibility of different reactions. For instance, breeding Adélie penguins appear to be able to compensate for an earlier reduction in sea-ice extent by switching prey (Beaulieu *et al.* 2009a). Yet, we showed (box 1) that this was not the norm and such a behaviour could be reserved to individuals of high quality. Depending on their quality, individuals would consequently not respond similarly to climate modification. Similarly, we showed in little penguins that parental effort appeared to be the mirror of parents' quality, *i.e.* parents of good quality are able to maintain a high level of parental care even in unfavourable conditions, while parents of lower quality return less often to care for their chicks (Article 4: Saraux *et al.* 2011c). Inter-individual differences (often described as individual quality, see Wilson & Nussey 2010) might thus play an important role in the response to climate that is not accounted for in these models.

Additionally, the overall breeding success considered in this matrix corresponds to the proportion of breeders times the breeding success of the individuals that breed. The proportion of breeders has been kept constant in this model. However, we observed in chapter VI (Article 6) a possible increase of the bias in sex ratio with SST. In case of warming, the increased bias in sex-ratio may lead to an unbalanced population, where part of the population would not be able to breed due to the absence of potential partners. This would decrease the proportion of breeders and therefore the overall breeding success, resulting in a diminution of the population growth rate. These data have to be taken carefully, as this corresponds to sex ratio at fledging and we could not infer the consequences on the operational sex ratio and as we have no explanations for this non-directional (either towards female or towards male) increase in bias. In any case, this conducts again to worse scenarios and cannot infirm the extinction previsions.

Importantly, only adult survival and breeding success were allowed to respond to climate, the other parameters being fixed. In chapter V, we observed that the relationship between juvenile survival and SST was opposed to that observed in adults, a warming leading to an increase in the return rates of the birds (Article 3, Saraux *et al.* 2011b). This may well attenuate the population decline observed with warming. According to elasticity[26] analyses, changes in survival at early ages (≤ 5 yr-old) may compensate the effect of similar changes in adult survival on population growth rate (Le Bohec *et al.* in prep; Appendix 3). Further,

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[26] ELASTICITY: proportional response to proportional or relative, rather than absolute, perturbations. Here this corresponds to proportional changes in population growth rate to proportional changes of vital rates (*e.g.* how much would λ respond to a 10% change in adult survival?).

juvenile survival is often thought to vary more than adult survival in long-lived species (Gaillard & Yoccoz 2003) so that the effect of climate on this parameter could play an important role in future population trends. However, the relationship between juvenile survival and SST obtained in chapter 5 was not as strong as the one obtained for adult survival (lower explained deviance), so that the effect of warming on juvenile survival may be attenuated.

Finally, another process has not been accounted for in these analyses. Integrated effects of environment are described in chapter I and correspond to delayed effects such as the effect of early-life conditions on later life-history traits. In chapter V (Article 3, Saraux *et al.* 2011b), we showed that conditions during the rearing period had a quadratic effect on juvenile return rate in king penguins. Juveniles fledged under unfavourable conditions exhibited low return rates in the following three years. The direct effect of climate experienced in the first year of life is visible through the dependence of breeding success on SST but the further consequences on later life-history traits such as survival of the following age classes through different phenotypic quality (*e.g.* body size) is not accounted for in the model. Additionally, if mortality increases due to warming, selection mechanisms should occur earlier than before, and only the best individuals would remain (Newton 1989; Martin 1995). This may lead to an increase in older age class survival rate and breeding success, consequently reducing the decline in population growth rate. Selection mechanisms may explain why return rates did not increase linearly with favourable rearing conditions. King penguin chicks fledged under favourable conditions may be of highly heterogeneous quality as a result of low selection pressure, affecting later survival of these individuals (Article 3: Saraux *et al.* 2011b; see also Braasch *et al.* 2009 in common terns). Early conditions in life may thus affect later age classes either positively through increased phenotypic quality or negatively through selection mechanisms.

Some parameters (juvenile survival and selection mechanism) may improve population growth rate of the king penguin population and let us hope for better scenarios. However these are small improvements which are probably not enough to reverse the scenarios of declining population of king penguins.

IV. Potential adaptations to climate change?

Importantly, it should be noted that previsions, such as those above, assume that animals will react in the future to the same extent as they did during the past, *i.e.* they will **not** adapt in response to predicted changes. However, penguins might react differently to global warming and even be able to cope with climate change if they could either adapt through micro-evolution or phenotypic plasticity (Nussey *et al.* 2005; Nussey *et al.* 2007; Visser 2008, Charmantier *et al.* 2008) or disperse.

> *« It is not the strongest of the species that survive, nor the most intelligent, but the one most responsive to change »*
> ***Charles Darwin***

1) Micro-evolution & phenotypic plasticity

Population models (such as the one above) typically assume that the relationships established between organisms and their environments do not evolve through time (Grémillet & Boulinier 2009). However this is highly unlikely to be the case as functional relationships may shift due to phenotypic plasticity. For instance, as mentioned in chapter II, modifications in breeding timing and growth stages of penguins have occurred in some species as the climate changes, whether this shift results from a passive adaptation to environmental condition or corresponds to an active decision taken by the birds. Flexibility in behaviour is often a pre-requisite of phenotypic plasticity. In seabirds, foraging is one of the key mechanisms on which climate change should have an effect through availability and distribution of prey. Offshore seabirds are usually thought to present much more flexibility in their foraging strategies than inshore birds. Typically, inshore birds make short trips close to their colonies without much variation. Still, we showed (chapter VII, Article 7: Saraux *et al.* 2011d) that little penguins, a good model for inshore birds, exhibit flexibility in their foraging strategies during the post-guard stage. Indeed they alternate between short and long trips for two distinct purposes, short trips being mostly for the chicks, while long trips enabled them to rebuild their reserves (Article 7: Saraux *et al.* 2011d). This enables them to raise their offspring without jeopardizing their own survival and to respond to environmental variability by adjusting the number of short trips conducted in a row. Plasticity in foraging strategies have also been shown in Adélie penguins, which adjust their foraging to maintain a sufficient body condition in years of contrasted environmental conditions (Ballard *et al.* 2010). For instance, Adélie penguins have been shown to be able to adjust their diet to krill quality and abundance by switching towards other prey such as fish in years of early sea-ice retreat (Beaulieu *et al.* 2009a). Yet our results suggest such plasticity only concerns part of the population, so that breeding success of the whole population is affected by sea-ice retreat (Box 1). Nonetheless, the fact that some individuals are able to adjust their foraging behaviour in the population shows that phenotypic plasticity exists in this species, which thus provides adaption potential to climate change. These results indicate that inshore penguins may well use phenotypic plasticity as much as offshore birds. Surprisingly, foraging of king penguins seemed less flexible, with winter longer trips occurring always in between the same dates whatever the year (Box 2).

If phenotypic plasticity can ensure responses to changes in environment, there are few chances that they account for adjustments to extreme climatic events. Indeed, environmental variability can affect differently life histories depending on its predictability (Levins 1968). Predictable variation may select for phenotypic plasticity, where reaction norms express the usual range of variation experienced by populations. However, extreme events are so rare that they may provide no selection at all to cope with such situations (Moreno & Møller 2011).

Beyond phenotypic plasticity, recent studies highlighted the importance of considering microevolution and its effect on individual and population responses to climate change (Visser 2008). A plastic genotype is typically unable to develop as extreme a phenotype as it is possible to produce via microevolutionnary responses. Microevolution can thus become the only way for organisms to adapt to environmental changes so important that plastic responses cannot anymore counteract the loss of fitness (Gienapp *et al.* 2008). Long-lived species respond slowly to new selective pressure due to their long generation time, and may consequently present a very slow rate of adaptation (Hughes 2000; Visser 2008). However, speed of current change in global climate has only rarely been observed before (IPCC 2007). Therefore it is unlikely that microevolution influences seabird responses as much as phenotypic plasticity, but it remains a largely unexplored and yet fascinating research avenue (Grémillet & Boulinier 2009). The possibility of adaptation through micro-evolution may play a role in the penguins' responses to climate change for those species with lower generation time, such as little penguins but could probably be dismissed for longer-lived species such as king penguins.

Finally, demographic strategies are often perceived as fixed. A species has its own place on the slow-fast continuum for instance. However, these strategies result from complex evolutionary trade-offs between demographic parameters, which depend on the environmental pressures applied to the organisms. Thus, demographic strategies may evolve. The effect on population trends of potential adaptations or adjustments of king penguins through changes in breeding behaviour have been investigated. Two situations were simulated (Figure VIII - 2), the first one corresponding to a shift in the selection gradient toward faster species through earlier recruitment and the second one to a decrease in the cost of reproduction by introducing sabbaticals. In this last scenario, birds only breed every second year but always early in the season with a higher breeding success. In both cases, the quasi-extinction was delayed but not stopped and the granted delay was smaller than 10 years (Figure VIII - 2).

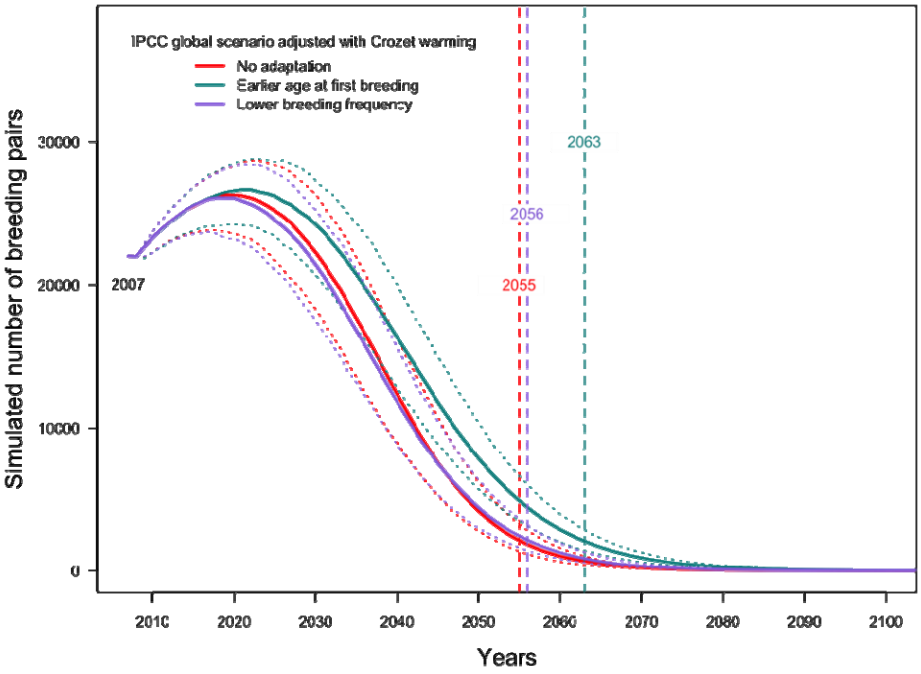

Figure VIII - 2: *Simulated Markov chain population trajectories under a climatic scenario with potential adaptations.*
Blue line corresponds to earlier recruitment in the breeding population. Purple line corresponds to king penguins breeding every second year with a breeding success of early breeders

2) Dispersal

Flightless penguin's migratory abilities do not match with those of flying procellariiformes species. For example, sub-Antarctic penguins are bound to their few, remote breeding sites and most of them cannot increase their foraging range during the breeding season if resources availability decreases around the sub-Antarctic islands. Furthermore, Antarctic penguins will see their geographic breeding range shrink with no possibility to go further south. For instance, a range contraction is already observed in the Adélie and emperor penguins on the

Antarctic peninsula, with the disappearance of most of the northern breeding sites (Forcada & Trathan 2009). Though dispersal and range shift are expected to increase in the near future, there are little chances that those factors will enable penguin population to establish themselves under more favourable conditions on a long-lasting basis.

To sum up, the results presented above lead to the worrying conclusion that the king penguin population of la "Baie du Marin" breeding on Possession Island, Crozet Archipelago, is likely to be on the verge of extinction, and may well become actually extinct within the next couple of centuries. Whereas there may yet be few improvements brought to our simulations, and at least limited plasticity in the behavioural responses of those animals to increasingly warming temperatures, the outcome certainly looks gloomy. Nonetheless, one should bear in mind that those predictions concern one of the many king penguin colonies to be found in the Southern Ocean. In addition, human settlements have been in close contact with this colony for over 50-years, and potential deleterious effects also should be accounted for (see chapter IX). Further studies are urgently needed to investigate whether such results extend to all populations of the species, and whether we are facing yet another loss in our natural heritage.

V. What to do? What are our roles as scientists?

The predictions presented above are frightening. King penguins (at least those of this colony) will go extinct within less than 100 years (before 2096). Of course the date has no real meaning and as for the SRES scenario, the probability that any of these extinction scenarios occurs is highly uncertain. However, there are strong chances for the reality to be in the range of these scenarios. We know that this is the situation we face for most of our biodiversity, but putting numbers on it gives reality on something we try to forget to lighten our conscience. ***So what should we do, what are our roles as scientists?***

Scientists are supposed to relate the facts they observed and to stay out of politics, management decisions, *etc.* However, when the facts are so serious that the quasi-totality of the scientific community accords to say that we are facing the sixth big extinction crisis and that this is all because of a single species (humans), I wonder whether we do not have to go further. Popularization of science, transmission of the information to the widest public possible under a relatively simple form, is often considered as a depreciated task. However, if we want things to improve, people need to be conscious of the problem and what are at stake.

> *« La science ne doit pas être un plaisir égoïste: ceux qui ont la chance de pouvoir se consacrer aux études scientifiques doivent être aussi les premiers à mettre leurs connaissances au service de l'humanité. »*
>
> ***Paul Lafargue & Wilhelm Liebnknecht***
>
> *(Science should not be a selfish pleasure: those who have the chance to devote their time to scientific studies should also be the first ones to let mankind profit about their knowledge.)*

On a conservation point, the International Union for Conservation of the Nature (IUCN) statuses may need to be re-evaluated. For instance, no penguin species, as to 2009, is listed as critically endangered. However, recent studies, such as those on the most emblematic species, the emperor penguins (Jenouvrier *et al.* 2009a), are causes for concern: indeed, these models predict a high risk of extinction in the forthcoming 50-100 years, despite this species being flagged as least concerned today. King penguins as well are currently listed under the status of least concern. However, in the light of the above alarming findings, the king penguin should be listed as vulnerable or endangered.

Unfortunately, we are unlikely to reverse current climate change in the short-term and we should thus concentrate to reduce the other human-induced effects on marine ecosystems. In the Southern Ocean, human activities correspond to fishing, tourism and science. The direct effect of tourism and science on penguins is discussed in the next chapter and can affect penguin physiology or breeding habitat. Protective measures, such as minimal distances of approach for tourists, protected areas, interdictions of plane or helicopter flying over should reduce such impact (Giese 1998; Fernandez-Juricic *et al.* 2001). However, this pressure is still relatively low and most of human-induced impacts occur in the marine environment. General agreement is that seabirds would greatly benefit from an extended use of Marine Protected Areas (MPA; Grémillet & Boulinier 2009). For instance, dozens of colonies have been designated Antarctic Specially Protected Areas, internationally recognized under the Antarctic Treaty. However, such a network is difficult to set-up as seabirds can cover huge distances between their breeding site and foraging areas. A thorough scientific knowledge of foraging areas is thus required to be able to determine the boundaries of MPA. Another complexity results from the fact that this area can lie in territorial waters of different countries. Until now MPAs are national entities managed by countries. Propositions of common international MPAs would improve their management and allow for continuous areas to be protected. The focus here is on seabirds and penguins, however such protected areas would also benefit to the whole ecosystem. Institutions such as the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR) is thus of prime importance to coordinate the different protection measures. CCAMLR is responsible for the management of sustainable and rational harvesting of all living resources in the Southern Ocean, with the exception of seals and whales (under the Convention for the Conservation of Antarctic Seals and the International Whaling Commission, respectively). Ecosystem management and in particular fisheries management must be conducted with an understanding of the ecological consequences of climate change (Trathan & Agnew 2010). Again this implies a good scientific knowledge of these consequences. In a recent review, Trathan & Agnew (2010) strongly suggest CCAMLR to achieve a risk assessment before setting new rules of management and to study with special care the risk associated with increased accessibility due to the decrease in sea ice cover.

Penguins living under higher latitudes have greater interactions with fisheries. African penguins for instance have been decreasing following overfishing of sardines, *Sardinops sagax,* in the Benguela ecosystem (Crawford 2007). Little penguins were also affected by the disappearance of their main prey in the 90s, though they adapted by moving onto new dietary items and recovered in late 2000s (Chiaradia *et al.* 2010). Models used to help fishery management and calculate allowable catches need to incorporate seabirds and functional relationships between fish and their predators to ensure a sufficient quantity to be left for predators. Allowable catches should be calculated in order to ensure not only fish sustainability (though this would already be a good step for most of marine ecosystems) but also seabird productivity.

In summary, scientists "*have the exciting yet daunting task*" (Grémillet & Boulinier 2009) to participate in conservation plans of marine ecosystems through definitions of both appropriated MPA and conservation measures, especially concerning fisheries.

Chapter IX ○○○○○○○○●○

Critical view of this work

I. Use of penguins as bio-indicators

In the second chapter, I advocated the use of penguins as bio-indicators of their ecosystems. As I explained in this chapter, information on other trophic levels is scarce and difficult to obtain and there is an increasing need for species representative of their ecosystems. However, ecosystems are complex entities with numerous interactions between the species that compose them and one single species cannot translate every change of its ecosystem.

Penguins and other seabirds are often considered relevant indicators because of their place on top of the food chain. However, penguins are **not really top-predators** as eggs and chicks are predated by other birds, such as giant petrels and skuas, while adults can be predated by orcas or leopard seals in sub-Antarctic and Antarctic penguins (see Ridoux 1994 for instance or Pitman & Durban 2010). In some populated temperate areas, they can also be predated by non-native animals such as dogs and foxes. Still we decided to use them as indicators as they seemed one of the best compromises, being close to the top (thus integrating most of the changes in the food chain), abundant and widespread and easy to monitor as they come on land compared to orcas or leopard seals for instance.

The idea of using top-predators (or animals close to the top in this work) is that they should integrate the changes occurring lower in the food chain. However, this relies on the assumption that higher trophic levels are mostly controlled by bottom-up[27] processes (Aebischer *et al.* 1990; Frederiksen *et al.* 2006) but the reverse effect, *i.e.* **top-down[28] control may nonetheless also exist** (as suggested in Ainley *et al.* 2006) and blur the mechanisms by which penguin populations are regulated. Trophic cascades[29] are widely recognized in terrestrial stream and lake ecosystems but were usually assumed absent from the open-ocean systems. Yet, there seems to be accumulating evidence of their existence (Frank *et al.* 2005; Ainley *et al.* 2006; Osterblom *et al.* 2006; Estes *et al.* 2011; Johnson *et al.* 2011; and the classical example of the disappearance of sea-otters and its effect on kelp forest), its absence of several marine ecosystems being probably due to overfishing (Ainley *et al.* 2006). In the Ross Sea, devoid of fishing, Ainley and colleagues (2006) showed that Adélie penguins, minke whales and killer whales, along with other predators depleted middle-trophic level

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[27] BOTTOM-UP CONTROL: see page 40

[28] TOP-DOWN CONTROL: regulation of ecosystem components at low trophic levels by species at higher trophic levels (*i.e.* control by predation)

[29] TROPHIC CASCADES: reciprocal predator-prey effects that alter the abundance, biomass, or productivity of a population, community or trophic level across more than one link in a food web. (Pace *et al.* 1999).

preys, namely krill and silver fishes, which in turn decreased the grazing pressure on phytoplankton. Other studies proposed that control in marine food chains is dynamic and that it can alternate between bottom-up and top-down controls (Litzow & Ciannelli 2007; Cury *et al.* 2008). Depending on the mode of control, seabirds and more specifically penguins could be more or less suitable indicators. For instance in the top-down control, the system is regulated by predation and seabirds are then not indicators as changes in the trophic chains result from the top predators themselves (Durant *et al.* 2009).

Additionally, the interest of the top-predator as an integrator of the effects of climate on food chains may become a negative point. Indeed, top-predator populations are **not straightforward indicators of climate changes**. While reflecting changes lower in the food chain, changes in seabird numbers or life-history traits usually respond with a lag of several months or even years (Thompson & Grosbois 2002). For instance, if SST and sea-ice extent have direct effect on resources' locations they also affect marine productivity itself, which in turn affects the abundance of penguin prey through the food chain (Gregg *et al.* 2003). The **effect of climate** thus needs to be examined both as such and **with a lag** at least as big as two years for some species (Le Bohec *et al.* 2008a). Climate effects may thus not be visible immediately and the mechanisms involved in the changes observed in the top predator populations may be hard to disentangle.

Finally, penguins are **not strictly specialists** and often present a dietary diversification. While the variety of prey available to penguins remain low in short and simple trophic chains like the polar ecosystem (*i.e.* essentially krill *vs.* fish), the possibility to switch to completely novel prey is generally greater in lower latitudes. In such a case, changes in abundance or distribution of usual prey would not be visible at the top of the food chain and penguins would not fulfil their role as indicators. Yet, not all species would react in the same way: little penguins adapted, after a transition period, to the complete disappearance of their main prey and moved onto new dietary items (Chiaradia *et al.* 2010), but African Penguins seem for the moment unable to cope with the reduction in sardine availability in their foraging range (Crawford 2007).

While penguins are probably one of the best choices of bio-indicators in the Southern Ocean, and their study is of great importance for such a remote area, ecologists must keep in mind they are only part of a bigger picture. If we want to understand the processes involved in the effect of climate on these marine ecosystems, we need to extend our investigations to other species at other levels of the trophic web (see next chapter for some propositions).

II. Wild penguins: to what extent?

A lot of studies on animal behaviour or physiology are conducted in captivity. However, investigating the animal in its natural context should bring more relevant information in an ecological scientific context. This can render the situation much more difficult though, as conditions cannot be controlled. For instance, one will have to disentangle between the effects of different parameters that cannot be investigated alone.

The main question when working with wild animals is to minimize the impact of our studies on the animals both from an ethical point of view and from a scientific point of view. Ethics are a sensitive point, everybody has its own personal ethics and protocols can be perceived very differently by people. Further, what does minimizing mean? Again this is purely subjective. For some, it will be to reduce it to zero. Yet, no studies on animals can be done without affecting them. Just the fact of being there to study them could modify their behaviour. This is why every study should be weighed in terms of costs and benefits (May 2004). However, if one thinks that the benefits are overwhelming the costs, the next question to ask is whether data acquired will give us appropriate and representative information. One of the hard questions to solve for scientists, as stated before, is how to keep it simple without being wrong? A classical example is how to choose the sample size, trading-off between being large enough to be representative but small enough to be monitored and cause the least individuals to be disturbed. Further, the situation in the field can be very different from one in a zoo and as mentioned earlier, even marking individuals can become an issue. In this thesis, I tried to obtain datasets as unbiased as possible to assess penguin responses to climate. However, individuals had to be caught for further identification and other parameters were modified from natural context. In this paragraph, I will discuss the main disrupted parameters to see which bias could have been introduced.

> *« And I for one welcome the attention increasingly given to the rights of non-human animals (…) But field studies of ecology and behavior of non-human animals can also raise difficult questions of costs and benefits. As a sixth wave of mass extinction looms, conservation biologists desperately need the knowledge that comes from such field studies. »* ***Sir Robert May***

1) Artificial boxes & tourist attraction in Phillip Island

As explained in chapter III, the study site in Phillip Island is part of a nature park and home for a world-famous attraction, the “Penguin Parade”. Tourists come every night to observe the returns of little penguins crossing the beach. Up to half a million visitors a year come to enjoy the view of these little penguins (Anonymous 2009). Of course, this is far from what I imagined when I thought of working on wild animals. Concrete tiers have been built up to let people sit in front of the beach; lights are on as to better see the penguins and so forth and so on. However, the attraction is closely managed and visitor rules are respected. Rangers ensure people stays on the board walk back from the beach and the burrows, well out of reach of the penguins. After the first penguin is seen to cross the beach, the lights are on for 50 minutes and no more. As I said just above it could be surprising for one who is used to work on penguins in more remote areas. However, when penguins live in the proximity of inhabited lands, the challenge is different and Philip Island Nature Park is an interesting way of managing the interaction between humans and wild animals. In a study of a mixed colony of Humboldt and Magellanic penguins, Simeone & Schlatter (1998) observed damages resulting from heavy human disturbance such as non-regulated tourist activities. For instance, non-regulated tourism has been reported to disturb incubating penguins and cause nest trampling (Gandini *et al.* 1996). However, visitation may be compatible with penguin reproduction if visits are controlled (Yorio & Boersma 1992). Similarly, Villanueva and colleagues did not observe any adverse effects of the ecotourism on Magellanic penguins at San Lorenzo colony (Argentina). Importantly, the need for species-specific management has been highlighted, as different species under the same stress will react differently (Ellenberg *et al.* 2006). In Phillip Island, tourists have been visiting this area since 1928 when local tourist operators began organizing penguin tours (Dann 1992). Later the present infrastructure has been developed in order to control people and what they are doing. According to Dann (1992), similar rates of recruitment and breeding productivity have been recorded in the area open to tourists and adjacent areas of the peninsula without public access, giving evidence that the interference from tourism is not affecting little penguin life-history traits. However, this does not mean that behavioural or physiological responses are not modified. A study on Magellanic penguins showed that chicks exhibit a higher corticosterone stress response at hatching and behavioural habituation to human contact by the time they are ready to fledge (Walker *et al.* 2005). Adults also exhibit behavioural and physiological habituation to human presence (Yorio *et al.* 2001). Yet, consequences of these changes are poorly known and further studies would be required.

Phillip Island has been greatly modified since European settlement in the 1840s. Agriculture but also recreation and housing have resulted in large-scale habitat loss and change, introduction of plants and animals, urban expansion and intense human activities. Concomitantly, 9 out of the ten little penguin colonies known to have existed on the island have disappeared and the only remaining one has been significantly reduced in size (Dann 1992). Following this report, the Victorian Government developed a protection plan including the cessation of building in the area and the buy-back of land and dwellings to restore habitat for penguins. Additionally, measures to limit predation by dogs and foxes have been taken and a traffic control system has been established to avoid road killings. The artificial burrows used in the study (wooden boxes) are also part of these measures of conservation to provide habitat in degraded areas. Breeding conditions in these boxes could be different from those in natural burrows and introduce a bias in our work. There has been no study on this subject in this colony. Temperatures inside such boxes have been evaluated in another place, in Western Australia and were always higher than in natural burrows (Ropert-Coudert *et al.* 2004b). However, conditions of sunlight are different in the two locations, as most of the boxes in Phillip Island are situated in shaded areas, thus reducing the over-heating of the burrows. Further, the conditions in the box should not affect much the parameters we studied, as we focused mostly on the post-guard phase, when adults return only at night, spending a few hours inside or around the burrow before leaving again.

2) Impact of scientific presence

Yet, human activities and impacts are not limited to tourism. In Dumont D’urville, Adélie penguins live all around the buildings of the scientific base and human presence and activities may affect penguins. First, when the scientific bases were installed, it reduced their breeding habitat. On Possession Island in Crozet for instance, the base was first established in the middle of the king penguin colony I studied. Most of the features of this base are still present now, reducing the colony area by 30% (Weimeskirch *et al.* 1992). But nowadays penguins are mostly subjected to the presence of scientists working there every day (see Carney & Sydeman 1999 for a review on human disturbance both for tourism and scientific purposes). It is hard to measure the impact scientists may have on penguins (see Le Maho *et al.* 1992 on stress due to handling in geese). The question is whether this colony of “Baie du Marin” is representative of the other king penguin colonies. A lot of people working on king penguins are amazed at how penguins react to humans in this colony. It seems easier to approach and handle them. This could be signs of a behavioural habituation to human presence. But does that really affect the parameters we are investigating? The effect of climate on king penguins seems to be mainly mediated through oceanographic conditions and prey availability; and habituation to humans should not have any repercussions on these parameters.

Yet, when comparing with other colonies, the "Baie du Marin" is the only king penguin colony of the Possession Island that decreased throughout the whole period from 1962 to 2001 (Delord *et al.* 2004; Figure IX - 1). Though no explanations are suggested in this study, we can think that the disturbance caused by human activities is one of the reasons of this decrease. Disturbed habitat or increased stress (due to human presence and several captures) may have led penguins to seek for another place to breed. Interestingly, the Colony called "La Chaloupe" (colony c in Figure IX - 1) situated very close to the "Baie du Marin" formed during that time with the first pairs observed to breed in the 60s.

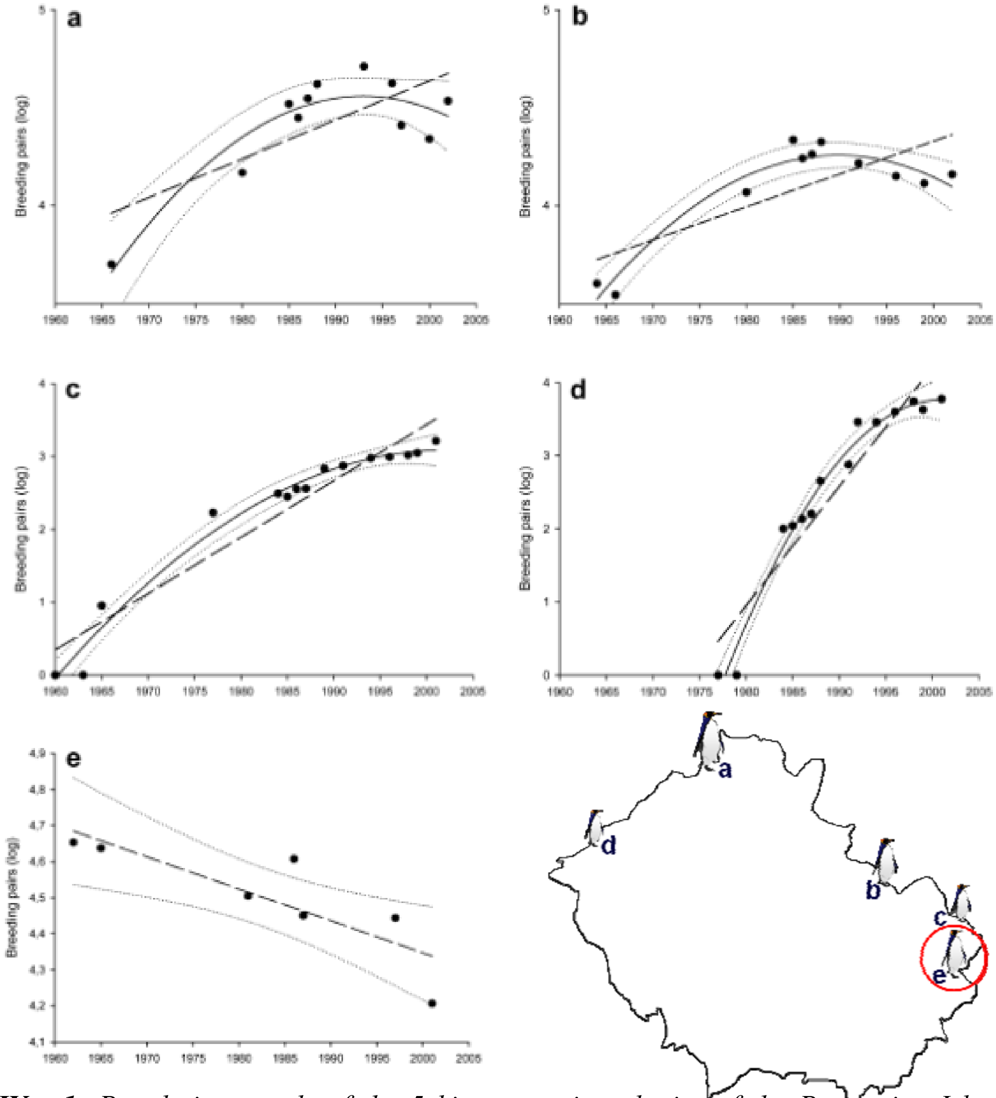

Figure IX - 1: *Population trends of the 5 king penguin colonies of the Possession Island, Crozet Archipelago. Figure taken from Delord et al. 2004, modified by the addition of the island map.*
Each lettered panel represents the colony indicated on the map by the correspondent letter.

Differences in dispersal and emigration could thus be different in this colony due to human disturbance. This would create a bias in our studies by modifying the apparent survival and return rate to the colony.

Generally, scale at which changes are considered may lead to misinterpretations. Focusing on the trend of a single colony is similar to observing the tree that masks the forest: local trends may not reflect accurately the overall trend of the species across its complete breeding range. Species that breed over a large range of latitudes may simply shift the centre of their distribution but an observer that does not access to the big picture may report the disappearance of those small colonies that are situated at the extremities of the distribution and conclude incorrectly that the whole species is affected. This is especially true for Adélie penguin populations which have been reported to shift their distribution polewards.

III. Return to the colony *vs.* survival

Survival is prone to error since it is often estimated through a measure of return rate of individuals from one year to the next. Such a parameter does not solely result from mortality, but also includes emigration and even partner or breeding site changes within a given colony. Return rates are thus underestimates of survival. To take emigration into account, one would need to monitor several colonies at the same time (see propositions in the next chapter). Apart from penguin disturbance, which seems to be minimal, RFID systems thus present another potential problem to study penguins. Indeed our three study sites represent only part of colonies. In Crozet the ‘ANTAVIA’ sub-colony represents about one third of the colony and is really close to the other parts. Philopatry is considered to be very high in king penguins (94% of site fidelity in Barrat 1976), meaning that they will return where they were born to breed. Observations even indicated that site fidelity lead penguins to return no more than a few meters away the following year (Barrat 1976; Gauthier-Clerc unpublished). Chicks raised in the ‘ANTAVIA’ part should thus breed in the same part. Still, some penguins could well move inside the colony and return to breed outside the ‘ANTAVIA’ part. In such cases, penguins would not be detected as the antennas concern only this part of the colony, introducing potential bias in survival estimates. In this work we investigated the return rates of juvenile king penguins after their fledging. At their return to the colony, juveniles seem to be very mobile. For instance, the number of passages over the antennas per day is more than 7 times higher for juveniles than adults (mean = 1.5 *vs*. 0.2 passages per day). As they are not constrained by breeding purposes, they wander about and chances that they do not cross the antennas are very few. Therefore, I do not think that studying a sub-colony instead of the whole colony biased significantly this study. Further, concerning adult survival, again emigration could not be taken into account. However, the RFID system allows for a continuous 24-hour monitoring (*i.e.* a constant recapture effort that is much more powerful than visual observations of bands), resulting in a high reliability of survival estimates. In study 2 (Saraux *et al.* 2011a) for instance, we did not observe a single gap in the individual capture histories, as all adults detected during a given summer had been detected the previous year. We therefore considered the re-sighting probability of a bird to be one, provided that it was alive and did not emigrate. In Dumont D'urville the studied colony is only a small part of the whole island population but is relatively distinct from the other colonies, thus limiting the possible exchanges between sub-colonies. Further, similarly to king penguins, on their first return to the colony, most Adélie penguins spend time in the vicinity of where they hatched (Ainley 2002), so that estimates of juvenile returns should not be biased. The site where Adélie penguins first breed is also related to where they hatched (Ainley 2002), so that the use of RFID systems is justified. However, adult survival rates are probably underestimated as some birds will necessarily move to other sub-colonies.

Finally in Phillip Island I did not investigate survival or return rates, so that exchanges from one year to another between sub-colonies did not affect our studies.

IV. Importance of extreme events

To predict penguin populations' response to climate change, one must both understand how the species react to climate variability and project future climate conditions. Relatively few studies have addressed this problem on penguin species and most of them have done so using an average predicted climate (such as Le Bohec *et al.* in prep). This does not allow taking into account extreme climatic events[30] (but see Jenouvrier *et al.* 2009a), which are often ecologically more relevant than are fluctuations in the mean climate (Parmesan *et al.* 2000). Extreme climatic events may have stronger effects on population dynamics than the average climate (see review in Moreno & Møller 2011). In penguins, this is also illustrated for instance by the importance of thermoclines in the foraging zone of little penguins and their disappearance when violent storms mix the water column (Ropert-Coudert *et al.* 2009).

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[30] EXTREME CLIMATIC EVENTS: rare occurrences happening 5% or less of the time as gauged from the expected distribution of the climate variable in question (Moreno & Møller 2011)

Extreme climatic events are predicted to increase in frequency in most future climate scenarios (Easterling *et al.* 2000; IPCC 2007). An increase in frequency of extreme events could severely impact a population and marine ecosystems are especially subject to rapid changes in climate and ocean environment (*e.g.* Humboldt Current, Alheit & Niquen 2004). Therefore, it is very important to investigate the effect of such extreme climatic events and not only the continuous effect of climate variability, as I did in this work. The time necessary for a population to recover from an extreme event depends on its growth rate (Gardmark *et al.* 2003) or generation time (Rosenheim & Tabashnik 1991). As penguins are long-lived species, they exhibit low population growth rates which is the result of their life-history traits: low breeding success, late recruitment and high survival (Stearns 1992). Therefore, they should present a slow recovery rate. If recovery time exceeds intervals between such weather disruptions as their frequency increases in a scenario of global climate change, extreme events could increase considerably the risk of population decrease and ultimately extinction.

Chapter X ○○○○○○○○○●

Future Studies

Over the course of my PhD, I obtained different results on life-history traits of penguins (see synthesis in Table VIII - 1). However, every new piece of knowledge raises new questions and below is a summary of what could be done to deepen our understanding of the effect of climate on penguins.

I. Understand underlying mechanisms of indirect effects of climate:

1) Missing link with prey

In this work I used penguins as bio-indicators of Southern Ocean ecosystems. Though they are good candidates for such a role, this approach also has its limitations (see chapter IX). A single species or trophic level cannot account for everything that happens in the ecosystem. Further, almost all changes apparent on penguin species were indirect effects of climate mediated by lower trophic level. To understand these indirect changes, we do need to know better the links between penguins and their prey and have information on prey stocks. Currently, diet analyses by stomach flushing or stable isotopes have given information on the types and proportion of prey foraged (see Ridoux 1994; Cherel & Hobson 2007; Cherel *et al.* 2007; Chiaradia *et al.* 2010 for instance). However, very few data are available concerning the distribution and availability of prey in response to climatic variables. **There is a need for a multi-year dataset on prey availability and distribution**.

Inter-annual variability of the prey (in response to climate and oceanographic conditions) needs to be evaluated to know the constraints that apply on penguins. In order to acquire such data, one needs first to **determine the relevant areas to sample** (*i.e.* foraging grounds). **GPS** fixed on the back of penguins have been used to know in which areas they are foraging. However, this raises several issues. First, GPS needs to be as small as possible to avoid too much drag effect, to be situated at the right place to keep balance, *etc.* (see recommendations in Casper 2009 and references on penguins therein, see also Chiaradia *et al.* 2005; Ropert-Coudert *et al.* 2007a, b). Further, penguins can go out at sea for a long time and both batteries and memory need to last long enough to get the whole trip. The last issue is to retrieve the GPS to get the data (note that Argos system enables to get data in live through satellites but is particularly expensive). Indeed, if we want to deploy loggers on a sufficient number of individuals and have a representative sample, the technique needs to be less costly.

