Thèse présentée pour obtenir le grade de
Docteur de l'Université Louis Pasteur Strasbourg I
Discipline: Sciences du Vivant

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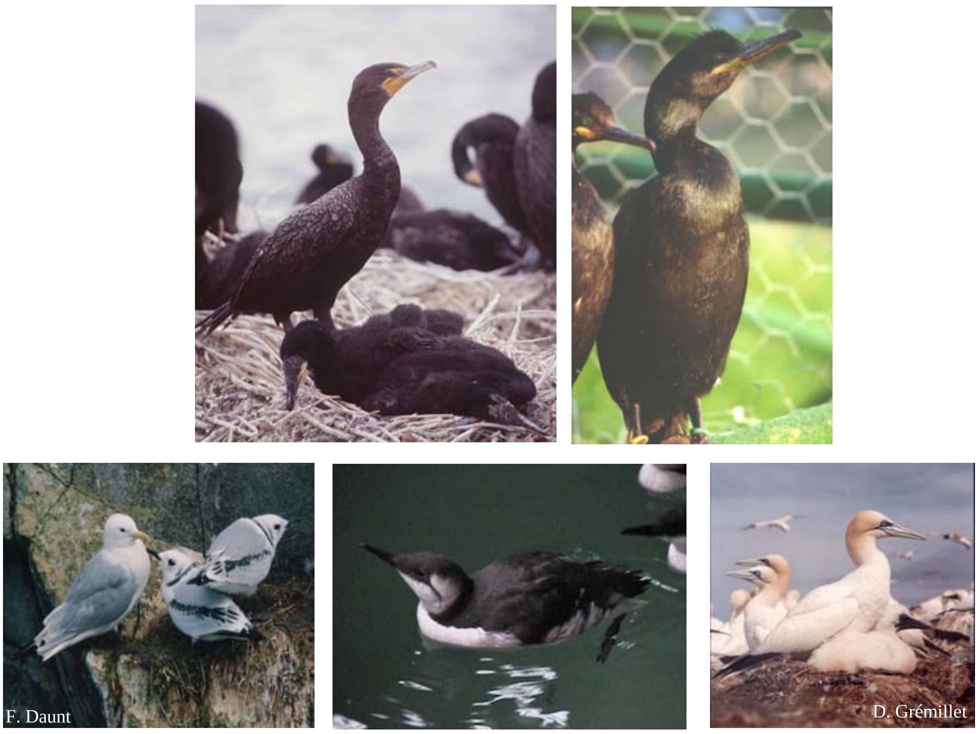
Diving energetics and fine scale foraging behaviour of avian divers and their capacity to buffer environmental change

Etude des besoins énergétiques et des tactiques prédatrices des oiseaux plongeurs ainsi que de leur capacité d'adaptation aux changements environnementaux



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Résumé

Les oiseaux marins sont présents sur toutes les mers du globe et dans des zones climatiques extrêmement différentes, allant des tropiques jusqu’aux régions polaires. Un grand nombre d’espèces vivent en haute mer et capturent leurs proies sous l’eau. L’élément liquide possède un énorme pouvoir de refroidissement et génère de fortes contraintes thermiques sur ces homéothermes. Ces contraintes ont certainement influencé les modes de colonisation des écosystèmes aquatiques par les oiseaux marins. Dans ces milieux hostiles, les oiseaux assurent leur survie par le biais de deux stratégies (non exclusives). (1) Augmentation de l’isolation périphérique afin de minimiser les pertes de chaleur au contact de l’eau; (2) exploitation de zones riches en nourriture afin de maximiser leurs gains d’énergie au cours de la recherche alimentaire. La combinaison de ces deux stratégies permet l’optimisation de l’efficacité énergétique au cours de la recherche alimentaire.

Afin de comprendre comment les oiseaux marins se sont adaptés au milieu aquatique au cours de leur trajectoire évolutive et de définir leur rôle au sein des écosystèmes actuels, il est donc de toute première importance d’étudier les mécanismes qui régissent leurs dépenses énergétiques ainsi que leurs gains en énergie au cours de la recherche alimentaire.

Au cours des deux dernières décennies, les avancées technologiques ont permis la réalisation d’un grand nombre d’études concernant le comportement alimentaire des oiseaux marins ainsi que leurs besoins énergétiques. Ces deux volets ont pourtant rarement été considérés conjointement et certains aspects fondamentaux restent négligés. Par exemple, l’effet de la pression sur l’isolation thermique et sur la flottabilité des oiseaux plongeurs, ainsi que ses conséquences sur les coûts énergétiques de la plongée n’ont pas encore été mesurés directement. En outre, le comportement prédateur des oiseaux plongeurs a principalement été déduit de mesures effectuées par des capteurs embarqués. Des observations directes et détaillées des techniques de pêche ainsi que des études de l’impact de divers facteurs biotiques et abiotiques sur ces stratégies restent extrêmement rares.

Le comportement des oiseaux marins est d’autre part principalement étudié à l’échelle de l’individu. Il est cependant nécessaire et urgent de prédire les réactions des communautés d’oiseaux marins aux changements environnementaux, qu’ils soient d’origine naturelle ou anthropique. Ces stress environnementaux provoquent en effet à l’heure actuelle des changements de régime et de structure variés au sein des écosystèmes marins. Des informations détaillées concernant les processus d’acquisition et de dépense d’énergie chez différentes espèces d’oiseaux marins constituent donc la base de modèles bio-énergétiques qui

permettront une approche fonctionnelle prédictive du rôle des oiseaux marins au faîte des réseaux trophiques aquatiques. La collecte de données écophysiologiques ainsi que leur synthèse dans le cadre d'exercices de modélisation, nous permettra donc de juger de la capacité d'adaptation des prédateurs marins aux changements environnementaux (tels qu'une baisse de la disponibilité des proies).

Mes travaux de thèse, qui traitent de l'écophysiologie de la recherche alimentaire chez les oiseaux plongeurs ont principalement concerné les cormorans. Des études récentes ont suggéré que les coûts de la recherche alimentaire sont particulièrement élevés chez ces oiseaux, mais que ceux-ci adaptent leur comportement prédateur afin de minimiser la durée totale de la recherche alimentaire (par le biais d'une augmentation de l'efficacité prédatrice). Cette stratégie nécessite l'exploitation de ressources alimentaires particulièrement profitables (forte densité des proies et/ou grande valeur calorifique). On peut donc prédire que les cormorans seront particulièrement sensibles aux contraintes environnementales affectant les conditions de la recherche alimentaire et/ou la disponibilité des proies. Ce sont donc d'excellents modèles d'étude de l'impact de ce type de changements sur les prédateurs marins.

Mes travaux de thèse s'articulent en sept chapitres. A l'issue d'une introduction générale (chapitre 1), je présente deux études de la dépense énergétique associée à la recherche alimentaire chez les oiseaux plongeurs (chapitres 2 et 3). Plus spécifiquement, j'ai étudié l'influence de la température de l'eau, de la profondeur des plongées ainsi que du statut nutritif des oiseaux sur les coûts énergétiques de la plongée chez les cormorans huppés (*Phalacrocorax aristotelis*) et les cormorans à aigrettes (*Phalacrocorax auritus*). Je détaille par la suite les comportements associés à la recherche alimentaire chez les oiseaux plongeurs (chapitres 4 et 5). Il s'agit d'une analyse détaillée des techniques de capture des poissons chez les cormorans à aigrettes et les grands cormorans (*Phalacrocorax carbo*) en fonction de divers paramètres biotiques et abiotiques. Enfin, je combine certains de ces résultats avec des données tirées de la littérature afin de développer un modèle bio-énergétique (chapitre 6). Ce modèle, élargi à quatre espèces d'oiseaux marins de la Mer du Nord, m'a permis de calculer leurs besoins alimentaires théoriques pendant la phase d'élevage des poussins. Il m'a également permis de tester la capacité d'adaptation de ces différentes espèces à une baisse de la disponibilité de leurs proies principales. Ces diverses études débouchent sur des conclusions et perspectives qui sont présentées dans le chapitre 7.

Dépense énergétique au cours de la plongée chez les cormorans (chapitres 2 et 3)

Dans un premier temps (chapitre 2), j'ai mesuré le métabolisme de base (BMR) de cormorans huppés au repos à terre, à la surface de l'eau et au cours de la plongée en eau peu profonde (1 m) par calorimétrie indirecte. Les coûts de la plongée ont été déterminés en fonction de la température de l'eau et du statut nutritif des oiseaux. Au cours d'une seconde étude (chapitre 3), j'ai mesuré les mêmes paramètres chez les cormorans à aigrettes, mais j'ai aussi étudié l'effet de la profondeur des plongées sur la dépense énergétique. Chez ces deux espèces, j'ai également enregistré la température abdominale au cours de la plongée (au moyen d'enregistreurs miniaturisés), afin de détecter d'éventuels phénomènes d'hypothermie permettant de réduire la dépense énergétique. Ces études ont montré que les coûts de la plongée en eau peu profonde sont nettement plus faibles chez les cormorans huppés et les cormorans à aigrettes que chez les grands cormorans (*P. carbo*) et qu'ils sont comparables à ceux d'autres oiseaux plongeurs à propulsion postérieure. Je montre par ailleurs que les coûts de la plongée augmentent avec la profondeur, mais que cette augmentation est moins importante que le suggéraient des modèles thermodynamiques. Des baisses de la température de l'air au cours du repos, et de la température de l'eau au cours du repos et de la plongée, induisent également une augmentation significative de la dépense métabolique. La prise alimentaire entraîne d'autre part une augmentation de la dépense énergétique de 13-15% pendant 5 heures au maximum chez les cormorans huppés, et de 5-8% pendant 2 heures chez les cormorans à aigrettes. La température abdominale augmente significativement chez les deux espèces au cours de la plongée. Les phénomènes d'hypothermie sont donc exclus. La température abdominale est plus basse au moment du repos de jour et minimale au cours du repos de nuit.

Techniques de pêche chez les cormorans (chapitres 4 et 5)

Il est difficile de juger de l'impact des changements environnementaux sur les communautés d'oiseaux marins. La pêche industrielle affecte entre autre la disponibilité des proies, mais nous ne savons pas comment des prédateurs tels que les oiseaux marins réagiront à ces changements. J'ai testé l'hypothèse selon laquelle les oiseaux marins augmentent leur effort de recherche alimentaire en fonction de la densité des proies, ainsi que l'existence d'une valeur seuil en deçà de laquelle la recherche alimentaire n'est plus rentable. Une étude de ce type est techniquement difficile dans des conditions de terrain, j'ai donc choisi une approche en milieu confiné permettant de contrôler un maximum de paramètres. J'ai utilisé un système de vidéo sous-marine afin d'analyser le comportement de prédation de cormorans à aigrettes sur des truites arc-en-ciel (*Oncorhynchus mykiss*) dans une fosse à plongeur (chapitre 4). Les techniques de capture des proies ont été analysées en fonction de la disponibilité des proies (densité par unité de volume), de leur taille, de leur comportement, des niveaux de luminosité, de la température de l'eau, de la profondeur et de la condition corporelle des oiseaux. J'ai montré que la densité des proies avait l'effet le plus marqué sur la performance prédatrice des cormorans (relation linéaire). De plus, une baisse de la densité des proies entraînait une augmentation du temps alloué à la recherche alimentaire, ainsi qu'une baisse de la proportion des plongées au cours desquelles des proies ont été poursuivies. Ces deux dernières relations ne sont pas linéaires, les changements deviennent exponentiels en deçà d'une densité seuil de 2 $g \cdot m^{-3}$. Mes résultats indiquent également que le comportement des proies influence le succès prédateur des oiseaux. Celui-ci baisse de manière significative en présence d'un banc de poissons (40,5 % de succès pour un individu au sein d'un banc et 70,8 % pour un individu isolé). Les oiseaux mettaient également plus de temps à capturer un individu issu d'un banc qu'un individu seul (10,2 s contre 5,2 s). La taille des proies, la profondeur de l'eau, les conditions de lumière, la température de l'eau et la condition corporelle des oiseaux n'avaient pas d'influence significative sur la performance prédatrice des oiseaux, tout du moins pour l'éventail des conditions biotiques et abiotiques considérées au cours de cette étude. Par la suite j'ai combiné mes résultats concernant le comportement de capture des proies chez les cormorans à aigrettes avec des données similaires enregistrées chez des grands cormorans chinois (chapitre 5). Ces cormorans apprivoisés ont été munis de caméras miniaturisées qui ont permis de les filmer au cours de la nage sub-aquatique et de la capture des proies. Les données recueillies ont montré que les deux espèces de cormorans concernées ne sont pas aussi efficaces que prévu : presque la moitié des attaques effectuées sur des poissons sont avortées ($n = 676$). Nous montrons cependant qu'une très faible proportion (0.4%) des poissons sont blessés sans être consommés par les cormorans. Ces résultats sont importants pour la gestion des populations de grands cormorans en Europe et de cormorans à aigrettes en Amérique du Nord, car ces oiseaux sont accusés de blesser un grand nombre de proies sans pour autant les manger.

Modélisation de l'impact de la disponibilité des proies sur les communautés d'oiseaux marins (chapitre 6)

Le dernier volet de ma thèse (chapitre 6) détaille un modèle bio-énergétique qui permet le calcul des besoins alimentaires des cormorans huppés, des guillemots de Troïl (*Uria aalge*), des fous de Bassan (*Morus bassanus*) et des mouettes tridactyles (*Rissa tridactyla*) pendant la période d'élevage des jeunes en Ecosse. J'ai utilisé les budgets-temps/activités des oiseaux (obtenus à partir de données enregistrées avec des appareils électroniques fixés sur des adultes reproducteurs en mer) et le coût métabolique associé à chaque activité (estimé soit à partir de mesures faites dans cette étude, soit à partir de données publiées dans la littérature) pour calculer la quantité de nourriture journalière nécessaire (DFI) à ces oiseaux. J'ai aussi estimé le taux de capture de proies (*catch per unit effort*, CPUE) requis dans différents scénarios qui examinaient la capacité des individus des quatre espèces à compenser une réduction dans l'accessibilité des ressources par une modification de leur comportement de prospection alimentaire. Mes résultats ont mis en évidence l'importance de la prise en compte des contraintes énergétiques des espèces afin d'évaluer précisément leur capacité à faire face à une réduction de l'accès aux ressources. Il est suggéré que dans les conditions actuelles de la Mer du Nord, les cormorans huppés et les guillemots ont suffisamment de temps et d'énergie disponibles pour augmenter leur effort de prospection alimentaire dans des proportions considérables, alors que les mouettes et les fous n'ont respectivement pas assez de temps ou d'énergie pour le faire. Des quatre espèces considérées ici, les fous sont ceux qui présentent le niveau métabolique le plus élevé durant la période d'élevage des jeunes et, par conséquent, sont ceux qui sont les moins capables, d'un point de vue physiologique, d'augmenter leur effort de prospection, les rendant potentiellement très sensibles à des phases de réduction de l'accessibilité aux ressources. Toutefois, les fous peuvent probablement tirer parti d'une niche écologique particulièrement profitable pour compenser les coûts importants qu'implique leur mode de vie.

Mon étude représente, à ce jour, l'examen le plus détaillé de l'influence de divers facteurs biotiques et abiotiques sur l'énergétique de la prospection alimentaire chez les oiseaux plongeurs. C'est la première étude dans laquelle les coûts énergétiques de la plongée sont mesurés en fonction de la profondeur. C'est également la première qui examine en détail les effets conjugués de différents facteurs biotiques et abiotiques sur le comportement et le succès prédateur des oiseaux plongeurs. Finalement, mes recherches illustrent l'importance d'une approche intégrative des stratégies énergétiques et comportementales dans le but d'estimer la capacité des communautés d'oiseaux de mer à faire face aux conséquences des modifications d'origine naturelle ou anthropique qui affectent leur environnement.