The two last points render the task especially difficult for investigations on **non-breeders**. Breeding birds return regularly to the colony and can be retrieved easily in the colony. However, non-breeding birds either immature or non-breeding adults can spend as long as several years out of the colony. Apart from the problem of battery and memory, this also means that a new way of fixation (not based on feathers due to moult) has to be found. **Stable isotopes** may be used in order to know in which area (Hobson 1999) and on which kind of prey they foraged (Hobson *et al.* 1994) during their time away of the colony. Yet, one needs to find a relevant tissue to answer these questions. Feathers or blood are easy to sample but may not have the ideal turnover rate (a few weeks for blood, period corresponding to right before moult for feathers; Hobson & Clark 1992). A tissue with continual growth would be ideal and sampling of claws or beak keratin should be considered, though beak would be difficult to sample and claws are worn out thin. This also means that we would have to estimate their growth phenology.

These difficulties explain the important lack of data we have on juvenile penguins. In chapter V (Article 3: Saraux *et al.* 2011b), it was showed that an increase in SST lead to an increase in return rates of king penguins. However, we do not know where juvenile king penguins go during their trip and thus averaged SST on a very large area then subdivided in smaller areas. Every area yielded the same result, but the sub-tropical area explained a higher proportion of the deviance in return rates. Information on whether juveniles exploit this area as feeding grounds would help understanding these results.

Once foraging grounds are better known, a first way to obtain data is to **work with fisheries** and rely on catches and location of these catches as indications of prey availability and distribution. However, this is possible only if fisheries target species that are also foraged by penguins. In the Southern Ocean, fisheries rely mostly on Antarctic krill and toothfish, the two largest monofisheries. Fisheries on Antarctic krill may provide important information for some penguin species such as Adélie, but it is to be mentioned that they act as direct competitors of the penguins and could bias the study by increasing krill depletion. Sub-Antarctic toothfishes are not part of the prey of penguins and are fished at depth different from those in which penguins forage. Data from fisheries may thus be more relevant for lower latitude penguins, such as little or African penguins. However, these data can only give indications of prey availability and are not always useful when catches amount to the allowed quota.

A second possibility is to use oceanographic campaigns to sample these areas on several successive years in order to investigate both the effect of climate on lower trophic levels but also the relation between penguin life-history traits and prey availability. For instance, survival of king penguins has been shown to decrease with SST (Le Bohec *et al.* 2008a) with a two year lag. This was explained by a delay between recruitment and abundance of the prey, but needs to be verified. However, ship-based sampling is very expensive and may not be possible on a repeated basis.

This could be partly compensated by the development of **modelling techniques** (Hulley & Duhamel 2011). Modelling on prey distribution could be realised using satellite-derived physical and biological oceanographic data (Koubbi *et al.* 2010). Further, the development of integrated ecosystemic models, the so-called “end-to-end” models (Travers *et al.* 2007; Fulton 2010; Shin *et al.* 2010) would enable to model interactions between penguins and the rest of the ecosystem and to predict the effect of climate or different conservation measures (MPA for instance) on seabirds more realistically by integrating all the interactions in the ecosystem. For instance, the Atlantis model has been used to provide important insights for ecosystem management in the last decade (Fulton *et al.* 2011). Such models relied on coupling different disciplinary models to account for changes occurring at different trophic levels. For instance, a model has been developed by Travers and colleagues (2009; 2010) coupling Regional Ocean Modeling System (ROMS) physical models, PlumeBio biogeochemical model and Object-oriented Simulator of Marine ecOSystems Exploitation (OSMOSE), multispecies and individual-based model of fish populations. Adding the superior trophic level of seabirds may help providing predictions of the seabird component according to different climate scenarios.

Finally, it is also important to know how dependent penguins are on a specific prey. To understand indirect effects of climate on penguins, we need to know **how they will react to a decrease in availability of their main prey or even its disappearance**. Little penguins for instance have been able to cope with the disappearance of pilchards by switching towards other prey (Chiaradia *et al.* 2010), while African penguins do not seem able to make such a switch (Crawford 2007). In order to understand their ability to adapt to new preys, it would be interesting to study diet evolution of several penguin species on a long-term basis. Again, this may be possible through the use of stable isotopes. A study based on excavations of Adélie penguin eggshells provided insights on their diet over a 38 000 year time series and showed a recent shift towards prey of lower trophic levels (Emslie & Patterson 2007). Similarly, a project conducted on little penguins and shearwaters (coordinated by Dr. Manuela Forero and Dr. André Chiaradia) aims at assessing such diet evolution through the last century. Samples have been collected on feathers of dead individuals through several museums and are currently analyzed. The use of two species breeding on the same grounds in Australia enable to compare diet evolution and see whether one of the species adapt more easily.

2) Hierarchic models or elasticity analyses on breeding success

Breeding success should be one of the most variable life-history traits in long-lived species (Stearns 1989) and thus one of the most affected by climate. It has for instance been shown to vary with SST in king penguins (Le Bohec *et al.* 2008a), while it is affected by sea-ice conditions in Adélie penguins (Ainley *et al.* 1998). However, breeding success results from a combination of different parameters, such as arrival and laying dates (*e.g.* Weimerskirch *et al.* 1992; Article 2: Saraux *et al.* 2011a for king penguins), body mass of parents at the onset of breeding (*e.g.* Robinson *et al.* 2005 in little penguins), foraging trip duration (*e.g.* Article 7: Saraux *et al.* 2011d in little penguins). Foraging performances are also affecting the amount of food brought back to the chicks and consequently their growth. In order to better understand the indirect mechanisms by which climate affects penguin breeding success, it is important to know the relative contribution of all these parameters and their sensitivity to climate.

Most of these parameters can be obtained through classical RFID-base automatic monitoring system and detections (dates and durations), while all data related to mass could be obtained either through automatic weighing system as part of the APMS or by directly weighing individuals (parents at the onset of breeding and chicks along their growth). Finally, foraging performances could be studied through the use of data-loggers such as accelerometers or beak-opening sensors (Hanuise *et al.* 2010).

The relative contribution of all the parameters could be estimated through **elasticity analyses** (Caswell 2001). However, parameters which have a high contribution should not be the ones more subjected to climate (Gaillard & Yoccoz 2003). **Hierarchical models** (relations between climate and these parameters and then these parameters and breeding success; Figure X - 1) may help answer this question by considering all indirect effects of climate on breeding success together and investigating each contribution.

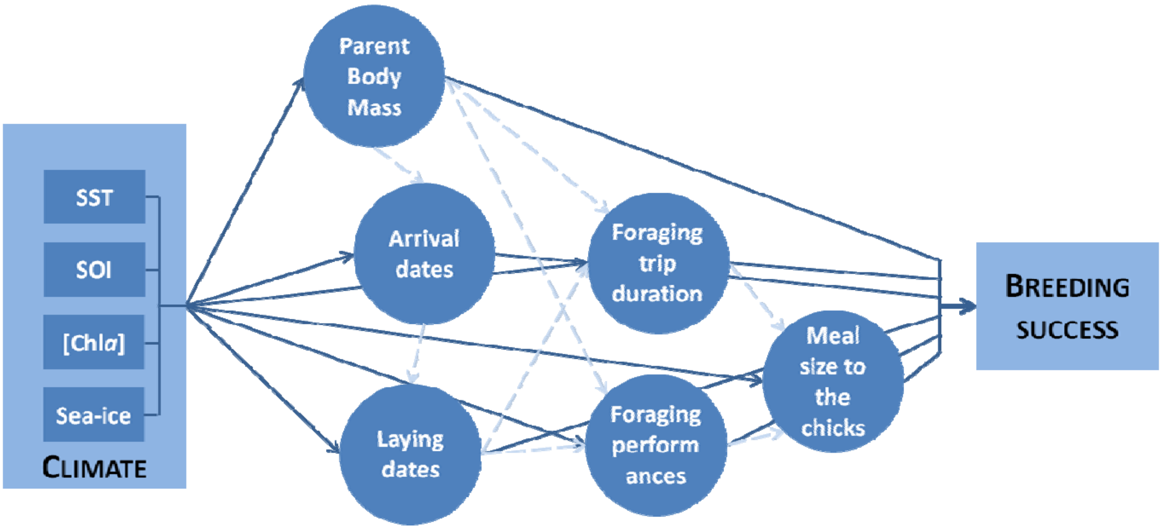

Figure X - 1: *Schematic of a hierarchical model of the impact of climate on breeding success.*

3) Investigating climate at smaller temporal scales

As shown in Chapter VI (Article 5: Saraux *et al.* in prep), little penguin breeding success may be driven by climate and oceanographic conditions at smaller temporal scale. Therefore, it would be very interesting to investigate temporal changes in environmental conditions within years, in particular in thermoclines, that have been shown to be important features of little penguin foraging success (Ropert-Coudert *et al.* 2009). Water stratification is supposed to depend on wind conditions, and storm frequency, which suggests potential rapid changes in thermoclines. The Commonwealth Scientific and Industrial Research Organisation (CSIRO) provided us with monthly temperature data on surface and at 50m deep from December 1999 to December 2006 on an area centred on Phillip Island little penguin foraging grounds (39°S-38°S; 143.5°E-145.5°E). Such data may give us relevant information on the temperature gradient in this area. Unfortunately for now we only have one data point per month corresponding at the measurement on one particular day. Therefore, we could not conduct analyses investigating the time scale of the changes for now. But similar data per day (or even mean per week) may allow us to answer this important question and to investigate whether changes in thermoclines are associated to changes in foraged prey mass (deduced from weighbridge data) and chick growth and mortality (obtained from the monitoring 3 times a week of the burrows). Another interesting question to investigate is the potential link between the onset of breeding and the appearance of thermoclines. Mean laying dates are highly variable in between season in little penguins (Salton *et al. in prep*) and the onset of breeding has been thought to be associated with a threshold in body condition of the birds (Robinson *et al.* 2005).

The appearance of a thermocline may thus be an important clue for them to decide to breed. Indeed, during the winter period there seems to be no water stratification at all (Figure X - 2), the difference in temperature between 0 and 50m appearing first around September or October depending on the year. It is also clear on this graph that the gradient is more important on certain years than others.

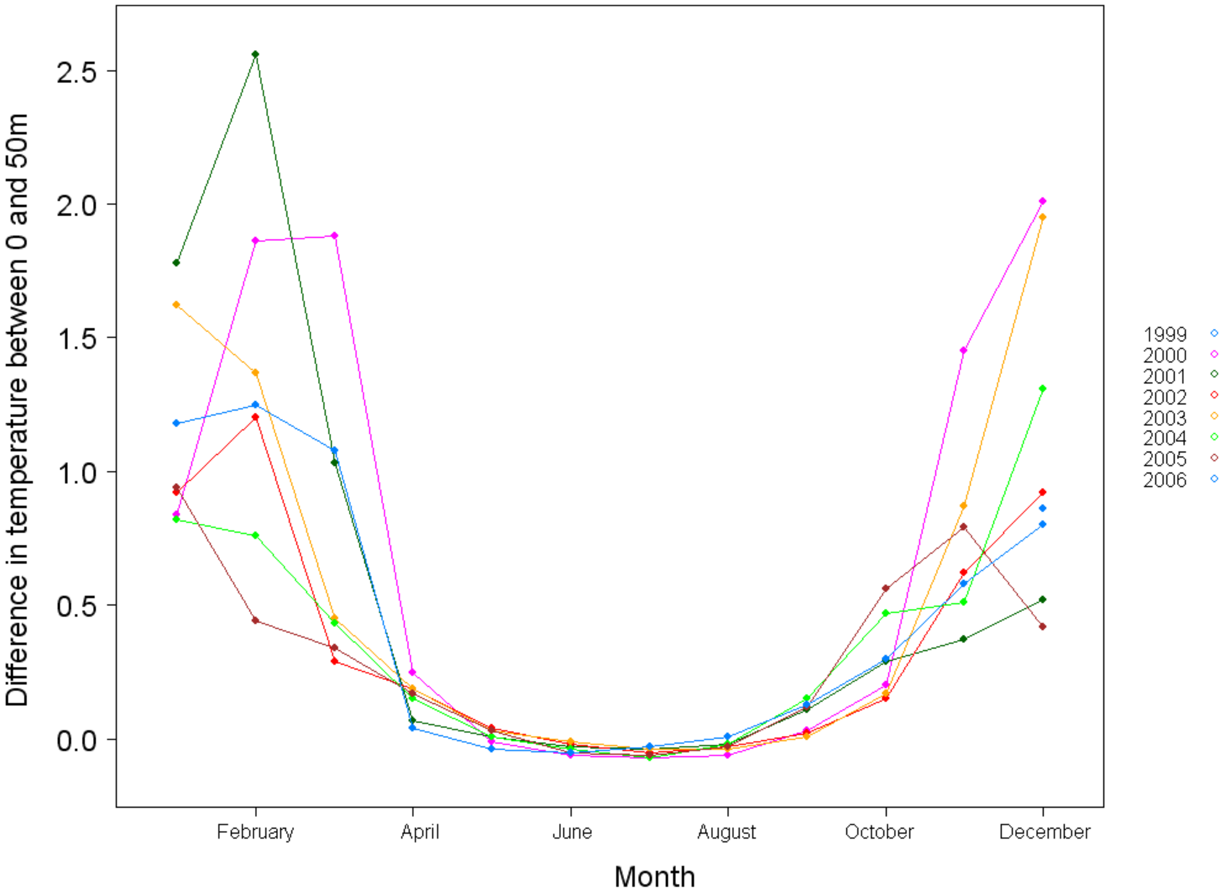

Figure X - 2: *Temperature difference between 0 and 50 meters in function of months for each year from 2000 to 2006 at Bass Strait, Australia.*

Climate change is supposed to increase the frequency of storms (IPCC 2007) and might then affect thermoclines. Such a study would then provide more relevant information on responses of little penguins to climate change from an ecological point of view than average warming.

4) Unravelling sex-ratio manipulation

In study 6, we investigated changes in king penguin sex-ratio. However, apart from one year our data were all collected at fledging and differences observed could either result from sex-ratio at hatching or from sex-specific mortality of the chicks between hatching and fledging or a combination of the two. Since 2010, we collect blood samples as close to hatching as possible, which may help us disentangle the two effects. Further, we collected abandoned eggs during the two last breeding seasons in order to study a potential manipulation of sex-ratio through maternal hormones invested in the egg yolk. Indeed if variations in sex-ratio have been mostly related to postzygotic mechanisms until now (Petrie *et al.* 2001), recent studies showed that sex-ratio could be biased as early as hatching (blue tit, *Parus caerulus,* Sheldon *et al.* 1999; collared flycatcher Ellegren *et al.* 1996). In the blue peawfol (*Pavo cristatus*), females have been shown to regulate their hormonal allocation according to their mate attractiveness, resulting in a bias towards females when corticosterone levels are high and towards male when testosterone levels are high (Pike & Petrie 2005). Such modulation of hormonal allocation has also been observed in blue tits (Sheldon *et al.* 1999; Griffith *et al.* 2003), zebra finches, *Poephila guttata* (Burley 1981; Gil *et al.* 1999) and collared flycatcher (Ellegren *et al.* 1996). Mother quality is also an important factor that can affect sexual allocation and can modulate sex-ratio through hormones. For instance, the quantity of androgens deposited in egg yolk increase with age and experience in the European starling, *Sturnus vulgaris* (Pilz *et al.* 2003). Petrie and colleagues suggested that maternal steroids could influence sex-chromosome segregation at the first meiotic division and thus provide ways of manipulating sex-ratio. In that regards, environmental conditions prior to breeding may also impact sex-ratio by affecting mother's condition. Finally, it is important to note that chicks were randomly sampled before fledging, so that they were alone and we consequently had no information on parents. As we just explained, parents' quality, age, experience and condition could affect importantly the sex of the offspring produced. It would thus be interesting to monitor chicks from known parents to investigate whether parents of better condition or older parents for instance preferentially raise chicks of one sex.

II. Accounting for integrated effects

Climate may affect organisms through delayed long-term effects. For instance, conditions early in life may affect later life-history traits (Gaillard *et al.* 1997; Lindström 1999;

Forchhammer *et al.* 2001, see Chapter I). In chapter V (Article 3: Saraux *et al.* 2011b), I showed that such delayed effects also occur in penguins, juvenile survival being affected by conditions during rearing in king penguins. Other conditions occurring early in life may affect later breeding success. Indeed, it was shown in this same article that king penguins return to the colony for the first time between 2 and 4 year old but breed only later (average age at first breeding: 6 yr-old). We suggested that these returns could be part of an important process of learning and gaining experience for future breeding events. Juveniles indeed return only during summer, the period of pairing, laying and brooding and could gain knowledge on habitats, courtships, *etc.* during this period. Several studies have investigated the effect of age on reproductive characteristics (see for instance Ainley 2002 for Adélie penguins). However, the relationships obtained can be modified by experience (Ainley 2002) and breeding success should be more dependent of actual experience in the colony (as the number of time they spent in the colony, the number of breeding events they already attempted, *etc.*) than age. In order to test our suggestion, it would be interesting to look at the effect of first returns on later breeding events. Juveniles returning first at 2-yr old should acquire experience earlier than those returning at 3-yr old or 4-yr old. Similarly juveniles staying longer in the colony may learn more than individuals only passing by. A study of both the effect of age at first return, time spent in the colony at this return and number of times they already visited the colony on age at first breeding and age at first success would help understand whether this strategy of early returns influences breeding events. Yet, only a few king penguins return at age 2, suggesting that there should be some associated costs if this is a beneficial strategy. If breeding earlier and being successful earlier mean a higher investment early in life, this could have consequences on survival or future breeding events (life-history trade-offs; Stearns 1989). Such a question could be addressed by the use of longitudinal data to study differences in mortality, rate of senescence (Nussey *et al.* 2008) or breeding success late in life between individuals starting to reproduce early and late. A study of the lifetime reproductive success could also help understanding which strategy is the more beneficial. However, if early returns are beneficial but costly, individuals that return early may be those of better quality that can afford such costs (for instance individuals of larger size tended to return earlier). In that case, differences in breeding success may result from differences in individual quality rather than experience (see Wilson & Nussey 2010 for a review on individual quality, ways to measure it, *etc.*). Separating the two may be difficult.

III. Coping with climate change

1) Emigration/Dispersal:

Penguins are thought to be highly philopatric species. In this thesis, I showed that king penguins exhibited very high return rates to their colony suggesting that dispersal is not an important driver of population dynamics (Chapter V, Article 3: Saraux *et al.* 2011b). Yet, most dead penguins disappear at sea and chances to record them are consequently low (see Dann 1992 for instance). Survival rate are thus associated with rates of return to the colony. However, birds not returning may well have emigrated somewhere else and survival is thus underestimated. If dispersal has usually been considered low not to say inexistent in penguins, this could change as one way to respond to climate change is to disperse towards more favourable areas. Dispersal is also known to increase in seabirds when breeding success is low (concept of "voting with the feet"; Danchin *et al.* 1998; Boulinier *et al.* 2008). Dispersal and emigration are thus increasingly important factors to study. However, this is probably one of the most difficult to investigate. This requires to monitor penguins at different places. Dispersal has mostly been studied through the use of bands, as they could be read by everyone, increasing the probabilities of resighting. However, bands have been shown to impair breeding success in king penguins (Article 2: Saraux *et al.* 2011a) and may thus bias the study of dispersal by increasing it. Several other methods can be developed to provide information on this parameter. First, multi-state recapture models (Lebreton & Pradel 2002) based on several automatic penguin monitoring system (APMS) situated at diverse colonies, may be developed. Different spatial scales need to be considered by monitoring colonies at different distances. As an example, the study of dispersal of the 'Baie du Marin' king penguin colony should be done by monitoring other colonies of the Possession Island, colonies of other islands in the Archipelago but also colonies in other archipelagos such as Kerguelen. Yet, such device would be very expensive with the necessity of installing APMS in all these places. Less costly, the monitoring of the dynamics of several colonies by counts and pictures may provide information on dispersal probability. For instance, concomitant to the decline of the king penguin colony in Baie du Marin, a new colony appeared (colony 'La Chaloupe' Delord *et al.* 2004). This suggests that the decline in the colony may not be due to increased mortality but to relocation of individuals in another colony. Similarly, a colony of emperor penguins has recently been discovered by an innovative way (detections of faecal strains on satellite images) on the Mertz glacier (Fretwell & Trathan 2009), relatively close to the colony of Pointe Géologie, which decreased by about half in the 70s. The question that arises is then whether this new colony derived from the Pointe Geologie one, explaining the disappearance of so many individuals. Genetics seem a promising way to answer this question. Genetic material sampled in different colonies may help understanding the flux of individuals between colonies and also how genetic diversity is maintained in a philopatric species. In birds, DNA can be extracted either from blood samples or even feathers and is thus easy to get with minimal disturbance of the birds. While mitochondrial DNA study reflects only part of the filiations (only mother's mitochondrions are transmitted to offspring; Waits *et al.* 1998), microsatellites seem good candidates to study genetic structure and diversity of population. Microsatellites are largely distributed in the genome and exhibit an important polymorphism providing information on kin relationships (Ahmed *et al.* 2010). Microsatellite markers have been determined in several penguin species (Roeder *et al.* 2002; Schlosser *et al.* 2003; Ahmed *et al.* 2009) but few studies have yet used these markers to study population genetic structure (but see Roeder *et al.* 2001; Bouzat *et al.* 2009). Comparisons of microsatellite morph distribution in between populations may enable us to determine whether they are issued from a common population and whether exchanges between populations exist and thus provide information on dispersal.

2) Adaptations

Exploring adaptations through microevolution or phenotypic plasticity is not possible through modeling and requires long-term field data (Grémillet & Boulinier 2009). In long-lived species such as penguins, adaptations should be slow and consequently hard to detect. Further, the drivers of behavioural or morphologic changes are hard to determine and only advanced genetic analyses enable to disentangle between microevolution and phenotypic plasticity. Nonetheless, adaptations are thought to occur more probably in species that exhibit flexibility and plasticity in their behaviour. The study of flexibility of parental or foraging strategies for instance may help understand whether a species or a population could be able to adapt easily to changes in their environment. We showed in chapter VII (Article 7: Saraux *et al.* 2011d) that breeding little penguins exhibited flexibility in their foraging strategies, by alternating between short and long trips to maintain their reserves while feeding their chicks as much as possible depending on the conditions. A thorough investigation of the transition rates between short and long trips may help confirm that they are triggered by adult body mass and that this strategy enables them to favour their own survival over reproduction. More explicit tests of the transition rates could be realized by the use of Hidden Markov Models (HMM). Rarely used in ecology until now (but see Hart *et al.* 2010), these models are one of the best ways to identify several distinct states, calculate transition rates between them and explain what determines the transition.

IV. Adélie penguins

Unfortunately, my work focused mainly on king and little penguins with only a few preliminary results on Adélie penguins. This was due to a too short dataset forbidding any testing of inter-annual variability and climate effects for now. However, data are accumulating and seem very promising. Development of algorithms to calculate precise body mass of penguins when they cross the weighbridge should allow investigating several questions without any need of recapture.

Investigations of the effect of climate on the ice-obligated Adélie penguins will really complement this work by allowing to investigate further the effect of the latitudinal gradient and the effect of sea-ice. Changes in sea-ice cover are predicted to be important in the near future (Meehl *et al.* 2007) and should play a role in the future of penguins, a question that has only been slightly investigated in this work. Interestingly, a lot of studies have already been conducted on the effect of sea-ice on Adélie penguins at other locations (*e.g.* Wilson *et al.* 2001; Kato *et al.* 2002). Information on this colony would add to our knowledge and understanding of the global picture of climate effect on Adélie penguins. Indeed, studied population trends vary according to locations and in particular to latitudes (see chapter II). The effect of sea-ice on population trends at this location has already been studied (Jenouvrier *et al.* 2006) but effect on life-history traits and mechanisms underlying still need to be assessed (but see Beaulieu *et al.* 2009a on a short-time period).

Further, most of our knowledge on Adélie penguins relies on banded birds, which could be handicapped (Dugger *et al.* 2006; Saraux *et al.* 2011a). We saw in the preliminary results presented in chapter V that return rates obtained seem much higher than previously evaluated. We discuss three potential reasons for this difference in this chapter: difference in location, time or bands. An increase of studies on non-banded birds would help answer this question and know whether vital rates need to be re-evaluated in Adélie penguins.

Our preliminary results also witnessed of potential important inter-annual variability in the timing juveniles spent out of the colony before returning for the first time. Such a study needs to be carried on for several years to assess the potential effect of climate on return rates and timing.

Additionally, the use of the weighbridge offers fantastic opportunities to investigate performances at sea depending on environmental conditions (*e.g.* Ballard *et al.* 2010). Foraging trip duration can be evaluated along with the mass of prey foraged (difference between return mass and departing mass). This may help understand how Adélie penguins adjust their foraging according to prey availability and oceanographic conditions. For instance, in case of low availability, is the mass of prey foraged kept relatively constant by increasing foraging duration or does it decrease?

In the years to come, similar study than those conducted on king penguins may allow to determine vital rates, their response to climate and to run population models.

CONCLUSION

In this thesis, we proposed to investigate the effects of the rapid and strong climate change on Southern Ocean ecosystems through the monitoring of top-predators, the penguins. Working on three different species, we found contrasted responses to climate between these species and highlighted the necessity of using different time-scales to investigate these effects depending on the biology of the species. The response to climate was also dependent on the life-history traits considered within a species, a warming in sea surface temperature leading to an increase in juvenile survival opposed to the negative consequences previously found on breeding success and adult survival. Finally, our results also pointed out the existence of behavioural plasticity in penguins, mainly in foraging strategies, suggesting the possibility to adapt (at least partially) to environmental changes through phenotypic plasticity. Yet, the rapidity and intensity of these changes seem to leave little hope for such long-lived and geographically constrained animals. Future studies on trophic interactions of penguins with their prey should provide valuable insights for a better understanding of the mechanisms underlying the indirect effects of climate that was highlighted in this work.

References

REFERENCES

A

Adams N. & Klages N. 1987. Seasonal variation in the diet of the king penguin (Aptenodytes patagonicus) at sub Antarctic Marion Island. *Journal of Zoology* **212**:303-324.

Aebischer N. J., Coulson J. C., Colebrook J. M. 1990. Parallel long-term trends across 4 marine trophic levels and weather. *Nature* **347**:753–755.

Ahmed M. O., Salem F. B., Bedhiaf S., M'Naouer D. 2010. Analyse moléculaire de la diversité génétique des dromadaires (Camelus dromedarius) en Tunisie. *Biotechnol. Agron. Soc. Environ* **14**:399-408.

Ahmed S., Hart T., Dawson D. A., Horsburgh G. J., Trathan P. N., Rogers A. D. 2009. Isolation and characterization of macaroni penguin (Eudyptes chrysolophus) microsatellite loci and their utility in other penguin species (Spheniscidae, AVES). *Molecular Ecology Resources* **9**:1530-1535.

Aho T., Kuitunen M., Suhonen J., Hakkari T., Jantti A. 1997. Effects of male removal on female foraging behaviour in the Eurasian tree-creeper. *Behavioral Ecology and Sociobiology* **41**:49-53.

Ainley D.G. & LeResche R. E. 1973. The effect of weather and ice-conditions on breeding in Adélie penguins. *The Condor* **75:** 235-255.

Ainley D.G. & Demaster D. 1980. Survival and mortality in a population of Adelie penguins. *Ecology* **61**: 522-530.

Ainley D. G., Wilson P. R., Barton K. J., Ballard G., Nur N., Karl B. 1998. Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology* **20**:311-319.

Ainley D.G. 2002. The Adélie penguin: bellwether of climate change. Columbia University Press, New York, 310 p.

Ainley D. G., Ballard G., Emslie S. D., Fraser W. R., Wilson P. R., Woehler E. J. 2003a. Adélie Penguins and Environmental Change. *Science* **300**: 429-430

Ainley D. G., Ford R. G., Brown E. D., Suryan R. M., Irons D. B. 2003b. Prey resources, competition and geographic structure of kittiwake colonies in Prince William Sound. *Ecology* **84**:709-723.

Ainley D. G., Ribic C. A., Ballard G., Heath S., Gaffney I., Karl B. J., Barton K. J., Wilson P. R., Webb S. 2004. Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. *Ecological monographs* **74**:159-178.

Ainley D. G., Clarke E. D., Arrigo K., Fraser W. R., Kato A., Barton K. J., Wilson P. R. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science* **17**: 171-182.

Ainley D. G., Ballard G., Dugger K. M. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. *Ecology* **87**: 2080-2093.

Albon S., Clutton-Brock T., Guinness F. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *The Journal of Animal Ecology* **56**:69-81.

Alheit J. & Niquen M. 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* **60**: 201-222.

Allen J. A. & Clarke B. C. 1984. Frequency-dependent selection -- homage to Poulton, E.B. *Biological Journal of the Linnean Society* **23:** 15-18.

Alm G. 1959. Connection between maturity, size and age in fishes. *Report of the Institute of Freshwater Research, Drottningholm* **40**:5-145.

Ancel A., Visser H., Handrich Y., Masman D., Le Maho Y. 1997. Energy saving in huddling penguins. *Nature* **385**: 304-305.

Andersson M. 1994. Sexual selection. Princeton, Princeton University press.

Anderegg W. R. L., Prall J. W., Harold J., Schneider S. H. 2010. Expert credibility in climate change. *Proceedings of the National Academy of Sciences* **107**:12107.

Anonymous 2009. Annual Report of the Phillip Island Penguin Reserve Committee of Management.

Arnould J. P., Dann P., Cullen J. M. 2004. Determining the sex of Little Penguins (*Eudyptula minor*) in northern Bass Strait using morphometric measurements. *Emu* **104**:261-265.

Atkinson A., Siegel V., Pakhomov E., Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**:100-103.

Ausubel J.H. 1999. Towards a Census of Marine Life. *Oceanography* **12**: 4-5.

B

Ballerini T., Tavecchia G., Olmastroni S., Pezzo F., Focardi S. 2009. Nonlinear effects of winter sea ice on the survival probabilities of Adelie penguins. *Oecologia* **161**: 253-265

Ballard G., Dugger K., Nur N., Ainley D. G. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Mar Ecol Prog Ser* **405**:287-302.

Barbraud C. & Weimerskirch H. 2001. Emperor penguins and climate change. *Nature* **411**: 183-186.

Barbraud C. & Weimerskirch H. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society of London Series B* **270**: 2111–2116.

Barbraud C. & Weimerskirch H. 2006. Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Science* **103**: 6248–6251.

Barbraud C., Weimerskirch H., Bost C. A., Forcada J., Trathan P. N., Ainley D. G. 2008. Are king penguin populations threatened by Southern Ocean warming? A Reply. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 26.

Barbraud C., Gavrilo M., Mizin Y., Weimerskirch H. 2011a. Comparison of emperor penguin declines between Pointe Géologie and Haswell Island over the past 50 years. *Antarctic Science, in press.*

Barbraud C., Rivalan P., Inchausti P., Nevoux M., Rolland V., Weimerskirch H. 2011b. Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *Journal of Animal Ecology* **80**: 89-100.

Bard E. 2003. Evolution du climat et de l'océan. Fayard, France

Barlow K. E. & Croxall J. P. 2002. Provisioning and parental expenditures by Macaroni penguins at South Georgia. *Ibis* **144**:248–258.

Barrat A. 1976. Quelques aspects de la biologie et de l'écologie du Manchot Royal (*Aptenodytes patagonicus*) des îles Crozet. *Comité National Français de la Recherche Antarctique* **40:** 9-51.

Barta Z., Houston A., McNamara J., Szekely T. 2002. Sexual conflict about parental care: the role of reserves. *American Naturalist* **159**:687-705.

Bates D. & Maechler M. 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-31.: http://CRAN.R-project.org/package=lme4.

Baudinette R., Gill P., O'driscoll M. 1986. Energetics of the Little Penguin, Eudyptula Minor: Temperature Regulation, the Calorigenic Effect of Food, and Moulting. *Australian Journal of Zoology* **34**:35-45.

Beaulieu M., Dervaux A., Thierry A.-M., Lazin D., Le Maho Y., Ropert-Coudert Y., Spée M., Raclot T., Ancel A. 2009a. When sea-ice clock is ahead of Adelie penguins' clock. *Functional Ecology* **24**: 93 - 102.

Beaulieu M., Raclot T., Dervaux A., Le Maho Y., Ropert-Coudert Y., Ancel A. 2009b. Can a disadvantaged parent rely on its partner? An experimental study within Adélie penguin pairs. *Animal Behaviour* **78**:313-320.

Beauplet G. & Guinet C. 2007 Phenotypic determinants of individual fitness in female fur seals: larger is better. *Proceedings of the Royal Society of London Series B* **274**: 1877-1883.

Behrenfeld M. J., O'Malley R. T., Siegel D. A., McClain C. R., Sarmiento J. L., Feldman G. C., Milligan A. J., Falkowski P. G., Letelier R. M., Boss E. S. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* **444** (7120): 752–755.

Belkin I. M. 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography* **81**:207-213.

Belkin I. M. & Gordon A. L. 1996. Southern Ocean fronts from the Greenwich meridian to Tasmania. *Journal of Geophysical Research* **101**:3675-3696.

Benvenuti S., Bonadonna F., Dall Antonia L., Gudmundsson G. A. 1998. Foraging flight of breeding thick-billed murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* **115**:57–66.

Bergeron P., Baeta R., Pelletier F., Reale D., Garant D. 2010. Individual quality: tautology or biological reality? *Journal of Animal Ecology* **80**: 361-364.

Bethge P., Nicol S., Culik B. M., Wilson R. P. 1997. Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*). *Journal of Zoology London* **242**:483-502.

Bindoff N. L., Willebrand J., Artale V., Cazenave A., Gregory J., Gulev S., Hanawa K., Le Quéré C., Levitus S., Nojiri Y., Shum C. K., Talley L. D., Unnikrishnan A. 2007. Observations: Oceanic Climate Change and Sea Level. in: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Birkhead T. R. & Furness R. W. 1985. Regulation of seabird populations. In: Sibly R. M., Smith R. H. (ed) Behavioural ecology, ecological consequences of adaptive behaviour. Blackwell London, p. 147-167.

Biuw M., Boehme L., Guinet C., Hindell M., Costa D. P., Charrassin J.-B., Roquet F., Bailleul F., Meredith M., Thorpe S., Tremblay Y., McDonald B., Park Y.-H., Rintoul S., Bindoff N., Goebel M., Crocker D. E., Lovell P., Nicholson J., Monks F., Fedak M. A. 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Science* **104**: 13705–13710.

Bize P., Criscuolo F., Metcalfe N. B., Nasir L., Monaghan P. 2009. Telomere dynamics rather than age predict life expectancy in the wild. *Proceedings of the royal society of London B* **276**:1679-1683.

Block B. A., Costa D. P., Boehlert G. W., Kochevar R. E. 2003. Revealing pelagic habitat use: the tagging of Pacific pelagics program. *Oceanologica acta* **25**: 255-266.

Boersma P. D. 1998. Population Trends of the Galapagos Penguin: Impacts of El Niño and La Niña. *The Condor* **100**: 245-253.

Boersma P. D. 2008. Penguins as marine sentinels. *BioScience* **58**: 597-607.

Boersma D. P. & Rebstock G. A. 2009. Flipper-bands do not affect foraging-trip duration of Magellanic Penguins. *J. Field Ornithol.* **80:** 408-418.

Boersma D. P. & Rebstock G. A. 2010. Effects of double bands on Magellanic penguins. *J. Field Ornithol.* **81**: 195-205.

Bonner J. T. 1965. Size and cycle. University of Princeton.

Booth A. M., Minot E. O., Fordham R. A., Imber M. J. 2000. Co-ordinated food provisioning in the little shearwater *Puffinus assimilis haurakiensis*: a previously undescribed foraging strategy in the Procellariidae. *Ibis* **142**:144-146.

Bost C.-A. & Le Maho Y. 1993. Seabirds as bio-indicators of changing marine ecosystems: new perspectives. *Acta Oecologica* **14**:463-470.

Bost C.-A., Georges J.-Y., Guinet C., Cherel Y., Putz K., Charrassin J.-B., Handrich Y., Zorn T., Lage J., Le Maho Y. 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology Progress Series* **150**: 21-33.

Bost C.-A., Charrassin J.-B., Clerquin Y., Ropert-Coudert Y., Le Maho Y. 2004. Exploitation of distant marginal ice zones by king penguins during winter. *Marine Ecology Progress Series* **283**: 293-297.

Bost C.A., Cotté C., Bailleul F., Cherel Y., Charrassin J.B., Guinet C., Ainley D. G., Weimerskirch H. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Special Issue on Processes at Oceanic Fronts of the Journal of Marine Systems (JMS-SIOF). Journal of Marine Systems* **78**: 363-376.

Boulinier T., McCoy K. D., Yoccoz N. G., Gasparini J., Tveraa T. 2008. Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters* **4**: 538–540.

Bouzat J. L., Walker B. G., Boersma P. D. 2009. Regional genetic structure in the Magellanic Penguin (Spheniscus magellanicus) suggests metapopulation dynamics. *The Auk* **126**:326-334.

Bowden R. M., Ewert M. A., Nelson, C. E. 2000. Environmental sex determination in a reptile varies seasonally and with yolk hormones. *Proceedings of the Royal Society of London* **267**: 1745-1749.

Boyce D. G., Lewis M. R., Worm B. 2010. Global phytoplankton decline over the past century. *Nature* **466**:591-596.

Boyd I. L. & Arnbom T. 1991. Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology* **11**: 259-266.

Boyd I. L. & Murray A. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology* **70**: 747-760.

Boyd I. L., Wanless S., Camphuysen C. J. 2006. Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press

Braasch A., Schauroth C., Becker P. 2009. Post-fledging body mass as a determinant of juvenile survival in Common Terns hirundo. *Journal of Ornithology* **150**: 401-407.

Brierley A. S. & Thomas D. N. 2002. Ecology of Southern Ocean pack ice. *Advances in Marine Biology* **43**:171-276.

Bucciarelli E., Blain S., Tréguer P. 2001. Iron and manganese in the wake of the Kerguelen Islands (Southern Ocean). *Marine Chemistry* **73**:21-36.

Bull J. 1980. Sex determination in reptiles. *Quarterly Review of Biology* **55**:3-21.

Bull L. 2000. Fidelity and breeding success of the blue penguin *Eudypyula minor* on Matiu-Somes island, Wellington, New-Zealand. *New-Zealand Journal of Zoology* **27**:291-298.

Burley N. 1981. Sex Ratio Manipulation and Selection for Attractiveness. *Science* **211**: 721-722.

Busalacchi A. J. 2004. The role of the Southern Ocean in global processes: an earth system science approach. *Antarctic Science* **16**: 363-368.