Publications

Présentées dans la thèse:

Enstipp, M.R., Grémillet, D. and Jones, D.R. (*en préparation*). Prey capture behaviour of double-crested cormorants (*Phalacrocorax auritus*) and its constraints.

Enstipp, M.R., Grémillet, D. and Jones, D.R. (soumis à *J. Exp. Biol.*). The effects of depth, temperature and food on the diving energetics of double-crested cormorants (*Phalacrocorax auritus*).

Grémillet, D., Enstipp, M.R., Boudiffa, M. and Liu, H. (*sous presse*). Do cormorants injure fish without eating them? An underwater video study. *Mar. Biol.*

Enstipp, M.R., Daunt, F., Wanless, S., Humphreys, E.M., Hamer, K.C., Benvenuti, S. and Grémillet, D. (*sous presse*). Foraging energetics of North Sea birds confronted with fluctuating prey availability. In *Management of marine ecosystems: monitoring change in upper trophic levels* (Symposium of the Zoological Society London; ed. I.L. Boyd and S. Wanless). Cambridge: Cambridge Univ. Press.

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Non présentées dans la thèse:

Enstipp, M.R., Andrews, R.A. and Jones, D.R. (2001). The effect of depth on the cardiac and behavioural responses of double-crested cormorants (*Phalacrocorax auritus*) during voluntary diving. *J. Exp. Biol.* **204**: 4081-4092.

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Enstipp, M.R., Grémillet, D. and Jones, D.R. Fine scale foraging behaviour of cormorants.

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International Conference and Workshop IMPRESS: Understanding marine foodweb processes – an ecosystem approach to sustainable sandeel fisheries in the North Sea. Hamburg, F.R.G., Nov. 2001
Enstipp, M.R. and Grémillet, D. Metabolic and behavioural studies in diving seabirds – providing input values for ecological modelling.

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Enstipp, M.R., Andrews, R.A. and Jones, D.R. Cardiac physiology and diving behaviour of double-crested cormorants (*Phalacrocorax auritus*).

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Enstipp, M.R., Andrews, R.A. and Jones, D.R. The effect of depth on the cardiac response of double-crested cormorants (*Phalacrocorax auritus*) during voluntary diving.

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Enstipp, M.R., Andrews, R.A. and Jones, D.R. Cardiac adjustments to voluntary diving in double-crested cormorants (*Phalacrocorax auritus*).

Abstract

Avian divers are confronted with a number of physiological challenges when foraging in cold water, especially at depth. Diving is believed to be particularly costly in cormorants (*Phalacrocoracidae*) because of their poor insulation and less efficient foot-propulsion. I used open-circuit respirometry to study the energetic requirements of two *Phalacrocorax* species, the European shag (*P. aristotelis*) and the double-crested cormorant (*P. auritus*) when diving in a shallow (1 m) and deep (10 m) dive tank. I also investigated the modifying effects of water temperature and feeding status on dive costs. My results indicate that the energetic costs during shallow diving in European shags and double-crested cormorants are comparable to other foot-propelled divers. Metabolic rate was significantly increased when diving to greater depth and at lower water temperatures, while feeding before diving increased metabolic rate, albeit not significantly. The strong effects of depth and water temperature on cormorant diving metabolic rate are most likely a consequence of their partially wettable plumage and their reduced plumage air volume, which makes them prone to heat loss and, hence, increases thermoregulatory costs.

The energetic requirements of animals have to be satisfied by intake of resources from the environment. Hence, the quest for food is a central aspect of animal behavior. Although the study of seabird foraging behaviour has greatly profited from recent technological developments, we still know little about predator-prey interactions on a fine scale. I used an underwater video array to investigate the prey-capture behaviour of double-crested cormorants foraging on live rainbow trout (*Oncorhynchus mykiss*). I tested the effects of a variety of factors on the underwater foraging behaviour of cormorants and established a functional link between prey density and cormorant prey capture rate. Prey density and behaviour both significantly affected predator performance. At prey densities below 2-3 g fish m^{-3} birds increased their search time during a trial drastically, while prey-encounter rate was greatly decreased. When cormorants attacked shoaling rather than solitary trout, their capture success was significantly reduced, while pursuit duration was significantly increased.

Seabird energetics and behaviour are typically studied on the individual or species level. However, if we want to understand how seabirds react to environmental changes, we have to consider entire communities. In the western North Sea, a large seabird assemblage critically depends on a single fish species, the lesser sandeel (*Ammodytes marinus*), which is also exploited by an industrial fishery. I developed an algorithm to test for the capacity of four seabird species during chick-rearing in Scotland to buffer a potential decline in sandeel abundance by increasing their foraging effort in various ways. My results show that under the conditions currently operating in this region shags and guillemots (*Uria aalge*) may have sufficient time and energy to allow them to increase their foraging effort considerably, while Kittiwakes (*Rissa tridactyla*) and gannets (*Morus bassanus*) appear more constrained by time and energy respectively. My study suggests that during chick-rearing gannets are working at the highest metabolic level of all species considered and hence, have the least physiological capacity to increase foraging effort. This indicates that gannets could potentially be very sensitive to a reduction in sandeel abundance. My thesis emphasises the importance of taking into account seabird energetics as well as fine scale behavioural requirements, when trying to develop management schemes for fisheries that will allow the coexistence of both seabirds and human fishery in a sustainable way.

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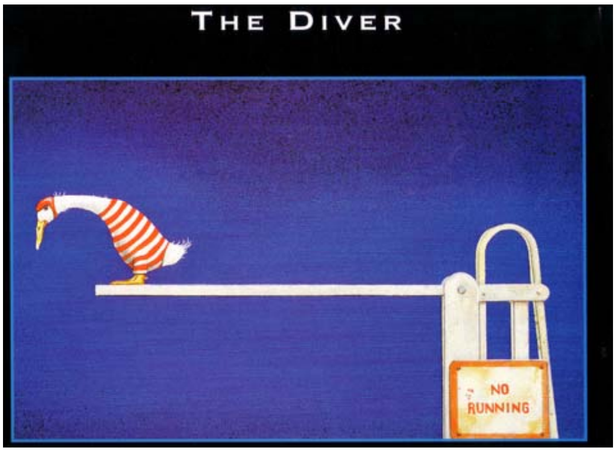
Acknowledgements

Many people provided support in various ways for this thesis work (practically, intellectually, emotionally, financially). I would like to truly thank all of you because without your help none of the following pages would have been possible.

Specific support for the various projects of this thesis work is acknowledged within each chapter. Here I would like to stay more global and thank, first of all, my supervisor, David Grémillet, who hired me for an ambitious project and supported me throughout, while keeping the leash at the right length. Thanks David for the many things that made my stay in Strasbourg enjoyable. I would also like to thank my co-supervisor in Vancouver, Dave Jones, for his continued unconditional support. While Vancouver is always a pleasant place to work, his generosity and sense of humor made me feel home. Being able to use the superb diving facilities in Dave's lab and, furthermore, to use the cormorants, which I had raised in captivity and Dave had the foresight to maintain over the years (Art Vanderhorst made sure of that), was crucial for the successful completion of this project.



Thanks also to Yvon Le Maho and all my colleagues at the CEPE for their support and who overcame their own language inhibitions to accommodate a stranger who successfully refused to speak french. Thanks especially to Amélie Lescroël, Céline Le Bohec, Lorien Pichegru and Peggy Berringer for their help with my french attempts. Jean-Yves Georges and Sylvie Massemin are thanked for stats advice and all the rest. Thanks to Lovena Toolsy for her help during the long hours of video analysis and to J.-P. Robin for his expertise in line fitting procedures.