Buse A. & Good J.E.G. 1996. Synchronisation of larval emergence in winter moth (Operophtera brumata L.) and budburst in pedunculate oak (Quercus robur L.) under simulated climate change. *Ecological Entomology* **21**: 335–343.

C

Cam E. & Monnat J.-Y. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *Journal of Animal Ecology* **69**:380–394

Cam E., Monnat J.-Y., Hines J. E. 2003. Long-term fitness consequences of early conditions in the kittiwake. *Journal of Animal Ecology* **72**: 411–424.

Cameron M. F. & Siniff D. B. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (Leptonychotes weddellii) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* **82**:601-615.

Cannell B. L. & Cullen J. M. 1998. The foraging behaviour of little penguins *Eudyptula minor* at different light levels. *Ibis* **140**:467-471.

Carlini A. R., Coria N. R., Santos M., Negrete J., Juares M., Daneri G. 2009. Responses of Pygoscelis adeliae and P. papua populations to environmental changes at Isla 25 de Mayo (King George Island). *Polar Biology* **32:** 1427-1433.

Carney K. M. & Sydeman W. J. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* **22**:68-79.

Casper R. M. 2009. Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour* **78:** 1477–1483.

Caswell H. 2001. Matrix population models: construction analysis and interpretation. Sinuar associates Inc., Sunderland, Massachussets

Cazenave A. & Llovel W. 2010. Contemporary sea level rise. *Annual Review of Marine Science* **2**:145-173.

Chambers L. E. 2004a. The impact of climate on Little Penguin breeding success. (ed. B. o. M. R. Center), pp. 62. Melbourne: Australian Bureau of Meterology.

Chambers L. E. 2004b. Delayed breeding in Little Penguins – evidence of climate change? *Australian Meteorological Magazine* **53:** 13-19.

Chambers L. E., Hughes L., Weston M. A. 2005. Climate change and its impact on Australia's avifauna. *Emu* **105**:1-20.

Charmantier A., McCleery R. H., Cole L. R., Perrins C., Kruuk L. E. B., Sheldon B. C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, **320**: 800-803.

Charnov E. L., 1982. The theory of sex allocation. Princeton: *Princeton University Press*.

Charrassin J.-B. & Bost C.-A. 2001. Utilisation of the oceanic habitat by king penguins over the annual cycle. *Marine Ecology Progress Series* **221:** 285-297.

Charrassin J.-B., Park Y.-H., Le Maho Y., Bost C.-A. 2002. Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters* **5:** 317-319.

Chaurand T. & Weimerskirch H. 1994. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J Anim Ecol* **63**:275–282.

Cherel Y. & Le Maho Y. 1985. Five months of fasting in king penguin chicks: body mass loss and fuel metabolism. *American Journal of Physiology* **249**:R387–R392.

Cherel Y., Stahl J. C., Le Maho Y. 1987. Ecology and Physiology of Fasting in King Penguin Chicks. *Auk* **104**:254-262.

Cherel Y., Robin J-P., Walch O., Karmann H., Netchitailo P. Le Maho Y. 1988. Fasting in king penguin I. Hormonal and metabolic changes during breeding. *American Journal of Physiology* **254:** R170-R177.

Cherel Y. & Ridoux V. 1992. Prey species and nutritive value of food fed during summer to king penguin Aptenodytes patagonica chicks at Possession Island, Crozet Archipelago. *Ibis* **134**:118-127.

Cherel Y., Fréby F, Gilles J., Robin J.P. 1993a. Comparative fuel metabolism in gentoo and king penguins: adaptation to brief versus prolonged fasting. *Polar Biology* **13**: 263-269.

Cherel Y., Verdon C., Ridoux V. 1993b. Seasonal importance of oceanic myctophids in king penguin diet at Crozet Islands. *Polar Biology* **13**:355-357.

Cherel Y., Ridoux V., Rodhouse P. 1996. Fish and squid in the diet of king penguin chicks, Aptenodytes patagonicus, during winter at sub-Antarctic Crozet Islands. *Marine Biology* **126**:559-570.

Cherel Y. & Hobson K. A. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series* **329**:281-287.

Cherel Y., Hobson K. A., Guinet C., Vanpe C. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *Journal of Animal Ecology* **76**:826-836.

Chiaradia A. F. 1999. Breeding biology and feeding ecology of little penguins Eudyptula minor at Phillip Island - a basis for a monitoring program. Hobart, University of Tasmania: 109 pages.

Chiaradia A. & Kerry K. R. 1999. Daily nest attendance and breeding performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology* **27**:13-20.

Chiaradia A., Costalunga A., Kerry K. R. 2003. The diet of Little Penguins *Eudyptula minor* at Phillip Island, Victoria, following the 1995 mass mortality of one of their main prey, the Pilchard *Sardinops sagax*. *Emu* **103**:43–48.

Chiaradia A., Ropert-Coudert Y., Healy M., Knott N. 2005. Finding the balance: the effect of positioning of external devices on little penguins. *Polar Research* **18**: 46 - 53.

Chiaradia A. & Nisbet I. C. T. 2006. Plasticity in parental provisioning and chick growth in Little Penguins *Eudyptula minor* in years of high and low breeding success. *Ardea* **94**:257–270.

Chiaradia A., Forero M. G., Hobson K. A., Cullen J. M. 2010. Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES Journal of Marine Science* **67**: 1710-1720.

Ciannelli L., Hjermann D., Lehodey P., Ottersen G., Duffy-Anderson J., Stenseth N. 2005. Climate forcing, food web structure and community dynamics in pelagic marine ecosystems. *in Aquatic Food Webs: An Ecosystem Approach*. A. Belgrano, editor. Pages 143–169.

Clark A. B. 1978. Sex ratio and resource competition in a prosimian primate. *Science* **201**: 163-165.

Clutton-Brock T. H. 1986. Sex ratio variation in birds. *Ibis* **128**: 317-329.

Clutton-Brock T. H., Major M., Albon S. D., Guinness F. E. 1987. Early development and population dynamics in red deers. I Density-dependent effects on juvenile survival. *Journal of Animal Ecology* **56**: 53-67.

Clutton-Brock T. H. 1991. The Evolution of Parental Care, Princeton University Press.

Clutton–Brock T. H. & Coulson T. 2002. Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **357**:1285-1298.

Cockburn A., Legge S., Double M. C. 2002 Sex ratios in birds and mammals: can the hypotheses be disentangled? In: *Sex ratios: concepts and research methods* (Hardy I. C. W. eds) Pages 266-286.

Cole L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* **29**:103-137.

Collins M., Cullen J. M., Dann P. 1999. Seasonal and annual foraging movements of little penguins from Phillip Island, Victoria. *Wildlife Research* **26**:705-721.

Collins M., An S. I., Cai W., Ganachaud A., Guilyardi E., Jin F. F., Jochum M., Lengaigne M., Power S., Timmermann A. 2010. The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature Geoscience* **3**:391-397.

Congdon B. C., Krockenberger A. K., Smithers B. V. 2005. Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the wedge-tailed shearwater. *Marine Ecology Progress Series* **301**: 293-301.

Conroy J. & White M. 1972. The breeding status of the king penguin (*Aptenodytes patagonica*). *British Antarctic Survey Bulletin* **32**: 31-40.

Corbel H. 2008. Envol chez le poussin d'oiseau. Rôle de l'investisseùent parental et mécanismes proximaux. PhD of Strasbourg University. 283 pages.

Corbel H., Morlon F., Geiger S., Groscolas R. 2009. State-dependant decisions during the fledging process of king penguin chicks. *Animal Behaviour* **78**: 829-838.

Cornet A. & Jouventin P. 1980. Le phoque de Weddell (*Leptonychotes weddelli*) à Pointe Géologie et sa plasticité sociale. *Mammalia* **44**: 497-521.

Costa D. P. 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *Am Zool* **31**:111-130.

Costa D. P., Hickstadt L. A., Crocker D. E., McDonald B. I., Goebel M. E., Fedak M. A. 2010. Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integrative and Comparative Biology* **50:** 1018-1030.

Costanza R., Arge R., Groot R. D., Farberk S., Grasso M., Hannon B., Limburg K., Naeem S., Neill R. V. O., Paruelo J. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**:253-260.

Côté S. D. & Festa-Bianchet M. 2001. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). *Behavioral Ecology and Sociobiology* **49**: 260-265.

Cotté C., Park Y.-H., Guinet C., Bost C.-A. 2007. Movements of foraging king penguins through marine mesoscale eddies. *Proceedings of the Royal Society of London Series B* **274:** 2385-2391.

Coulson T., Gaillard J. M., Festa-Bianchet M. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology* **74**:789-801.

Crawford R. J. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* **148:** S253-S260.

Crews D. 1996. Temperature-Dependent Sex Determination: The Interplay of Steroid Hormones and Temperature. *Zoological science* **13**: 1-13.

Criscuolo F., Monaghan P., Nasir L., Metcalfe N. B. 2008. Early nutrition and phenotypic development:'catch-up'growth leads to elevated metabolic rate in adulthood. *Proceedings of the Royal Society B: Biological Sciences* **275**:1565.

Crocker D. E., Costa D. P., Le Boeuf B. J., Webb P. M., Houser D. S. 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. *Marine ecology progress series* **309**: 1-10.

Croxall J. 1984. Seabirds.

Croxall J. P., McCann T. S., Prince P. A., Rothery P. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976-1987: implications for Southern Ocean monitoring studies. In: Sahrhage D (ed.) *Antarctic Ocean and Resources Variability*, Springer Berlin, pp 261-285.

Croxall J. P., Callaghan T., Cervellati R., Walton D. 1992. Southern Ocean Environmental Changes: Effects on Seabird, Seal and Whale Populations. *Philosophical Transactions of the Royal Society of London series B* **338**: 319-328.

Croxall J. P., Trathan P. N., Murphy E. J. 2002. Environmental change and Antarctic seabird populations. *Science* **297**: 1510-1514.

Culik B., Wilson R., Bannasch R. 1993. Flipper-bands on penguins: what is the cost of a life-long commitment? *Marine Ecology Progress Series* **98**:209-214.

Culik B. M., Hennicke J., Martin T. 2000. Humboldt penguins outmanoeuvring El Nino. *Journal of Experimental Biology* **203:** 2311-2322.

Cullen J. M., Chambers L. E., Coutin P. C., Dann P. 2009. Predicting onset and success of breeding in little penguins Eudyptula minor from ocean temperatures. *Marine Ecology Progress Series* **378:** 269–278.

Cury P. M., Shin Y. J., Planque B., Durant J. M., Fromentin J.-M., Kramer-Schadt S., Stenseth N. Ch., Travers M., Grimm V. 2008. Ecosystem oceanography for global change in fisheries. *Trends in Ecology and Evolution* **23**: 338-346.

Cushing D. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* **26**:249-293.

D

Danchin E., Boulinier T., Massot M. 1998. Conspecific reproductive success and breeding habitat selection implications for the study of coloniality. *Ecology* **79**:2415-2428.

Daniel T. A., Chiaradia A., Logan M., Quinn G., Reina R. 2007. Synchronized group association in little penguins, *Eudyptula minor*. *Animal behaviour* **74**:1241-1248.

Dann P. 1988. An experimental manipulation of clutch size in the little penguin *Eudyptula minor*. *Emu* **88**:101-103.

Dann P. & Cullen J. M. 1990. Survival, patterns of reproduction, and lifetime reproductive output in little blue penguins *Eudyptula minor* on Phillip Island, Victoria, Australia. In: *Penguin biology* (Davis LS, Darby JT eds), Academic Press, Sydney, pp. 63-84.

Dann P. 1992. Distribution, population trends and factors influencing the population size of little penguins, Eudyptula minor on Phillip Island, Victoria. *Emu* **91**: 263-272.

Daunt F., Wanless S., Harris M. P., Money L., Monaghan P. 2007. Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology* **21**:561-567.

Davies N. & Green R. 1976. The development and ecological significance of feeding techniques in the reed warbler (Acrocephalus scirpaceus). *Animal Behaviour* **24**: 223-229.

Davis M. B., Shaw R. G., Etterson J. R. 2005. Evolutionary responses to changing climate. *Ecology* **86**:1704-1714.

De Brooke M. d. L. 2004. The food consumption of the world's seabirds. *Proceeding of the Royal Society of London Series B* **271:** S246–S248.

Delord K., Barbraud C., Weimerskirch H. 2004. Long-term trends in the population size of king penguins at Crozet archipelago: environmental variability and density dependence? *Polar Biology* **27:** 793–800.

Descamps S., Gauthier-Clerc M., Gendner J. P., Le Maho Y. 2002. The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet). *Avian Science* **2**: 87-98.

Descamps S., Gauthier-Clerc M., Le Bohec C., Gendner J. P., Le Maho Y. 2005. Impact of predation on king penguin Aptenodytes patagonicus in Crozet Archipelago. *Polar Biology* **28:** 303-310.

Deser C. & Wallace J. M. 1987. El Niño events and their relation to the southern oscillation: 1925-1986. *Geophysical Research Letters* **92**: 14189-14196.

deYoung B., Harris R., Carlotti F., Mackas D., Poggiale J-C. 2006. Integrating Process Studies and Modelling of Marine Zooplankton. *Global Change Newsletter* **66**: 5-8

Dobson F. S. & Oli M. K. 2001. The demographic basis of population regulation in Columbian ground squirrels. *American Naturalist* **158**:236-247.

Dobson F. S. & Oli M. K. 2007. Fast and slow life histories of mammals. *Ecoscience* **14**:292-299.

Drake J. M. 2005. Population effects of increased climate variation. *Proceedings of the Royal Society B: Biological Sciences* **272**:1823-1827.

Drent R. & Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**:225–252.

Ducklow H. W., Baker K., Martinson D. G., Quetin L. B., Ross R. M., Smith R. C., Stammerjohn S. E., Vernet M., Fraser W. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London series B* **362:** 67-94.

Dugger K., Ballard G., Ainley D., Barton K. 2006. Effects of flipper-bands on foraging behavior and survival of Adélie Penguins (*Pygoscelis Adeliae*). *The Auk* **123**: 858-869.

Durant J. M., Hjermann D. Ø., Ottersen G., Stenseth N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* **33**:271-283.

Durant J. M., Hjermann D. Ø., Frederiksen M., Charrassin J.B., Le Maho Y., Sabarros P. S., Crawford R. J. M., Stenseth N. Ch. 2009. The pros and cons of using seabirds as ecological indicators. *Climate Research* **39**: 115-129.

E

Easterling D. R., Evans J. L., Groisman P. Y., Karl T. R., Kunkel K. E., Ambenje P. 2000. Observed variability and trends in extreme climate events: A brief review. *Bulletin of the American Meteorology Society* **81**: 417–425.

Edwards M. & Richardson A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**:881-884.

Ellenberg U., Mattern T., Seddon P. J., Jorquera G. L. 2006. Physiological and reproductive consequences of human disturbance in Humboldt penguins: the need for species-specific visitor management. *Biological Conservation* **133**:95-106.

Ellegren H., Gustafsson L., Sheldon B. C. 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proceedings of the National Academy of Sciences* **93**: 11723-11728.

Ellis S., Woehler E. J., Skewgar E., Boersma P. D. 2007. Penguin Conservation Assessment: summary document. pp. 15. Ushuaia: IUCN/SSC Conservation Breeding Specialists Group.

Emlen S. T., Emlen M., Levin S. A. 1986. Sex ratio selection in species with helpers-at-the-nest. *The American Naturalist* **127**: 1–8.

Emmerson L. & Southwell C. 2008. Sea ice cover and its influence on Adelie penguin reproductive performance *Ecology* **89:** 2096-2102.

Emslie S. D. & McDaniel J. D. 2002. Adelie penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula. *Polar Biology* **25:** 222-229.

Emslie S. D. & Patterson W. P. 2007. Abrupt recent shift in 13C and 15N values in Adélie penguin eggshell in Antarctica. *Proceedings of the National Academy of Sciences* **104**:11666.

Ericsson G. & Wallin K. 2001. Age-specific moose(Alces alces) mortality in a predator-free environment: Evidence for senescence in females. *Ecoscience* **8**:157-163.

Ericsson G., Wallin K., Ball J. P., Broberg M. 2001. Age-related reproductive effort and senescence in free-ranging moose, Alces alces. *Ecology* **82**:1613-1620.

Estes J. A., Terborgh J., Brashares J. S., Power M. E., Berger J., Bond W. J., Carpenter S. R., Essington T. E., Holt R. D., Jackson J. B. C., Marquis R. J., Oksanen L., Oksanen T., Paine R. T., Pikitch E. K., Ripple W. J., Sandin S. A., Scheffer M., Schoener T. W., Shurin J. B., Sinclair A. R. E., Soulé M. E., Virtanen R., Wardle D. A. 2011. Trophic Downgrading of Planet Earth. *Science* **333**:301-306.

F

Fahlman A., Halsey L. G., Butler P. J., Jones D. R., Schmidt A., Durant S., Froget G., Bost C.-A., Woakes A. J., Duchamp C., Handrich Y. 2006. Accounting for body condition improves allometric estimates of resting metabolic rates in fasting king penguins, Aptenodytes patagonicus. *Polar Biology* **29**: 609-614.

Fallow P., Chiaradia A., Ropert-Coudert Y., Kato A., Reina R. 2009. Flipper-bands modify the short-term diving behaviour of Little penguins. *J. Wildl. Manag.* **73**: 1348-1354.

Fasola M. & Saino N. 1995. Sex-biased parental care allocation in 3 tern species (Laridae, Aves). *Canadian Journal of Zoology* **73**:1461-1467.

Fernandez-Juricic E., Jimenez M. D., Lucas E. 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental conservation* **28:** 263-269.

Festa-Bianchet M., Gaillard J.-M., Jorgenson J. T. 1998. Mass- and Density- dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* **152**: 367-379.

Fisher R. A. 1930. The genetical theory of natural selection. Oxford: Clarendon, 318 pages.

Forcada J., Trathan P. N., Reid K., Murphy E., Croxall, J. P. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* **12:** 411-423.

Forcada J., Trathan P. N., Murphy E. J. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology* **14**:2473-2488.

Forcada J. & Trathan P. N. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* **15:** 1618–1630.

Forchhammer M. C. & Post E. 2000. Climatic signatures in ecology. *Trends in Ecology & Evolution* **15**:286-286.

Forchhammer M. C., Clutton Brock T. H., Lindström J., Albon S. D. 2001. Climate and population density induce long term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**:721-729.

Forero M. G., Donázar J. A., Hiraldo F. 2002. Causes and fitness consequences of natal dispersal in a population of black kites. *Ecology* **83**: 858-872.

Fortescue M. 1995. Biology of the Little Penguin Eudyptula minor on Bowen Island and at other Australian colonies. *in The Penguins: Ecology and Management.* I. N. a. P. R. P. Dann,editor. Pages 364–392.

Frank S. A. 1990. Sex allocation theory for birds and mammals. *Annu. Rev. Ecol. Syst.* **21**:13-55.

Frank K. T., Petrie B., Choi J. S., Leggett W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**:1621.

Fraser W. R. & Patterson D. L. 1997. Human disturbance and long-term changes in Adelie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. In *Antarctic Communities: Species, Structure and Survival.* eds. B. Battaglia, J. Valencia & D. Walton), pp. 445-452. New York: Cambridge University Press.

Fraser W. R. & Hofmann E. E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* **265:** 1–15.

Frederiksen M., Edwards M., Richardson A. J., Halliday N. C., Wanless S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* **75:** 1259–1268.

Fretwell P. T. & Trathan P. N. 2009. Penguins from space: faecal stains reveal the location of emperor penguin colonies. *Global Ecology and Biogeography* **18:** 543–552.

Fridolfsson AK. & Ellegren H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30:** 116-121.

Froget G., Gauthier-Clerc M., Le Maho Y., Handrich Y. 1998. Is penguin banding harmless? *Polar Biol.* **20**: 409–413.

Fulton E. A. 2010. Approaches to end-to-end ecosystem models. *Journal of Marine Systems* **81**:171-183.

Fulton E. A., Link J. S., Kaplan I. C., Savina Rolland M., Johnson P., Ainsworth C., Horne P., Gorton R., Gamble R. J., Smith A. D. M. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* **12**:171-188.

Furness R.W. & Camphuysen C.J. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* **54**:726–737.

G

Gårdmark A., Enberg K., Ripa J., Laakso J., Kaitala V. 2003. The ecology of recovery. *Annales Zoologici Fennici* **40**: 131-144

Gaillard J.-M., Pontier D., Allaine D., Lebreton J., Trouvilliez J., Clobert J. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* **56**:59-76.

Gaillard J.-M., Boutin J. M., Delorme D., Van Laere G., Duncan P., Lebreton J. D. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**:502-513.

Gaillard J.-M., Festa-Bianchet M., Yoccoz N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**: 58-63.

Gaillard J.-M. & Yoccoz N. G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**:3294-3306.

Gales R.P. & Pemberton D. 1990. Seasonal and local variation in the diet of the little penguin, *Eudyptula minor*, in Tasmania. *Australian Journal of Wildlife Research* **17**:231-259.

Gandini P., Frere E., Boersma P. D. 1996. Status and conservation of Magellanic Penguins Spheniscus magellanicus in Patagonia, Argentina. *Bird Conservation International* **6**: 307-316.

Gaston A. 1997. Mass and date at departure affect the survival of Ancient Murrelet Synthliboramphus antiquus chicks after leaving the colony. *Ibis* **139**: 673-678.

Gauthier-Clerc M., Le Maho Y., Gendner J.-P., Handrich Y. 2001. State-dependent decisions in long-term fasting king penguins, *Aptenodytes patagonicus*, during courtship and incubation. *Animal Behaviour* **62**:661-669.

Gauthier-Clerc M., Le Maho Y., Gendner J.-P., Handrich Y. 2002. Moulting fast and time constraint for reproduction in the king penguin. *Polar Biology* **25**:288-295.

Gauthier-Clerc M., Gendner J.-P., Ribic C. A., Fraser W. A., Woehler E. J., Descamps S., Gilly C., Le Bohec C., Le Maho Y. 2004. Long-term effects of flipper-bands on penguins. *Proc. R. Soc. Lond. B* **271**: S423–S426.

Gendner J.-P., Gilles J., Challet E., Verdon C., Plumere C., Reboud X., Handrich Y., Le Maho Y. 1992. Automatic weighing and identification of breeding king penguins. In: *Wildlife telemetry. Remote monitoring and tracking of animals.* (eds. G. Priede & S. M. Swift), pp. 29-30. Melksham, England: Redwood Press.

Gendner J.P., Gauthier-Clerc M., Le Bohec C., Descamps S., Le Maho Y. 2005. A new application for transponders in studying of penguins. *J. Field Ornithol.* **76**: 138-142.

Gienapp P., Teplitsky C., Alho J., Mills J., Merila J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* **17**:167-178.

Giese M. 1998. Guidelines for people approaching breeding groups of Adélie penguins (*Pygoscelis Adeliae*). *Polar Record* **34:** 287-292.

Gil D., Graves J., Hazon N., Wells A. 1999. Male Attractiveness and Differential Testosterone Investment in Zebra Finch Eggs. *Science* **286**: 126-128.

Goodey W. & Lill A. 1993. Parental care by the Willie Wagtail in Southern Victoria. *Emu* **93**:180-187.

Goodman D. 1974. Natural selection and cost of ceiling on reproductive effort. *American Naturalist* **108**:247-268.

Granadeiro J. P., Nunes M., Silva M., Furness R. W. 1998. Flexible foraging strategy of Cory's shearwarter, *Calonectris diomedea*, during the chickrearing period. *Animal Behaviour* **56**:1169–1176.

Gregg W. W., Conkright M. E., Ginoux P., O'Reilly J. E., Casey N. W. 2003. Ocean primary production and climate: Global decadal changes. *Geophysical Research Letters* **30**: 1809-1812.

Grémillet D., Lewis S., Drapeau L., von den Lingen C. D., Huggett J. A., Coetzee J. C., Verheye H. M., Daunt F., Wanless S., Ryan P. G. 2008. Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology* **45:** 610–621.

Grémillet D. & Boulinier T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series* **391**:121-137.

Griffith S. C., Örnborg J., Russell A. F., Andersson S., Sheldon B. C. 2003. Correlations between ultraviolet coloration, overwinter survival and offspring sex ratio in the blue tit. *Journal of Evolutionary Biology* **16**: 1045-1054.

Griffiths R., Double M. C., Orr K., Dawson R. J. G. 1998. A DNA test to sex most birds. *Molecular Ecology* **7**: 1071-1075.

Groscolas R. & Robin J.-P. 2001. Long-term fasting and re-feeding in penguins. *Compar. Biochem. Physiol. Part A* **128**: 645-655.

Grüebler M. U. & Naef-Daenzer B. 2010. Fitness consequences of timing of breeding in birds: date effects in the course of a reproductive episode. *Journal of Avian Biology* **41**: 282-291.

Guerra M. & Drummond H. 1995. Reversed sexual size dimorphism and parental care – minimal division of labor in the Blue-Footed Booby. *Behaviour* **132**:479-496.

Guinard E., Weimerskirch H., Jouventin P. 1998. Population Changes and Demography of the Northern Rockhopper Penguin on Amsterdam and Saint Paul Islands. *Colonial Waterbirds* **21:** 222-228.

Guinet C., Jouventin P., Malacamp J. 1995. Satellite remote sensing in monitoring change of seabirds: use of Spot Image in king penguin population increase at Ile aux Cochons, Crozet Archipelago. *Polar Biology* **15**: 511-515.

H

Hallett T., Coulson T., Pilkington J., Clutton-Brock T., Pemberton J., Grenfell B. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**:71-75.

Halpern B. S., Walbridge S., Selkoe K. A., Kappel C. V., Micheli F., D'Agrosa C., Bruno J. F., Casey K. S., Ebert C., Fox H. E., Fujita R., Heinemann D., Lenihan H. S., Madin E. M. P., Perry M. T., Selig E. R., Spalding M., Steneck R., Watson R. 2008. A global map of human impact on marine ecosystems. *Science* **319** (5865): 948–952.

Hamer K. & Furness R. 1991. Age-specific breeding performance and reproductive effort in great skuas Catharacta skua. *The Journal of Animal Ecology* **60**:693-704.

Hamer K. C., Quillfedt P., Masello J. F., Fletcher K. L. 2006. Sex differences in provisioning rules: responses of Manx shearwaters to supplementary chick feeding. *Behavioral Ecology* **17**:132-137.

Hamilton W. D. 1967. Extraordinary sex ratios. *Science* **156**: 477-488.

Hansen J., Sato M., Ruedy R., Lo K., Lea D. W., Medina-Elizade M. 2006. Global temperature change. *Proceedings of the National Academy of Sciences* **103**:14288.

Hanuise N., Bost C. A., Huin W., Auber A., Halsey L. G., Handrich Y. 2010. Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. *Journal of Experimental Biology* **213**:3874-3880.

Hare S. R. & Mantua N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* **47**:103-145.

Harrell F.E. 2001. Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression and Survival Analysis. Springer, New York. Pages.335-337.

Harris M.P., Halley D.J., Wanless S. 1991. The post-fledging survival of young guillemots Uria algae in relation to hatching date and growth. *Ibis* **134**:335–339.

Harris M.P., Frederiksen M., Wanless S. 2007. Within- and between year variation in the juvenile survival of common guillemots Uria aalge. *Ibis* **149**: 472–481.

Hart T., Mann R., Coulson T., Pettorelli N., Trathan P. N. 2010. Behavioural switching in a central place forager: patterns of diving behaviour in the macaroni penguin (Eudyptes chrysolophus). *Marine Biology* **157**:1543-1553.

Hasselquist D. & Kempenaers B. 2002. Parental care and adaptive brood sex ratio manipulation in birds. *Philosophical Transactions of the Royal Society of London B* **357**: 363–372.

Hays J., Imbrie J., Shackleton N. 1976. Variations in the Earth's Orbit: Pacemaker of the Ice Ages. *Science* **194**:1121.

Hays G. C., Richardson A. J., Robinson C. 2005. Climate change and marine plankton. *Trends in Ecology & Evolution* **20**:337-344.

Hedd A. 1998. Foraging ecology of Shy Albatrosses *Thalassarche cauta* breeding in Australia: Implications for interactions with longline fisheries. PhD, University of Tasmania.

Hedgren S. 1981. Effects of fledging weight and time of fledging on survival of guillemot Uria aalge chicks. *Ornis Scandinavica* **12**: 51–54.

Hewison A. J. M. & Gaillard J.-M. 1996. Birth-sex ratios and local resource competition in roe deer, Caproelus caproelus. *Behavioral Ecology* **7**: 461-464.

Hewison A. J. M. & Gaillard J.-M. 1999. Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology and Evolution* **14**: 229-234.

Hewison A. J. M., Gaillard J.-M., Kjellander P., Toïgo C., Liberg O., Delorme D. 2005. Big mothers invest more in daughters – reversed sex-allocation in a weekly polygynous mammal. *Ecology Letters* **8:** 430-437.

Hindell M. A., Lea M.-A., Hull C. L. 1996. The effects of flipper bands on adult survival rate and reproduction in the royal penguin, Eudyptes schlegeli. *Ibis* **138**: 557-560.

Hinke J. T., Salwicka K., Trivelpiece S. G., Watters G. M., Trivelpiece W. Z. 2007. Divergent responses of Pygoscelis penguins reveal a common environmental driver. *Oecologia* **153:** 845-855.

Hobson K. A. & Clark R. G. 1992. Assessing avian diets using stable isotopes I: turnover of 13C in tissues. *Condor* **94**:181-188.

Hobson K. A., Piatt J. F., Pitocchelli J. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* **63**:786-798.

Hobson K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**:314-326.

Hoegh-Guldberg O. & Bruno J. F. 2010. The impact of climate change on the world's marine ecosystems. *Science* **328**:1523.

Hoffman A. A. & Parsons P.A. 1997. Extreme environmental change and evolution. Cambridge University Press.

Horvizt C., Schemske D. W., Caswell H. 1997. The relative ‘‘importance’’ of life-history stages to population growth: prospective and retrospective analyses. In: *Structured population models in marine, terrestrial and freshwater systems.* (Tuljapurkar S. & Caswell H. eds) Kluwer Academic Publishers. Pages. 247-271.

Houston A. I., Szekely T., McNamara J. M. 2005. Conflict between parents over care. *Trends in Ecology & Evolution* **20**:33–38.

Hughes L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* **15**:56-61.

Huin N. & Prince P.A. 2000. Chick growth in albatrosses: curve fitting with a twist. *J. Avian Biol.* **31**: 418–425.

Hulley P. A. & Duhamel G. 2011. Aspects of lanternfish distribution in the Kergelen plateau region. In: *The Kerguelen Plateau: marine ecosystem and fisheries*. (Duhamel G. & Welsford D. eds) Pages 183-195.

Hunt G., Mehlum F., Russell R., Irons D., Decker M., Becker P. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. *Proceedings of the 22 International Ornithological Congress, Durban,* pp. 2040–2056. Johannesburg: BirdLife South Africa.

Hunt B., Pakhomov E., McQuaid C. 2001. Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology* **138**:369-381.

I

Irvine L. G., Clarke J. R., Kerry K. R. 2000. Low breeding success of the Adélie penguin at Berchervaise island in the 1998/1999 season. *CCAMLR Science* **7:** 151-167.

IUCN. 2009. IUCN Red List of Threatened Species. Version 2009.1 www.iucnredlist..org

IPCC. 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.

J

Jackson J. B. C. 1985 Distribution and ecology of clonal and aclonal benthic invertebrates. In *Population biology and evolution of clonal organisms* (ed. J. B. C. Jackson, L. W. Buss & R. E. Cook, pp. 297-355. New Haven: Yale University Press.

Jackson S. & Wilson R. P. 2002. The potential costs of flipper-bands to penguins. *Func. Ecol.* **16**: 141-148.

Jansen E., Overpeck J., Briffa K. R., Duplessy J.-C., Joos F., Masson-Delmotte V., Olago D., Otto-Bliesner B., Peltier W. R., Rahmstorf S., Ramesh R., Raynaud D., Rind D., Solomina O., Villalba R., Zhang D. 2007. Palaeoclimate. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M., Miller H.L. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Janzen F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences* **91**:7487-7490.

Jarvis M. J. F. 1974. The ecological significance of clutch size in the South African gannet Sula capensis (Lichtenstein). *Journal of Animal Ecology* **43**: 1–17.

Jenouvrier S., Barbraud C., Weimerskirch H. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* **72**:576-587.

Jenouvrier S., Weimerskirch H., Barbraud C., Park Y.-H., Cazelles B. 2005a. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. *Proceedings of the Royal Society of London Series B* **272:** 887–895.

Jenouvrier S., Barbraud C., Weimerskirch H. 2005b. Long-term contrasted responses to climate of two antarctic seabird species. *Ecology* **86:** 2889-2903.

Jenouvrier S., Barbraud C., Weimerskirch H. 2006. Sea ice affects the population dynamics of Adelie penguins in Terre Adelie. *Polar Biology* **29:** 413–423.

Jenouvrier S., Caswell H., Barbraud C., Holland M., Stroeve J., Weimerskirch H. 2009a. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Science* **106:** 1844-1847.

Jenouvrier S., Barbraud C., Weimerskirch H., Caswell H. 2009b. Limitation of population recovery: a stochastic approach to the case of the emperor penguin. *Oikos* **118:** 1292-1298.

Johnson C. R., Banks S. C., Barrett N. S., Cazassus F., Dunstan P. K., Edgar G. J., Frusher S. D., Gardner C., Haddon M., Helidoniotis F., Hill K. L., Holbrook N. J., Hosie G. W., Last P. R., Ling S. D., Melbourne-Thomas J., Miller K., Pecl G. T., Richardson A. J., Ridgway K. R., Rintoul S. R., Ritz D. A., Ross D. J., Sanderson J. C., Shepherd S. A., Slotwinski A., Swadling K. M., Taw N. 2011. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* **400**:17-32.

Jones O. R., Gaillard J. M., Tuljapurkar S., Alho J. S., Armitage K. B., Becker P. H., Bize P., Brommer J., Charmantier A., Charpentier M. 2008. Senescence rates are determined by ranking on the fast–slow life history continuum. *Ecology Letters* **11**:664-673.

Jouventin P., Stahl J., Weimerskirch H., Mougin J. 1984. The seabirds of the French subantarctic islands and Adelie Land, their status and conservation. In: *Status and Conservation of the World's Seabirds*.ICBP Technical Publication Pages 609-625.

Jouventin P. & Weimerskirch H. 1990. Satellite-tracking of wandering albatrosses. *Nature* **343:** 746-748.

Jouzel J., Masson-Delmotte V., Cattani O., Dreyfus G., Falourd S., Hoffmann G., Minster B., Nouet J., Barnola J., Chappellaz J. 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science* **317**:793.

K

Kaplan A., Cane M. A., Kushnir Y., Clement A. C., Blumenthal M. B., Rajagopalan B. 1998. Analyses of global sea surface temperature 1856-1991. *Journal of Geophysical Research* **103**:567–518.

Kappelle M., Van Vuuren M. M. I., Baas P. 1999. Effects of climate change on biodiversity: a review and identification of key research issues. *Biodiversity and Conservation* **8**:1383-1397.

Karr J.R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* **6**: 21-27.

Kato A., Ropert-Coudert Y., Naito Y. 2002. Changes in Adélie penguin breeding populations in Lützow-Holm Bay, Antarctica, in relation to sea-ice conditions. *Polar Biology* **25:** 934 - 938.

Kato A., Ropert-Coudert Y., Chiaradia A. 2008. Regulation of trip duration in an inshore forager, the little penguin (*Eudyptula minor*), during incubation. *The Auk* **125**:588-593.

Kearney M. & Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**:334-350.

Keeling C. D., Chin J., Whorf T. 1996. Increased activity of northern vegetation inferred from atmospheric CO2 measurements. *Nature* **382**:146-149.

Keller L. F. & Van Noordwijk A. J. 1994. Effects of local environmental conditions on nestling growth in the great tit Parus major. *Ardea* **82**:349-349.

Kerry K. R., Clarke J. R., Else G. D. 1993. Identification of sex of Adélie penguins from observations of incubating birds. *Wildlife Research* **20**:725–732.

Keyfitz N. & Flieger W. 1971. *Population: Facts and Methods of Demography.* Freeman, San Francisco.

Klomp N. I. & Wooller R. D. 1991. Patterns of arrival and depature by breeding little penguins at Penguin Island, Western Australia. *EMU* **91**:32-35.

Komdeur J. 1996. Influence of age on reproductive performance in the Seychelles warbler. *Behavioral Ecology* **7**:417-425.

Kooyman G. L., Ainley D. G., Ballard G., Ponganis, P. J. 2007. Effects of giant icebergs on two emperor penguin colonies in the Ross Sea, Antarctica. *Antarctic Science* **19:** 31-38.

Korpimäki E. & Lagerström M. 1988. Survival and natal dispersal of fledglings of Tengmalm's owl in relation to fluctuating food conditions and hatching date. *Journal of Animal Ecology* **57**:433–441.

Koubbi P., Ozouf-Costaz C., Goarant A., Moteki M., Hulley P. A., Causse R., Dettai A., Duhamel G., Pruvost P., Tavernier E., Post A. L., Beaman R. J., Rintoul S. R., Hirawake

T., Hirano D., Ishimaru T., Riddle M., Hosie G. 2010. Estimating the biodiversity of the East Antarctic shelf and oceanic zone for ecoregionalisation: Example of the ichthyofauna of the CEAMARC (Collaborative East Antarctic Marine Census) CAML surveys. *Polar Science* **4**: 115-133.

Kozlov A. N. & Tarverdiyevma I. 1989. Feeding of different species of Myctophidae in different parts of the Southern Ocean. *Journal of Ichthyology* **29**: 160–167.

Kozlov A. N., Shust K., Zemsky A. 1991. Seasonal and inter-annual variability in the distribution of Electrona carlsbergi in the Southern Polar Front area (The area to the north of South Georgia is used as an example). *Selected Scientific Papers, Scientific Committee for the Conservation of Antarctic Living Resources (CCAMLR)*:320-337.

Kozlov M. V. 2000. Climatic signatures in ecology. *Trends in Ecology and Evolution* **15**: 286-287.

Krishnankutty N. 2006. Effect of 2004 tsunami on ecosystems – a perspective from the concept of disturbance. *Current Science* **90**: 772-773.

Kruuk L. E. B., Clutton-Brock T. H., Albon S. D., Pemberton J. M., Guinness F. E. 1999. Population density affects sex ratio variation in red deer. *Nature* **399**: 459-461.

L

Lack D. L. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press

Lack D. L. 1968. Ecological adaptations for breeding in birds. London: Methuem.

Lalonde R. G. 1991. Optimal offspring provisioning when resources are not predictable. *American Naturalist* **138**:680-686.

Lancraft T. M., Torres J. J., Hopkins T. L. 1989. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones. *Polar Biology* **9**: 225-233.

Laws R. 1977. Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* **279**:81-96.