Thanks to all the people in Trondheim and surroundings who helped me during my first season. Svein-Håkon Lorentsen of NINA was amazingly efficient in helping me to set myself up in the middle of nowhere during a busy time for himself. His kindness and rømmegrøt won't be forgotten. Claus Bech of Trondheim University (NTNU) supported me throughout my time in Norway. Thanks to Geir Håvard Nymoen for his help during our 'chick-collecting' trip. Sissel Smistad was curios and bighearted enough to provide space for the 'skarvenes herre' and his strange work and Kro John's authentic norwegian cuisine was greatly appreciated (and now for something completely different: potatoes). Thanks to Olaf Vadstein and Vera Sandlund of NTNU for unlimited access to the facilities at Sletvik Feltstasjon.

I would like to thank all the people in Vancouver that helped me in ways too numerous to account for but, above all, for their friendship: Harald Jurk, Volker Deecke, Christine Stewart, Kevin Fort, Tom Hoeg and Russ Andrews. Thanks to all the people in the Jones' lab: Kim Borg, Manuela Gardner, Todd Jones, Mervin, and especially Martha Gutierrez, who helped with the 'stiff bird research'. Arthur Vanderhorst and Sam Gopaul of the UBC Animal Care Centre were always there for me and my birds. Bruce Gillespie and Don Brandies of the UBC Zoology Mechanical Workshop were of great help for technical questions. Robin Liley tolerated the take over of his fish tanks and John Gosline provided the time machine for my video set-up. Ken Scheer from the Fraser Valley Trout Hatchery is thanked for generously donating live rainbow trout and Andrew Lotto (UBC Forestry) for his fish transportation tank. Thanks to the UBC Animal Care Committee which granted permits for the proposed research and to the BC Ministry of Environment which granted holding permits for the double-crested cormorants. Canadian Wildlife Service (CWS) issued catching permits for the capture of the murre chicks and BC Parks authorised the capture. Thanks to Ron Ydenberg and his research team at SFU in Burnaby and Mark Hipfner of the CWS for arranging the capture of the chicks and to Eric Davies, who actually caught them. David Hancock generously shared his expertise and knowledge about raising alcid chicks in captivity and was a great source of inspiration. Anne McDonald of the Night Owl Bird Hospital and Tamara Godbey of the UBC Animal Care Centre provided veterinary support. I'm sure my next attempt with murres will be successful. Thanks to Jan Ropert-Coudert for the swim speed loggers and to Gerry Stensgaard and Gary Novlesky at Ocean Engineering (BC Research) who kindly provided access to a 60 m tow tank at which they could be calibrated. Dave Rosen is thanked for his help with datacan and the logger calibration.

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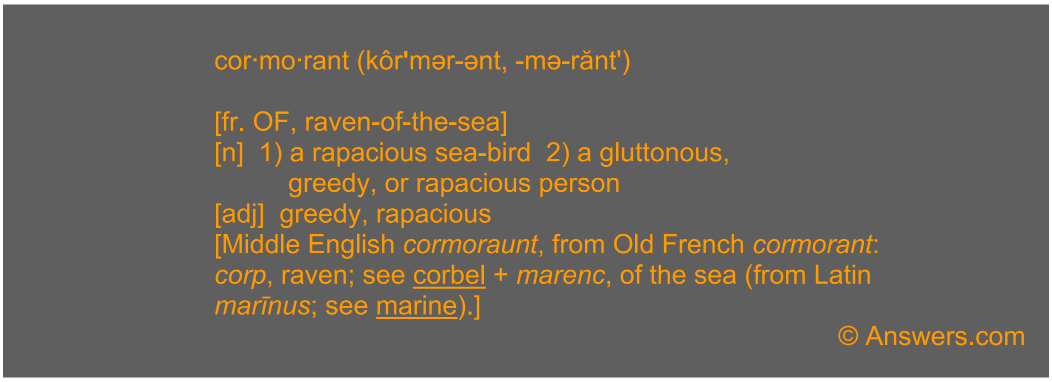
Thanks to the other IMPRESS people, who inspired many good discussions on seabird biology. I'm particularly grateful to Francis Daunt, who helped with stats, Gerrit Peters who provided excellent technical support for his data loggers, Liz Humphreys, and Sarah Wanless and Mike Harris for their hospitality in Scotland.

I would like to thank Jim Lovvorn for his support and some great discussions on the biomechanics of underwater locomotion, and Yves Handrich for fruitful discussions on thermoregulation during diving. Thanks to Pat Butler and Jean-Louis Gendrault for being part of my ‘Jury de thèse’.

Magali Grantham tolerated my ‘obsession’ with diving birds for many years and helped on all levels; thanks for everything Magali.



cor·mo·rant (kôr'mər-ənt, -mə-rănt')

[fr. OF, raven-of-the-sea]
[n] 1) a rapacious sea-bird 2) a gluttonous,
greedy, or rapacious person
[adj] greedy, rapacious
[Middle English *cormoraunt*, from Old French *cormorant*: *corp*, raven; see corbel + *marenc*, of the sea (from Latin *marīnus*; see marine).]

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I would like to acknowledge the financial support of the European Commission that funded my research within the framework of the project ‘Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864). Financial support was also provided by a ‘discovery grant’ and equipment grants from NSERC Canada to D.R. Jones.

Finally, I would like to thank Gunna Weingartner for all her help with my work throughout the years, too numerous to mention here but also, for being there.

Chapter 1

General Introduction

Thesis outline

My thesis is comprised of 7 chapters. Chapter 1 gives a brief outline and introduces the main themes of this thesis. Chapters 2-6 are written as individual, self-contained manuscripts and have been or will be submitted for publication in various journals. Since all of these are based on collaborations with colleagues, they are written in the plural form ‘we’ rather than the singular ‘I’. Chapters 2 and 3 investigate in detail the energetic costs associated with diving in two foot-propelled pursuit divers, the European shag (*Phalacrocorax aristotelis*) and the double-crested cormorant (*Phalacrocorax auritus*). Using an open-circuit respirometry system in a captive setting, I examined how dive depth, water temperature and feeding status modify their metabolic rate during diving. I also monitored stomach temperatures during captive dive trials to investigate if birds pursue a strategy that would enable them to prolong aerobic dive duration (i.e. hypothermia). Chapter 4 investigates the prey-capture behaviour of double-crested cormorants foraging on juvenile rainbow trout (*Oncorhynchus mykiss*). Here I examined how a variety of factors (prey density, prey size, light conditions, prey behaviour, water temperature, and depth) influence the foraging performance of cormorants and established a functional relationship between prey density and cormorant prey-capture rate. Chapter 5 uses the prey-capture experiments reported in chapter 4, to assess how often cormorants might injure fish during foraging without eating them. This aspect has important management implications, since some interest groups, affected by the recent recovery of cormorant populations in Europe and North-America, claim that cormorants injure substantial amounts of fish without ingesting them. Chapter 6 explores the capacity of four North Sea seabird species during chick-rearing to buffer the potential decline in abundance of their major prey, the lesser sandeel (*Ammodytes marinus*). To this end, I developed an algorithm to calculate the daily energy expenditure (DEE) of adult breeders, their required daily food intake (DFI) and their required prey-capture rate (catch per unit effort, CPUE). After establishing a ‘baseline situation’ for all four species, I examined a number of hypothetical scenarios during which birds increased their foraging effort in various ways, to investigate how birds might be buffered against reduced sandeel abundance. I examined especially how time, energy and food quality might constrain the buffering capacity of the four species.

Finally, chapter 7 summarizes the main findings of this thesis, sets them into a wider context, and defines the work ahead of us.

Why study seabirds?

Dramatic changes within marine ecosystems have occurred in the last decades and are usually attributed to both climatic and anthropogenic factors. Commercial fisheries continue to drastically alter marine ecosystems and biodiversity worldwide as we are ‘fishing down marine food webs’ (Pauly et al., 1998; for a historical perspective on overfishing see Jackson et al., 2001). Moreover, regime shifts have been recently identified in the North Pacific and the North Sea, suggesting changes in climate-ocean interactions throughout the temperate zone of the Northern Hemisphere (Hare and Mantua, 2000; Weijerman, et al., 2005). Certainly, the combined effects of climate change and overfishing will have consequences for the marine environment (Frederiksen et al., 2004) and far beyond. If we want to minimise the anthropogenic impact on these complex systems and if we want to move towards a sustainable resource extraction, we have to develop management schemes with predictable outcomes. Unfortunately, marine ecosystems are highly dynamic and we often know little about the mechanisms that operate within them. Oceanographic conditions structure marine food chains from bottom to top. Many organisms at the bottom and intermediate trophic level of marine food webs undergo strong spatial and temporal fluctuations, which hampers efficient monitoring of their populations. In contrast, top predators, such as seabirds, are the conspicuous elements of marine food chains. Seabirds breed in dense colonies that are often accessible, so that their populations can be monitored with relative ease. As a group, seabirds are important consumers at various levels within marine systems. A recent estimate of the food consumption of the world’s seabirds suggests an annual consumption similar to global marine fisheries landings (Brooke, 2004), which could imply competition for prey sources. As top predators, they exert a profound influence on the structure of marine food webs from top to bottom and thereby integrate ecological processes occurring within the lower trophic levels. This status has two important, interrelated implications: (1) Seabirds are vulnerable to changes within their environment, and, for instance, years of low prey abundance often coincide with a reduced reproductive success (Furness and Tasker, 2000; Rindorf et al., 2000). It is therefore crucial to understand how seabirds function within their natural environment if we want to ensure the persistence of their populations. (2) Beyond the protection of seabird populations, studying these predators is important because the development of their populations might reflect the conditions within marine food chains, making them potentially reliable indicators for the state of entire marine ecosystems (Cairns, 1987; Montevecchi, 1993; Furness and Camphuysen, 1997). Hence, studying seabirds is important to ensure the efficient management of their populations but also because they are functional in assessing the status of marine systems. The study of seabirds might therefore provide insights into the mechanisms operating within marine food webs across a wide range of temporal and spatial scales.

Why study seabird energy requirements and energy acquisition?

To understand the role of seabirds in the nutrient fluxes of marine ecosystems, it is crucial to study (1) how much energy they require and (2) how this energy is acquired. All living organisms must obtain and convert energy from the environment to maintain themselves, grow and reproduce. Hence, the quest for food is a fundamental driving force in determining animal behaviour. How much energy an organism requires depends on a variety of factors, with the biggest difference being between animals that are able to maintain high and relatively stable body temperatures independent of ambient temperature (endotherms) and those that are not (ectotherms). The capacity for aerobic metabolism in endotherms exceeds that of ectotherms by an order of magnitude (Bennet and Ruben, 1979). A higher and stable body temperature enables endotherms to stay active over a generally broader range of environmental temperatures when compared with ectotherms. While this might have facilitated niche expansion for endotherms, especially into cooler climates, it comes at the cost of a metabolic machinery that is expensive to maintain.

As endotherms, seabirds were able to colonize all climatic zones from the Tropics to Polar regions. Many species spend extended periods at sea and some only return to land to breed. As consumers, they are found at most trophic levels of the marine food web, ranging from zooplankton feeders like little auks (*Alle alle*) to gannets (*Sulidae*) and some penguins (*Spheniscidae*) that take pelagic fish and squid, to gulls (*Laridae*) and albatrosses (*Diomedeidae*) that scavenge on animal remains. Seabirds make use of a range of foraging techniques to exploit the ocean’s food resources. Shealer (2002) distinguishes between 3 different strategies amongst seabirds to obtain food. Coastal and inshore species, such as gulls, that are predominantly surface feeders and gather to feed in areas where food is abundant and forced to the surface. Diving seabirds, like cormorants, alcids and penguins, which exploit a greater range of depth to obtain food. Finally, pelagic species, such as albatrosses, that roam the world’s oceans to search widely dispersed food near the surface.

Foraging in seabirds involves two activities that are energetically expensive, flight and/or diving. The energetic costs of diving differ between species and seem to be generally more costly in foot-propelled divers (e.g. ducks, cormorants), when compared with wing-propelled divers (e.g. alcids, penguins; Ellis and Gabrielsen, 2002). Apart from biomechanical considerations, diving birds face an energetically demanding situation when foraging underwater because of the considerable cooling properties of water. Unless properly insulated, they will lose heat rapidly, especially in cold water and thermoregulatory costs will greatly increase the overall energy requirements.

The mechanical power requirements of aerial flight also vary widely, being lower in species with a high aspect ratio, especially when combined with a low wing loading (Norberg, 1996). Many avian divers also use their wings for underwater flight. However, diving and aerial flight place conflicting biomechanical demands on avian divers, whereby dive costs must be balanced against flight costs (Lovvorn and Jones, 1994), and wing shape design has to compromise between these different constraints. For example, to reduce dive costs, it would be advantageous for shallow divers to increase body density by decreasing mass-specific air volumes (Lovvorn and Jones, 1991). Stephenson et al. (1989) showed that tufted ducks (*Aythya fuligula*) in an experimental setting adapted to shallow diving by increasing blood volume and, hence, blood oxygen stores, while decreasing respiratory volume. However, while such a change would decrease dive costs (as buoyancy is reduced), it would also increase body mass and, therefore, wing loading and flight costs (Lovvorn and Jones, 1994). Generally speaking, flight costs are higher in species that have to balance the demands imposed upon them by aerial flight and by diving (e.g. alcids), limiting their foraging range during the breeding season. In contrast, pelagic species, such as albatrosses travel great distances at very low energetic costs (Bevan et al., 1995a).

Because of these mechanical and thermoregulatory constraints, life in the marine environment might be energetically costly for birds. Food sources within that environment, however, are patchily distributed, often unpredictable and extremely ephemeral (Gaston, 2004) and it might therefore be difficult for seabirds to balance their energetic requirements (Ashmole, 1963). If we want to learn more about the constraints that seabirds are facing in the marine environment, it is crucial to study their energetic requirements and how they are met. Not surprisingly, foraging energetics and foraging behaviour are central aspects of seabird biology.

Studying seabird energetics

The study of seabird energetics is central in understanding the mechanisms and constraints underlying seabird life history and demography. Diving beneath the surface to locate, pursue and capture their prey is a common method of food acquisition in many seabird species. It is also an energetically demanding activity and, hence, dive costs are an important component of the time-energy budgets of diving seabirds. Underwater foraging allows them to exploit the rich food sources of productive aquatic ecosystems that are out of reach for surface feeding species, such as gulls and terns. However, it also confronts them with a number of physiological and energetic challenges. As air breathers avian divers have to return to the water surface frequently to reload their oxygen stores and unload accumulated CO_2. Therefore, a central aspect of their diving behaviour is the economic use of finite oxygen stores during submergence to maximise underwater foraging time. Cardiovascular mechanisms facilitating the economic use of the limited oxygen stores during diving in endotherms have been extensively studied (for review see Butler and Jones, 1997). Despite this, we are still at pain to explain how some divers extend their dive duration on a regular basis beyond what we calculate to be their aerobic dive time, without any significant contribution from anaerobic metabolism. The most likely scenario is a greatly reduced metabolic rate during these dives, so that metabolism falls even below the resting level (hypometabolism). A mechanism by which this could be at least partly accomplished is the regional reduction in body temperature (hypothermia) that has been observed in some species (for review see Butler, 2004). If we want to understand the complex balance of behaviour and physiology that shapes the foraging strategies of air-breathing animals exploiting an underwater prey resource, it is essential to study their energetic requirements during diving.