Le Bohec C., Gauthier-Clerc M., Grémillet D., Pradel R., Béchet A., Gendner J.-P., Le Maho Y. 2007. Population dynamics in a long-lived seabird: I. Impact on breeding activity on survival and breeding probability in unbanded King Penguins. *Journal of Animal Ecology* **76**: 1149-1160.

Le Bohec C., Durant J. M., Gauthier-Clerc M., Stenseth N. Ch., Park Y.-H., Pradel R., Grémillet D., Gendner J.-P., Le Maho Y. 2008a. King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy of Science* **105:** 2493-2497.

Le Bohec C., Durant J. M., Gauthier-Clerc M., Stenseth N. C., Park Y.-H., Pradel R., Grémillet D., Gendner J.-P., Le Maho Y. 2008b. Reply to Barbraud *et al.*: King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 26.

Lebreton J. D. 1981. Contribution à la dynamique des populations d'oiseaux. Modèles mathématiques en temps discret. *Unpublished thesis.* Lyon, France

Lebreton J. D. & Clobert J. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling. In: Perrins C.M., Lebreton J.D., Hirons G.J.M. (Eds) *Bird population studies: their relevance to conservation and management*. Oxford University Press, Oxford, pp. 105-125.

Lebreton J. D., Burnham K. P., Clobert J., Anderson D. R. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* **62**: 67-118.

Lebreton J. D. & Pradel R. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* **29:** 353-369.

Lee D. E. & Sydeman W. J. 2009. North Pacific climate mediates offspring sex ratio in northern elephant seals. *Journal of mammalogy* **90**: 1-8.

Le Maho Y., Vu Van Kha H., Koubi H., Dewasme G., Girard J. Ferré P., Cagnard M. 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. *American Journal of Physiology* **241**: E342-E354.

Le Maho Y., Karmann H., Briot D., Handrich Y., Robin J.-P., Mioskowski E., Cherel Y., Farni J. 1992. Stress in birds due to routine handling and a technique to avoid it. *American Journal of Physiology* **263**: R775-R781.

Le Maho Y., Gendner J.-P., Challet E., Bost C.-A., Gilles J., Verdon C., Plumere C., Robin J.-P., Handrich Y. 1993. Undisturbed breeding penguins as indicators of changes in marine resources. *Marine Ecology Progress Series* **95:** 1-6.

Le Maho Y. 2002. Nature and function. *Nature* **416**:21.

Le Maho Y., Saraux C., Durant J., Viblanc V. A., Gauthier-Clerc M., Yoccoz N., Stenseth N. Ch., Le Bohec C. 2011. An ethical issue on biodiversity science: The monitoring of penguins with flipper-bands. *Comptes Rendus Biologie* **334**: 378-384

Le Quéré C., Bopp L., Tegen I. 2002. Antarctic circumpolar wave impact on marine biology: A natural laboratory for climate change study. *Geophysical Research Letters* **29**: 1407.

Lescroël A. & Bost C.-A. 2005. Foraging under contrasting oceanographic conditions; the gentoo penguin at Kerguelen Archipelago. *Mar Ecol Prog Ser* **302**:245-261.

Lescroël A., Dugger K. M., Ballard G., Ainley D. G. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology* **78:** 798 - 806.

Leslie P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* **33**: 183-212.

Leslie P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* **35:** 213-245.

Lessells C. M. & Avery M. I. 1987. Sex ratio selection in species with helpers at the nest: some extensions of the repayment model. *The American Naturalist* ***1*29**: 610–620.

Lessells C. M., Mateman A. C., Visser J. 1996. Great tit hatchling sex ratios. *Journal of Avian Biology* **27**: 135–142.

Levins R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press.

Lewis S., Sheratt T. N., Hamer K. C., Wanless S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* **412**:816-819.

Lewis S., Benvenuti S., Dall'Antonia L., Griffiths R., Money L., Sherratt T., Wanless S., Hamer K.C. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London series B* **269**:1687-1693.

Lewis S., Schreiber E., Daunt F., Schenk G.A., Orr K., Adams A., Wanless S., Hamer K.C. 2005. Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* **147**:408–414.

Lewontin R. C. 1965. Selection for colonizing ability. Pages 79–94 *in The genetics of colonizing species* (H. G. Baker and G. L. Stebbins, eds.) Academic Press, New York.

Lewontin R. C. & Cohen D. 1969. On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences* **62**:1056.

Linden M., Gustaffson L., Pärt T. 1992. Selection on fledging mass in the Collared Flycatcher and the Great Tit. *Ecology* **73**: 336-343.

Lindström J. 1999. Early development and fitness in birds and mammals. *Trend in Ecology and Evolution* **14**: 343–348.

Lishman G. 1985. The food and feeding ecology of Adélie penguins (Pygoscelis adeliae) and chinstrap penguins (Pygoscelis antarctica) at Signy Island, South Orkney Islands. *J Zool* **205**:245-263.

Litzow M. A. & Ciannelli L. 2007. Oscillating trophic control induces community reorganization in a marine environment. *Ecology Letters* **10**: 1124-1134.

Loeb V., Siegel V., Holm-Hansen O., Hewitt R., Fraser W. R., Trivelpiece W. Z., Trivelpiece S. G. 1997. Effects of sea-ice extent and krill or salp dominance on theAntarctic foodweb. *Nature* **387:** 897-900.

Loison A., Festa-Bianchet M., Gaillard J.-M., Jorgenson J. T., Jullien J. M. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* **80**:2539-2554.

Lorrain A., Graham B., Ménard F., Popp B., Bouillon S., Breugel P. v., Cherel Y. 2009. Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. *Marine Ecology Progress Series* **391:** 293–306.

Louw G. 1993. Physiological animal ecology. Longman Scientific and Technical.

Lubimova T., Shust K., Popkov V. 1987. Some features of the ecology of mesopelagic fish of family Myctophidae in the Southern Ocean. *Biological resources of the Arctic and Antarctic. Nauka, Moscow*:320–337.

Lynnes A., Reid K., Croxall J. 2004. Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biology* **27**:544-554.

M

MacArthur R. H. 1962. Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences of the United States of America* **48**:1893-1897.

MacArthur R. H. & Wilson E. O. 1967. The theory of island biogeography. Princeton Univ Pr.

Mangin S., Gauthier-Clerc M., Frenot Y., Gendner J.-P., Le Maho Y. 2003. Ticks *Ixodes uriae* and the breeding performance of a colonial seabird, king penguin *Aptenodytes patagonicus. Journal of avian biology* **34**: 30-34.

Mann K. H. & Lazier J. L. 1991. Dynamics of marine ecosystems. Blackwell Scientific Publishers, London, England.

Marchant S. & Higgins P. 1990. *Handbook of Australian, New Zealand and Antarctic Birds*. Sharp, M. (ed.) volume I: Oxford University Press, Melbourne.

Marchetti K. & Price T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Review* **64**: 41-70.

Markman S., Pinshow B., Wright J., Kotler B. P. 2004. Food patch use by parent birds: to gather food for themselves or for their chicks? *Journal of Animal Ecology* **73**:747-755.

Martin K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist* **35**: 340–348.

Mauck R.A. & Grubb Jr T.C. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Animal Behaviour* **49**: 999–1008.

May R. M. 2004. Ethics and amphibians *Nature* **431**: 403.

Maynard Smith J. 1977a. The sex habit in plants and animals. In Measuring Selection in Natural Populations, ed. FB Christiansen,TMFenchel, pp. 265–73. Berlin: Springer-Verlag.

Maynard Smith J. 1977b. Parental investment: a prospective analysis. *Animal Behaviour* **25**: 1-9.

Mayr E. 1939. The Sex Ratio in Wild Birds. *The American Naturalist* **73**: 156-179.

McCarty J. P. 2001. Ecological Consequences of Recent Climate Change. *Conservation Biology* **15**:320-331.

McNamara J. M. & Houston A. I. 1996. State-dependent life histories. *Nature* **380**: 215-221.

Meehl G. A., Stocker T. F., Collins W. D., Friedlingstein P., Gaye A. T., Gregory J. M., Kitoh A., Knutti R., Murphy J. M., Noda A., Raper S. C. B., Watterson I. G., Weaver A. J., Zhao Z.-C. 2007. Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M., Miller H.L. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Menzel A. & Fabian P. 1999. Growing season extended in Europe. *Nature* **397**:659-659.

Mickelson M., Dann P., Cullen J. 1991. Sea Temperature in Bass Strait and Breeding Success of the Little Penguin Eudyptula minor at Phillip Island, South-eastern Australia. *Emu* **91**:355-368.

Middleton J. F., Arthur C., Van Ruth P., Ward T. M., McClean J. L., Maltrud M. E., Gill P., Levings A. Middleton S. 2007. El-Niño effects and upwelling off South Australia. *Journal of Physical Oceanography* **37:** 2458-2477.

Minster J.-F. 1998. *La machine Ocean*: Flammarion.

Moline M. A., Claustre H., Frazer T. K., Schofield O., Vernet M. 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology* **10**:1973-1980.

Moline M. A., Karnovsky N. J., Brown Z., Divoky G. J., Frazer T. K., Jacoby C. A., Torres J. J., Fraser W. R. 2008. High latitude changes in ice dynamics and their impact on polar marine ecosystems. *Annals of the New York Academy of Sciences* **1134**:267-319.

Monaghan P. & Haussmann M.F. 2006. Do telomere dynamics link lifestyle and lifespan? *Trends in Ecology and Evolution* **21**:47-53.

Montaigne F. 2010. Fraser's Penguins: A Journey to the Future in Antarctica.

Montes-Hugo M., Vernet M., Martinson D., Smith R., Iannuzzi R. 2008. Variability on phytoplankton size structure in the western Antarctic Peninsula (1997-2006). *Deep Sea Research Part II: Topical Studies in Oceanography* **55**:2106-2117.

Montevecchi W.A. 1993. Birds as indicators of change in marine prey stocks. In: *Birds as monitors of environmental change.* (Furness RW, Greenwood DJ: eds) Chapman & Hall, London, p 217–266.

Moore J. K., Abbott M. R., Richman J. G. 1999. Location and dynamics of the Antarctic polar front from satellite sea surface temperature data. *Geophysical Research Letter* **104**: 3059-3073.

Moore J. K. & Abbott M. R. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *Journal of Geophysical Research* **105**: 709-722.

Moore S. E. 2008. Marine mammals as ecosystem sentinels. *Journal of Mammalogy* **89**:534-540.

Moreno J., Barbosa A., Potti J., Merino S. 1997. The effects of hatching date and parental quality on chick growth and crèching age in the chinstrap penguin Pygoscelis antarctica: a field experiment. *The Auk* **114**: 47–54.

Moreno J. & Møller A. P. 2011. Extreme climatic events in relation to global change and their impact on life histories. *Current Zoology* **57**: 375-389.

Morris W. F., Pfister C. A., Tuljapurkar S., Haridas C. V., Boggs C. L., Boyce M. S., Bruna E. M., Church D. R., Coulson T., Doak D. F. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89**:19-25.

Murphy M. E. 1996. Nutrition and metabolism. Avian Energetics and Nutritional Ecology (ed. C. Carey), pp. 31– 60. Chapman & Hall, New York.

Murphy E.J., Watkins J. L., Trathan P. N., Reid K., Meredith M. P., Thorpe S. E., Johnston N. M., Clarke A., Tarling G. A. Collins M. A., Forcada J., Shreeve R. S., Atkinson A., Korb R., Whitehouse M. J., Ward P., Rodhouse P. G., Enderlein P., Hirst A. G., Martin A. R., Hill S. L., Staniland I. J., Pond D. W., Briggs D. R., Cunningham N. J., Fleming A. H. 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Philosophical Transactions of the Royal Society of London B* **362**: 113-148.

Myneni R. B., Keeling C., Tucker C., Asrar G., Nemani R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**:698-702.

N

Naef-Daenzer B. & Nuber W. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**: 730-738.

Nager R. G., Monaghan P., Griffiths R., Houston D. C., Dawson R. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Sciences USA* **96**: 570-573.

Nager R. G., Monaghan P., Houston D. C., Genovart M. 2000. Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (Larus fuscus). *Behavioral ecology and Sociobiology* **48:** 452-457.

Naito Y. 2004. Bio-logging Science. *Memoirs of the National Institute of Polar Research, Special issue* **58**: 118-132.

Newton I. 1989. Lifetime Reproduction in Birds. Academic Press, London.

Nicolaus M., Le Bohec C., Nolan P. M., Gauthier-Clerc M., Le Maho Y., Komdeur J., Jouventin P. 2007. Ornamental colors reveal age in the king penguin. *Polar Biology* **31**: 53-61.

Nicolaus M., Bouwman K., Dingemanse N. 2009. Effect of PIT tags on the survival and recruitment of Great Tits. *Ardea* **96:** 286-292.

Nisbet I. C. T. & Dann P. 2009. Reproductive performance of little penguins Eudyptula minor in relation to year, age, pair-bond duration, breeding date and individual quality. *Journal of Avian Biology* **40**: 296-308.

Numata M., Davis L.S., Renner M. 2000. Prolonged foraging trips and egg desertion in little penguins Eudyptula minor. *New Zealand Journal of Zoology* **27**:277 - 289.

Nunney L. 1999. The effective size of a hierarchically structured population. *Evolution* **53**: 1-10.

Nur N. 1988. The cost of reproduction in birds: an examination of the evidence. *Ardea* **76**:155-168.

Nussey D. H., Postma E., Gienapp P., Visser M. E. 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**:304.

Nussey D. H., Wilson A., Brommer J. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* **20**:831-844.

Nussey D. H., Coulson T., Festa Bianchet M., Gaillard J.-M. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology* **22**:393-406.

O

Oli M. K. & Dobson F. S. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole’s prediction revisited. *American Naturalist* **161**: 422-440.

Oli M. K. & Armitage K. B. 2004. Yellow-bellied marmot population dynamics: demographic mechanism of growth and decline. *Ecology* **85**: 2446-2455.

Olsson O. 1996. Seasonal effects of timing and reproduction in the King penguin : a unique breeding cycle. *Journal of Avian Biology* **27**: 7-14.

Olsson O., Bonnedahl J., Anker-Nilssen P. 2001. Mate switching and copulation behaviour in King Penguins. *Journal of Avian biology* **32**: 139-145.

Olsson O. & Van der Jeugd H. P. 2002. Survival in king penguins Aptenodytes patagonicus: temporal and sex- specific effects of environmental variability. *Oecologia* **132**: 509–516.

Orians G. H. & Pearson N. E. 1979. On the theory of central place foraging. In: Analysis of ecological systems (Horn DJ, Mitchell RD, Stairs GR, eds). Columbus: Ohio State University Press; 154-177.

Österblom H., Casini M., Olsson O., Bignert A. 2006. Fish, seabirds and trophic cascades in the Baltic Sea. *Marine Ecology Progress Series* **323**:233-238.

Ottersen G., Planque B., Belgrano A., Post E., Reid P. C., Stenseth N. C. 2001. Ecological effects of the North Atlantic oscillation. *Oecologia* **128**:1-14.

Owen M. & Black J. M. 1989. Factors Affecting the Survival of Barnacle Geese on Migration from the Breeding Grounds. *Journal of Animal Ecology* **58**:603–617.

P

Pace M. L., Cole J. J., Carpenter S. R., Kitchell J. F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* **14**:483-488.

Pakhomov E. A., Perissinotto R., McQuaid C. D. 1994. Comparative structure of the macrozooplankton micronekton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series* **111**: 155–169.

Park Y. H., Gamberoni L., Charriaud E. 1993. Frontal Structure, Water Masses, and Circulation in the Crozet Basin. *Journal of geophysical research* **98**: 12361-12385.

Park Y. H. & Gamberoni L. 1997. Cross-frontal exchange of Antarctic intermediate water and Antarctic bottom water in the Crozet Basin. *Deep Sea Research Part II: Topical Studies in Oceanography* **44**:963-986.

Park Y-H., Roquet F., Vivier F. 2004. Quasi-stationary ENSO wave signals versus the Antarctic Circumpolar Wave scenario. *Geophys Res Lett* **31**: L09315.

Parmesan C., Root T. L., Willig M. R. 2000. Impacts of Extreme Weather and Climate on Terrestrial Biota. *Bulletin of the American Meteorological Society* **81:** 443-450.

Parmesan C. & Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**:637-669.

Partridge L. & Green P. 1985. Intraspecific feeding specializations and population dynamics. In Behavioural Ecology: Ecological Consequences of Adaptive Behaviour (ed. R. M. Sibly and R. H. Smith), pp. 207-226. Blackwell Scientific Publications, Oxford.

Perissinotto R. & Duncombe Rae C. 1990. Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phytoplankton biomass and production. *Deep Sea Research Part A. Oceanographic Research Papers* **37**:777-793.

Perrins C. M., Harris M. P., Britton C. K. 1973. Survival of young Manx shearwaters Puffinus puffinus. *Ibis* **115**: 535–548.

Petit J., Jouzel J., Raynaud D., Barkov N., Barnola J., Basile I., Bender M., Chappellaz J., Davis M., Delaygue G. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**:429-436.

Petrie M., Schwabl H., Brande-Lavridsen N., Burke T. 2001. Maternal investment Sex differences in avian yolk hormone levels. *Nature* **412**: 498-499.

Pettersson L. B., Ramnarine I. W., Becher S. A., Mahabir R., Magurran A. E. 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata*. *Behavioral Ecology and Sociobiology* **55**: 461-468.

Pfister C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proc. Natl Acad. Sci. USA* **95:** 213-218.

Pianka E. R. 1970. On r-and K-selection. *The American Naturalist* **104**:592-597.

Piatt J. P., Sydeman W. J., Wiese F. 2007. Introduction: a modern role for seabirds as indicators. *Marine Ecology Progress Series* **352**: 199-204.

Pike T. W. & Petrie M. 2005. Offspring sex ratio is related to paternal train elaboration and yolk corticosterone in peafowl. *Biology Letters* **1**: 204–207.

Pilz K. M., Smith H. G., Sandell M. I., Schwabl H. 2003. Interfemale variation in egg yolk androgen allocation in the European starling: do high-quality females invest more? *Animal behaviour* **65**: 841– 850.

Pitman R. L. & Durban J. W. 2010. Killer whale predation on penguins in Antarctica. *Polar Biology* **33**:1589-1594.

Porter W. P. & Kearney M. 2009. Size, shape, and the thermal niche of endotherms. *Proceedings of the National Academy of Sciences* **106**:19666.

Pörtner H. O. & Farrell A. P. 2008. Physiology and climate change. *Science* **322**:690.

Post E. & Stenseth N. Ch. 1998. Large scale climatic fluctuation and population dynamics of moose and white tailed deer. *Journal of Animal Ecology* **67**:537-543.

Post E. & Stenseth N. Ch. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**:1322-1339.

Post E. & Forchhammer M. C. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature* **420**:168-171.

Prézelin B. B., Hofmann E. E., Mengelt C., Klinck J. M. 2000. The linkage between Upper Circumpolar Deep Water (UCDW) and phytoplankton assemblages on the west Antarctic Peninsula continental shelf. *Journal of Marine Research* **58**:165-202.

Q

Quillfeldt P., Masello J., Hamer K.C. 2004. Sex differences in provisioning rules and honest signalling of need in Manx shearwaters *Puffinus puffinus*. *Animal Behaviour* **68**:613-620.

R

R Development Core Team 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Reid K. & Croxall J. P. 2001. Environment response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London Series B* **268:** 377-384.

Reid J., Bignal E., Bignal S., McCracken D., Monaghan P. 2003. Age specific reproductive performance in red billed choughs Pyrrhocorax pyrrhocorax: patterns and processes in a natural population. *Journal of Animal Ecology* **72**:765-776.

Reilly P. & Cullen J. 1981. The Little Penguin Eudyptula minor in Victoria, II: Breeding. *Emu* **81**:1-19.

Reynolds R. W., Rayner N. A., Smith T. M., Stokes D. C., Wang W. 2002. An improved in situ and satellite SST analysis for climate. *Journal of Climate* **15**:1609-1625.

Richardson A. J. & Schoeman D. S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* **305**:1609.

Richardson A. J. & Poloczanska E. S. 2008. Ocean science: under-resourced, under threat. *Science* **320**: 1294–1295.

Ricklefs R. E. 1998. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *American Naturalist* **152**:24-44.

Ridoux V. 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Marine Ornithology* **22**:1-192.

Robinson S., Chiaradia A., Hindell M. A. 2005. The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. *Ibis* **147**:483–489.

Rochet M. J. 2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. *ICES Journal of Marine Science: Journal du Conseil* **57**:228.

Rodary D., Bonneau W., Le Maho Y., Bost C.-A. 2000. Benthic diving in male emperor penguins Aptenodytes forsteri foraging in winter. *Marine Ecology Progress Series* **207:** 171-181.

Roeder A. D., Marshall R. K., Mitchelson A. J., Visagathilagar T., Ritchie P. A., Love D. R., Pakai T. J., McPartlan H. C., Murray N. D., Robinson N. A. 2001. Gene flow on the ice: genetic differentiation among Adélie penguin colonies around Antarctica. *Molecular Ecology* **10**:1645-1656.

Roeder A. D., Ritchie P. A., Lambert D. M. 2002. New DNA markers for penguins. *Conservation genetics* **3**:341-344.

Root T. L., Price J. T., Hall K. R., Schneider S. H., Rosenzweig C., Pounds J. A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**:57-60.

Ropelewski C.F. & Halpert M.S. 1987. Global and regional precipitation associated with El Niño/Southern Oscillation. *Monthly Weather Review* **115**: 1606-1626.

Ropert-Coudert Y., Wilson R. P., Daunt F., Kato A. 2004a. Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. *Behavioral Ecology* **15**:824-830.

Ropert-Coudert Y., Cannell B., Kato A. 2004b. Temperature inside nest boxes of little penguins. *Wildlife Society Bulletin* **32**: 177-182.

Ropert-Coudert Y. & Wilson R. P. 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3:** 437–444.

Ropert-Coudert Y., Kato A., Wilson R. P. 2006a. The Penguiness book. pp. http://polaris.nipr.ac.jp/~penguin/penguiness/. Tokyo: National Institute of Polar Research.

Ropert-Coudert Y., Kato A., Wilson R. P., Cannell B. 2006b. Foraging strategies and prey encounter rate of free-ranging little penguins. *Marine Biology* **149**: 139-148.

Ropert-Coudert Y., Knott N., Chiaradia A., Kato A. 2007a. How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep-Sea Research part II* **54:** 415–423.

Ropert-Coudert Y., Wilson R. P., Yoda K., Kato A. 2007b. Assessing performance constraints in penguins with externally-attached devices. *Marine Ecology Progress Series* **333:** 281-289.

Ropert-Coudert Y., Ainley D. G., Ballard G., Kato A., Lyver P., Olmastroni S., Southwell C., Takahashi A., Trathan P., Wilson P. R., Le Maho Y. 2007c. Automatic Monitoring of Penguin PoPulation (AMPPoP): Circumpolar monitoring of the biology of key-species in relation to environmental changes. In *IPY Symposium, Asian Collaboration in IPY2007-2008* (ed. M. Shiobara). Tokyo: National Institute of Polar Research.

Ropert-Coudert Y., Kato A., Chiaradia A. 2009. Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the little penguin. *Proceedings of the Royal Society of London Series B* **276:** 4105-4109.

Rosenheim J.A. & Tabashnik B.E. 1991. Influence of generation time on the rate of response to selection. *American Naturalist* **137**: 527-541.

Rosivall B., Török J., Hasselquist D., Bensch S. 2004. Brood sex ratio adjustment in collared flycatchers (Ficedula albicollis): results differ between populations. *Behavioral Ecology and Sociobiology* **56**: 346–351.

S

Saether B.-E. 1990. Age-specific variation in reproductive performance of birds. *Current ornithology* **7**:251-283.

Sæther B. E. & Bakke Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642-653.

Sander M., Balbão T. C., Costa E. S., Santos C. R. d., Petry M. V. 2007a. Decline of the breeding population of Pygoscelis antarctica and Pygoscelis adeliae on Penguin Island, South Shetland, Antarctica. *Polar Biology* **30:** 651–654.

Sander M., Balbão T. C., Polito M. J., Costa E. S., Carneiro A. P. B. 2007b. Recent decrease in chinstrap penguin (Pygoscelis antarctica) populations at two of Admiralty Bay's islets on King George Island, South Shetland Islands, Antarctica. *Polar Biology* **30:** 659–661.

Saraux C., Le Bohec C., Durant J. M., Viblanc V. A., Gauthier-Clerc M., Beaune D., Park Y.H., Yoccoz N., Stenseth N. Chr., Le Maho Y. 2011a. Reliability of flipper-banded penguins as indicators of climate change. Nature **469**: 203-206.

Saraux C., Viblanc V. A., Hanuise N., Le Maho Y., Le Bohec C. 2011b. Effects of Individual pre-fledging traits and environmental conditions on return patterns in juvenile king penguins. *PLoS ONE* **6**: e20407.

Saraux C., Chiaradia A., Le Maho Y., Ropert-Coudert Y. 2011c. Everybody needs somebody : unequal parental effort in little penguins. *Behavioral Ecology* **22**: 837-845.

Saraux C., Robinson-Laverick S., Ropert-Coudert Y., Le Maho Y., Chiaradia A. 2011d. Plasticity in foraging strategies of inshore birds: how little penguins maintain body reserves while feeding offspring. *Ecology* **92**: 1909-1916.

Satheesh S. & Wesley S.G. 2009. Impact of December 26, 2004 tsunami on hydrobiology of Kudankulam coast, Gulf of Mannar, India. *Environmental Monitoring & Assessment* **156**: 131-139.

Schlosser J., Garner T., Dubach J., McElligott A. 2003. Characterization of microsatellite loci in Humboldt penguin (Spheniscus humboldti) and cross amplification in other penguin species. *Molecular Ecology Notes* **3**:62-64.

Schmidt-Nielsen K. 1984. Scaling: why is animal size so important? Cambridge University Press, Cambridge.

Schmutz J.A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. *Condor* **95**:222-225.

Schreiber E.A. 2001. Climate and Weather Effects on Seabirds. in: Schreiber E.A. & Burger J. (eds) Biology of Marine Birds. CRC Press, Boca Raton, Florida.

Schulte-Hostedde A., Zinner B., Millar J.S., Hickling G. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* **86**: 155-163.

Schultz M. A. & Klomp N. I. 2000. Does the foraging strategy of adult short-tailed shearwaters cause obesity in their chicks? *Journal of Avian Biology* **31**:287 - 294.

Schwagmeyer P. L. & Mock D. W. 2003. How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. *Ethology* **109**:303–313.

Schwagmeyer P. L. & Mock D.W. 2008. Parental provisioning and offspring fitness: size matters. *Animal Behaviour* **75**: 291-298.

Sheldon B. C., Andersson S., Griffith S. C., Örnborg J., Sendecka J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**: 874-877.

Sherley R. B., Burghardt T., Barham P. J., Campbell N., Cuthill I. C. 2010. Spotting the difference: towards fully-automated population monitoring of African penguins Spheniscus demersus. *Endangered Species Research* **11**:101-111.

Shin Y.-J., Travers M., Maury O. 2010. Coupling models low and high trophic levels models: towards a pathways-orientated approach for end-to-end models. *Progress in Oceanography* **84**: 105-112.

Sidhu L. A., Catchpole E. A., Dann P. 2007. Mark-recapture-recovery modeling and age-related survival in little penguins (Eudyptula minor). *Auk* **124**:815–827.

Simeone A. & Schlatter R. P. 1998. Threats to a mixed species colony of Spheniscus penguins in Southern Chile. *Colonial Waterbirds* **21**: 418-421.

Skelly D. K., Joseph L. N., Possingham H. P., Kealoha Freidenburg L., Farrugia T. J., Kinnison M. T., Hendry A. P. 2007. Evolutionary responses to climate change. *Conservation Biology* **21:** 1353-1355.

Smetacek V. & Nicol S. 2005. Polar ocean ecosystems in a changing world. *Nature* **437**:362-368.

Smith R. C., Ainley D., Baker K., Domack E., Emslie S., Fraser B., Kennett J., Leventer A., Mosley-Thompson E., Stammerjohn S. 1999. Marine ecosystem sensitivity to climate change. *BioScience* **49**:393-404.

Sousa W.P. 1984. The role of disturbance in natural communities. *Annual review of ecology and systematics* **15**: 353-391.

Spear L. & Nur N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *Journal of Animal Ecology* **63**: 283–298.

SRES 2000. Special Report on Emissions Scenarios. IPCC

Stahel C. & Gales R. 1987. Little penguin: fairy penguins in Australia. Nswu Press.

Stahl J. T. & Oli M. K. 2006. Relative importance of avian life-history variables to population growth rate. *Ecological modelling* **198:** 23-39.

Stearns S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3-47.

Stearns S.C. 1989. Trade-offs in life-history evolution. *Functional Ecology* **3**: 259-268.

Stearns S.C. 1992. The Evolution of Life Histories. Oxford Univ Press, Oxford

Stenseth N. Ch., Mysterud A., Ottersen G., Hurrell J. W., Chan K.-S., Lima M. 2002. Ecological Effects of Climate Fluctuations. *Science* **297:** 1292-1296.

Stenseth N. Ch., Ottersen G., Hurrell J. W., Mysterud A., Lima M., Chan K.-S., Yoccoz N. G., Adlandsvik B. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. *Proceedings of the Royal Society of London Series B* **270:** 2087–2096.

Stenseth N. Ch. & Mysterud A. 2005. Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology* **74**: 1195-1198.

Stonehouse B. 1960. The king penguin Aptenodytes patagonica of South Georgia. I. Breeding behaviour and development. *Falkland Islands Dependencies Survey. Scientific report* **23**: 1-81.

Sullivan K. 1989. Predation and starvation: age-specific mortality in juvenile juncos (Junco Phaenotus). *Journal of Animal Ecology* **58**: 275-286.

Sullivan C., Arrigo K., McClain C., Comiso J., Firestone J. 1993. Distributions of phytoplankton blooms in the Southern Ocean. *Science* **262**:1832-1837.

T

Takahashi A., Dunn M., Trathan P. N., Sato K., Naito Y., Croxall J. P. 2003a. Foraging strategies of Chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series* **250:** 279-289.

Takahashi A., Watanuki Y., Sato K., Kato A., Arai N., Nishikawa J., Naito Y. 2003b. Parental foraging effort and offspring growth in Adélie Penguins: does working hard improve reproductive success? *Functional Ecology* **17**:590-597.

Tansley A. G. 1935. The Use and Abuse of Vegetational Concepts and Terms. *Ecology* **16**: 284-307.

Tewksbury J. J., Huey R. B., Deutsch C. A. 2008. Putting the Heat on Tropical Animals. *Science* **320**:1296.

Thomas D. W., Blondel J., Perret P., Lambrechts M. M., Speakman J. R. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291**:2598–2600.

Thomas C. D., Cameron A., Green R. E., Bakkenes M., Beaumont L. J., Collingham Y. C., Erasmus B. F. N., Ferreira de Siqueira M., Grainger A., Hannah L. 2004. Extinction risk from climate change. *Nature* **427**:145-148.

Thompson P. M. & Grosbois V. 2002. Effects of climate variation on seabird population dynamics. *Directions in Science* **1**: 50-52.

Timmermann A., Oberhuber J., Bacher A., Esch M., Latif M., Roeckner E. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**:694-697.

Tinbergen J. M. & Boerlijst M. C. 1990. Nestling weight and survival in individual Great Tits (Parus major). *Journal of Animal Ecology* **59**: 1113-1127.

Trathan P. N., Forcada J., Murphy E. J. 2007. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society of London B* **362**: 2351-2365.

Trathan P. N. & Agnew D. 2010. Climate change and the Antarctic marine ecosystem: an essay on management implications. *Antarctic Science* **22**:387-398.

Travers M., Shin Y. J., Jennings S., Cury P. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography* **75**:751-770.

Travers M., Shin Y.-J., Jennings S., Machu E., Huggett J.A., Field J., Cury P. 2009. Two-way coupling versus one-way forcing of plankton and fish models to predict ecosystem changes in the Benguela. *Ecological Modelling* **220**: 3089-3099.

Travers M., Watermeyer K., Shannon L. J., Shin Y.-J. 2010. Changes in food web structure under scenarios of overfishing in the southern Benguela: comparison of the Ecosim and OSMOSE modelling approaches. *Journal of Marine Systems* **79**: 101-111.

Tremblay Y. & Cherel Y. 2000. Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Marine Ecology Progress Series* **204:** 257-267.

Trenberth K. E., Jones P. D., Ambenje P., Bojariu R., Easterling D., Klein Tank A., Parker D., Rahimzadeh F., Renwick J. A., Rusticucci M., Soden B., Zhai P. 2007. Observations: Surface and Atmospheric Climate Change. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Trivelpiece W. Z., Hinke J. T., Miller A. K., Reiss C. S., Trivelpiece S. G., Watters G. M. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* **108**:7625-7628.

Trivers R. L. 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man 1871–1971 (Campbell B, ed). Chicago: Aldine Press; 136–179.

Trivers R. L. & Willard D. E. 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. *Science* **179**: 90-92.

Trivers R. L. 1974. Parent-offspring conflict. *American Zoologist* **14**:249-264.

Tsuda T. T., Tsuda M., Naruse T., Kawata H., Ando A., Shiina T., Fukuda M., Kurita M., Le Maho Y., Kulski J. K., Inoko H. 2001. Phylogenetic analysis of penguin (Spheniscidae) species based on sequence variation in MHC class II genes. *Immunogenetics* **53:** 712-716.

Tuljapurkar S., Li N., Feldman M. W. 1995. High sex ratios in China's future. *Science* **267**: 874-876.

Tynan C. T. 1998. Ecological importance of the southern boundary of the Antarctic Circumpolar current. *Nature* **392**: 708-710.

V

Van der Jeugd H.P. & Larsson K. 1998. Pre-breeding survival of barnacle geese Branta leucopsis in relation to fledging characteristics. *Journal of Animal Ecology* **67**: 953-966.

Vargas F. H., Harrison S., Rea, S., Macdonald D. W. 2006. Biological effects of El Nino on the Galapagos penguin. *Biological Conservation* **127:** 107-114.

Vargas F. H., Lacy R. C., Johnson P. J., Steinfurth A., Crawford R. J., Boersma P. D., Macdonald D. W. 2007. Modelling the effect of El Nino on the persistence of small populations: The Galapagos penguin as a case study. *Biological Conservation* **137:** 138-148.

Vaupel J. W., Manton K. G., Stallard E. 1979. The Impact of Heterogeneity in Individual Frailty on the Dynamics of Mortality. *Demography* **16**:439-454

Velando A, Alonso-Alvarez C. 2003. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *Journal of Animal Ecology* **72**:846–856.

Veran S. & Beissinger S. R. 2009. Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters* **12**: 129-143.

Verity P. G., Smetacek V., Smayda T. J. 2002. Status, trends and the future of the marine pelagic ecosystem. *Environmental Conservation* **29:** 207–237.

Viblanc V. A., Arnaud C. M., Dobson F. S., Murie J. O. 2010. Kin selection in Columbian ground squirrels (Urocitellus colombianus): littermate kin provide individual fitness benefits. *Proceedings of the Royal Society of London Series B* **277**: 889-894.

Viera V., Le Bohec C., Côté S., Groscolas R. 2006. Massive breeding failures following a tsunami in a colonial seabird. *Polar Biology* **29**: 713-716.

Villanueva C., Bertellotti M., Walker B. 2010. Ecotourism effects on Magellanic penguins at San Lorenzo colony, Peninsula Valdes, Argentina. *Oral presentation at the 7th International Penguin Conference*.

Vimeux F., Masson V., Jouzel J., Stievenard M., Petit J. 1999. Glacial–interglacial changes in ocean surface conditions in the Southern Hemisphere. *Nature* **398**:410-413.

Visser M. E. & Holleman L. J. M. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B* **268**:289-294.

Visser M. E., Adriaensen F., van Balen J. H., Blondel J., Dhondt A. A., van Dongen S., du Feu C., Ivankina E. V., Kerimov A. B., de Laet J., Matthysen E., McCleery R., Orell M., Thomson D. L. 2003. Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society of London Series B* **270**: 367-372.

Visser M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London Series B* **275**: 649-661.

Volkman N. J., Pressler P., Trivelpiece W. 1980. Diets of Pygoscelid penguins at King George Island, Antarctica. *Condor* **82**:373–378

W

Wade M. J. & Schuster S. M. 2002. The evolution of parental care in the context of sexual selection: a critical reassessment of parental investment theory. *American naturalist* **160**: 285-292.

Waits L. P., Talbot S. L., Ward R., Shields G. 1998. Mitochondrial DNA phylogeography of the North American brown bear and implications for conservation. *Conservation Biology* **12**:408-417.

Walker B. G., Boersma P., Wingfield J. C. 2005. Physiological and behavioral differences in Magellanic penguin chicks in undisturbed and tourist visited locations of a colony. *Conservation Biology* **19**:1571-1577.

Walther G. R., Post E., Convey P., Menzel A., Parmesan C., Beebee T., Fromentin J. M., Hoegh-Guldberg O., Bairlein F. 2002. Ecological responses to recent climate change. *Nature* **416**:389-395.

Warham J. 1996. The behaviour, population biology and physiology of the petrels. Academic Press London.

Watanuki Y., Miyamoto Y., Kato A. 1999. Dive bouts and feeding sites of Adelie penguins rearing chicks in an area with fast sea-ice. *Waterbirds* **22:** 120-129.

Weatherhead P. J. & Forbes M. R. L. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* **5**:426-433.

Weavers B. W. 1992. Seasonal foraging ranges and travels at sea of little penguins Eudyptula minor, determined by radiotracking. *EMU* **91**:302-317.

Webb J. N., Houston A., McNamara J., Skezely T. 1999. Multiple patterns of parental care. *Animal Behaviour* **58**: 983-993.

Weimerskirch H., Jouventin P., Stahl J. C. 1986. Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* **128**:195-213.

Weimerskirch H. 1992. Reproductive effort in long-lived birds: Age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* **64**:464-473.

Weimerskirch H., Stahl J.C., Jouventin P. 1992. The breeding biology and population-dynamics of King Penguins Aptenodytes patagonica on the Crozet Islands. *Ibis* **134**: 107-117.

Weimerskirch H., Chastel O., Chaurand T., Ackerman L., Hindermeyer X., Judas J. 1994. Alternate long and short foraging trips in pelagic seabird parent. *Anim Behav* **47**:472–476.

Weimerskirch H., Cherel Y., Cuenot-Chaillet F., Ridoux V. 1997a. Alternative foraging strategies and resource allocation by male and female Wandering albatrosses. *Ecology* **78**: 2051-2063.

Weimerskirch H., Mougey T., Hindermeyer X. 1997b. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behav Ecol* **8**:635-643.

Weimerskirch H. 1998. How can a pelagic seabird provision its chick when relying on a distant resource? Cyclic attendance, foraging decision and body condition in sooty shearwaters. *J Anim Ecol* **67**:99–109.