From an energetics point of view, divers have to overcome three forces when submerging: buoyancy, drag and inertia. Stephenson (1994) showed that buoyancy is the dominant factor determining dive costs in lesser scaup ducks (*Aythya affinis*). Other avian divers, notably cormorants, are less buoyant than ducks, which reduces the amount of mechanical work required during descent. The increase in ambient pressure when diving to depth will decrease the amount of air trapped within the plumage, so that work against buoyancy will decline even further. However, this will also reduce plumage insulation and, hence, increase heat loss to the water, unless other means of insulation are deployed. Some avian divers (e.g. penguins) use subcutaneous fat for insulation. For penguins this is a viable strategy because they don't have to answer to the demands of aerial flight. For species that retained the ability of aerial flight, however, this mass increase could be problematic, since it would increase their flight costs.

Although a body of information on the diving energetics of wing-propelled divers (especially penguins) has emerged in recent years (for review see Ellis and Gabrielsen, 2002), measurements of diving costs for foot-propelled divers are scarce. Few studies have looked in detail how biotic and abiotic factors, such as water temperature, influence dive costs in birds (Bevan and Butler, 1992; de Leeuw, 1996; Grémillet et al., 2003). Furthermore, almost all of these studies were conducted with animals diving in shallow tanks or channels. I am only aware of one study to date that investigated the energetic consequences of diving to depth. De Leeuw (1996) found that dives to 2.2 m and 5.5 m depth were equally costly in tufted ducks. He attributed this to the increase in thermoregulatory costs during dives to greater depth cancelling out the accompanying decrease in mechanical costs. However, given the small depth range covered in this study, the complex effects that dive depth might have on diving energetics over a significant depth range, naturally encountered by the diver, still remains unclear. To understand how physiology constrains the foraging behaviour of avian divers, we need a profound knowledge of their energy requirements during diving. This includes the understanding of how the various biotic and abiotic factors that are naturally encountered by these animals will modify their energetic requirements.

Estimating the energy requirements of free-ranging animals is, however, a challenging task. Today, there are three different approaches to studying the field energetics of animals. (1) Establishing a time-energy budget (TEB) by combining a detailed time-activity-budget (TAB) with laboratory measurements of activity-specific metabolic rates, while also taking into account a variety of biotic and abiotic factors (e.g. temperature), that influence the energy requirements. From the knowledge of how long an animal engages in each activity on a daily basis and the energetic cost associated with each activity, daily energy expenditure can be calculated (Goldstein, 1988). (2) The doubly-labelled water (DLW) method (Lifson et al., 1955) estimates the rate of CO_2 production from the difference in the rate of loss of labelled hydrogen (^{2}H or ^{3}H) and oxygen (^{18}O) from the body. The biggest drawback with this method is that it only provides a mean value of energy expenditure over the entire study period, i.e. it is not possible to assess the costs of specific activities. (3) The heart rate method (Butler, 1993) exploits the physiological relationship between heart rate (f_H) and oxygen consumption rate ($\dot{V}o_2$) and requires calibration of both variables against each other under controlled conditions. $\dot{V}o_2$ can then be estimated from f_H recorded in free ranging animals (for a comparison of DLW and heart rate methods see Butler et al., 2004). While this method requires surgical implantation and might currently not be feasible for animals below a mass of 1 kg, recent development of a miniaturized data-logger that allows data collection over extended periods (up to one year; see Grémillet et al., 2005b) makes this an attractive method for future studies.

Estimating dive costs in avian divers is central to our understanding of their energy requirements in the field. In the following section I will evaluate the usefulness of the methods introduced above, in estimating dive costs.

(1) The accuracy of time-energy budgets in estimating field energetics of animals critically depends on the accuracy of its input values. Hence, it is important to have detailed and precise activity data that can be linked with the appropriate activity-specific energy costs. In the past many time-energy budgets incorporated dive costs that had been determined in animals diving in shallow tanks and that might therefore not be representative of animals diving in the wild. Consequently, it is important to investigate the affects of a range of biotic and abiotic factors naturally encountered by the diver on dive costs, so that these can be incorporated in future bio-energetic models. In case of shallow avian divers, like many diving ducks and some cormorant species (e.g. double-crested cormorants), it is possible to reconstruct semi-natural conditions in a captive setting (dive depth, temperature, feeding conditions, light conditions, etc.), so that dive costs can be measured directly via respirometry.

Another promising approach for estimating dive costs is to use biomechanical models to calculate the mechanical costs required for locomotion and convert these into metabolic requirements using a value for aerobic efficiency (mechanical power output/aerobic power input), which has to be determined experimentally (Lovvorn, 1994; Lovvorn and Gillingham, 1996). This method that has been extensively used to estimate flight costs (Pennycuick, 1989). The recent deployment of instruments measuring mechanical variables (e.g. acceleration, swim speed, etc.) in animals foraging in the wild (Lovvorn et al., 2004; Watanuki et al., 2005), will help to improve the accuracy of biomechanical models in the future.

(2) As already pointed out, the DLW method integrates costs of all activities over the measurement period and, hence, does not allow estimation of the energetic costs associated with particular activities, like diving.

(3) The heart rate method (Butler, 1993; Butler et al., 2004) is a promising approach for studying the energetic requirements of undisturbed animals in the field with a fine time resolution. However, heart rate data has to be calibrated against measurements of energy

expenditure during exercise with captive animals. Depending on species and type of locomotion investigated, it might not be possible to reproduce natural conditions. Typically the calibration procedure is carried out with animals exercising on a treadmill (e.g. Bevan et al., 1994; Bevan et al., 1995b; Froget et al., 2001). It is not clear, however, how well we can extrapolate from such calibrations to a natural situation, when different muscle groups are used under both circumstances (e.g. walking on a treadmill vs. flying in air or water). Similarly, Froget et al. (2002) showed that the relationship between heart rate and oxygen consumption differs for different physiological demands (exercise vs. thermoregulation), while McPhee et al. (2003) found that an increase in oxygen consumption after feeding in Stellar sea lions (*Eumetopias jubatus*) was not accompanied by a change in heart rate. Clearly, more validation studies are needed to assess the effects of the various factors under different conditions on the relationship between heart rate and oxygen consumption. In the context of breath-hold diving, abrupt physiological changes at the onset of a dive (heart rate decline, peripheral vasoconstriction, etc.) will influence the relationship between heart rate and oxygen consumption. As a consequence, heart rate cannot be used to estimate oxygen consumption during submergence. However, if heart rate is averaged over complete dive cycles or dive bouts, it is a good predictor of oxygen consumption during these periods (Fedak, 1986; Bevan et al., 1992; Butler, 1993).

In summary, all currently available methods to estimate dive costs in aquatic birds require controlled experiments with captive animals to measure oxygen consumption. The experimentally determined $\dot{V}o_2$ can then be incorporated into time-energy budgets or biomechanical models or it can be used to calibrate against heart rate data. Hence, measurements of the kind conducted within the framework of this thesis, form the basis for any bio-energetics modelling that might enable us to assess the energetic requirements of animals foraging in the wild.

Studying seabird fine scale foraging behaviour

The energetic requirements of seabirds have to be satisfied by intake of resources from the environment. Despite its obvious relevance, the behaviour of seabirds at sea has been virtually impossible to study until the development of radio-telemetry (e.g. Wanless and Harris, 1992; but see Dewar, 1924). Ship based surveys studied the distribution of seabirds at sea but their capacity to investigate seabird foraging behaviour was limited, especially when diving species were concerned. Since then, the study of seabird foraging behaviour has greatly profited from technological developments. Especially in the last two decades, through the development of miniaturized mechanical and electronic devices (e.g. Burger and Wilson, 1988; Wilson et al., 1989; Woakes, 1995; Andrews, 1998), it has become possible to study the foraging behaviour of seabirds in the wild in great detail (e.g. Croxall et al., 1991; Wanless et al., 1992), often collecting physiological data alongside (e.g. Bevan et al., 1997). However, how much do we know about the interactions of seabird predators and their prey? In the introduction to an influential book, John Croxall (1987) wrote: "Understanding predator-prey relationships requires much information about the diet, distribution and bioenergetics of both predators and prey and on the detailed nature of their interactions." How much have we learnt since? How well do we understand predator-prey relationships in the marine environment? There has been a fair amount of research investigating diet, distribution and bioenergetics of predator and prey organisms (see Shealer, 2002; Brooke, 2002; Ellis and Gabrielsen, 2002). However, rarely have these studies integrated the various aspects of predator-prey interaction. How much have we learnt about the 'detailed nature' of predator-prey interactions? Direct observation of marine predators foraging underwater is obviously a challenging task, which is hampered by numerous practical difficulties and is therefore rare (Axelsen et al., 2001; Similae and Ugarte, 1993). Data-logger recordings from animals foraging in the wild have enabled us to deduce a wealth of information concerning the overall foraging patterns of marine predators (location, dive depth, dive duration, etc.) but we still know little about predator-prey interactions on a fine scale. Furthermore, experimental investigation of predator-prey interactions in the aquatic environment have mostly been restricted to fish (Neil and Cullen, 1974; Turesson and Broenmark, 2004), while studies on diving birds or mammals are lacking. In the few studies that experimentally investigated the foraging behaviour of aquatic birds (Wood and Hand, 1985; Ulenaers et al., 1992; Fox, 1994), observation was restricted to surface behaviour, omitting all underwater activity (i.e. search, pursuit, capture, handling) from analysis.