Weimerskirch H., Barbraud C., Lys P. 2000. Sex Differences in Parental Investment and Chick Growth in Wandering Albatrosses: Fitness Consequences. *Ecology* **81**: 309-318.

Weimerskirch H., Inchausti P., Guinet C., Barbraud C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* **15:** 249–256.

Weladji R. B., Klein D. R., Holand Ø., Mysterud A. 2002. Comparative response of Rangifer tarandus and other northern ungulates to climatic variability. *Rangifer* **22**:33-50.

Welcker J., Harding A. M. A., Kamovsky N. J., Steen H., Strom H., Gabrielsen G. W. 2009. Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk Alle alle. *Journal of Avian Biology* **40**: 388-399.

Western D. 1979. Size, life history and ecology in mammals. *African Journal of Ecology* **17**:185-204.

White W. B. & Peterson R. G. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380:** 699-702.

Williams G. C. 1966. Natural selection, the cost of reproduction and a refinment of Lack's principle. *American Naturalist* **100**:687-690.

Williams T. D. & Rothery P. 1990. Factors affecting variation in foraging and activity patterns of gentoo penguins (*Pygoscelis papua*) during the breeding season at Bird Island, South Georgia. *J Appl Ecol* **27**:1042-1054.

Williams T. D. 1995. The penguins. Oxford University Press.

Wilson R. P., Nagy K. A., Obst B. 1989a. The foraging range of penguins. *Polar Records* **25**: 303-307.

Wilson R. P., Ryan P. G., Wilson M. P. 1989b. Sharing food in the stomachs of seabirds between adults and chicks - a case for delayed gastric emptying. *Comp. Biochem. Physiol.* **94**(A): 461 - 466.

Wilson R. P., Ainley D. G., Nur N., Jacobs S. S., Barton K. J., Ballard G., Comiso J.C. 2001. Adélie penguin population change in the pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. *Marine Ecology Progress Series* **213**: 301-309.

Wilson A. J. & Nussey D.H. 2010. What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution* **25**:207-214.

Wilson R. P. 2011. The price tag. *Nature* **469**:164-165.

Witkander U., Olsson O., Nilsson S.G. 2000. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* **31**:447-456.

Woehler E. J., Penney R. L., Creet S. M., Burton H. R. 1994. Impacts of human visitors on breeding success and long-term population trends in Adélie penguins at Casey, Antarctica. *Polar Biology* **14**: 269-274.

Woehler E. J. 1995. Consumption of Southern Ocean marine resources by penguins. *in The penguins: ecology and management.* . N. I. Dann P., Reilly P. N.,editor. Chipping Norton: Surrey Beatty & Sons. Pages 266–295.

Woehler E. J. 1996. Concurrent decreases in five species of Southern Ocean seabirds in Prydz Bay. *Polar Biology* **16**:379-382.

Woehler E. J., Cooper J., Croxall J. P., Fraser W. R., Kooyman G. L., Miller G., Nel D., Patterson D., Peter H.-U., Ribic C. A., Salwicka K., Trivelpiece W. Z., Weimerskirch H. 2001. A statistical assessment of the status and trends of Antarctic and subantarctic seabirds. In *SCAR-BBS Workshop on Southern Ocean Seabird Populations.* Hobart: SCAR-CCAMLR.

Wolfaardt A. C. & Nel D. C. 2003. Breeding productivity and annual cycle of rehabilitated African Penguins following chronic oiling. In: Nel DC, Whittington PA (eds) The Rehabilitation of Oiled African Penguins: a Conservation Success Story. Cape Town: Bird Life South Africa and Avian Demography Unit, University of Cape Town, pp 18-24.

Woodward F. I. 1987. Climate and plant distribution. Cambridge University Press. UK

Wooller R., Bradley J., Skira I., Serventy D. 1990. Reproductive success of short-tailed shearwaters Puffinus tenuirostris in relation to their age and breeding experience. *The Journal of Animal Ecology* **59**:161-170.

Wunderle J. 1991. Age-specific foraging proficiency in birds. *Current Ornithology* **8**: 273–324.

Y

Yamagata T., Behera S. K., Luo J.-J., Masson S., Jury M. R., Rao S. A. 2004. Coupled ocean-atmosphere variability in the tropical Indian Ocean. *Geophysical Monographs* **147:** 189-212.

Yorio P. & Boersma P. D. 1992. The effects of human disturbance on Magellanic Penguin Spheniscus magellanicus behaviour and breeding success. *Bird Conservation International* **2**: 161-73.

Yorio P., Frere E., Gandini P., Schiavini A. 2001. Tourism and recreation at seabird breeding sites in Patagonia, Argentina: current concerns and future prospects. *Bird Conservation International* **11**:231-245.

Yorke J., Ward S., Chiaradia A. 2004. Diving behaviour of little penguins *Eudyptula minor* at different stages of breeding at Phillip Island, Australia. *New Zealand Journal of Zoology* **31**: 115–116.

Z

Zimmer I., Ropert-Coudert Y., Kato A., Ancel A., Chiaradia A. 2011. Does foraging performance change with age in female little penguins (Eudyptula minor)? *PLoS ONE* **6**(1): e16098.

Zon R. 1915. Seed production of western white pine. US Dept. of Agriculture.

Zwally H. J., Comiso J. C., Parkinson C. L., Cavalieri D. J., Gloersen P. 2002. Variability of Antarctic sea ice 1979–1998. *J. Geophys. Res* **107**:3041.

ABBREVIATIONS

ACC: Antarctic Circumpolar Current
AIC: Akaike's Information Criterion
ANTAVIA: ANTennes AVIAires (system developed by the DEPE lab to monitor penguins automatically)
APMS: Automatic Penguin Monitoring System
ASR: Adult Sex Ratio

CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources
[Chla]: concentration in chlorophyll a

ENSO: El-Niño Southern Oscillation

GHG: Greenhouse Gas
GLM: Generalized Linear Model
GLMM: Generalized Linear Mixed Model

IPCC: Intergovernmental Panel on Climate Change

LM: Linear Model
LR: Logistic Regression
LRS: Lifetime Reproductive Success

NAO: North Atlantic Oscillation
NPP: Net Primary Production

OSR: Operational Sex Ratio

PCR: Polymerase Chain Reaction
PF: Polar Front

RFID: Radio-Frequency-Identification

SeaWiFS: Sea-viewing Wide Field of view Sensor
SOI: Southern Oscillation Index
SSH: Sea Surface Height
SST: Sea Surface Temperature

TAAF: Terres Australes et Antarctiques Françaises (French Southern and Sub-Antarctic Territories)

Appendices

APPENDIX 1: IPCC: Integrating Penguins in Climate Change (Article 1)

IPCC: Integrating Penguins in Climate Change

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Short running title: penguins and climate change

As scientists working with a main emphasis on penguins' biology we are often confronted to the following question: why do people study penguins? There are many different possible answers. Of course penguins are extraordinary divers and their physiological adaptations to extreme hydrostatic pressure, to low temperatures, to hunt visually in almost complete darkness, are some of the features that make them attractive models for scientists. However, those peculiar birds also present another, more global facet. They act as important ecological indicators of their increasingly changing environment, and may serve as predicators of environmental change, *i.e.* "a bellwether of the climate" to paraphrase David Ainley in his book of the same name. In the present review, we consider the pros and cons of using penguins to examine changes occurring in the oceans of the southern hemisphere and review how these environmental changes might impact the different life-history traits of penguins. We also propose some avenues for future research on penguins, in order for scientists to optimize their use as living observatories of the Southern Ocean ecosystems.

Key Words: climate change, spheniscidae, mechanisms, population trends, foraging

A thorough understanding of marine and coastal ecosystems is a global priority if we are to detect early signs of climate changes, and more importantly if we wish to predict the response of animal populations to these changes. The 2007 Intergovernmental Panel on Climate Change (IPCC) report highlighted our limited knowledge on the response of marine environments to climate changes and an urgent need to remedy to this lack of information (cf. Richardson & Poloczanska 2008), especially in regards of the role of oceans in the world climate regulation (Minster 1998). Whereas substantial information may be collected at the level of primary producers of the euphotic zone *via* remote sensing, the data on subsequent levels of the food-web (primary and sometimes even secondary consumers) are scarce. Indeed, humans are far removed from the ocean expense and most marine ecosystems are hardly accessible and poorly sampled (Richardson & Poloczanska 2008). Despite the efforts of international programs, such as the Census of Marine Life (Ausubel 1999), collecting data remains a tremendous challenge. We lack practical methods to examine and monitor the structure of marine ecosystems both at the spatial (most sampling is done only on some transects along the ships' roads) and temporal scales (difficulties of having repeatable measurements from year to year when using commercial ship trips or fisheries data), that are appropriate to understand the consequences of climate changes on biodiversity erosion. One way around consists in investigating the whole system through sentinel species that are chosen at the top of trophic webs. The effects of climate forcing on primary and secondary production of the short oceanic food webs may indeed be integrated at higher levels of the food chain (Croxall *et al.* 1988, Le Maho *et al.* 1993, Boyd & Murray 2001) and thus amplified in top-level predators, such as seabirds. Top-predators thus are sensitive indicators of environmental changes and reflect the trophic dynamics of their ecosystems (Verity *et al.* 2002), an illustration of this being the large-scale, top-down approach proposed by the Tagging Of Pacific Pelagics project (Block *et al.* 2003). Seabirds and marine mammals are thus increasingly used as ecological indicators (*e.g.* Durant *et al.* 2009), *i.e.* as species that can reveal alteration in their environment through proximal (physiological or behavioural) or distal (population) changes. The term bioindicator is often used to characterize top predators in such a situation but it traditionally refers to species that reflect the level of pollutants in an ecosystem and not ecosystemic or trophic changes (*sensu* Karr 1981). With this in mind, a pertinent eco-indicating species should be abundant and widespread, possess a well-documented foraging ecology, a high degree of dietary specialization and show a close association to oceanic structures (Bost *et al.* 2009). In the circumpolar Southern Ocean, which communicates with the three other oceanic basins and thus greatly contributes to world climate regulation (Busalacchi 2004), penguins are an iconic family of seabirds most famously known for their impressive swimming performances (see Ropert-Coudert *et al.* 2006), their extraordinary fasting capacities (Cherel *et al.* 1993b) or their remarkable resistance to extreme environments (*e.g.* Emperor Penguins *Aptenodytes forsteri* are able to withstand temperatures well below 0°C, Ancel *et al.* 1997). Yet it is less known by the general audience that penguins are also good models for climate change studies (but see Dee Boersma 2008 and Forcada & Trathan 2009), and represent, therefore, one of the main family of ecological indicators of the marine southern hemisphere (Ellis *et al.* 2007). Here, we review the use of penguins as indicators of climate changes in the literature.

An interesting model

All penguin species exploit the oceans of the southern hemisphere and are often associated to cold upwelling currents like the Benguela current in southern Africa. These oceans are all linked via the Southern Ocean which contains most of the world sea ice. As such, it is one of the most important world climate regulators (Busalacchi 2004) and is expected to be strongly affected by climate change due to its high latitude position. Furthermore, the Southern Ocean is the most productive marine region of our planet (Tynan 1998). It has even been referred to as a "natural laboratory for climate change study" (Le Quéré *et al.* 2002). A number of climatic indices can be used to characterize the oceanic sectors used by penguins, the most well-known being the El Niño Southern Oscillation (ENSO), the Antarctic Circumpolar Wave (White & Peterson 1996) and the Indian Ocean Dipole (Yamagata *et al.* 2004). Through the Great Conveyor Belt, any anomaly occurring in other oceans are linked to the circumpolar main eastward circulation. All penguins species can thus potentially be affected even though they are situated far away from the centre of emergence of an anomaly. An ENSO event in the Pacific basin, for example, may be carried out as far as to the Australian coast and affect local currents there (Ropelewski & Halpert 1987). Among the species that live in the southern oceans, marine top predators are particularly suited as ecological indicators of the marine environment (see Bost *et al.* 2009), since 1) they are amazing prospectors, covering huge distances (*e.g.* Jouventin and Weimerskirch 1990) and ii) they concentrate their at-sea activity to oceanographic features that are of key importance to the functioning of the world oceanic system, such as upwellings (*e.g.* Biuw *et al.* 2007), oceanic fronts (Bost *et al.* 2009), eddies (Cotté *et al.* 2007), or thermoclines (*e.g.* Boyd and Arnbom 1991, Ropert-Coudert *et al.* 2009). Seabirds and marine mammals are particularly interesting since they entirely rely on marine resources but breed and moult on land and are thus easily accessible for investigations during those periods ashore. While Procellariformes are often used as ecological indicators, penguins (Spheniscidae) account for the majority of the seabird biomass in the Southern Ocean (Woehler *et al.* 2001) and are equally important consumers of the marine ecosystems (de Brook 2004). Their populations are large and widespread, all around the southern hemisphere (Marchant and Higgins 1990), from the tropics to the south polar circle (Fig. 1), although the Pacific sector of the southern hemisphere is probably less extensively covered than the Indian Ocean one.

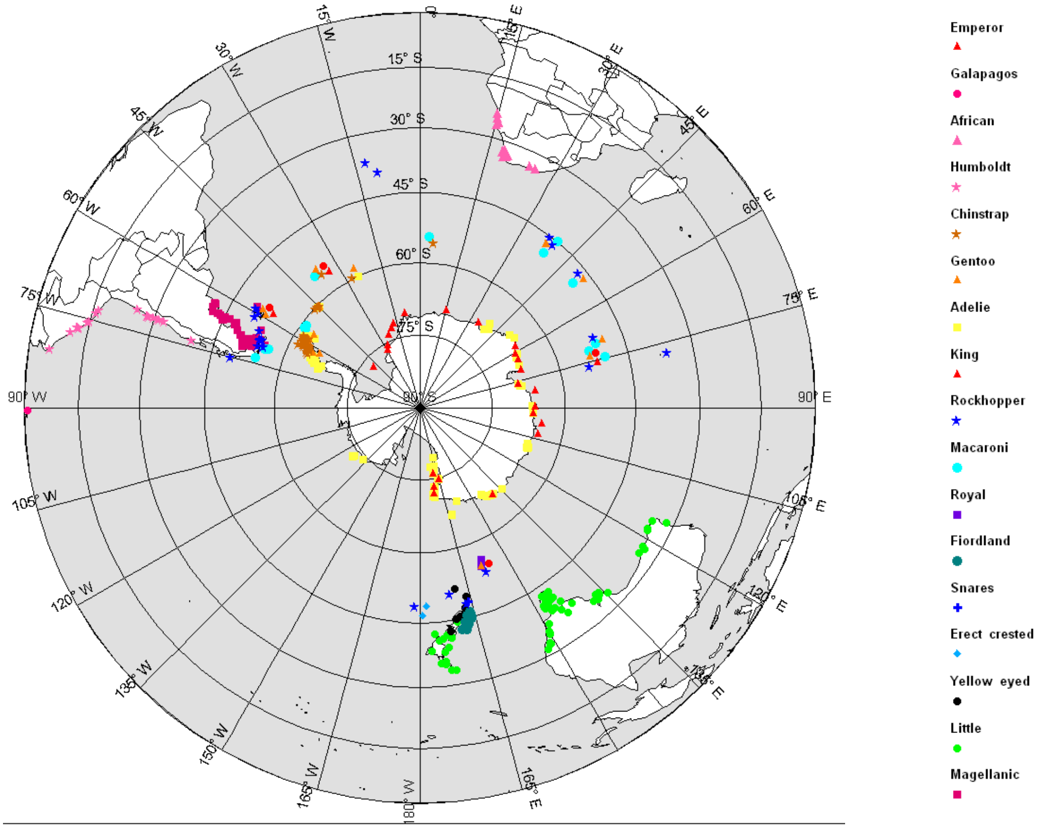

Figure 1. *Location of major penguin colonies in the Southern Ocean (information about sites taken from Ellis et al. 1998, Marchant & Higgins 1990). For clarity of presentation Northern and Southern Rockhopper Penguins, as well as New Zealand and Australian species of Little Penguins, have been merged into Rockhoppers and Little Penguins, respectively.*

Even though *Spheniscus* spp. occasionally share their on-land habitats with man, interactions are limited in the vast areas of Patagonia or along the beaches of southern Africa. The situation can be drastically different for species inhabiting the sometimes crowded shores of Australia and New Zealand. Adding to their extensive circumpolar on-land distribution penguins are extraordinary divers which enable them to prospect a large vertical volume of southern hemisphere oceans, from right underneath the surface (*e.g.* Watanuki *et al.* 1999) to the benthos (Rodary *et al.* 2000, Tremblay & Cherel 2000, Takahashi *et al.* 2003). Despite being flightless - the horizontal distances travelled by penguins are on average 10 times less wide than that of flying species (Wilson *et al.* 1989) - they forage from coastal (*e.g.* Collins *et al.* 1992) to offshore areas (Bost *et al.* 1997), reaching sometimes distances as far as 4095km from the colonies in the case of the King Penguins *A. patagonicus* in winter (Bost *et al.* 2004). Compared with other seabirds, penguins can be captured and recaptured at ease having lost the ability to fly, but this only applies during the breeding season. Information remains, however, scarce during the non-breeding season (winter for the seasonal breeders and the immature period for all species). The morphological adaptations to flightlessness represent a further enhancement to using them in scientific studies compared with Procellariforms for example: their bodies are dense and relatively large and can thus accommodate diverse recording systems that are either attached onto or implanted into them, an approach referred to as bio-logging (Naito 2004, Ropert-Coudert & Wilson 2005). Of course, such an approach requires specific guidelines to be strictly followed so as to limit the impact that devices could incur onto the fitness or performances of the birds (cf. Casper 2009 and references on penguins therein, see also Ropert-Coudert *et al.* 2007a, b).

Penguins – at least those big enough to carry large, multi-channel recorders – have been used as bioplatforms where the animal-attached data recorders not only provide information about the bird's activity but also measure the physical properties of their environment (*e.g.* Charrassin *et al.* 2002). Note that large top predators, like elephant seals are also big enough to be considered as bio-plateforms (see Costa *et al.* 2010) but their visits ashore are less predictable than that of reproducing penguins and their population are much smaller.

The different ways climate impact penguins

The impact of climate change on penguin populations in the Southern Ocean *sensu stricto*, *i.e.* south of the polar convergence (*i.e.* restricted to polar and sub-polar species) has been recently reviewed in great details (Forcada & Trathan 2009). The following will further expand the discussion to other penguin species and their respective environments.

Effect on population trends: The impact of climatic anomalies has been mostly discussed at population scale where scientists try and correlate long-term datasets on population trends to long-term climate datasets (*e.g.* Kato *et al.* 2002, Croxall *et al.* 2002, Ainley *et al.* 2005, Jenouvrier *et al.* 2009a among others). Such an approach is based on the indirect effects that climate change can have on an ecosystem, which are expected to be reflected in the penguins' responses (Stenseth *et al.* 2002). For instance, an increase in Sea Surface Temperature (SST) mediated by climate change may lead to a decrease in the ocean's productivity (Gregg *et al.* 2003), which, in turn, would affect the food webs via cascading bottom-up effects (see Frederiksen *et al.* 2006). Hence, linking similarly long timescale climatic and penguin population datasets may provide clues to understanding ecosystemic processes and also represents a powerful *a posteriori* approach to predict future trends as these can be extrapolated from the shape of the relationship established over the past. The effect of periodic climatic events, such as ENSO, can thus be easily highlighted (*e.g.* Dee Boersma 1998). In this context, amplitudes of anomalies may often be more important in understanding population trends than the occurrence of the anomalies itself. This is especially true since the definition of ENSO events may vary according to the index used, and/or the thresholds depicting the occurrence of these events. Thus we encourage studies to investigate the effect of climatic indices on a continuous basis, in order to avoid subjectively fixed limits. In addition, strong ENSO events can crash down populations but the subsequent succession of smaller-scale events can prevent the population to recover, as is the case in Galápagos Penguins (Vargas *et al.* 2006, 2007). Yet, at population level, highly diverse trends have been observed in association with climate change across species. Galápagos penguin populations have declined because of changes in oceanographic conditions, paralleling an overall warming in the Pacific during the last twenty years of the twentieth century associated with more frequent El Niño and less frequent La Niña events (Dee Boersma 1998). In contrast, other penguins' declines have been linked to a decrease in SST like in Northern Rockhopper Penguins *Eudyptes moseleyi* on Amsterdam Island (37°50'S, 77°31'E, Guinard *et al.* 1998).

Effect on demographic parameters: Impact of climatic anomalies can also be investigated on parameters such as breeding success and/or individual survival. If some parameters, *e.g.* dates of egg laying, can be visually assessed for most penguins species, others are more difficult to measure, especially since huge gatherings may render the task close to insurmountable (but see Emmerson & Southwell 2008). Besides, most demographic parameters are declined into binary figures (failure or success) and are thus reproducible from one year to the next, thus allowing to test for them as a function of the annual conditions. Survival, however, is more prone to error since it is often estimated through a measure of return rate of individuals from one year to the next. Such a parameter does not solely result from mortality, and includes emigration and even partner or breeding site changes within a given colony. Here, the spatial scale at which one chooses to work is determinant in shaping the relationship between demographic parameters and the extent of the anomaly. For instance, local SST anomalies may impact drastically the mean egg laying date, the number of successfully fledged chicks and the body mass of Little Penguin *Eudyptula minor* chicks at fledging, while the Little Penguins' hatching success is linked to global-scale ENSO related SST anomalies (Chambers 2004a). Time scale is also of importance since SST presents an immediate effect on King Penguins' breeding success but a 2-year time lag effect on survival (Le Bohec *et al.* 2008a but see Barbraud *et al.* 2008). Interestingly, if climate warming is expected to delay the onset of breeding in emperor and Adélie Penguins *Pygoscelis adeliae* (Barbraud & Weimerskirch 2006), it will advance it in Little Penguins (Chambers 2004b, Cullen *et al.* 2009). Nonetheless, effects of climate on penguin life history traits will always remain difficult to interpret since they can be both direct and immediate (Fraser & Hoffman 2003 and see below) or indirect through modifications in the food chain for instance and appear only later.

Direct effects on behaviour: Compared with the growing body of literature linking large scale population trends to climate change, a mechanistic approach that would explain how physical changes directly impact foraging efficiency and thus breeding success is clearly lacking. Yet foraging activity clearly conditions the success of reproduction and is thus an important parameter to understand penguins' responses to climate change (Fraser & Hoffman 2003). The difficulty of relating climate change to foraging activity is that the latter is often measured at short time scales that differ from climatic measurements. However, IPCC (2007) scenario augurs for an increase in extreme weather events linked to climate change. The influence of such severe conditions on foraging activity has, to the best of our knowledge, only been reported once: Little Penguins' foraging success – and consequently breeding success – has been shown to be reduced in years when violent storms mixed the water column, leading to a disappearance of the 25-m deep thermocline where prey of the penguins concentrate preferentially in years of good resource availability (Ropert-Coudert *et al.* 2009). These observations are yet to be investigated in other penguin species. As another example, SST anomalies can directly affect the location of penguins' feeding grounds, such as the polar front for sub-Antarctic penguins (Moore *et al.* 1999) and force them to migrate distances as long as 900 km in the case of the Humboldt Penguin *S. humboldti* to find new profitable grounds (Culik *et al.* 2000). This will thus impact directly chick provisioning. Foraging activity can definitely tell us a lot about the plasticity of penguins to face climate change. For instance, recent studies on Adélie Penguins highlighted the interest of examining the match between the peak of penguin at-sea activity and the peak of resource availability (Beaulieu *et al.* 2009).

A case-study; the sea-ice: Antarctic marine ecosystem appears intuitively fragile in facing global warming effects, as sea ice plays an important role there (Loeb *et al.* 1997). The ecology of the two penguin species living only in continental Antarctica, Adélie and Emperor Penguins, is highly associated with sea-ice conditions. Due to logistical difficulties of monitoring birds breeding on fast ice in the harsh Antarctic winter, relatively less information are available for Emperor (but see Barbraud & Weimerskirch 2001, Jenouvrier *et al.* 2009b) than for Adélie Penguins, for which a large number of studies has been conducted all around Antarctica over the past 50 years. For instances, modification in sea-ice conditions is known to affect foraging behaviour (Watanuki *et al.* 1997, Rodary *et al.* 2000), breeding success (Ainley & Le Resche 1973, Ainley *et al.* 1998, Irvine *et al.* 2000), winter survival (Wilson *et al.* 2001, Jenouvrier *et al.* 2006) and consequently the population trends (Fraser & Patterson 1997, Wilson *et al.* 2001, Kato *et al.* 2002) of Adélie Penguins, which are often regarded as "creatures of the Antarctic pack ice" (Ainley 2002). Trends of penguin populations in the Antarctic, and especially the peninsula region (which suffered the quickest rate of warming on Earth), deserve a review of their own. Smith *et al.* (1999) proposed a conceptual model that synthesizes the long-term impact of climate change on the three Pygoscelid species in this particular region. This model links penguin population growth to sea-ice concentration. The rapid warming in the lower latitudes of the Antarctic continent has induced the decline of sea ice extent and duration, alterations in phytoplankton and zooplankton community composition and changes in krill recruitment, abundance and availability to predators (Smith *et al.* 1999, Forcada *et al.* 2006, Ducklow *et al.* 2007). This reduction in sea ice at lower latitudes is thus accompanied by a decreasing trend in Adélie population (Fraser & Patterson 1997, Forcada *et al.* 2006, Carlini *et al.* 2009). The situation is different in southern Antarctica as Adélie Penguin populations there are increasing (Ross Sea and East Antarctic regions, Jenouvrier *et al.* 2006, Woehler *et al.* 2001). In contrast to Adélie Penguin population, the closely related but ice-intolerant Gentoo Penguins *P. papua* are increasing in most of the Antarctic Peninsula (Forcada *et al.* 2006, Ducklow *et al.* 2007, Carlini *et al.* 2009, Ballerini *et al.* 2009). The case of Chinstrap Penguins *P. Antarctica* appears more complex since populations are either decreasing (South Orkney Islands 60°35′S, 45°30′W, Forcada *et al.* 2006; King George Island 62°06'S, 57°56'W, Sander *et al.* 2007a, b) or stable/increasing (Anvers Island 64°46′ S, 64°3′W, Ducklow *et al.* 2007, Hinke *et al.* 2007). Although penguins, like Adélie for instance, are able to adjust their behaviour to local change in sea-ice condition until some level (Beaulieu *et al.* 2009), prolonged warming will inevitably lead to population decline and distribution changes. The recent production of giant icebergs in the Ross Sea has tremendously impacted Adélie and Emperor Penguin colonies in this region (Kooyman *et al.* 2007). Further to the point, it would be too restrictive to believe that modifications in sea-ice conditions would only affect the species mentioned above, as sub-Antarctic King Penguins also depend on sea ice at the winter stage of their breeding cycle (Bost *et al.* 2004).

Confounding factors

Unfortunately, penguin populations are not always straightforward indicators of climate changes. If SST and sea-ice extent have direct effects on resources' locations they also affect marine productivity itself, which in turn affects the abundance of penguin prey through the food chain (Gregg *et al.* 2003). The effect of climate thus needs to be examined both as such and with a lag as big as two years for some species (Le Bohec *et al.* 2008a). Furthermore, populations are affected by environmental conditions, locally as well as globally (Stenseth *et al.* 2002), and both local and global indices thus have to be considered to explore the effect of climate variability. The use of 'weather packages' (Stenseth & Mysterud 2005) and large-scale climatic indices may give a better representation of climatic effects than the use of a local weather variable (Stenseth *et al.* 2003). An observed decrease in foraging or breeding efficiency of penguins may result from a series of factors acting independently or in combination. Density dependence, for instance, is a well-known parameter likely to affect those populations where penguins breed in dense, large colonies (see Croxall *et al.* 2002, Barbraud & Weimerskirch 2003). Population processes are known to differ between small and big populations of Galápagos Penguins (Vargas *et al.* 2007). Such confounding factor has indeed been suggested to affect *Aptenodytes* spp. (Delord *et al.* 2004) and *Pygoscelis* spp. (Ainley *et al.* 2006), and would also certainly impact *Eudyptes* spp. and *Spheniscus* spp., although evidence of density-dependence has yet to be established for these latter species. The reduced foraging range of Little Penguins further adds to density-dependence issues as this concentrate birds' foraging activity on a geographically reduced zone and may lead to rapid prey depletion. Yet, at lower latitudes, man's activities, both on land (habitat destruction) and at sea (fisheries and leisure boating), present an additional impact onto penguin population. For example, it is difficult to disentangle the effects of both intense fishery activities and climate change to explain the Benguela ecosystem shift, where sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* progressively distribute further eastward, forcing top predators to either follow the move or to switch to new prey (Grémillet *et al.* 2008). The negative consequences of such a shift are obviously illustrated by the decline of African Penguins *S. demersus* around the southern African coast (Crawford 2007). On land too, man's extension on the coastlines has impacted negatively the populations of Australian and New Zealand, African and south American penguin species that were already subjected to greater predatory pressure (at least on land) than high latitude penguins breeding in remote places. However, the protection offered by the harsh environmental conditions found below the 40° South is fragile. Already in the past, King Penguin populations went down to extremely low levels when they were exploited for oil (and also as food items) during the 18th and 19th centuries. Exploitation probably ceased in the early 20th century when colonies were reduced or even extinct but they subsequently increased substantially at all breeding sites (Croxall *et al.* 1992, Weimerskirch *et al.* 1992). Recovery processes might be accelerated by an increased food supply probably made available by the concomitant reduction of the whale stock (Conroy & White 1972). Yet, nowadays other factors are superimposing to the effects of climate in the Southern Ocean. Tourism, for example, develops rapidly in sub-Antarctic and Antarctic regions (Fraser & Patterson 1997). As such, tourists may – if not properly supervised – destroy habitats, approach breeders without care and increase the birds' stress, even leading to the abandonment of reproduction in the worst case (Woehler *et al.* 1994). In addition to tourism, oiling is still a vivid problem in many regions of the Southern Ocean (although this particular subject would deserve a review of its own). On a purely methodological note, differences in models and population estimators, as well as in monitoring means, among research teams add to the difficulty of establishing accurate censuses and predicting accurately the response of populations (*e.g.* Ellis *et al.* 2007). As mentioned above, scale at which changes are considered may also lead to misinterpretations. Focusing on the trend of a single colony is similar to observing the tree that masks the forest: local trends may not reflect accurately the overall trend of the species across its complete breeding range. Species that breed over a large range of latitudes may simply shift the centre of their distribution but an observer that does not access to the big picture may report the disappearance of those small colonies that are situated at the extremities of the distribution and conclude incorrectly that the whole species is affected. We already mentioned how effect of climate change may be reflected in the penguin population via a bottom-up process but the reverse effect, *i.e.* top-down control, may also exist (Ainley *et al.* 2006) and blur the mechanisms by which penguin populations are regulated. Finally, penguins are not strictly specialists and often present a dietary diversification. While the variety of prey available to penguins remain low in short and simple trophic chains like the polar ecosystem (*i.e.* essentially krill *vs.* fish), the possibility to switch to completely novel prey is generally greater in lower latitudes. Yet, not all species would react in the same way: Little Penguins adapted, after a short transition period, to the complete disappearance of their main prey and moved onto new dietary items (Chiaradia *et al.* 2003), but African Penguins seem for the moment unable to cope with the reduction in sardines availability in their foraging range (Crawford 2007).

Perspectives

To predict penguin populations' response to climate change, one must both understand how the species react to climate variability and project future climate conditions. Relatively few studies have addressed this problem on penguin species and most of them have done so using an average predicted climate. This does not allow taking into account extreme weather events (but see Jenouvrier *et al.* 2009a), which are often ecologically more relevant than are fluctuations in the mean climate (Parmesan *et al.* 2000), as illustrated above by the importance of thermoclines in the foraging zone of Little Penguins and their disappearance when violent storms mix the water column (Ropert-Coudert *et al.* 2009). An increase in frequency of extreme events could severely impact a population and marine ecosystems are especially subject to rapid changes in climate and ocean environment (*e.g.* Humboldt Current, Alheit & Niquen 2004). The time necessary for a population to recover from an extreme event depends on its growth rate (Gardmark *et al.* 2003) or generation time (Rosenheim & Tabashnik 1991). As penguins are long-lived species, they exhibit low population growth rates which is the result of their life-history traits: low breeding success, late recruitment and high survival (Stearns 1992). Therefore, they should present a slow recovery rate and extreme events could thus increase considerably the risk of extinction or decline of penguins' populations. Emperor Penguins in Terre Adélie, for example, never recovered from their decrease in the 1970s (Jenouvrier *et al.* 2009b). Another important point to underline is that previsions relied on the fact that animals will react in the future to the same extent as they did during the past. Penguins could indeed react differently to global warming and could be able to cope with climate change if they could adapt by microevolutionnary changes or phenotypic plasticity (Visser 2008, Charmantier *et al.* 2008). As mentioned before, modifications in breeding timing and growth stages of penguins have occurred in some species as the climate changes whether this shift results from a passive adaptation to environmental condition or corresponds to an active decision taken by the birds. Long-lived species respond slowly to new selective pressure due to their long generation time, and may consequently present a very slow rate of adaptation (Visser 2008). However, speed of current change in global climate has only rarely been observed before (IPCC 2007). The possibility of adaptation could thus play an important role in the penguins' responses to climate change for those species with lower generation time, such as Little Penguins but could probably be dismissed for species such as King Penguins or Emperor Penguins. Due to their inability to fly penguin's migratory abilities do not match with those of procellariiformes species. For example, sub-Antarctic penguins are bound to their few, remote breeding sites and most of them cannot increase their foraging range during the breeding season if resources availability decreases around the sub-Antarctic islands. Furthermore, Antarctic penguins will see their geographic breeding range shrink with no possibility to go further south. A range contraction is already observed in Adélie and Emperor Penguins on the Antarctica peninsula, with the disappearance of most of the northern breeding sites (Forcada & Trathan 2009). These parameters (adaptation and migration), together with recovery plasticity, need to be computed into models to predict populations' responses to climate change.

In the end, can we use penguins as bio-sentinels? Obviously, this is a species-specific question. There is, for instance, less concerns when monitoring Adélie Penguins, which are numerous and rather resilient, than when monitoring Snares Penguins *Eudyptes robustus*, which are highly endangered and in small numbers. While an endangered species could be seen as a particularly relevant ecological indicator, its fragility means that there are concerns when using approaches such as oceanic bioplateforms on these species as these may impact their foraging and/or breeding successes. In endangered species less invasive methods should thus be preferred and could even only be restricted to censuses and *a posteriori* approaches (cf. above). Bearing in mind the risk of further endangering an already-fragile species we suggest to use the following spheniscid species as ecological indicators with increasing care (based on their IUCN (2009) status and overall number of pairs taken in Ellis *et al.* 2007):

- Least Concerned species: Chinstrap Penguins (4 million) > Adélie Penguins (2.6 million) > King Penguins (> 1.6 million) > Little Penguins (350–600 000), and to a lesser extent Emperor Penguins (195 000, but see Jenouvrier *et al.* 2009a and local trends around the Antarctic);
- Near Threatened species: Magellanic Penguins *S. magellanicus* (1.3 million) > Gentoo Penguins (314 000);
- Vulnerable species: Macaroni Penguins *Eudyptes chrysocome* (9 million) > Southern Rockhopper Penguins (1.45 million) > Royal Penguins *E. schlegeli* (851 000) > Humboldt Penguins (41-47 000).

Although classified as Vulnerables 'only', Snares Penguins (30 000), and especially the 3000 pairs of Fjordland Penguins *Eudyptes pachyrhynchus*, should be considered in an intermediate levels between this category and the one just below due to their relatively small numbers and rapidly decreasing trends;

- Endangered species: Northern Rockhopper Penguins (> 500 000 but decreasing at a fast rate) > Erect-crested Penguins *Eudyptes sclateri* (80 000) > African Penguins (59 000) > Yellow-eyed Penguins *Megadyptes antipodes* (3587) > Galápagos Penguins (600).

This sphenoscale is of course tentative and cannot be used as an official guideline, but it reinforces the idea that Pygoscelid populations are particularly adapted to be used as a "Bellwether of Climate Change" (*sensu* Ainley 2002). It is fortunate that the four least concerned species offer a gradation from polar to temperate species, from coastal to pelagic species, from ancestral (Little Penguins were the first to diverge from the other species, Tsuda *et al.* 2001) to modern species, and from small-sized (Little Penguins) to large-sized (King Penguins). Yet, even for these species, the IUCN statuses may soon need to be re-evaluated as trends are highly divergent from sites to sites and within sites. For instance, no penguin species, as to 2009, is listed as critically endangered. However, recent studies, such as those on the most emblematic species, the Emperor Penguins (Jenouvrier *et al.* 2009a), are causes for concern: indeed, these models predict a high risk of extinction in the forthcoming 50-100 years, despite this species being flagged as least concerned today. In the light of the above, population censuses are of prime importance and institutions like the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR), must receive support from international financing agencies. Yet to further understand the causes for the variability in population trends there is a need for a parallel approach in which a dual on-land versus at-sea monitoring is emphasized. We propose here that an international effort should be made to create a network of monitoring stations throughout the southern hemisphere (such as was proposed by the AMPPoP project of the International Polar Year, Ropert-Coudert *et al.* 2007c). Such observatories would consist of two parallel approaches. First, population processes could be investigated through the use of Automatic Identification Systems (AIS), an alternative – yet more costly – approach to studying climate effect on penguins (Saraux *et al.* 2011a) than traditional methods using flipper bands. In AIS approaches, a large number of individuals are uniquely identified by means of a subcutaneously inserted transponder that can be read by antennae placed on the natural path of the penguins between the colony and the sea (Fig. 2a, Gendner *et al.* 1992, Kerry *et al.* 1993, Le Maho *et al.* 1993, Chiaradia & Kerry 1999). In parallel, the foraging activity of these known-individuals should be investigated using a bio-logging approach (Ropert-Coudert & Wilson 2005, Naito 2009, Fig. 2b) so as to correlate population trends to the individual eco-physiological capacity of birds to face the consequences of climate change in their oceanic feeding grounds (Lescroël *et al.* 2009).

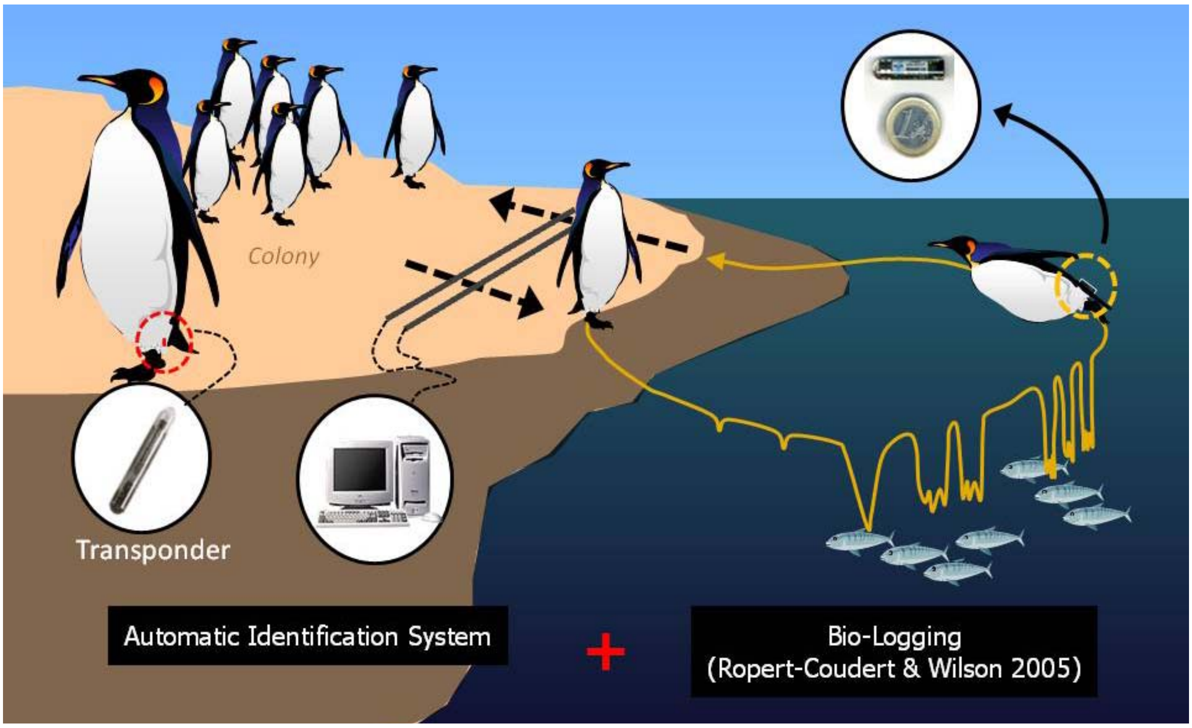

Figure 2. *A proposal to build a "penguin observatory" by combining two monitoring procedures that provide real-time (or near real time) information on penguins activity on land and at sea, with minimum perturbations: automatic identification systems and bio-logging. Together with classical population censuses, the setup of such observatories in key sites in the Southern Ocean would constitute a network of information, which, if properly compiled in online databases, could serve at investigating the impact of changes on the penguins' biology.*

As suggested above, bio-logging allows scientists to monitor changes occurring in the environment of penguins at the same spatial and temporal scale than the one at which activity – and reactivity – is measured (see Ropert-Coudert *et al.* 2009). AIS already exist and are used in a few penguin colonies throughout the Southern Ocean (Table 1) and advances in miniaturization means that nowadays miniature localization and diving activity recorders are readily available. This strictly methodological approach would not be efficient though if the data from the different observatories are not processed in a similar manner between the different research groups and compiled in a database accessible to anyone (*e.g.* SCAR-marBIN, http://www.scarmarbin.be/). Homogenization of monitoring procedures is already a major goal of the CCAMLR Ecosystem Monitoring Program.

Table 1. *Location of automated identification systems (AIS) in the Southern Ocean. Countries into parentheses represent sectors of the Antarctic continent. All systems are still operational as of 2010, except for the prototype, enclosed version of the AIS in Crozet on king penguins, which was replaced by an open version in 1998 where antennae are buried underground.*

Colony name	**Location**	**Species monitored**	**Specificities**
Cape Crozier (USA)	77°31'S, 169°23'E	*Pygoscelis adeliae*	Identification and weighing (1996~)
Cape Royds (USA)	77°34'S, 166°11'E	*Pygoscelis adeliae*	Identification and weighing (1996~)
Cape Bird (New Zealand)	77°13'S, 166°28'E	*Pygoscelis adeliae*	Identification and weighing (1996~)
Edmonson Point (Italy)	74°19'S, 165°04'E	*Pygoscelis adeliae*	Identification and weighing (1994~)
Dumont d'Urville (France)	66°70'S, 140°00'E	*Pygoscelis adeliae*	Identification and weighing (2006~)
Phillip Island (Australia)	38°29'S, 145°14'E	*Eudyptula minor*	Identification and weighing (1999~)
Bechervaise Island (Australia)	67°35'S, 62°49'E	*Pygoscelis adeliae*	Identification and weighing (1990~)
Crozet Archipelago (France)	46°25'S, 51°45'E	*Aptenodytes patagonicus*	Identification and weighing, enclosed (1990-97)
Crozet Archipelago (France)	46°25'S, 51°45'E	*Aptenodytes patagonicus*	Identification, open (1998~)
Robben Island (South Africa)	33°48'S, 18°21'E	*Spheniscus demersus*	Video-identification (2004~)
Bird Island, South Georgia (UK)	38°00'S, 54°00'W	*Eudyptes chrysolophus*	Identification and weighing (2003~)

Finally, new methodologies have also been flourishing recently and must be considered in the panel of approaches to optimize our use of penguin populations as ecological indicators. Among these, i) satellite imagery to identify new colonies (Fretwell & Trathan 2009), ii) stable isotopes analysis to reconstruct trophic interactions with little impact on the penguins (Lorrain *et al.* 2009), and iii) the use of paleological records to better understand population and diet fluctuations with past climate (Emslie & McDaniel 2002) appear particularly promising.

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An ethical issue in biodiversity science: The monitoring of penguins with flipper bands

Science et ethique : le suivi des manchots par le baguage à l'aileron

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ABSTRACT

Individual marking is essential to study the life-history traits of animals and to track them in all kinds of ecological, behavioural or physiological studies. Unlike other birds, penguins cannot be banded on their legs due to their leg joint anatomy and a band is instead fixed around a flipper. However, there is now detailed evidence that flipper-banding has a detrimental impact on individuals. It can severely injure flipper tissues, and the drag effect of their flipper bands results in a higher energy expenditure when birds are moving through the water. It also results in lower efficiency in foraging, since they require longer foraging trips, as well as in lower survival and lower breeding success. Moreover, due to the uncertainty of the rate of band loss, flipper bands induce a scientific bias. These problems, which obviously have serious ethical implications, can be avoided with alternative methods such as radiofrequency identification techniques.

Mots clés :
Bagues
Dynamique de populations
Perturbation
Impact
Biais scientifiques

RÉSUMÉ

Un marquage individuel est indispensable à la fois pour étudier les traits d'histoire de vie des animaux et pour assurer un suivi des individus dans toutes sortes d'études, aussi bien écologiques que comportementales ou physiologiques. Du fait de leur anatomie particulière, les manchots ne peuvent cependant être bagués aux pattes contrairement aux autres espèces d'oiseaux. Or, on sait aujourd'hui que le baguage à l'aileron a un effet délétère. Il peut notamment blesser sévèrement les tissus de l'aileron, et la gêne hydrodynamique occasionnée par la bague induit une augmentation de la dépense énergétique des oiseaux lorsqu'ils se meuvent dans l'eau. Il en résulte une diminution de leur efficacité dans la prospection alimentaire comme le montre l'augmentation de la durée de leurs voyages alimentaires en mer. Leur survie et leur succès reproducteur sont également réduits. Si l'on ajoute l'incertitude liée à la

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perte de bagues, il en résulte un biais dans les investigations scientifiques. Ces problèmes, qui ont évidemment d'importantes implications éthiques, peuvent être évités grâce à des méthodes alternatives telles que l'identification électronique par radiofréquence.

1. Introduction

Much of our present knowledge on the ecology and behaviour of animals is derived from longitudinal studies of individuals. Long-term datasets are essential to study life-history traits (e.g. age-specific survival, age at first reproduction, reproductive lifetime) [1], and to understand how variations in those traits might impact population dynamics and behavioural strategies. However, the collection of such datasets requires the ability to identify individuals repeatedly over time, i.e. by individual markings. For most bird species, monitoring is possible by means of ringing, a method by which observers are able to read an individual identification number on a leg ring, either at distance using binoculars or a telescope, or by recapturing birds (particularly in the case of smaller sized species). For instance, in the current context of increasing anthropogenic pressures, capture-mark-recapture data obtained from banding have enabled researchers to model how seabird populations may be impacted by fisheries and climatic variations through changes in breeding success and survival [2–5]. However, leg rings are not suitable for all bird species. For instance, due to anatomical peculiarities of their leg joint, penguins cannot be banded with traditional leg rings. Nonetheless, obtaining longitudinal data from penguin populations is crucial, as some species are endangered and others live in extreme habitats where climate changes and their impact on marine prey are predicted to be important. They are thus particularly relevant biological models for investigating changes in life-history traits and population dynamics, and may act as bellwethers of climate change [2] and marine ecosystem health (Fig. 1).

Consequently, since the 1950s, flipper bands have been widely used [2,6,7] to study the life-history traits and behaviour of various penguin species but also to track individuals used in physiological investigations. Data from flipper-banding have also been used to explain observed changes in penguin populations in relation to climate changes [8,9], ultimately predicting the future impact of climate on these populations [10]. However, since the 1970s, detrimental effects of flipper-banding have been reported (for review, see [11,12]). In an early reaction to this, at the end of the 1980s, the observation of tissue injuries induced by flipper bands resulted in the cessation of many penguin flipper-banding projects as a matter of precaution. However, the harmlessness of flipper bands remains a controversial issue and continues to be subject to much debate and dispute. Flipper-banding is still being used in research and conservation projects, such as for investigating the survival of penguins rehabilitated after an oil spill [13]. Some teams, who are still using large scale banding schemes, claim that flipper bands have no significant effects, at least in some species [14,15].

In this context, one may question the reliability of data based on flipper-banding if it has an impact on the life-history traits of penguins. Moreover, "it raises practical and larger ethical questions about costs and benefits of procedures in field studies" [16]. For those teams that have abandoned banding, can data previously obtained from banded birds be used without discussing the various implications of flipper-banding impacts? Is available information sufficient to accurately correct for banding effects?

In the context of global change, obtaining data on penguin biology and ecology is unquestionably necessary for scientists to address future threats. Here, we review the *pros* and *cons* of the three penguin monitoring methods known in use today. More specifically, we compare flipper bands to Radio Frequency IDentification (RFID) tags, which appear to be the main alternative to flipper bands since their introduction in 1991 in king penguins, *Aptenodytes patagonicus* [17]. We will also discuss the advantages and disadvantages of web tags, i.e. small-animal identification tags which are attached to the outer webbing of penguin feet [15].

2. Advantages of flipper bands

2.1. Avoidance of capture stress

Flipper-banding usually requires a single initial capture to fit the band. Since the band number can be read from a distance with binoculars, recapture is not needed for further identification, except [15] when bands become loose and need to be securely reattached. Flipper bands therefore enable the monitoring of penguins throughout their whole life with a single capture, thus avoiding the further stress associated with recaptures, such as in many other bird species (i.e. for which recapture is necessary in order to read tag numbers on smaller scaled rings).

RFID tags share this advantage with flipper bands since identification may be automatically performed using fixed antennas on the typical passageways of the birds. The main limitation of RFID however, is the short reading distance of antennas which is required to identify the tag, i.e. with a maximum of about 1 m for the 31 mm transponders used in the Texas Instruments Radio Frequency Identification TIRIS system (see [18]). Thus, to settle such systems requires the existence of bottleneck locations, where birds will always pass when travelling between the colony and the sea. Further, to identify penguins in the colony, a portable hand reader is needed and the birds must to be approached very closely by observers with the subsequent consequences of human disturbance.

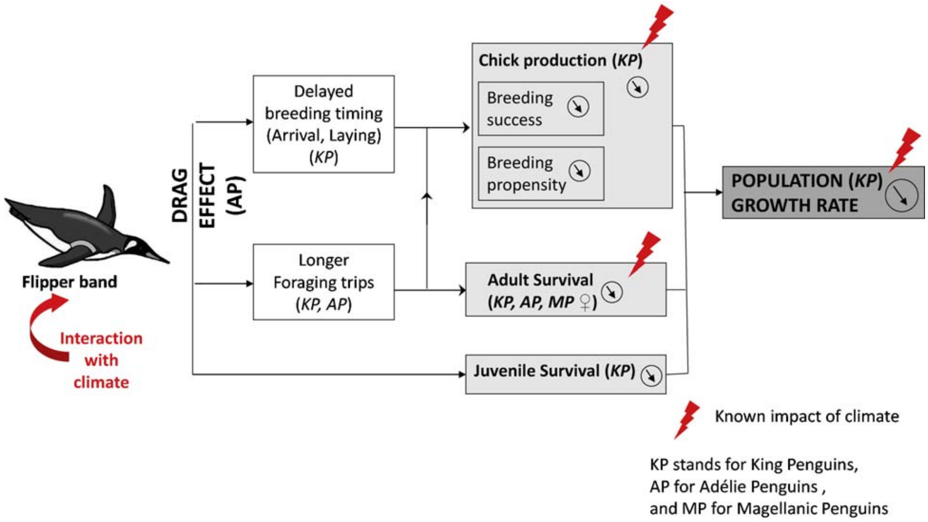

Fig. 1. Effects of flipper bands on penguin populations and their interaction with climate. The small black arrows into circles indicate where flipper bands induce a reduction, e.g. such as a reduction in breeding success.

The use of web tags definitely requires both an initial capture of the birds and subsequent recapturing to be able to read the small markings of the tags [15]. Thus, it incurs an even higher disturbance cost to birds and is therefore not favoured as a method for marking individuals.

2.2. *An easy and cheap means to identify penguins*

Flipper bands, either in plastic or metal, are easily visible for an observer, at least when both flippers of the penguin are visible. Moreover, when the carcass of a banded penguin is found, removing the band or recording the number is simple. Thus, even if the person finding the carcass is not the scientist involved in penguin monitoring, it is likely that the band or the number will be forwarded (the correspondence address is usually indicated on the band itself). In contrast, RFID tags can only be read with dedicated equipment, therefore precluding any identification when such equipment is not available. Moreover, they are not visible and hard to detect as they are implanted under the skin and are small (they weigh less than a gram).

In addition, the cost of flipper bands is extremely low (less than 1 € a piece), as are the small ear tags (0.1 € a piece) designed for rodents that have been adapted for the use on penguins [15]. On the other hand, whereas RFID tags are also affordable (around 2–3 €), the cost of a hand RFID reader is much more expensive (about 500 €) and the cost of a fixed set-up with series of antennas, readers and computers, and spare equipment (such as used for the king penguin colony on Possession Island in Crozet archipelago [18]) can reach 20 to 30 k€, depending on the number of passageways that need to be equipped. Moreover, those figures include spare equipment, but do not account for accessory costs for sheltering the equipment and for maintenance. Yet, to ensure its continuous functioning in the field, the full time presence of an engineer is compulsory, or there is a higher risk of gaps in data collection due to equipment failure. But note that a RFID system generates a huge number of data even if there are some interruptions. For an identification set-up to run at a remote field site, solar cell systems and/or batteries are needed and can also require daily maintenance (with in some cases the added problem of poor light, such as in Antarctica during the winter). Note, however, that the reading of a band number at a distance also requires people to be continuously in the field. But, in contrast to an automatic system, human based informations do not allow the same constant recapture effort and individual birds can be missed.

3. Disadvantages of flipper bands

Hereafter, we will only consider the effects of single flipper bands compared to those of RFID and web tags, as most banding schemes usually involve monitoring penguins with a single flipper band. The main effects of flipper bands are summarized in Fig. 1.

3.1. *Tissue injuries*

The moulting process causes penguin flippers to swell [19] and, particularly at that time, flipper bands, which can easily be fitted too tightly or not properly secured (with a slight opening), may induce severe injuries to flipper tissues [15,20]. Wound depth in flipper joints may be 1 cm or more, thus damaging tendons and muscles. In extreme cases, presumably due to infections, this can lead to death [21]. The effects of flipper bands, however, depend both on band material and shape; some bands are worse than others. For instance, aluminium bands are known to be more harmful than stainless-steel bands, as they can deform easily, especially under the high pressures encountered while diving [15]. No infections have yet been reported with transponder injection or web tag piercing.

3.2. Increased drag

Culik et al. [22] found in 1993 a 24% increase in the energetic cost of subsurface swimming in Adélie penguins *Pygoscelis adeliae* in a water canal. This was an important finding, because it revealed the importance of the increased drag resulting from flipper bands. The authors estimated that the increased cost would reduce by half the prey captured by free-ranging banded penguins.

The drag increase associated with any external device fitted to a penguin, depends on the shape and material of the device [23]. Accordingly, Barham et al. [24] found that stainless-steel flipper bands caused more drag on swimming African penguins *Spheniscus demersus* than experimental silicone rubber bands. RFID tags, since they are implanted under penguin's skin, avoid any possible drag effect. The same presumably applies to web tags since penguins use their flippers instead of their feet to propel themselves when they swim, and web tags are located on the feet positioned within the continuity of a streamlined body. It can therefore be assumed that they cause little if any drag, and thus their energetic cost to a penguin is negligible [15].

3.3. Lengthening of foraging trips

If flipper-banded birds are not able to compensate for the handicap resulting from increased drag, longer foraging trips are to be expected as a consequence of lower swimming and foraging efficiency compared to non-banded birds. By monitoring breeding male and female Adélie penguins with subcutaneous RFID tags over four years (about half of which were banded with stainless-steel flipper bands), Dugger et al. [25] found an 8% significant increase (3.5 hours) in the duration of the foraging trips of banded birds relative to their non-banded conspecifics. Investigating 60 breeding male Magellanic penguins *Spheniscus magellanicus* over a 13-month period (half of the birds had either stainless-steel flipper bands or a web tag), Boersma and Rebstock [14] found an eight-hour difference in foraging trip length between banded and non-banded birds. However, the difference (almost 20%) was not significant, possibly due to large variability in the data (standard deviation of 13 to 21 hours for an average duration between 43 and 52 hours). Saraux et al. [26], who investigated over 10 years 100 RFID tagged king penguins of which half had a stainless-steel flipper band, found that banded birds made significantly longer trips at sea during all incubation and brooding shifts (that is when both mates alternate on the egg and chick, respectively) than non-banded ones (i.e. of 12.7 versus 11.6 days). The mean increase in the duration of foraging trips was 9% [26], and therefore similar to that observed for banded Adélie penguins [25]. Importantly, the effect was still observed after a decade [26], thus arguing against the assumption advanced in some studies [8] that penguins are ultimately able to adapt to their band.

3.4. Reduced breeding success

The significant impact of flipper-banding on breeding success was first shown in 2004 in a five-year study on king penguins [27], already indicating that the effect of flipper bands on breeding success does not disappear after one or two years [27]. Saraux et al. [26] recently demonstrated that banded birds, even after a 10-year period from initial banding, still exhibited a reduced breeding success compared to non-banded birds. Altogether, chick production over ten years was nearly twice as large for non-banded birds as for banded king penguins: the 50 non-banded king penguins produced 80 chicks whereas the 49 banded birds produced only 47. What are the drivers of such a poor breeding success? We found that banded king penguins arrived later at the colony to breed [26], laid their egg later in the season, and in accordance with previous studies [7,27–29], that delaying reproduction onset resulted in lower breeding success [26]. The delay at the onset of breeding can be attributed to a lower efficiency in storing body fuels. Moreover, the proportion of returning birds engaged in breeding was lower for banded than for non-banded birds, suggesting that those non-breeding banded birds may have been unable to store sufficient body fuels. Note that a bird with a delayed start in breeding also has reduced choice in mate selection.

3.5. Reduced survival in adults

In their study, Dugger et al. [25] found that adult survival was 11–13% lower in flipper-banded Adélie penguins over the 2002–2003 season. Over a longer period, they however observed a high variability in survival, including years of high survival for banded birds, which could be associated primarily with variable environmental conditions. Their data showed that previous studies [30] had underestimated bands' effect, which likely occurred throughout the lifetime of the animal.

These effects of flipper bands on penguin survival were investigated in more detail in king penguins [26]. Over a decade, adult birds marked with stainless-steel bands had an average survival of 20% compared to 36% for non-banded birds. Plotting residuals of the model suggested that differences in survival increased up to 54 ± 3 months, i.e. 4.5 years. Those birds (banded and non-banded) which died during that period had a lower breeding success than the birds which survived, therefore suggesting that the lower survival in banded birds concerned poorer performers [26].

3.6. Reduced survival of juveniles

The survival rate of non-banded juvenile king penguins is about 75–80% after 2–3 winters [27], which is approximately twice as large as that reported in previous studies of flipper-banded chicks (47% in Brodin et al. [29] and 6–39% in Weimerskirch et al. [7]).

4. Scientific bias due to flipper bands

The impact of flipper bands on the survival and breeding success of penguins obviously introduces a bias in those studies where the changes in these traits are used as indicators of the impact of climate change on populations. The real question concerning flipper-band data is thus whether data obtained from flipper-banded birds may be corrected.

4.1. Uncertainty in the rate of band loss

As reported by Boersma and Rebstock [15], the rate of band loss can vary between 5 and 22% for aluminium bands, which open more easily, compared to a rate of loss of only 0–2% for stainless-steel bands. Moreover, the method used to determine the rate of band loss, i.e. by tracking double flipper-banded birds to calculate the proportion of those losing one band [8], is biased. Indeed, the survival of doubly banded birds is lower than that of single banded birds [31].

In contrast, the rate of RFID tag loss is negligible for 31 mm tags if inserted properly under the skin, i.e. in a way preventing their ejection after initial insertion [26]. However, Boersma and Rebstock [14] found a tag loss of 2.6% for 12 mm RFID tags injected under the skin of penguins' feet. The small size and the location of these tags may explain their high rate of loss. Indeed, such small tags have a very short reading distance of about 10–20 cm and cannot be implanted under the better-protected abdominal skin if they are to be read by underground antennas. In the feet, transponders may be less likely to get trapped in subcutaneous blubber, and thus are subjected to higher physical stress and ejection as penguins walk. It is therefore preferable to use tags with greater detection distances. Concerning web tags, they may pull out, therefore leaving a small tear in the webbing [15].

4.2. Scientific bias

Since flipper bands can affect adult survival and/or reproduction, any study using raw (uncorrected) data collected through flipper-banding schemes takes the risk of confounding banding effects with the investigated climate or anthropogenic effects, thus leading to incorrect inferences.

Correcting data by accounting for banding effects therefore seems the obvious solution. However, the major problem with such an approach is that flipper-banded penguins are differently affected by climate when compared to non-banded birds. In banded Adélie penguins for instance, the increase in foraging duration varies according to the year [25], whereas African penguins only seem to be negatively affected by banding during periods of reduced prey availability [32]. In king penguins [26], the population growth rates of banded and non-banded birds did not respond similarly to variations in sea surface temperature. Indeed, differences between the two groups were most apparent in "intermediate" years. Food availability at sea could be so poor for a given year that even those birds not handicapped by a band might fail in large numbers. In contrast, in years of very favourable environmental conditions, the environmental pressure on banded king penguins is weak and the extra cost inflicted by banding may then be less visible, explaining the absence of or slight difference observed between banded and non-banded birds in cold and favourable years [26].

A major difficulty also arises for studies investigating the impact of climate change on penguin dispersal. Indeed, a drop in breeding success increases dispersal in seabirds [33]. Thus, the reduced breeding success of banded birds may result in increased dispersal, resulting in an additional bias in ecological investigations. Presently, penguin dispersal is almost exclusively studied based on banded birds because one cannot surround all existing colonies with RFID antennas. However, the significance of such data is therefore put into question, as dispersal based on banded birds may not be representative of actual population dispersal in free-ranging penguins.

5. Conclusions

The long-term impact of flipper bands on the survival of juvenile penguins, and on the breeding success, survival and duration of foraging trips of adult penguins, as well as their relationships with climate, are only known in detail for king penguins. The observed impacts can be essentially attributed to the drag effect of the bands, and possibly also to flipper injuries, since, in accordance with data for Adélie penguins [25], they are associated with longer foraging trips [26], and most likely greater energy expenditure. This result is also in accordance with the pioneering studies of Wilson et al. that highlighted increased metabolic rates for banded swimming penguins, which suggested decreases in foraging efficiency [11,22,23]. In contrast to previous assumptions [8], the impact of flipper bands (at least for king penguins) is not limited in time. Birds which survived beyond the five first years following banding continued to display longer foraging trips and reduced breeding success [26]. Banded birds therefore seem unable to compensate for the handicap resulting from the increased band-induced drag, except when marine resources are unusually abundant [26]. Delays and/or failure/inability to engage in breeding altogether indicate that the main effect of flipper-banding is through a serious weakening of an individual body condition.

Due to the large size of the section of the colony that was surrounded by RFID antennas, we never observed two flipper-banded birds as a mated pair. In a smaller population where the chance of banded pairs would be higher, the effect on breeding would then presumably be even higher. Still, the observed impact certainly cannot be neglected since, for king penguins, the survival of banded chicks after 2–3 winters is approximately half that of non-banded chicks; the survival of banded adults over 10 years is of 20% instead of 36% for non-banded birds and their breeding success is about 40% lower than that of non-banded birds [26,27]. Moreover, it should be emphasized that the results presented were obtained using stainless-steel flipper bands, which are known to be much less harmful than the aluminium bands [17] still widely used in population studies of penguins. We may therefore assume that the bias on data obtained with aluminium bands [7–10] on previous investigations was far greater. However, since this impact has not yet been measured, any correction for the effect of banding that can be made for existing data in population dynamics investigations would be highly speculative. The study of king penguins [26] can at least be used as a benchmark for sensitivity analyses.

An important question is whether the impact of flipper bands is the same in different penguin species. In other words, can the data for king penguins be generalized to other penguins and, particularly to smaller penguins, since the king penguin is the second largest species after the emperor penguin *Aptenodytes forsteri*?

Since the drag increases as a square of the speed and the power that is required to overcome drag increases as a cube of the speed, the effect is expected to be smaller in smaller penguins if they swim at lower speeds than king penguins. But there is no clear relationship between size and swimming speed in penguins [34], and thus there is no reason for drag effects to be disproportionally higher in the large king penguins. The drag effect might even be higher for smaller penguins because their flipper bands are proportionally larger than for penguins of greater size. Yet, as indicated above, the measured increase in swimming metabolic rate induced by flipper bands in the small Adélie penguin is as much as 24% [22]. A specific problem for the emperor penguin is that it is the only bird to breed during the severe Antarctic winter, and we do not know the effect of temperatures well below freezing on wet flipper bands when the penguins jump out from water, or the impact of the bands during blizzards, i.e. while the birds are standing on sea ice.

It is sometimes argued that using flipper bands is the only way to investigate the dispersal of penguins. However, breeding success is a main trigger of dispersal [33], and its drop induced by flipper bands introduces a bias that raises questions about its costs and benefits. As pointed out by Robert May [16], there are therefore good reasons why we need to think more carefully about some present practices in field investigations.

Altogether, taking into account the important and long-term impact of stainless-steel flipper bands on juvenile and adult penguins, the finding that aluminium bands are even more harmful [15], and considering the uncertainties about the rate of band loss and the dispersal of banded birds, the continuation of banding schemes should be seriously reconsidered. We cannot be sure that there is no effect of RFID tags in penguins [12] but this is very unlikely since no negative effects have been found either in juveniles or adults in tits [35]. The much larger survival and breeding success of RFID tagged penguins is anyway a strong argument for the use of RFID as an alternative to flipper bands and for developing technical innovations to counteract the limitations of RFID. Compared to flipper-banding, another clear advantage of an automated RFID identification based on antennas surrounding a colony is that it enables an identification of penguins day and night at the right time they get in or out this colony. The number of individuals which can be monitored is also quite unlimited, therefore enabling investigations at a real population scale without a huge human involvement. Note that there is also a fully-automated population monitoring of penguins through a computer vision system that is using the natural markings in the chest plumage of African penguins [36]. However, such non-invasive system cannot be used on most species of penguins because they do not have such natural markings.

The data on the breeding success and survival of penguins based on banded birds, and particularly aluminium-banded birds [7–10], should also be reconsidered. Climate change is clearly having negative impacts on some penguin populations [37,38], but developing reliable forecasts requires unbiased estimates of the relationships between climatic variables and penguin demography.

Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

References

[1] J.D. Lebreton, K.P. Burnham, J. Clobert, D.R. Anderson, Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies, Ecol. Monogr. 62 (1992) 67–118.

[2] D. Ainley, The Adélie penguin: bellwether of climate change, Columbia University Press, New York, 2002.

[3] J.P. Croxall, P.N. Trathan, E.J. Murphy, Environmental change and Antarctic seabird populations, Science 297 (2002) 1510–1514.

[4] N.C. Stenseth, A. Mysterud, G. Ottersen, J.W. Hurrell, K.S. Chan, M. Lima, Ecological effects of climate fluctuations, Science 297 (2002) 1292–1296.

[5] C. Barbraud, P. Rivalan, P. Inchausti, M. Nevoux, V. Rolland, H. Weimerskirch, Contrasted demographic responses facing future climate change in Southern Ocean seabirds, J. Anim. Ecol. 80 (2011) 89–100.

[6] W.J.L. Sladen, R.L. Penney, Penguin flipper-bands used by the USARP bird-banding program 1958-60, Bird-Banding 31 (1960) 79–82.

[7] H. Weimerskirch, J.-C. Stahl, P. Jouventin, The breeding biology and population dynamics of king penguins *Aptenodytes patagonica*, Ibis 134 (1992) 107–117.

[8] C. Barbraud, H. Weimerskirch, Emperor penguins and climate change, Nature 411 (2001) 183–186.

[9] S. Jenouvrier, C. Barbraud, H. Weimerskirch, Long-term contrasted responses to climate of two Antarctic seabirds species, Ecology 86 (2005) 2889–2903.

[10] S. Jenouvrier, et al., Demographic models and IPCC climate projections predict the decline of an emperor penguin population, Proc. Nat. Acad. Sci. U S A 106 (2009) 1844–1847.

[11] S. Jackson, R.P. Wilson, The potential costs of flipper-bands to penguins, Funct. Ecol. 16 (2002) 141–148.

[12] R.P. Wilson, The price tag, Nature 469 (2011) 164–165.

[13] L.G. Underhill, et al., Mortality and survival of African penguins *Spheniscus demersus* involved in the Apollo Sea oil spill: an evaluation of rehabilitation efforts, Ibis 141 (1999) 29–37.

[14] D.P. Boersma, G.A. Rebstock, Flipper-bands do not affect foraging-trip duration of Magellanic Penguins, JFO 80 (2009) 408–418.

[15] D.P. Boersma, G.A. Rebstock, Effects of double bands on Magellanic penguins, JFO 81 (2010) 195–205.

[16] R.M. May, Ethics and amphibians, Nature 431 (2004) 403.

[17] J.-P. Gendner, J. Gilles, E. Challet, C. Verdon, C. Plumere, X. Reboud, Y. Handrich, Y. Le Maho, Automatic weighing and identification of breeding king penguins, in: I.G. Priede, S.M. Swift (Eds.), Wildlife Telemetry, Remote Monitoring and Tracking of Animals, Ellis Horwood, Chichester, 1992, pp. 29–30.

[18] J.-P. Gendner, M. Gauthier-Clerc, C. Le Bohec, S. Descamps, Y. Le Maho, A new application for transponders in studying of penguins, JFO 76 (2005) 138–142.

[19] R. Groscolas, Study of molt fasting in the emperor penguin *Aptenodytes forsteri*: relationship between feather growth, body weight loss, body temperature and plasma fuel levels, Com. Physiol. Biochem. A. Comp. Physiol. 61 (1978) 287–295.

[20] M. Sallaberry, M.J. Valencia, Wounds due to flipper bands on penguins, JFO 56 (1985) 275–277.

[21] D.G. Ainley, R.E. Leresche, W.J.L. Sladen, Breeding biology of the Adélie Penguin, University of California Press, Berkeley, 1983.

[22] B.M. Culik, R.P. Wilson, R. Bannasch, Flipper-bands on penguins: what is the cost of a lifelong commitment? MEPS 98 (1993) 209–214.

[23] B.M. Culik, R. Bannasch, R.P. Wilson, External devices on penguins: how important is shape? Mar. Biol. 118 (1994) 353–357.

[24] P.J. Barham, L.G. Underhill, R.J.M. Crawford, T.M. Leshoro, D.A. Bolton, Impact of flipper-banding on breeding success of African Penguins *Spheniscus demersus* at Robben Island: comparisons among silicone rubber bands, stainless-steel bands and no bands, Afr. J. Mar. Sci. 30 (2008) 595–602.

[25] K. Dugger, G. Ballard, D. Ainley, K. Barton, Effects of flipper-bands on foraging behavior and survival of Adélie Penguins (*Pygoscelis Adeliae*), Auk 123 (2006) 858–869.

[26] C. Saraux, C. Le Bohec, J.M. Durant, V.A. Viblanc, M. Gauthier-Clerc, D. Beaune, Y.-H. Park, N.G. Yoccoz, N.C. Stenseth, Y. Le Maho, Reliability of flipper-banded penguins as indicators of climate change, Nature 469 (2011) 203–206.

[27] M. Gauthier-Clerc, J.-P. Gendner, C.A. Ribic, W.R. Fraser, E.J. Woehler, S. Descamps, C. Gilly, C. Le Bohec, Y. Le Maho, Long-term effects of flipper-bands on penguins, Proc. Royal Soc. London. B (suppl.) 271 (2004) S423–S426.

[28] O. Olsson, Seasonal effects of timing and reproduction in the king penguin: a unique breeding cycle, J. Avian. Biol. 27 (1996) 7–14.

[29] A. Brodin, O. Olsson, C.W. Clark, Modeling the breeding cycle of long-lived birds – why do king penguins try to breed late? Auk 115 (1998) 767–771.

[30] D.G. Ainley, D.P. DeMaster, Survival and mortality in a population of Adélie Penguins, Ecology 61 (1980) 522–530.

[31] G. Froget, M. Gauthier-Clerc, Y. Le Maho, Y. Handrich, Is penguin banding harmless? Polar Biol. 20 (1998) 409–413.

[32] S.L. Hampton, P.G. Ryan, L.G. Underhill, The effect of flipper-banding on the breeding success of African Penguins *Spheniscus demersus* at Boulders Beach South Africa, Ostrich 80 (2009) 77–80.

[33] T. Boulinier, K.D. McCoy, N.G. Yoccoz, J. Gasparini, T. Tveraa, Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours, Biol. Lett. 4 (2008) 538–540.

[34] R.P. Wilson, Y. Ropert-Coudert, A. Kato, Rush and grab strategies in foraging marine endotherms: the case for haste in penguins, Anim. Behav. 63 (2002) 85–95.

[35] M. Nicolaus, K. Bouwman, N.J. Dingemanse, Effects of PIT tags on the survival and recruitment of great tits, Ardea 96 (2009) 286–292.

[36] R.B. Sherley, T. Burghardt, P.J. Barham, N. Campbell, I.C. Cuthill, Spotting the difference: towards fully automated population monitoring of African penguins *Spheniscus demersus*, ESR 11 (2010) 101–111.

[37] C. Le Bohec, King penguin population threatened by Southern Ocean warming, Proc. Nat. Acad. Sci. USA 105 (2008) 2493–2497.

[38] F. Montaigne, Fraser's penguins: a journey to the future in Antarctica, Henry Holt, New York, 2010.

APPENDIX 3: King penguins on the verge of extinction

King penguins on the verge of extinction?

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The extinction of colonies of emperor penguins in Antarctica and of king penguins in the sub-Antarctic is predicted to occur within the 21st century. These predictions however need to be re-examined because they are based on flipper-banded birds or non-banded birds of unknown age. Using for the first time data available for non-banded birds of known age from the world largest population of king penguins settled on Crozet Archipelago, we built annual stage-structured matrices from 1999 to 2007 to reassess the population changes of the past decade in relation to climate variability. Population growth rate is mainly sensitive to changes in temperature-dependent population parameters such as survival and breeding success of adult birds but also post-fledging survival. Population projections were simulated according to several IPCC warming scenarios. These projections indicate that the colony would reach quasi-extinction (decline of 90% of the initial population size) before the end of the 21st century (between 2055 and 2096 according to the warming scenario). With the rate of current global changes, king penguins will probably not be able to cope and reverse the predicted population decline with micro-evolutionary changes or behavioral adjustments.

Global climate is predicted to become warmer. Animal populations are particularly sensitive to the frequency and rate of climate variations, and the rate of current changes in global climate is unnaturally rapid (IPCC 2007). Predicting the impact of upcoming climate changes on populations and biodiversity is therefore a critical task assigned to scientists nowadays. It is however challenging to investigate the impact of climate on the whole ecosystem, and this is why ecological indicators such as upper-level predators have been of growing interest (Durant *et al.* 2009). Top-predator populations can indeed be used as ecological indicators since they integrate the effect of climate change on lower trophic levels (Durant *et al.* 2009). They generally are long-lived organisms that are particularly sensitive and thus vulnerable to rapid environmental changes. Because of both a delayed maturity and low fecundity, even small changes in adult survival can drastically reduce their lifetime reproductive success (Stearns 1992), and thereby population persistence. Population dynamics of long-lived species are expected to be more sensitive to the same relative changes in survival than in reproductive success (Stearns 1992; Saether & Bakke 2000). Not all age classes contribute equally to fitness (Charlesworth 1994), and the effect of environmental forcing on populations therefore depends on which age classes are affected. According to life history theory (Stearns 1992; Lebreton & Clobert 1991), adult survival is the parameter that has the highest elasticity, *i.e.* contributes the most to the population growth rate in long-lived species. It is therefore expected to be the life history trait on which the effect of environmental variability is the least apparent (Gaillard & Yoccoz 2003).

Polar areas, in addition to the major role of their oceanic circulation in global climate (Busalacchi 2004), host some of the most important fauna biomass of our planet (Tynan 1998). Polar ecosystems are presumed to be strongly affected by current global warming (Hoegh-Guldbreg & Bruno 2010). As a consequence, resource abundance and availability in polar areas will be rapidly altered (Fraser & Hofmann 2003), affecting ultimately their population dynamics and trends through deleterious effects on their demographic traits, as it has already been observed in numerous upper-level marine predators (Croxall *et al.* 2002; Ainley *et al.* 2005; Trathan *et al.* 2007; Barbraud *et al.* 2011b). It is therefore timely to explore the effects of climate on population dynamics in seabirds from the Southern Ocean, such as the King penguin (*Aptenodytes patagonicus*), and the limits of potential adaptive strategies shaped by this species to cope with future climate change. As about two thirds of the world's king penguin population breed in Crozet Archipelago, Southern Indian Ocean (Guinet *et al.* 1995), we decided to evaluate the persistence of this population in relation to the ongoing global warming assuming that it would give us some picture of what the world population might at least be expected to encounter.

King penguins feed on small mesopelagics and primarily on myctophids (Cherel & Ridoux 1992), which are highly abundant in the Antarctic Polar Frontal Zone (*i.e.* 49 to 53° S; Duhamel *et al.* 2000). However, despite the key role of myctophids in the Southern Ocean ecosystem, information on their stock dynamics and monitoring is still lacking. It is thus only through environmental indices providing information on marine productivity and fish stock changes (Stenseth *et al.* 2002; Henson *et al.* 2010), that we are currently able to understand the dynamic of king penguins and to detect the potential extinction risk of the population of king penguins from 'La Grande Manchotière' under the current climate change patterns.