However, if we want to understand the constraints that seabirds face during foraging, it is essential to study the relationships that link these predators with their prey. How does prey abundance and behaviour affect predator performance? The functional links between these variables are crucial for our understanding of seabird foraging behaviour and their capacity to respond to changes within the marine environment. Hence, experimental studies investigating the underwater prey capture behaviour of seabirds in relation to a variety of biotic and abiotic factors are urgently needed. While this is an impossible task in the field, in a captive setting logistic problems can be overcome and a variety of factors can be altered systematically, which allows the study of predator-prey interactions in great detail.

Why study cormorants and shags?

Double-crested cormorants (*Phalacrocorax auritus*) and European shags (*Phalacrocorax aristotelis*) are foot-propelled pursuit divers that forage on benthic and pelagic fish, which they catch inshore. Both species range from mild temperate climatic zones to thermally challenging arctic zones (Johnsgard, 1993). The plumage of great cormorants is partially wettable (Grémillet et al., 2005a) and their plumage air volume is reduced when compared with other aquatic birds (Wilson et al., 1992; Grémillet et al., 2005a), reducing buoyancy. These features are probably characteristic for a range of cormorant and shag species. European shags (Grémillet et al., 2005a) and double-crested cormorants (pers. observation) both possess the same dual feather structure as great cormorants, with a wettable outer portion and a highly waterproof inner section. The plumage air volume of double-crested cormorants is similar to that of great cormorants (0.13 vs. 0.17 x 10^{-3} $m^3 \cdot kg^{-1}$; pers. observ.; Grémillet et al., 2005a). While reduced buoyancy in cormorants has often been described as an adaptation for diving, decreasing the mechanical costs, it also makes them prone to heat loss. This effect is particularly marked because, unlike in penguins, the sub-cutaneous fat layer of shags and cormorants is negligible and they have to rely on plumage air as an insulating layer when diving in cold water. Hence, dive costs in cormorants and shags might be strongly influenced by water temperature. This effect is predicted to be further enhanced during dives to depth, when the increase in ambient pressure will reduce the insulative air layer even further. We might therefore expect to see a clear difference in dive costs of cormorants and shags with a change in depth, as heat loss during deep diving might outweigh any energetic savings related to the decreased buoyancy at greater depth. This is unlike the situation in tufted ducks, where dives to 2.2 m and 5.5 m were equally costly (de Leeuw, 1996). Another advantage when studying cormorants is that the depth range typically exploited by them in the wild can be relatively easy duplicated in a captive setting (Ross, 1974 observed a depth range for double-crested cormorants of 1.5-7.9 m). Hence, it is possible to investigate the impact of depth on the diving energetics of an avian diver over a significant depth range, encountered in the wild. Finally, dive costs and, hence, foraging costs are believed to be relatively expensive in the *Phalacrocoracidae* (Schmid et al., 1995). This is of great importance in a conservation context, since it might make them especially vulnerable to natural or manmade fluctuations in the abundance of their prey. These attributes make cormorants and shags good model species to study the energetic requirements associated with diving in seabirds.

From individuals to communities: sandeel fishery and North Sea seabirds

Seabird behaviour and energetics are typically studied on the individual or species level. However, if we want to understand how seabirds react to environmental changes, we have to consider entire communities. Currently anthropogenic and natural stresses are causing dramatic changes in the structure of marine food webs. Detailed information on energy acquisition and energy allocation of seabird species form the basis for any bioenergetics modelling that will allow us to investigate the effects of these changes on seabird communities (Boyd, 2002). Looking at a variety of species with different strategies with respect to energy acquisition and energy allocation will allow us to contrast the different buffer capacities of these species to changes in the marine environment (e.g. decline in prey abundance).

In the western North Sea, a large seabird assemblage exploits a small number of fish species. Sandeels, especially the lesser sandeel (*Ammodytes marinus*), are important prey items in this system and comprise a major component of the diet of seabirds, marine mammals, and predatory fish (see Furness and Tasker, 2000). Sandeel populations show strong spatial and temporal variability, which is poorly understood. A marked decline in sandeels around Shetland in the mid 1980s had adverse effects on many seabird species. Surface feeders like Arctic terns (*Sterna paradisaea*) and black-legged kittiwakes (*Rissa tridactyla*) had greatly reduced breeding success, whilst diving species like common guillemots (*Uria aalge*) were able to compensate for the reduction in sandeel availability to some extent by increasing their foraging effort (Monaghan, 1992; Monaghan et al., 1996). In 1990 a sandeel fishery opened around the Firth of Forth area (south-east Scotland) and expanded rapidly coinciding with a decline in breeding performance of kittiwakes from nearby colonies (Tasker et al., 2000). Concern for the future of these predators culminated in the closure of the fishery in 2000.

Furness and Tasker (2000) found that small seabirds with high energetic costs during foraging and a limited ability to switch diet (e.g. many surface feeders such as terns) were potentially most sensitive to a reduction in sandeel abundance. Larger species with less costly foraging modes and a greater ability to switch diet (e.g. many pursuit-diving species) were potentially less sensitive. Furness and Tasker were, however, uncertain about the relative importance of some factors, such as foraging energetics. In fact, energetic and behavioural constraints during foraging might limit the capacity of seabirds to buffer a decline in sandeel abundance. Furthermore, seabird species in the North Sea pursue various foraging strategies that have different energetic costs associated with them. Hence, the buffering capacity for decreased sandeel abundance might differ between species, depending on how close they operate to their metabolic ceiling.

During the breeding season energy requirements of seabirds are especially high, because they have to meet the energy demands of their chicks in addition to their own. During chick-rearing seabirds are ‘central place foragers’ (Orians and Pearson, 1979) that have to return to the colony to feed their chicks. Feeding frequency varies between species, with single prey loaders such as the common guillemot commuting throughout daylight hours to feed its chick, while some penguin and albatross species go on extensive foraging trips that may last several days or even weeks and during which birds might cover thousands of kilometres (Weimerskirch et al., 1994). During this period seabirds will be constrained by a variety of factors, most importantly by (1) the time available for foraging, (2) energy expenditure during foraging, and (3) food availability. If foraging conditions are unfavourable during the breeding season (e.g. low prey abundance) adult birds might be able to compensate to a certain degree by increasing their foraging effort and/or switching to other prey species. Many species have been shown to adjust their time activity budgets in response to changes in food availability (Burger and Piatt, 1990). However, increasing foraging effort will also increase energy expenditure. In the long run, birds can only sustain an energy expenditure that is below their metabolic ceiling (Weiner, 1992), before physiological limits are reached and fitness costs may be incurred (e.g. reduced survival; Drent and Daan, 1980). Ultimately birds face a trade off between investing in current chick survival and ensuring their own survival for future reproduction (Williams, 1966). If conditions are sufficiently bad, they might discontinue breeding. Reproductive success in seabird colonies is therefore reduced in years with low food availability (Furness and Tasker, 2000; Rindorf et al., 2000). During years with climatic anomalies (e.g. El Niño Southern Oscillation), when food is scarce, complete reproductive failures might occur. Furthermore, the effects of large scale climatic variation may not be limited to reproductive success but might also influence adult survival (Croxall et al., 2002; Grosbois and Thompson, 2005), with important consequences for seabird population dynamics.