The onset of long-term monitoring studies decades ago makes it now possible to analyze longitudinal capture–mark–recapture (CMR) data on individuals from many natural populations (Barbraud *et al.* 2011b), and to use modern statistical models for their analysis (Lebreton *et al.* 1992). Recently, such studies modeled the dynamic of a penguin population to predict their future trends according to various climate change scenarios (Barbraud & Weimerskirch 2001; Jenouvrier *et al.* 2009). However, errors in estimates of the vital rates due to methodological problems (deleterious effects of flipper-band on penguin reproductive success and survival, see Gauthier-Clerc *et al.* 2004; Dugger *et al.* 2006; Saraux *et al.* 2011a), produce inaccuracies in the estimation of the population growth rate **λ**. This is particularly true for vital rates such as the adult survival to which **λ** is the most sensitive and that appear to play a key role in a range of species. We did monitor non-banded adult king penguins for nine years, using an automated system of identification of micro-tagged birds. Our data showed in 2008 that both survival and breeding success of king penguins breeding on Possession Island (Crozet Archipelago) are negatively affected by Ocean warming (Le Bohec *et al.* 2008a). But the age of these birds was unknown, which did not allow us to include the impact of age-structure on the dynamics of this population.

Here we present the first results on king penguin population dynamics and projections of population trends in relation to climate change scenarios that are based on data of 2201 known-aged king penguins that have never been flipper-banded for monitoring purposes, but instead fitted with subcutaneous electronic tags. In addition to obtaining unbiased demographic information from these non-banded birds, the strength of our system is also in its constant recapture effort coupled with the high fidelity of penguins to their natal site, thus providing a huge amount of information each year for each age class (Gendner *et al.* 2005). This possibility to have access to parameter estimates such as the age at first reproduction, age-specific reproductive and survival rates, that are often not estimated precisely (Altwegg *et al.* 2005), allows us to build accurate population matrices. We constructed stage-based population projection matrices (Caswell 2001) using Capture-Mark-Recapture estimates of age-specific survival and field estimates of fecundity to (*i*) calculate annual population growth rates λ and identify the life stages and vital rates that strongly contribute to the variation of λ (using Life Table Response Experiment analysis), and (*ii*) estimate the extinction risk of this king penguin population under projections of warming-climate stochastic scenarios forecasted by the Intergovernmental Panel on Climate Change for the upcoming decades.

Materials and Methods

Study Details. Our study was conducted during austral summers between 1997/1998 and 2007/2008 on the Possession Island (colony ‘La Grande Manchotière’; 46°25’S, 51°45’E) in the Crozet Archipelago where almost two third of the world king penguin population breed (Guinet *et al.* 1995). Individuals were fitted with subcutaneous electronic tags. These transponder tags weigh 0.8g and have no known adverse effects. They were shown to affect neither recruitment nor survival in tits (Nicolaus *et al.* 2009). Tests in pressurized chamber do not alter transponder tags (pers. comm. B. Friess). Antennas used to read the tags are permanently buried on penguin usual pathways and are connected to a computerized reading system (Gendner *et al.* 2005). The sequence of signals from the antennas reveals whether a transponded bird is entering or leaving the breeding site. This identification system does not require bird recapture or visual observation by a human and allows continuous automatic data collection all year round (Gendner *et al.* 2005). The breeding cycles and parameters of 2201 birds of known-aged (7 cohorts of birds tagged as 10-month old chicks, just before fledging, between 1998 and 2004) and 449 unknown-aged adult birds (unknown-aged birds tagged as breeders between 1996 and 1999) were established by interpreting the movements of the birds between the breeding area and the sea (see Descamps *et al.* 2005 and Le Bohec *et al.* 2007 for details). This unique long-term monitoring on the daily movements of birds enabled us to determine individual breeding activities and survival probabilities of penguins each year. The proportion of breeders was estimated as the number of birds attempting to reproduce in a given year relative to the number of birds still alive in this particular year, calculated from the capture recapture data. When they reproduce, king penguins lay a single egg per year, and the breeding cycle (incubation and chick rearing period) lasts over a year (*ca* 14 months, Descamps *et al.* 2002), meaning that a successful breeding cycle encompasses two civil years (*i.e.* a successful breeding cycle noted *Year t* will start with a molting period from *ca*

September *t*-1 to finish in *ca* November *t*). The breeding success was estimated as the number of eggs producing fledglings, and the overall breeding success (at the population scale) was the product of breeding proportion and breeding success.

Environmental descriptors. King penguins feed mainly on myctophid fishes and onychoteuthid squids (Cherel *et al.* 1996; Cherel & Weimerskirch 1999), which in turn feed on the meso- and macroplankton whose fecundity and growth both depend on phytoplankton production (Richardson & Verheye 1998). Since primary production is related to local physical conditions (Gregg *et al.* 2003), sea surface temperature (SST, in °C) variation gives information on both phytoplankton and zooplankton change of abundance. Concentration of chlorophyll *a* (Chl*a,* in mg.m^{-3}) is a proxy of primary productivity that can be used to locate in time and space the bloom of phytoplankton that affects the abundance of prey for king penguins through the food chain (Gregg *et al.* 2003). Since individuals are affected by environmental conditions, locally as well as globally (Stenseth *et al.* 2002), both local and global indexes have to be considered to explore the effect of climate variability on population. The use of ‘weather packages’ (Stenseth & Mysterud 2005) and large-scale climatic indexes may give a better representation of climatic effects than the use of a local weather variable (Stenseth *et al.* 2003). Thus, the Southern Oscillation Index (SOI, calculated from the monthly fluctuation in the air pressure difference between Tahiti and Darwin, Australia), as a global index encompassing a combination of weather features, could be a good explanatory variable of the effects of climate variability for top-predators, such as penguins (Le Bohec *et al.* 2008a; Jenouvrier *et al.* 2006). Negative SOI values indicate a warm phase of El Niño Southern Oscillation (Deser & Wallace 1987).

Chl*a* concentrations, obtained from the sea-viewing wide field sensor, were averaged on a subsector centered on Crozet Archipelago (bounded by [43–47°S, 46–56°E]) during annual king penguin rearing period (January-December) and during spring-summer period (September to April). This subsector corresponds to the yearly most productive subsector in the region (Perissinotto & Duncombe Rae 1990). Annual values of SOI were averaged and used as global environmental descriptors. Finally, we used mean SSTs, obtained from the Australian Bureau of Meteorology at the National Ocean and Atmospheric Administration, centered on Crozet ([43–47°S, 46–56°E] during the bloom of chlorophyll) and at the Marginal Ice Zone ([56–57°S, 46–56°E] during annual king penguin breeding) in the functional relationships with the demographic parameters (survival and breeding success, respectively, see Saraux *et al.* 2011a; Le Bohec *et al.* 2008a) in order to perform population trajectories under climate change scenarios.

Demographic modeling

Survival Analysis

Data collected from November 1998 to May 2008 (k = 10 occasions) were analyzed in a capture-mark-recapture framework following protocols defined by Lebreton *et al.* (1992). Using maximum-likelihood methods implemented in programs M- and E-SURGE (Choquet *et al.* 2004; Choquet *et al.* 2009), we estimated survival probabilities of the unknown-aged adults and known-aged juveniles using single-state or multi-state mark-recapture models respectively. Survival ϕ_t was defined as the probability of surviving between summer t (November of year t-1 to May of year t) and summer t+1 (November of year t to May of year t+1).

First, we used goodness-of-fit tests (GOF) computed by the software U-CARE (Choquet *et al.* 2009) to check that our most general model fitted the data. The overall GOF test of the unknown-aged adult population showed that the general Cormack–Jolly–Seber (CJS) model [$p_t \phi_t$] satisfactorily fitted our data (χ^2_2= 0.26, P = 0.61). Component 2.CT of the GOF tests ran for each cohort in the known-aged birds' dataset detected heterogeneity of capture within each cohort (Global test: χ^2_{28} = 104.17, P < 0.01). Most of the heterogeneity appeared to arise from the two first years after fledging (*i.e.* before the first return). By removing these first encounters, some heterogeneity was still remaining. However, contingency tables, checking if individuals not seen one year after fledging might have more chance to be absent after they had returned, did not show any such problem: late-returning individuals were no less catchable than early-returning ones. We therefore calculated an overdispersion factor $\hat{c}$ to account for the remaining lack of fit ($\hat{c}$ = 1.268; Global test: χ^2_{41} = 51.93, P = 0.12), and we ran multi-event models distinguishing the state 'before the first return' and 'after the first return' (see below).

Due to the high performance of the identification system used in our study (Gendner *et al.* 2005) and the high site fidelity in this species (even within the colony), there was no gap in the series of observations of all unknown-aged adults, thus the probability of detecting an adult (breeding or non-breeding) p_i was equal to 1 (see Le Bohec *et al.* 2007; Le Bohec *et al.* 2008a). The multi-state CMR models used for 1-year old marked birds were fitted under the general 'umbrella' of multi-event models (Pradel 2005). Models were fully described by linking states at successive sampling occasions by the matrix of survival ⁄ transition probabilities (Φ-matrix, the set of states is E = ['before the first return', 'after the first return', 'dead']), while the events were linked to states by the matrix of event probabilities (B-matrix, the set of events is Ω = ['seen', 'not seen']). Φ was separated in two steps: S-matrix for survival probabilities and T-matrix for transition probabilities conditional on survival.

Finally, we used Akaike's information criterion (AIC) or the modified version of the criterion QAIC, (Burnham & Anderson 2002), to select the best model, in terms of both parsimony (fewest model parameters) and adequate description of the data (*i.e.* deviance explained, Table S1). Models with the lowest values of these criterions were retained as the best candidate models (see Lebreton *et al.* 1992). We calculated AIC weights as a measure of the relative plausibility of the different candidate models. The constrained time-dependent model on survival for unknown-aged adults, and time- and age-dependent model on survival for the known-age birds provided better descriptions of the data (Table S1).

Matrix Population Modeling

To predict population trends in relation to climate changes and thereby address the question of population persistence, we used stage-structured matrix modeling (Caswell 2001). Penguins being fitted with transponders at one-year of age since 1998, we gradually had access to age-specific survival rates obtained from CMR models described above and age-specific reproductive rates for birds between 2 and 8-year old, to which parameters of a class of unknown-aged breeding adults (considered older than 8 years) have been added. For a given year t, vital rates for different age classes were then summarized in an annual population transition matrix (time-varying after birth-pulse matrix $\mathbf{A}_t$, see Caswell 2001 and Fig. S1a). Because all the elements of the full stage-structured matrices (*i.e.* 9 stages) were not available for the first years of the study, we therefore used a global transition matrix $\mathbf{A}$ (which included the mean values of the demographic rates obtained over our study period, *i.e.* linear time-invariant model, see (Caswell 2001) to which actual annual estimated parameters were incremented year after year. The annual population growth rate λ was given by the dominant Eigenvalue of $\mathbf{A}_t$ (Caswell 2001). Population persistence is linked to whether the matrix model has a dominant Eigenvalue greater than one or not ($\lambda < 1$ indicates a decrease of the population). We thus used this technique to produce nine annual Leslie matrices for which we assessed the effects of variation in fitness components on population growth using Life Table Response Experiment (LTRE) analyses (Caswell 2001).

Figure S1 a) *Annual population transition matrix (time-varying matrix A_t).* ***b)*** *Transition matrix implementing the significant relationships found i- between the overall adult breeding success and the Sea Surface Temperature (SST) of the area around Crozet Archipelago ($OBS_{Ads} \sim 2.9941SSTcro - 0.4914$, $P < 0.0104$), and ii- the adult survival and the SST at the Marginal Ice Zone (MIZ) with a 2-year lag ($S_{Ads} \sim 7.0404SSTmiz - 3.9055$, $P < 0.0001$).* ***c)*** *Earlier age at first breeding: age-structured recruitment pattern shifted 1 year earlier in the annual population transition matrix.* ***d)*** *Lower breeding frequency: only early breeding events following with a non-breeding year (P_B : probability of breeding). For all matrices* $\boldsymbol{A_t}$*, the first row describes the age-specific overall breeding success (OBS_{age}), and the diagonal the age-specific survival (S_{age}).*

a)

$$\mathrm{A}_t = \begin{pmatrix} 0 & 0 & 0 & OBS_4 & OBS_5 & OBS_6 & OBS_7 & OBS_8 & OBS_{Ads} \\ S_{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{45} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{56} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{67} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{78} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{89} & S_{Ads} \end{pmatrix}$$

b)

$$\mathrm{A}_t = \begin{pmatrix} 0 & 0 & 0 & OBS_4 & OBS_5 & OBS_6 & OBS_7 & OBS_8 & OBS_{Ads} \sim SSTcro \\ S_{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{45} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{56} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{67} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{78} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{89} & S_{Ads} \sim SSTmiz \end{pmatrix}$$

c)

$$\mathrm{A}_t = \begin{pmatrix} 0 & 0 & OBS_4 & OBS_5 & OBS_6 & OBS_7 & OBS_8 & OBS_8 & OBS_{Ads} \\ S_{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{45} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{56} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{67} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{78} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{89} & S_{Ads} \end{pmatrix}$$

d)

$$\mathrm{A}_t = \begin{pmatrix} 0 & 0 & 0 & OBS_4 & OBS_5 & OBS_6 & OBS_7 & OBS_8 & OBS_{AdsEarly} & 0 \\ S_{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{34} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{45} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{56} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{67} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{78} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{89} & 0 & S_{AdsNonBreeder} \times \left(1 - P_{B_{AdsEarly}}\right) \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{AdsEarly} \times P_{B_{AdsEarly}} & 0 \end{pmatrix}$$

The LTRE method allowed us to quantify the contributions of each of the vital rates to the differences in population growth rate among years (Caswell 1989; Caswell 2001; Hunter *et al.* 2010). As reference year, we chose the year 2007, for which all the vital rates are available and λ reached one of the lowest values during the study period ($\lambda = 0.9976$). The proportional change in λ for a proportional change in the vital rates from the global transition matrix gave us a measure of relative sensitivity (or elasticity) of the population growth rate (Caswell 2001; Ezard & Coulson 2010). Matrix and statistical analyses were performed using the R statistical environment (version R 2.9.1, http://www.r-project.org; R development core team 2008).

Population growth change analysis

The core of our study consisted in exploring the influences of environmental variability on population growth rate. Since population growth rate encompasses multiple, decoupled spatiotemporally and non-linear functional relationships between demographic parameters and climate variables (Le Bohec *et al.* 2008a; Barbraud *et al.* 2011b; Saraux *et al.* 2011a), we used a global climate index (the Southern Oscillation Index SOI; Stenseth *et al.* 2002) and a measure of the primary production in the Crozet sector (reflected by chlorophyll *a* concentrations). We used generalized additive models (GAM) with nonparametric smooth functions that were fitted using penalized maximum likelihood and implemented in the 'mgcv' library available in R-2.9.1 (Wood & Augustin 2002) to explore the effect of climate on population growth rate. Specifically, let Y_t be the population growth at year *t*. Let $X_{i,t}$ be a vector of the explanatory variables at year *t* where *i* identifies a single components. Let f_i be nonparametric, smoothing functions, specifying the effect of the covariate X_i on the demographic variable Y_t. The formulation is:

$$Y_t = \alpha + \Sigma_i f_i(X_{i,t}) + \varepsilon_t$$

where α is an intercept and ε is a stochastic noise term. The GAM procedure chooses the degrees of freedom of the smoothing function f_i (*i.e.* how linear is the curve) based on the minimization of the Generalized Cross Validation (GCV) score. It includes a linear effect (*i.e.* $f_i(X_{i,t}) = b_i * X_{i,t}$ where b is the slope) as a special case.

We applied a backward selection strategy for GAM regressions based on minimization of the GCV score, and a measure of the model predictive squared error R^2 (Green & Silverman 1994). A covariate was retained if it caused a decrease of the model GCV score. Correlation between environmental variables was checked before including explanatory variables in the models. We found no auto-correlation in the residuals of the selected models.

Population Viability Modeling

To assess the extinction risk of the king penguin population, we first used the simple structure of the deterministic matrix model **A**. It allowed us to assess the relative importance of basic demographic parameters without stretching beyond the limits of the available data. However, while annual transition matrices integrate the environmental variation or density dependence (*i.e.* all vital rates are measured each year and vary with time), a potential density-dependence effect should be taken into account when using a global transition matrix. The population of 'La Grande Manchotière' remained stable during our study period. The main density-dependence effect is most likely to be the number of breeding site available, we therefore put a cap on the number of individuals that are allowed to breed at K assuming that all breeding age-classes are affected equally. We used K = 45 000 breeding pairs, *i.e.* the maximum population size N observed at 'La Grande Manchotière' since the 1960s (see Delord *et al.* 2004).

Stochastic variability in the vital rates composing the global transition matrix was simulated using the linear time-varying matrices model $\mathbf{A}_t$. Stochasticity was generated by sampling randomly input demographic parameters of the models (*i.e.* age-specific survival and breeding success) from their respective probabilistic distribution (with a mean value and accompanying standard deviation estimated during the study). A warming of the climate system over the past 100 years has been detected by the IPCC in changes of surface temperatures (oceanic and atmospheric) and in contributions to sea level rise. Taken together with additional information on radiative forcing, greenhouse gazes or aerosol concentrations for instance, the Special Report on Emissions Scenarios (SRES - (1) was able to provide projections of future changes in surface temperatures. During the same period as the one used by the IPCC to calculate some of their scenarios (*i.e.* 1906 to 2005), warming trends were observed in the Crozet sector ($y \sim 0.013x - 25.81$, $R^2 = 72.16$, $P < 0.001$). Using these IPCC storylines or actual warming in Crozet, and knowing that adult breeding success and survival of king penguins from the Crozet Archipelago are affected by the sea surface temperature around Crozet ([43–47°S, 46–56°E]) and at the Marginal Ice Zone (MIZ, [56–57°S, 46–56°E]) (see Fig. S1b, Le Bohec *et al.* 2008a), we were then able to implement predicted environmental change in our global transition matrix, taking into account the observed stochasticity (*i.e.* probabilistic distributions of the SST with mean values and standard deviations of the residuals estimated between 1906 and 2005). Six climate change scenarios were thus simulated for the next 200 years:

Scenario S1- no warming of the sea surface temperature in the Crozet sector, Scenario S2- current warming trends observed in the Crozet sector (*i.e.* using the slopes of warming trends observed around Crozet and at the MIZ between 1906 and 2005),

Scenario S3- a global warming of 0.2°C per decade of the surface temperature obtained by the SRES-IPCC scenarios,

Scenario S4- a global warming of 0.2°C per decade adjusted with existing warming trends in the Crozet sector, meaning that global warming of 0.2°C per decade was thus adjusted by the ratios between the slopes obtained for Crozet areas (*i.e.* trends of 1.25°C and 1.35°C were observed from 1906 to 2005 at Crozet and the MIZ, respectively) and the slope obtained by the IPCC value (*i.e.* linear increasing trend of 0.74°C of global surface temperature was observed from 1906 to 2005),

Scenario S5- future warming predicted by B1 scenario given by the SRES-IPCC (the global population stays the same, but with rapid global solutions to economic, social and environmental sustainability, meaning equity improvement, reductions in resource use, introduction of clean and resource-efficient technologies, but without additional climate initiatives),

Scenario S6- future warming predicted by A1B scenario given by the SRES-IPCC (same global population, but with economic growth balancing between the use of fossil-fuel and renewable energy sources).

At that stage, it was possible to estimate 6 projected annual population growth rates for the next 200 years. The population size in year $\mathbf{n}(t+1)$ was determined as the product of the population matrix $\mathbf{A}_t$ and the current year's population size $\mathbf{n}(t)$ ($\mathbf{n}(t+1) = \mathbf{A}_t\,\mathbf{n}(t)$) (Caswell 2001). Using the Markov Chain Monte Carlo method (Oro *et al.* 2004), population trajectories (1000 runs) over time were drawn to estimate the years of quasi-extinction. We defined our quasi-extinction times at 10% of our initial population size. This 10% threshold also match with the standardized minimum viable population size (median MVP) derived from the meta-analysis done by Traill *et al.* (2007) on 212 species (Traill *et al.* 2007) that has been corroborated by the MVP recommended census based on genetic data (Frankham 1995). As an initial value in our models, we took the breeding population estimated by photo-counting in our last year of observation (22 000 breeding pairs in 2007), and as a carrying capacity (*i.e.* maximal value of N) the highest of the available estimates of the breeding population to-date at 'La Grande Manchotière': 45 000 breeding pairs in 1962 (Delord *et al.* 2004). Finally, using the warming scenario S4 (global warming scenario of 0.2°C per decade adjusted with current warming trends in the Crozet sector), we investigated the limits of adaptations of the King penguin by simulating population trajectories when i) the age at first breeding is earlier, and ii) the breeding frequency is reduced to one early breeding event every 2 years (Fig. S1c and S1d). An age-structured recruitment pattern shifted 1 year earlier should mimic a movement on the selection gradient toward an *r* life-history strategy, while sabbaticals and no late breeding might limit the cost of reproduction in terms of future survival and breeding success. Generation time *T*, used to project population size reduction of ≥ 30% and ≥ 50% within a three generation period (‘Vulnerable’ and ‘Endangered’ categories according to the IUCN criterions, IUCN 2008), was calculated as $T = A + [\ S_{Ads} / (1 - S_{Ads})\ ]$ (Saether *et al.* 2005), where age at maturity A refers to the age at which regular breeding females first occurred (5-year old), and S_{Ads} is the expected adult survival rate (*i.e.* 0.89076, see Table S2).

Results

Vital rates and population growth rates for the study period.

The constrained time-dependent model on survival for unknown-aged adults, and time- and age-dependent model on survival for the known-age birds provide the best fit of the data (Model a2 and Model b5, Table S1 in *supporting information* SI).

Table S1 *Capture-Mark-Recapture model selection to estimate survival and capture probabilities of king penguins from the Crozet Archipelago. The highest AIC weight (wi) indicates the best model (shown in bold).*

Models	DEV	ΔAICi	NP	*w*i
a. Unknown-aged adult breeders				
Model (a1) $[p_i \phi_i]$	1806.060	38.7828	1	$0.4\ 10^{-8}$
Model (a2) $[p_i \phi_t]$	**1750.877**	**0**	**9**	**0.9999**
	DEV	ΔQAICi	NP	*w*i
b. Known-aged birds				
Model (b1) $[p_t\ \psi_{a_{2,3,4\_K}}\ \phi_i]$	9410.267	44.6020	14	$0.2\ 10^{-9}$
Model (b2) $[p_t\ \psi_{a_{2,3,4\_K}}\ \phi_t]$	9371.579	30.0913	22	$0.3\ 10^{-6}$
Model (b3) $[p_t\ \psi_{a_{2,3,4\_K}}\ \phi_a]$	9361.576	22.2027	22	$0.2\ 10^{-4}$
Model (b4) $[p_t\ \psi_{a_{2,3,4\_K}}\ \phi_{a*t}]$	9275.425	20.2603	55	$0.4\ 10^{-4}$
Model (b5) $[p_t\ \psi_{a_{2,3,4\_K}}\ \phi_{a+t}]$	**9313.135**	**0**	**30**	**0. 9999**

Model symbols and subscripts: p *= encounter probability;* ϕ *= survival probability;* ψ *= transition probability (conditional on survival), here the probability of returning to the colony; i = constant; t = time-dependence; a = age; + = additive model, * = model with interaction. DEV: Deviance, ΔAICi: Difference in value between AIC (Akaike's Information Criterion) of the most parsimonious model and the model in question, ΔQAICi: Difference in value between AIC based on quasi-likelihood (overdispersion (ĉ) was 1.268). NP: Number of estimated parameters, wi: AIC or QAIC weight.*

***Table S2** Demographic parameters (values from the global transition matrix **A**) and Life Table Response Experiment analysis (LTRE, measured relative to the year 2007) for the population growth rate **λ** of king penguins from the Crozet Archipelago.*

					Proportional contribution to the difference between λ_t et λ_{2007}							
Age	Estimates	SD	Sensitivity ($s_{ij} = \partial\lambda/\partial a_{ij}$)	$(\partial\lambda/\partial a_{ij})^2$ $V(a_{ij})$	1999	2000	2001	2002	2003	2004	2005	2006
Overall Breeding Success												
A4	0.00556	0.00593	0.04878	$1.41086\ 10^{-5}$	0.00059	0.00066	0.00060	0.00049	0.00351	0.00090	0.00685	0.00317
A5	0.05490	0.01525	0.04165	$2.64529\ 10^{-5}$	0.01290	0.01416	0.01297	0.01069	0.01508	0.01483	0.02605	0.00923
A6	0.10720	0.03361	0.03520	$4.16368\ 10^{-5}$	0.00334	0.00361	0.00329	0.00268	0.00397	0.01388	0.00203	0.01955
A7	0.18306	0.04548	0.03036	$4.19178\ 10^{-5}$	0.02111	0.02251	0.02043	0.01638	0.02552	0.01991	0.04166	0.01767
A8	0.18981	0.00477	0.02611	$3.24941\ 10^{-6}$	0.00132	0.00138	0.00125	0.00099	0.00162	0.00122	0.00135	0.00199
Adults	0.36319	0.09427	0.16476	$2.55900\ 10^{-3}$	**0.52446**	**0.63205**	**0.39756**	**0.58687**	**0.36106**	**0.78418**	**0.61896**	**0.4414**
Survival												
A2	0.83388	0.01241	0.09199	$1.04994\ 10^{-4}$	**0.04842**	**0.10450**	**0.06597**	**0.07006**	**0.05228**	**0.02578**	**0.02661**	**0.04134**
A3	0.93180	0.01146	0.08233	$7.77062\ 10^{-5}$	0.00053	0.03726	0.02376	0.02510	0.01952	0.00955	0.00986	0.01548
A4	0.92622	0.00776	0.08282	$5.32051\ 10^{-5}$	0.00492	0.00556	0.02381	0.02515	0.01956	0.00957	0.00988	0.01551
A5	0.88101	0.01072	0.08677	$8.06702\ 10^{-5}$	0.01118	0.01264	0.01196	0.03976	0.03055	0.01498	0.01540	0.02411
A6	0.87172	0.01300	0.08507	$9.40955\ 10^{-5}$	0.01682	0.01903	0.01802	0.01525	0.03069	0.01509	0.01544	0.02426
A7	0.88982	0.01433	0.07910	$8.96781\ 10^{-5}$	0.01250	0.01418	0.01346	0.01142	0.01453	0.01258	0.01274	0.01966
A8	0.88723	0.01882	0.07307	$1.00453\ 10^{-4}$	0.00835	0.00952	0.00907	0.00772	0.00967	0.00986	0.01247	0.01919
A9	0.88967	0.02946	0.06730	$1.33424\ 10^{-4}$	0.00872	0.01003	0.00960	0.00823	0.01004	0.01054	0.01084	0.01676
Adults	0.89076	0.01913	0.42592	$3.47043\ 10^{-3}$	**0.32482**	**0.11292**	**0.38825**	**0.17921**	**0.40239**	**0.05712**	**0.18986**	**0.33076**

LTRE analysis: values are expressed as proportional contributions to the difference between λ_t and λ_{2007} that can be decomposed into:

$$\lambda_t - \lambda_{2007} \approx \sum_i (a_i^t - a_i^{2007}) \frac{\partial\lambda}{\partial a_i}$$

where the sensitivity term s_i is calculated at the mean of the vital rates for the reference year and year t.
Each term in the summation is the relative contribution of one of the vital rates to the difference in the λ between the reference year and year t.
A parameter shows a high contribution if it highly differs among years or if λ is very sensitive to differences in that parameter (31, 69).

Whatever the year, king penguin survival from fledgling to the next summer (corresponding to their first winter at sea) was much lower (between 77.5% CI [72.1 – 82.0] and 89.8% CI [82.8 – 94.2]) than survival of older age-classes (from 3- to 9-year-old: between

85.8% CI [81.9 – 89.0] and 96.5% CI [93.3 – 98.2]). One single bird has attempted to breed, unsuccessfully, at 2-year-old during our study period. Only few birds attempted to breed at 3-year-old (6.1 ± 2.7%). Between 4 and 5 years of age, the proportion of birds breeding increased from 39.5 ± 2.9% to 64.5 ± 5.8%. First breeding success was observed at 4 year-old (0.6 ± 0.6% of surviving 4-year-old birds succeed to fledge a chick), and successful breeding events increased with age (from 5.5 ± 1.5% at 5-year-old to 19.0 ± 0.5% at 8-year-old; see the vital rate estimates in Table S2).

Table S3 *King penguin population growth rates obtained from annual population transition matrices* $\mathbf{A}_t$*. Population growth rates* λ *given by the dominant Eigenvalue of* $\mathbf{A}_t$*, the standard error of the estimated population growth rate SE(*λ*) calculated from the variances of the matrix entries using the series approximation methods (Chapter 12 in Caswell 2001). The null hypothesis (*H_0*:* $\lambda \geq 1$*) was tested by computing an approximate normal test of the z statistic (*$z = (1-\lambda)/SE(\lambda)$*) which under* H_0 *has a normal distribution with mean 0 and variance 1. In bold are presented the years when the king penguin population at Crozet decreased.*

Year	**λ**	**SE(λ)**	***z***	***P***
1999	1.01660	0.06421	-0.25861	0.602
2000	1.04342	0.06013	-0.72218	0.765
2001	1.05586	0.06069	-0.92047	0.821
2002	1.07869	0.05934	-1.32605	0.908
2003	**0.98524**	**0.06674**	**0.22118**	**0.412**
2004	1.05101	0.06676	-0.76418	0.778
2005	1.04600	0.06771	-0.67936	0.752
2006	**0.99679**	**0.07978**	**0.04757**	**0.481**
2007	**0.99764**	**0.08301**	**0.02957**	**0.488**
Study period	1.03148	0.00405	-7.77826	1.000

The annual stage-structured matrices $\mathbf{A}_t$ gave annual growth rates λ between 1.02 in 1999 and 0.10 in 2007, with lowest values in 2003, 2006 and 2007 ($\lambda < 1$, Table S3, Fig. 1). The population was projected to remain stable (all CIs overlap 1, Table S3), even though since 2002/2003 the population trend has slightly decreased (most λ values below 1, Fig. 1).

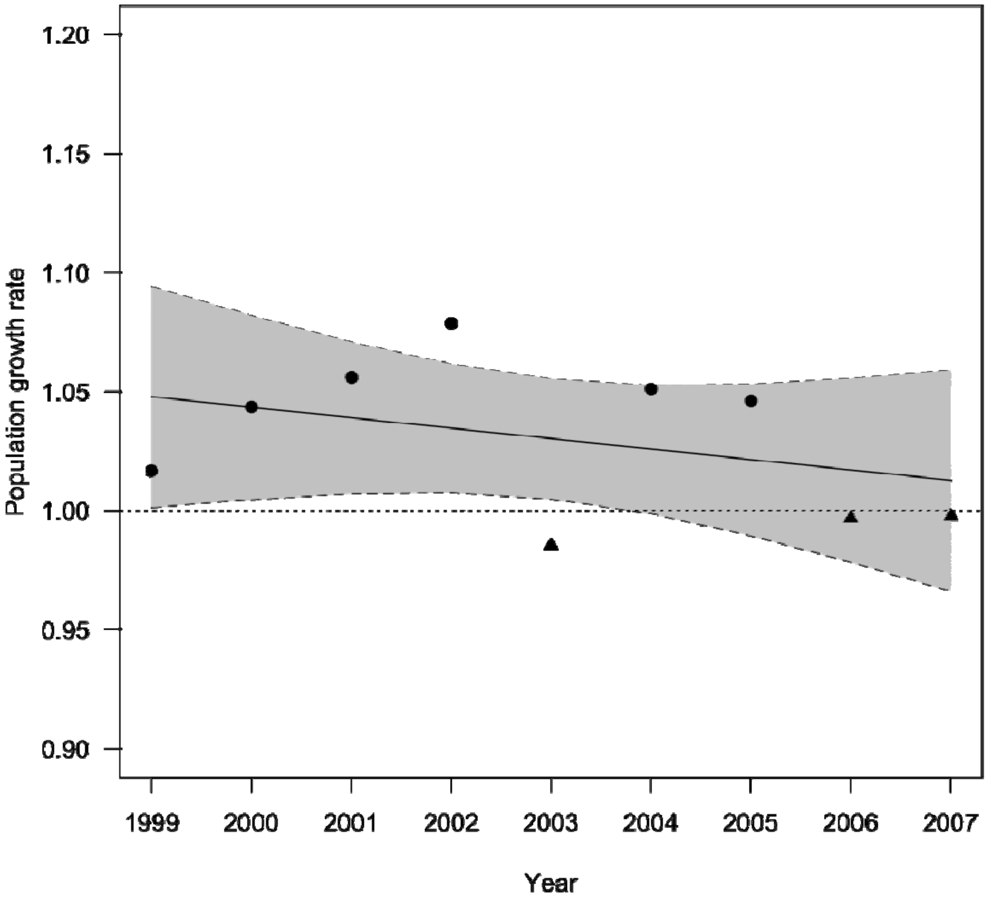

Figure 1 *Annual population growth rate (λ, the dominant Eigenvalue of A_t) of the King penguin colony of 'La Grande Manchotière - Crozet Archipelago' during the study. Fitted linear model and confident intervals are indicated with solid and dashed lines, respectively (y ~ – 0.004x + 9.816, R^2 = 0.017, P = 0.321).*

Life Table Response Experiment and sensitivity analyses. We used the annual stage-structured matrices and the deterministic global transition matrix to explore the sensitivity of the population growth rate to changes in fitness components. The LTRE results highlight that whatever the year, breeding success, adult survival and to a lesser extent 2-years-old juvenile survival, contribute the most of the variation in λ (ranges of [0.36-0.78], [0.06-0.39] and [0.03-0.10], respectively, see Table S2). Figure S2 confirms that λ is indeed highly sensitive to changes in survival at early ages (between 2 and 5 years, birds fledge at 1-year old and start their first breeding attempt at 5-year old in average). Reductions in population growth rate λ (2003 and 2006) appear to be driven by, and equally shared between, reduced adult survival and breeding success (Table S2).

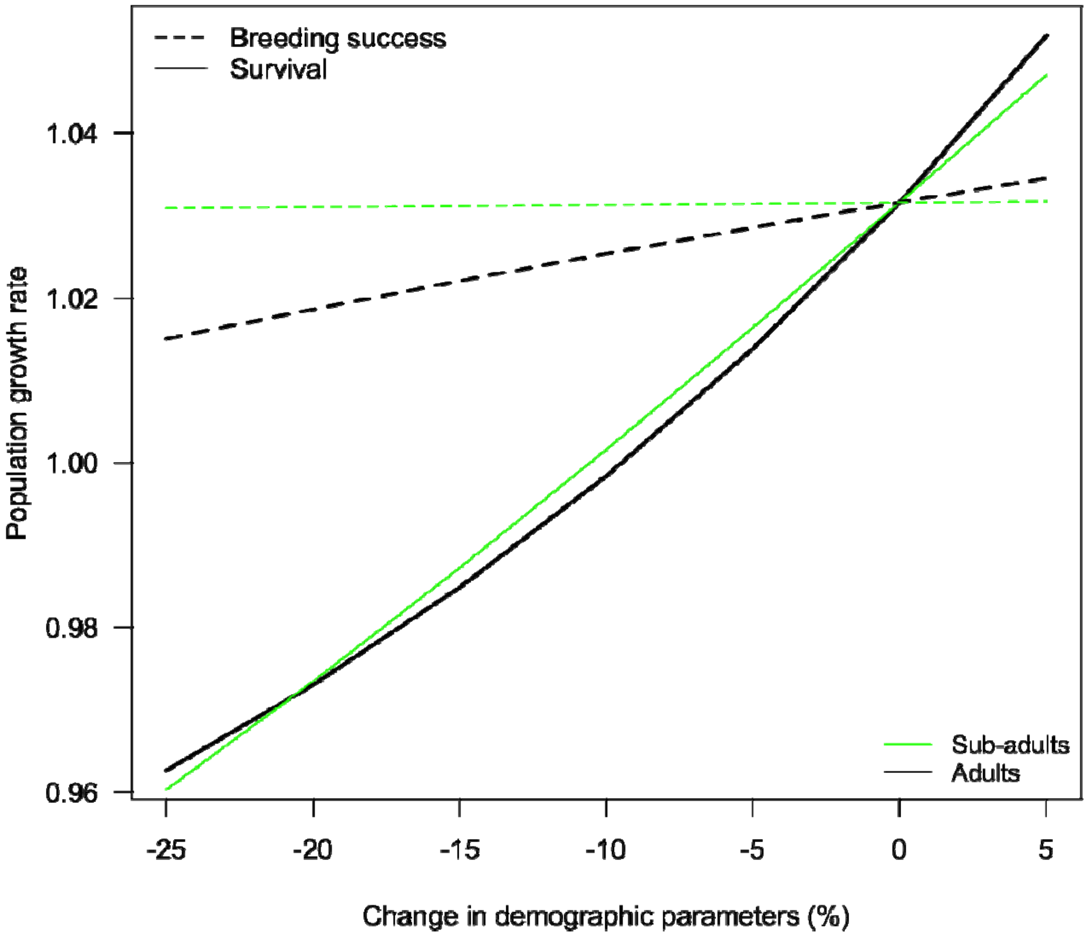

Figure S2 *Elasticity of the population growth rate (λ, the dominant Eigenvalue of* A_t*) to changes in various demographic parameters of the global transition matrix. Solid lines correspond to survival parameters and dashed lines to breeding success parameters. Green lines correspond to sub-adult stage (between 2 and 5 year-old) and black ones to adult stage (> 8 year-old).*

Climate and population growth rate fluctuations. Variations in the king penguin population growth rate can be explained by environmental variability (Table 1, and see SI for details on the environmental descriptors). Looking at the single variable analysis, models with a 2-years lag (M1: annual chlorophyll concentration ([Chl*a*]), M3: spring-summer [Chl*a*], M4: annual Southern Oscillation Index, SOI) are the best fitting models compared to the competitive models. The model including both environmental variables (annual [Chl*a*] and SOI) provides a better fit to the data with 86% of the deviance explained, although [Chl*a*] alone explains most of the deviance (76%, M1). Population growth rate appeared to be positively affected by annual [Chl*a*] around Crozet, with also a slight positive effect of annual SOI, with a 2-year lag (Table 1): the king penguin population decreased two years following low productivity around Crozet that might be linked to warm events (negative values of SOI associated with El Niño warm events).

Table 1 *Best models selected by generalized cross validation (GCV), based on fitting a generalized additive model (GAM) to variation in annual population growth rate* (**λ**) *of the colony 'La Grande Manchotière - Crozet Archipelago'* (**λ** *~ Climates).*

Model	**Formulation**	**R^2 adjusted**	**ED**	**GCV**	***F***	**p-value**
1	$\boldsymbol{\lambda_t = \alpha + f\,(\mathrm{Chl}a_{\mathrm{yr}\ t\text{-}2}) + \varepsilon_t}$	**0.675**	**75.6%**	**$\mathbf{0.54\ 10^{-3}}$**	**10.67**	**0.015**
2	$\boldsymbol{\lambda_t = \alpha + f_1(\mathrm{Chl}a_{\mathrm{yr}\ t\text{-}2}) + f_2(\mathrm{SOI}_{\mathrm{yr}\ t\text{-}2}) + \varepsilon_t}$	**0.764**	**86.1%**	**$\mathbf{0.50\ 10^{-3}}$**	**8.98** **2.39**	**0.032** **0.195**
3	$\boldsymbol{\lambda_t = \alpha + f(\mathrm{Chl}a_{\mathrm{Spsum}\ t\text{-}2}) + \varepsilon_t}$	**0.554**	**67.1%**	**$\mathbf{0.75\ 10^{-3}}$**	**6.20**	**0.044**
4	$\lambda_t = \alpha + f(\mathrm{SOI}_{\mathrm{yr}\ t\text{-}2}) + \varepsilon_t$	0.134	24.8%	$1.09\ 10^{-3}$	2.18	0.184
5	$\lambda_t = \alpha + f(\mathrm{SOI}_{\mathrm{yr}\ t\text{-}1}) + \varepsilon_t$	0.149	25.5%	$1.07\ 10^{-3}$	2.40	0.165
6	$\lambda_t = \alpha + f(\mathrm{Chl}a_{\mathrm{Sprsum}\ t\text{-}1}) + \varepsilon_t$	-0.024	10.4%	$1.28\ 10^{-3}$	0.81	0.397
7	$\lambda_t = \alpha + f(\mathrm{Chl}a_{\mathrm{yr}\ t\text{-}1}) + \varepsilon_t$	-0.140	0.3%	$1.43\ 10^{-3}$	0.02	0.890

Best models, selected by lowest GCV and highest adjusted R^2, are indicated in bold. Cha_{yr} is the mean annual chlorophyll concentration observed around Crozet [43–47°S, 46–56°E] and Cha_{Sprsum} is the mean chlorophyll concentration during Spring-summer (September t-1 to April t). SOI_{yr} is the mean annual value of the Southern Oscillation Index. f_i corresponds to nonparametric smoothing functions specifying the effect of the covariate x_i on the demographic variable λ_t. α and ε_t correspond to intercept and stochastic noise term, respectively. Models at t having no significant effects, we simplified the table with only models with lags t-1 and t-2.

Model projections under climate-warming scenarios. We assessed the probability of extinction of the king penguin population of 'La Grande Manchotière' in accordance to the several scenarios of environmental change provided by IPCC to which we included environmental stochasticity (see *Materials and Methods* in SI). First we projected the current warming trend observed in the Crozet area (*i.e.* using the slopes of warming trends observed between 1906 and 2005 around Crozet and at the Marginal Ice Zone south of Crozet Basin). Monte Carlo simulations show that in this case population trajectories (*i.e.* simulated population size over time) are expected to decrease over simulation time, and the quasi-extinction time (defined as population decline of 90%) of the king penguin population is predicted to happen before the end of our 21st century (*i.e.* 85 years from now, Fig. 2 in green). If the global warming scenario of 0.2°C per decade (projected by the SRES-IPCC 2007) is now adjusted with the current warming trends observed in Crozet areas, the population is predicted to reach quasi-extinction about 40 years sooner, *i.e.* in 44 years. Using A1B and B1 scenarios (distinction between storyline emphasizing on sustained economic development and storyline promoting environmental sustainability) generated by the SRES-IPCC 2007, quasi-extinction is projected to be on the same schedule (*i.e.* 44-45 years).

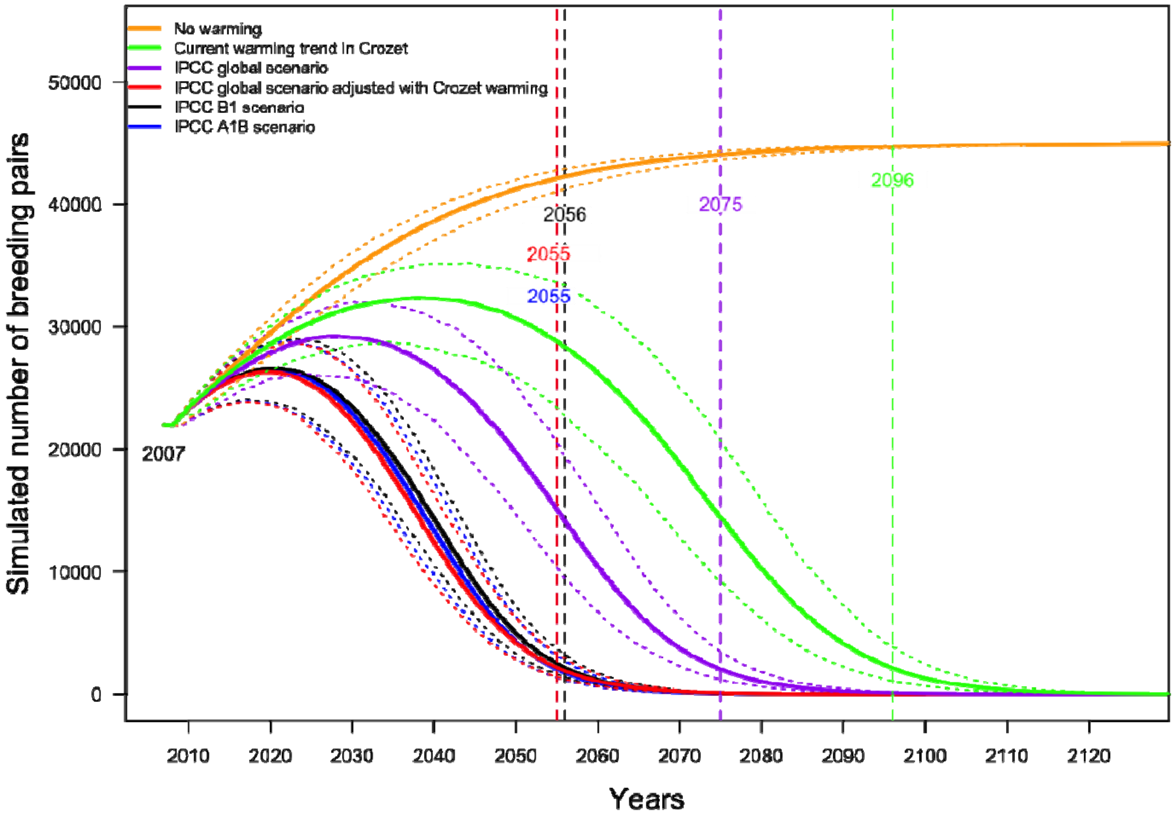

Figure 2 *Simulated Markov chain population trajectories (1000 runs) of the king penguin population of 'La Grande Manchotière - Crozet Archipelago' under environmental stochasticity coupled with environmental change scenarios for the next 200 years. The probabilities of annual adult overall breeding success and survival were generated according to six SST change scenarios: (S1) no warming (in yellow), (S2) current warming trend in Crozet (i.e. using the slopes of warming trends observed between 1906 and 2005 around Crozet and at the Marginal Ice Zone, in green), (S3) global warming of 0.2°C per decade obtained by the SRES IPCC scenarios (in magenta), (S4) global warming of 0.2°C per decade adjusted with current warming trend in Crozet (warming of 0.2°C was adjusted by the ratios between the warming slopes obtained in Crozet areas and by the IPCC between 1906 and 2005, in red), (S5) and (S6) future warming predicted by B1 (in black) and A1B (in blue) scenarios given by the SRES IPCC 2007. The lower and the upper confidence limits represent the 2.5 and 97.5 of the data (dashed lines). Vertical lines represent the quasi-extinction years (10% of our initial population size) calculated under the different scenarios.*

Potential adaptations or adjustments of the king penguin population through changes in breeding behavior, for instance breeding every second year (that should decrease costs of reproduction on future survival and breeding events) or recruiting earlier into the breeding population (moving from low to high turnover on fast-low continuum in the life-history (Bielby *et al.* 2007), see details in SI *Materials and Methods*), are expected to delay the quasi-extinction threshold of the penguin population by less than 10 years but does not counter the decline (Fig. 3).

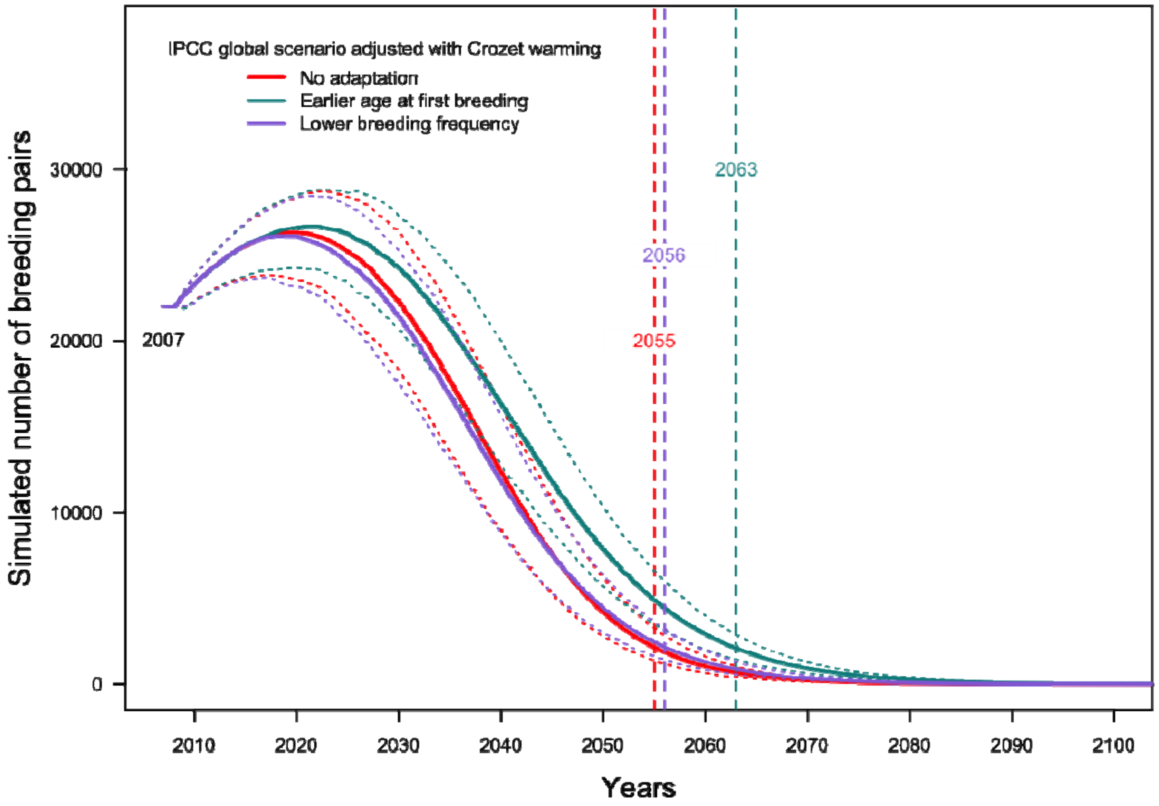

Figure 3 *Simulated Markov chain population trajectories of the king penguin population of 'La Grande Manchotière - Crozet Archipelago' under environmental stochasticity coupled with the Scenario S4 (i.e. global warming of 0.2°C per decade obtained by the SRES IPCC scenarios adjusted with current warming trend in Crozet) and over time, when 1- the population is able to adapt with an earlier recruitment (in cyan) or 2- by reducing the breeding frequency to one early breeding event every 2 years (in violet), and when 3- no adaptation occurred (in red). The lower and the upper confidence limits represent the 2.5 and 97.5 of the data (dashed line). Vertical lines represent the quasi-extinction years (10% of our initial population size) calculated under the different scenarios.*

Discussion

First and foremost, our study shows that low primary productivity, that is to some extent linked to warm events (negative values of SOI associated with El Niño warm events), affects negatively the population growth rate of king penguins from a geographical area that supports a large proportion of the world population (Guinet *et al.* 1995). The low population growth rates observed in 2003, 2006 and 2007 can be interpreted in the light of the functional processes by which warm events impact life history traits (*e.g.* Le Bohec *et al.* 2008a; Saraux *et al.* 2011a). Despite these sporadic decreases and a slight declining trend since 2002/2003, the king penguin population of 'La Grande Manchotière' has remained stable throughout the study period, *i.e.* the first decade of the 21st century. The two-year lag that characterizes the response of penguin life history traits to environmental change can be explained by the indirect effect of environmental conditions on top predators: a delayed recruitment of copepods grazing on phytoplankton (Fraser & Hofmann 2003) affects, with an additional time lag, the recruitment, growth and abundance of prey feeding on them and foraged at a specific size by king penguins. This upward cascade of effects combined with delayed reproductive costs in terms of future survival (linked to the particular up to 1-year breeding cycle of the king penguin, see Le Bohec *et al.* 2008a) might ultimately impact the population growth rate with a 2-year lag. Such a temporal lag effect is common in marine ecosystems (see refs in Durant *et al.* 2009). Hjermann *et al.* (2004) showed for instance how temperature and a global climate index (North Atlantic Oscillation, NAO) may indirectly affect the population dynamics of capelin*Mallotus villosus* in the Barents Sea with a 1 to 2-year lag by influencing the reproduction of herring and cod. Also, Thompson and Ollason (2001) showed that climate effects (NAO) require 5 years to be seen in northern fulmar *Fulmarus glacialis* population changes in the North Atlantic due to delayed maturity. In 2005, Sandvik and his colleagues confirmed with a meta-analysis that the presence of time lags in the NAO effect on North Atlantic seabird community is relatively common. In accordance with the life history theory and most of the previous studies in long-lived species, the population growth rate of king penguins appears to be more sensitive to changes in survival than in reproductive success (Stearns 1992; Saether & Bakke 2000). But less usual, our study reveals that in addition to adult survival, the population growth rate of these penguins is highly sensitive to changes in survival of juveniles (between their first year at sea and the mean age at first breeding, *i.e.* 2 to 5-year old). Very few studies, especially in birds, have demonstrated that traits related to early life stages (sub-adult survival and recruitment) also have a major impact on population growth rate (Oli & Armitage 2004). Information on immature individuals is difficult to obtain in the wild and the weight given to the adult subset of populations in the dynamics of long-lived species population might well be an artifact of a lack of information. The importance of stressors on early life stages has generally been considered as negligible (Barbraud & Weimerskirch 2001), with exceptions such as in Kitaysky *et al.* (2006). Methodological biases should obviously be avoided to properly assess datasets and perform robust analyses on population dynamics. In accordance with our preliminary data (Gauthier-Clerc *et al.* 2004), survival estimates of our non-banded micro-tagged chicks during the first year at sea is approximately twice as large as that reported in previous study on flipper-banded chicks (83.4% *vs* 40.3 – 51.1% in Weimerskirch *et al.* 1992). Contrary to previous results based on flipper-band, the proportion of birds attempting to breed at a given age is higher than the ones obtained with flipper-banded birds (6.1% *vs* 4.8% at 3-year old, 39.5% *vs* 6.6% at 4-year old and 64.5% *vs* 38.2% at 5-year old, see Weimerskirch *et al.* 1992). Also, by demonstrating that for adult king penguins (Gauthier-Clerc *et al.* 2004) the detrimental effect of flipper-banding on their breeding success and survival, and its interaction with climate on their life-history traits, we recommend that studies predicting future population trajectories with regard to changes in climate should seriously reconsider the biases associated with the use of flipper-banded birds (Saraux *et al.* 2011a).

There is growing evidence that climate change will become one of the major drivers of species extinction in the 21st century. To evaluate the extinction risk of populations of king penguins breeding on Crozet Archipelago, we used several projections of future warming from climate models given by the latest IPCC Fourth Assessment Report (2007). Using these climate-warming scenarios, we show that the study population may be under threat within 45 and 85 years from now. Considering the clear and rapid extinction risk that our data show for non-banded king penguins of known age, it is also very likely that despite being based on flipper-banded birds the prediction of Jenouvrier *et al.* (2009) that emperor penguin colonies will also decline dramatically by 2100 remains reasonable. Behavioral adjustment is a way to cope rapidly with a changing environment, without the necessity of permanent genetic changes (Charmantier *et al.* 2008). In addition to the phenotypic plasticity, microevolution on phenotypic traits might also provide the potential for organisms to respond effectively to environmental changes (Nussey *et al.* 2005). By testing the effect of reproducing every second year (a breeding strategy that occurs more frequently in some colony, see Stonehouse 1960) or starting to reproduce earlier, we demonstrated that these behavioral adaptations would delay the extinction of the king penguin population on Crozet (potential respite of less than a decade). This result substantiates that micro-evolutionary processes through natural selection improvements to fitness can influence population trajectories. Despite Crozet Archipelago alone supports the majority of king penguins, the predictions of the extinction risk are still obtained using information at a local scale. Therefore, in addition to the phenotypic and/or genotypic adaptability as referred above, we should also consider potential migration patterns (*i.e.* emigration) in response to modifications of their altered environment, and future sub-Antarctic type environments that would become available in the fast-melting Antarctic continent. Our knowledge on movements between king penguin colonies is poor due to logistical difficulties, thus revealing a need for more investigation in the future. Nevertheless, king penguins seem to have a poor ability to disperse to or to colonize a new (and possibly more suitable) range of habitats (Weimerskirch *et al.* 1992), which weights towards the vulnerability of this species. Moreover, the scarcity of Sub-Antarctic islands limits the possibility of settlement in new favorable habitats. Both extrinsic environmental factors and intrinsic demographic processes may have profound effects on population dynamics and extinction risk. The next step is to gauge the potential relevance of evolution to population dynamics and persistence by combining demographic matrix modeling and selection analyses (Schoener *et al.* 2011).

King penguins are specialist predators that mostly forage on myctophid fish but also on squids (Cherel & Ridoux 1992), making them more sensitive to change in their prey abundance and availability than are generalists that can switch to alternative prey (Pierotti & Annett 1990). Rapid changes in the environment would favor generalist/adaptable species and be detrimental to specialized species with a narrow trophic niche (Crick 2004). Myctophidae is the second major resource of the Southern Ocean after Antarctic krill in terms of biomass (Lubimova & Shust 1987) and are the major predators of zooplankton (Pakhomov *et al.* 1996). King penguins can be used as indicators of environmental changes in Southern Ocean ecosystems as they integrate alterations occurring at lower levels of the food chain (see Durant *et al.* 2009). In addition to its effects on oceanic processes (*i.e.* front positions, sea ice extent) and the spatio-temporal availability of seabird prey, climate change can disrupt interspecific interactions (*e.g.* krill-myctophids, myctophids-penguins). It is therefore necessary to investigate potential top-down effects of a reduction in penguins on the lower levels of the food chain. Inother words, will the decline or extinction of king penguin predation pressure propagate to the whole food chain in a cascade? Trophic cascades are not uncommon and the drastic effects of predator removal are well studied (see example in Sala & Sugihara 2005). For example, the reduction of sea otters led to the elimination of the kelp forest by the sea urchin, freed from predation by the otters (Estes *et al.* 1998). The functioning of the Southern Ocean still remains poorly understood and the effects of the predicted decline of king penguins at Crozet will require particular attention.

Extinction risk is a critical area of investigation for contemporary ecologists and conservation biologists, and practical conservation efforts for vulnerable species can be considerably enhanced by thoroughly understanding the ecological processes that interact to determine species persistence/extinction. In that context, our study underlines that while the King penguin is still currently classified as ‘Least Concern’ in the IUCN Red List of Threatened Species (International Union for Conservation of the Nature 2008, IUCN 2008), the situation of king penguins appears to be alarming under the ongoing global climate change patterns, considering that the Crozet Archipelago hosts about two thirds of the global taxon and that the extinction risk of this population is extremely high within a very short time-period according to our results. Using IUCN criterions (IUCN 2008), the King penguin should be listed as 'Vulnerable' (projected population size reduction of ≥ 30% within a three generation period, *i.e.* 39 years in our case (see Saether *et al.* 2005 for generation time estimation) and 'Endangered' (≥ 50%) from year 2047 according to the global warming projection forecasted by the IPCC and adjusted with the current warming trend observed in the Crozet area. However, political and administrative acceptance of conservation status is first needed to be able to implement an effective action plan for sensitive species. Among them, long-lived species need particular attention, because they are more susceptible to strong climate forcing due to their life-history characteristics (*i.e.* late maturity and high generation time, sensitivity of adult and immature survivals, low fecundity, *etc.*). Populations of long-lived species can severely be reduced by extreme climatic events, and an increase in frequency and/or intensity of these events may affect the population persistence in a shorter term than is currently expected by conservation agencies, possibly highlighting the need to redefine their criteria to flag species at risk by taking into account the compelling frenzied pace of current climate changes.

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Supplementary references

B. Charlesworth, *Current Biology* **4**, 1146 (1994).

P. N. Trathan, J. Forcada, E. J. Murphy, *Philos Trans R Soc Lond B* **362**, 2351 (2007).

G. Duhamel, P. Koubbi, C. Ravier, *Polar Biol* **23**, 106 (2000).

S. A. Henson *et al.*, *Biogeosciences* **7**, 621 (2010).

R. Altwegg, S. Dummermuth, B. R. Anholt, T. Flatt, *Oikos* **110**, 55 (2005).

D. O. Hjermann, N. C. Stenseth, G. Ottersen, *Mar Ecol Prog Ser* **273**, 229 (2004).

P. M. Thompson, J. C. Ollason, *Nature* **413**, 417 (2001).

H. Sandvik, K. E. Erikstad, R. T. Barrett, N. G. Yoccoz, *J Anim Ecol* **74**, 817 (2005).

A. S. Kitaysky, E. V. Kitaiskaia, J. F. Piatt, J. C. Wingfield, *Proceedings of the Royal Society B-Biological Sciences* **273**, 445 (2006).

R. Pierotti, C. A. Annett, *BioScience* **40**, 568 (1990).

H. Q. P. Crick, *Ibis* **146**, 48 (2004).

E. Sala, G. Sugihara, in *Aquatic food webs: an ecosystem approach,* A. Belgrano, U. M. Scharler, J. Dunne, R. E. Ulanowicz, Eds. (Oxford University Press, Oxford, 2005), pp. 170-183.

B. E. Saether *et al.*, *Nature* **436**, 99 (2005).

Y. Cherel, H. Weimerskirch, *Marine Ecology-Progress Series* **188**, 93 (1999).

A. J. Richardson, H. M. Verheye, *J Plankton Res* **20**, 2379 (1998).

R. Choquet, A. M. Reboulet, R. Pradel, O. Gimenez, J. D. Lebreton, *Animal Biodiversity and Conservation* **27**, 207 (2004).

R. Choquet, L. Rouan, R. Pradel, *Environmental and Ecological Statistics* **3**, 845 (2009).

R. Choquet, J. D. Lebreton, O. Gimenez, A. M. Reboulet, R. Pradel, *Ecography* **32**, 1071 (2009).

R. Pradel, *Biometrics* **61**, 442 (2005).

T. H. G. Ezard, T. Coulson, *Ecol Model* **221**, 191 (2010).

H. Caswell, *Ecol Model* **46**, 221 (1989).

C. M. Hunter *et al.*, *Ecology* **91**, 2883 (2010).

S. N. Wood, N. H. Augustin, *Ecol Model* **157**, 157 (2002).

D. Oro, J. S. Aguilar, J. M. Igual, M. Louzao, *Biol Conserv* **116**, 93 (2004).

L. W. Traill, C. J. A. Bradshaw, B. W. Brook, *Biol Conserv* **139**, 159 (2007).

R. Frankham, *Genetical Research* **66**, 95 (1995).

P. J. Green, B. W. Silverman, *Nonparametric Regression and Generalized Linear Models: a Roughness Penalty Approach*. (Chapman and Hall/CRC, London, New York, 1994).

APPENDIX 4: Résumé de la thèse en français

Si à l'échelle des temps géologiques, la température moyenne de la Terre a connu de très importantes variations, la réalité du changement climatique actuel semble sans équivoque. De plus, quel que soit le scénario économique envisagé, ce réchauffement global devrait se poursuivre dans les siècles à venir, avec une augmentation de la température moyenne du globe d'au moins 0,2°C par décennie d'après le dernier rapport du Groupe Intergouvernemental d'Experts sur l'Evolution du Climat (GIEC) en 2007. Toutes les espèces, animales comme végétales, doivent donc faire face à une nouvelle pression de sélection et la planète semble aujourd'hui traverser la sixième grande crise d'extinction des espèces. Nous savons déjà qu'un grand nombre de systèmes biologiques différents sont affectés par les perturbations liées aux changements environnementaux. Il reste néanmoins difficile de mettre en relation ce changement climatique et les bouleversements observés dans bon nombre d'écosystèmes en raison de la complexité de ces écosystèmes, mais aussi de problèmes méthodologiques (manque de données à long terme, difficulté de séparer les effets propres du climat de ceux d'autres activités anthropiques tels que la modification des habitats ou la surexploitation). Il est donc capital d'augmenter nos connaissances sur l'effet du changement climatique sur la biodiversité, cela afin de prédire l'impact des changements futurs sur la dynamique et la persistance des populations. Ceci est d'autant plus vrai pour les écosystèmes marins, écosystèmes pour lesquels le manque d'informations est le plus grand d'après le dernier rapport du GIEC, et ce alors même que les océans couvrent 71% de la surface du globe et jouent un rôle clé dans la régulation du climat. Aussi, apparaît-il primordial d'accroître les connaissances scientifiques concernant les effets potentiels du climat sur les écosystèmes marins. Plus particulièrement, l'océan Austral, véritable « laboratoire grandeur nature » pour étudier les changements climatiques selon Le Quéré, semble être un endroit idéal pour répondre à ses questions. En effet, il se situe à la confluence des autres océans du globe excepté l'océan Arctique, et toute perturbation climatique se produisant dans l'un de ces océans sera donc détectable dans l'océan Austral. Par ailleurs, l'hétérogénéité régionale du changement climatique se traduisant par des changements plus marqués au niveau des pôles, les écosystèmes de l'océan Austral, océan le plus productif au monde, pourraient être plus fortement touchés.

Dans ce travail de thèse, nous avons examiné l'impact du climat sur les écosystèmes de l'océan Austral au travers des manchots, prédateurs supérieurs répartis autour de cet océan sous des latitudes très différentes. De part leur position au sommet de courtes chaînes trophiques, les manchots constituent en effet d'excellents bio-indicateurs des perturbations de leurs écosystèmes marins puisqu'ils intègrent rapidement toute modification intervenant aux niveaux trophiques inférieurs. Nous avons réalisé un état des connaissances sur le sujet au travers d'un premier article de synthèse bibliographique (**Article 1**, Ropert-Coudert, Saraux & Kato in revision). A la suite de ce travail, l'étude de trois espèces différentes (manchots pygmées, *Eudyptula minor*, en Australie, manchots royaux, *Aptenodytes patagonica*, sur l'archipel de Crozet et manchots Adélie, *Pygoscelis Adeliae*, en Terre Adélie) nous a permis d'étudier la plasticité comportementale et populationnelle de ces différentes espèces face aux changements climatiques en fonction de la latitude. Ainsi nous avons tenté dans un premier temps d'approfondir les connaissances sur l'écologie de ces trois espèces, avant d'étudier l'impact des changements environnementaux sur leurs différents traits d'histoire de vie (ex. survie juvénile et adulte, reproduction, *etc.*).

Pour cela, un suivi à long-terme de nombreux individus est essentiel. Or, nous avons montré que les bagues alaires, majoritairement utilisées chez les manchots, entraînent une diminution importante et à long-terme de la survie et du succès reproducteur chez le manchot royal, biaisant ainsi l'étude de l'impact du climat sur les populations (**Article 2**, Saraux *et al.* 2011 Nature). Un système de détection automatique des manchots par RFID (Radio-Frequency Identification) similaire pour les trois espèces, nous a permis de (ré-)évaluer les paramètres démographiques des espèces étudiées ainsi que l'effet du climat sur ces derniers, tout en minimisant la perturbation des animaux.

La survie juvénile est un paramètre rarement étudié et pourtant capital dans la dynamique des populations. Une étude conduite sur 10 ans et plus de 2500 manchots royaux nous a permis de montrer que le taux de retour d'individus juvéniles à la colonie est bien supérieur à ce qui avait été précédemment évalué à l'aide de bagues alaires (77% *vs.* 5 à 39%), ce qui est synonyme d'une survie juvénile très élevée, proche de celle des adultes (**Article 3**, Saraux *et al.* 2011, PLoS ONE). Chez le manchot Adélie, les taux de retour des juvéniles semblent là aussi dépasser les 70%, estimation bien supérieure à ce que l'on connaissait (étude en cours, Saraux *et al.*). De plus, nous avons constaté que la survie juvénile des manchots royaux augmente avec la température de la mer (**Article 3**, Saraux *et al.* 2011, PLoS ONE), par opposition à la survie adulte et au succès reproducteur de cette espèce qui sont négativement affectés par le climat.

Le succès reproducteur des espèces dépend notamment des stratégies d'investissement parental utilisées. Si tous les manchots semblent présenter des stratégies similaires, avec la nécessité d'un élevage biparental pendant la quasi-totalité de l'élevage, nous avons montré que chez le manchot pygmée cet investissement n'est pas égalitaire puisque dans la majeure partie des couples l'un des deux parents revient plus souvent nourrir les poussins et leur procure en outre des repas plus importants (**Article 4**, Saraux *et al.* 2011 Behavioral Ecology). Cette différence entre les deux parents n'étant ni liée au sexe des individus ni à leur âge, et semblant être consistante au cours de leur vie, nous suggérons que ceci est le reflet de la différence de qualité entre deux parents. La différence observée s'atténue les années où les conditions sont favorables, laissant penser que le climat a un effet non négligeable sur l'investissement parental, et cela tout particulièrement pour le parent de moins bonne qualité (**Article 4**, Saraux *et al.* 2011 Behavioral Ecology). Chez ce même manchot pygmée, nous avons trouvé que le succès reproducteur est faiblement affecté par les moyennes saisonnières des températures de la mer, contrairement aux manchots royaux. Toutefois, une question d'échelle temporelle à laquelle l'effet du climat doit être étudié sur cette espèce se pose, puisqu'une une faible période (quelques semaines) défavorable est susceptible de mettre à mal la saison de reproduction dans sa totalité (**Article 5**, Saraux *et al.* in prep).

Enfin, nous avons également mis en évidence une relation entre la température de surface de la mer et le sexe ratio à l'envol des manchots royaux (**Article 6**, Bordier, Saraux *et al.* in prep). Les manchots étant des espèces monogames (au moins à l'échelle de la saison de reproduction), le sexe ratio de la population reproductrice doit être équilibré pour être optimal, condition nécessaire pour que tous les individus de la population puissent se reproduire. Or nous avons montré que plus la température de la mer est chaude plus le sexe ratio est biaisé, laissant craindre une éventuelle déviation de l'équilibre de la population avec le réchauffement prévu. Une telle déviation pourrait avoir des conséquences importantes sur la dynamique des populations, soit en poussant le sexe surnuméraire à émigrer soit en empêchant une partie de la population de se reproduire, diminuant ainsi le succès global de la population à se renouveler. La dispersion (ou émigration) est un paramètre peu ou pas étudié chez les manchots par manque de méthodologie adaptée mais qui pourrait jouer un rôle important dans la persistance des populations (*e.g.* échange génétique pour éviter la consanguinité, possibilité d'aller dans des zones moins affectées par le climat). Il serait donc très intéressant d'utiliser des modèles de capture- recapture multi-états dans le futur à l'aide de données récoltées par des systèmes automatiques de détection mis en place dans différentes zones. Des analyses génétiques des populations pourraient également être source de précieuses informations sur ce sujet.

La connaissance des traits d'histoire de vie d'une espèce et de leur réponse au climat permet par ailleurs de réaliser des modèles populationnels et de projeter l'évolution d'une population en relation avec des scénarios prédictifs du climat (scénarios du GIEC). Ainsi, la colonie de manchots royaux étudiée (contenant actuellement plus de 20 000 couples de manchots royaux) serait passible d'extinction dans les 200 prochaines années. Toutefois, ces prévisions présupposent que les manchots vont répondre au climat dans le futur de la même manière qu'ils ont répondu dans le passé. Il est donc nécessaire d'étudier également les possibles adaptations des manchots face à ce changement climatique. A contrario de la plupart des crises précédentes, la crise actuelle ne s'étale pas sur des milliers ou des millions d'années mais sur quelques siècles tout au plus, mettant la capacité d'adaptation des espèces à rude épreuve et ce d'autant plus chez des espèces longévives comme les manchots. En conséquence, des mécanismes évolutifs non-génétiques permettant l'adaptation d'une espèce sur un laps de temps court vont avoir une importance prédominante dans le devenir des populations animales actuelles. La plasticité phénotypique, ou encore la possibilité qu'un même génotype puisse conduire à différents phénotypes sous l'effet de l'environnement, et qui englobe la plasticité comportementale des espèces est susceptible de jouer un rôle important.

Nous avons étudié ce dernier paramètre au travers des stratégies alimentaires des parents pendant l'élevage des poussins. Alors que les espèces se nourrissant près de la côte sont généralement supposées comme étant moins flexibles, nous avons montré que le manchot pygmée est capable d'adapter la durée de ses voyages alimentaires à sa condition corporelle. Ainsi, les manchots pygmées alternent entre des voyages courts destinés à alimenter les poussins le plus fréquemment possible et des voyages longs, initiés lorsque leur masse corporelle est faible et ayant pour but de reconstruire leurs réserves (**Article 7**, Saraux *et al.* 2011 Ecology). Les conditions en mer affectent la proportion de voyages courts réalisés par les parents et ainsi la croissance et la survie du poussin, mais ce choix devrait permettre au manchot pygmée de ne pas compromettre sa survie.

Inversement, le manchot royal, espèce se nourrissant au large loin de la côte, semble présenter peu de flexibilité dans ses stratégies alimentaires. En effet, le cycle reproducteur de cette espèce est composé de trois grandes parties, une première pendant l'été où le poussin est nourri de façon relativement fréquente, une seconde pendant l'hiver où le poussin est très peu nourri et une dernière au printemps suivant où le poussin est à nouveau fortement nourri avant de prendre son envol. Le nombre de nourrissages effectués pendant chacune de ces 3 périodes varie en fonction des années et des conditions. En revanche les périodes auxquelles le nombre de nourrissages diminue en début ou ré-augmente en fin d'hiver semblent fixes (**Box 2**, Saraux *et al.* in prep).

Au cours de ce travail de thèse nous avons pu montrer que de nombreux traits d'histoire de vie des manchots sont affectés par le climat. En revanche, il existe une grande variabilité des réponses à l'échelle inter-spécifique mais aussi intra-spécifique entre les traits considérés. Par exemple, alors qu'une augmentation de température de la mer conduit à une diminution du succès reproducteur et de la survie chez les manchots royaux adultes, elle induit une augmentation des taux de survie des juvéniles. Cet effet différentiel de l'environnement en fonction des stades de vie rend compte de la complexité de l'étude et de la modélisation de l'impact des changements globaux sur les organismes vivants.

Les manchots sont souvent considérés comme de bons indicateurs de leurs écosystèmes de part leur position en bout de chaîne trophique. Néanmoins, une grande partie de l'effet du climat observé sur les manchots correspond à des effets indirects (visibles notamment par le délai entre les changements de l'environnement physique et les conséquences sur les individus). Pour mieux comprendre les mécanismes sous-jacents de l'impact du climat sur cette famille d'oiseaux inféodés au milieu marin, il semble donc indispensable d'étudier dans le futur l'effet du climat à la fois sur les maillons trophiques inférieurs, et sur les relations inter-trophiques.

La réponse contrastée observée chez le manchot royal mène tout de même à des prévisions de disparition de cette population dans les deux siècles à venir. Face à de tels résultats, une question revient sans cesse, « quel rôle doit-on jouer en tant que scientifique ? ». Dans un premier temps, il paraît indispensable de revoir la classification proposée par l'UICN afin d'augmenter le niveau de vulnérabilité des manchots. Il semble également important d'utiliser les outils législatifs développés récemment et d'instaurer des zones d'aires marines protégées en accord avec la biologie des espèces concernées. Par exemple, dans notre cas, toute la difficulté consisterait à étendre les zones protégées à celles réellement utilisées par les manchots lors de leurs voyages alimentaires en mer (zones pouvant s'étendre sur plusieurs centaines voire milliers de kilomètres, les manchots se nourrissant loin de leurs colonies) tout en s'assurant des moyens de protection efficaces (réserves naturelles terrestres et marines intégrales).

Global warming is now hardly a disputable matter. The rapid changes in climate are unequivocal and foreseen to continue drastically within the next centuries, profoundly affecting the biological component of our planet. As the 6th mass extinction crisis is looming, it is becoming urgently necessary to increase our understanding of ecosystems and their responses to climate change. This is especially true for the poorly known yet important marine ecosystems. Covering most of the Earth's surface, oceans are indeed key actors in climate regulation, and the responses of their ecosystems to climate change have been insufficiently studied. In particular, due to its geographical location at high latitudes which makes it strongly prone to the effects of climate, and due to its connectivity with all the other major oceans of the Earth, understanding how climate change might affect the remote Southern Ocean is a scientific priority.

In this thesis, we investigated the effects of climate on Southern Ocean ecosystems through the monitoring of their emblematic top-predators: the penguins. As top-predators, penguins are considered good indicators of their environment as they integrate the effects of climate which occur at every level of the food chain. The present work relied on data collected over several years on three penguin species (little penguins, king penguins and Adélie penguins) using automatic monitoring systems based on Radio-Frequency-IDentification, that we suggest to be a relatively harm-free method for monitoring individual penguins over the long-term.

We found juvenile survival in king penguins to be higher than previously thought and close to adult survival rate. Surprisingly, it increased in years of high sea surface temperature (SST), indicating contrasted effects of climate on king penguins depending on the life-history trait considered. SST has also been shown to possibly bias the sex ratio of king penguin fledglings, which may affect in return the population dynamics. The study of different species enabled us to highlight the importance of the time-scale at which the effect of climate is investigated and the necessity of adapting it to the species biology. For instance, in little penguins chick mortality was concentrated on some weeks, underlining the dependence of reproductive success on punctual conditions, probably due to the low reserves accumulated by the chicks. Finally, we also show the importance of taking into account individual heterogeneity and quality, leading to consistent differences in parental effort in little penguins and in the ability to face different sea-ice conditions in Adélie penguins. Such inter-individual differences along with the flexibility exhibited in some behaviour (such as foraging in little penguins) may help penguins to adapt to new environmental pressures through phenotypic plasticity, though the rapidity and strength of climate change under these latitudes leave little hope for these long-lived animals.

Keywords: climate change, juvenile survival, life-history traits, penguins, reproduction, seabirds, Southern Ocean ecosystems