My thesis work was conducted within the framework of the European Commission project ‘Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries’ (IMPRESS). The overall objective of the project was to determine the relationship between hydrography, relevant sandeel population characteristics (i.e. the temporal and spatial patterns in abundance and age- and size distributions), and the foraging performance of groups of seabirds. The ultimate goal was to develop exploitation strategies for the industrial sandeel fishery that mitigate the impact on seabirds. It is extremely difficult to establish a causal link between the sandeel fishery in the North Sea and the decreased reproductive performance of seabird species in the area. However, when trying to develop management schemes for the North Sea sandeel fishery that would minimise the possible impact on seabirds, it is essential to evaluate the overall performance of seabirds in their environment and investigate possible constraints. For this, we need detailed information about their foraging activity and the associated energetic costs. Based on this information we can estimate the daily energy expenditure (DEE) and, assuming that birds maintain an energetic balance, this should represent their required daily energy intake. If we also have information about the birds' diet composition, the energetic content of the diet, and digestive efficiencies, we can estimate the daily food intake (DFI). From a detailed time-activity budget we can then also estimate required prey-capture rates (e.g. expressed in g fish caught per time spent underwater). In the context of the sandeel fishery/seabird conflict in the North Sea, it is then possible to calculate the energetic requirements of particular seabird populations or colonies, and, ideally, to define the minimum sandeel abundance required within their foraging areas.

Within this thesis work I collected detailed information on the energetic requirements of two closely related pursuit-diving seabird species during diving, the European shag and the double-crested cormorant (chapters 2 and 3). By combining the energetic information gathered for the European shag with detailed time-activity budgets for this species during chick-rearing in Scotland, it was possible to calculate their DEE for that period (chapter 6). Taking information on diet and breeding success into account, it was also possible to calculate their required DFI and prey-capture rates (CPUE). This formed the basis for a model that allowed me to investigate the scope of birds to increase their foraging effort and thereby buffer against a potential decline in sandeel abundance (chapter 6). In chapter 4, I also investigated the prey-capture behaviour of double-crested cormorants (as a proxy for European shags) foraging on juvenile rainbow trout and established a functional link between fish density and cormorant prey-capture performance. Ideally, this functional relationship between prey density and predator performance together with sandeel abundance estimates for the relevant part of the North Sea should have been incorporated in our model (chapter 6). However, for timely reasons this was not possible, so that I will discuss the implications of the latter aspects for our model in chapter 7.

Research objectives

The main objectives of the research conducted within this thesis were:

(1) To investigate in detail the energetic costs associated with diving in two foot-propelled pursuit divers, the European shag and the double-crested cormorant and examine the importance of modifying factors (depth, water temperature, feeding status; chapters 2 and 3).

(2) To study the effect of a variety of factors (prey density, prey size, light conditions, prey behaviour, water temperature, and depth) on the prey-capture behaviour and the foraging performance of cormorants feeding on live prey, and to establish a functional relationship between prey density and cormorant prey-capture rate (chapter 4).

(3) To investigate the capacity of four North Sea seabird species during chick-rearing to buffer the potential decline in abundance of their major prey, the lesser sandeel, with emphasis on energetic constraints (chapter 6).

For all animal work conducted within this thesis, I decided to make use of a captive setting. This allowed the controlled manipulation of a variety of factors and a detailed examination on how these factors affect either energy expenditure or foraging performance, something still impossible to achieve in a field study. Focussing especially on the double-crested cormorant also meant that it was possible to duplicate natural foraging conditions in our captive setting with respect to dive depth.

Chapter 2

Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*)

Note: this article has been published in the *Journal of Experimental Biology*.

Enstipp, M.R., Grémillet, D. and Lorentsen, S.-H. (2005). Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*). *J. Exp. Biol.* **208**: 3451-3461.

Abstract

Diving is believed to be very costly in cormorants (*Phalacrocoracidae*) when compared with other avian divers because of their poor insulation and less efficient foot-propulsion. It was therefore suggested that cormorants might employ a behavioural strategy to reduce daily energy expenditure by minimizing the amount of time spent in water. However, European shags (*Phalacrocorax aristotelis*) have been observed to spend up to 7 h day^{-1} diving in water of around 5-6 ^{o}C. To gain a better understanding of the energetic requirements in European shags we measured their metabolic rates when resting in air/water and during shallow diving using respirometry. To investigate the effects of water temperature and feeding status on metabolic rate, birds dived at water temperatures ranging from 5-13 ^{o}C in both post-absorptive and absorptive states. In parallel with respirometry, stomach temperature loggers were deployed to monitor body temperature. Basal metabolic rate (BMR) was almost identical to allometric predictions at 4.73 W·kg^{-1}. Metabolic rate when resting on water, during diving, and after feeding was significantly elevated when compared with the resting in air rate. During diving the metabolic rate of post-absorptive shags increased to 22.66 W·kg^{-1}, which corresponds to 4.8 times BMR. Minimum cost of Transport (COT) was calculated at 17.8 J·kg^{-1}·m^{-1} at a swim speed of 1.3 m·s^{-1}. Feeding before diving elevated diving metabolic rate by 13 % for up to 5 h. There was a significant relationship between diving metabolic rate and water temperature, where metabolic rate increased as water temperature declined. Thermal conductance when resting in air at 10–19 ^{o}C was 2.05 W·m^{-2}·^{o}C^{-1} and quadrupled during diving (7.88 W·m^{-2}·^{o}C^{-1}). Stomach temperature when resting in air during the day was 40.6 ^{o}C and increased during activity. In dive trials lasting up to 50 min stomach temperature fluctuated around a peak value of 42.0 ^{o}C. Hence, there is no evidence that European shags might employ a strategy of regional hypothermia. The energetic costs during shallow diving in European shags are considerably lower than what has previously been reported for great cormorants (*P. carbo*) and are comparable to other foot-propelled divers. The lower dive costs in shags might be the consequence of a more streamlined body shape reducing hydrodynamic costs as well as a greater insulative plumage air layer (estimated to 2.71 mm), which reduces thermoregulatory costs. The latter might be of great importance for shags especially during winter when they spend extended periods foraging in cold water.

Keywords: metabolism, diving, thermoregulation, European shag, energetics, HIF.

Introduction

Seabirds face an energetically challenging situation when diving in cold water. As homeotherms, avian divers regulate their body temperature within a narrow range, with core body temperatures typically between 38 and 42 ^{o}C (Dawson and Whittow, 2000). Water has a heat capacity 4000 times greater than that of air and a thermal conductivity 25 times that of air. Hence, cold water is an enormous heat sink. Unless properly insulated, birds will lose heat very rapidly in cold water and the thermoregulatory costs might be a great burden to the overall energy budget. Although a body of information on the diving energetics of wing-propelled divers (especially penguins) has emerged in recent years (for review see Ellis and Gabrielsen, 2002), measurements of diving costs for foot-propelled divers are scarce. Apart from diving ducks, the only foot-propelled pursuit divers that have been investigated are the two sub-species of the great cormorant (*Phalacrocorax carbo sinensis*, Schmid et al., 1995; *P. carbo carbo*, Grémillet et al., 2001; Grémillet et al., 2003), while Ancel et al. (2000) investigated the metabolic rate of Brandt's cormorants (*P. penicillatus*) during surface swimming.

Great cormorants and European shags (Phalacrocorax aristotelis) are foot-propelled pursuit divers that forage on benthic and pelagic fish, which they catch inshore. Both species range from mild temperate climatic zones to thermally challenging arctic zones (Johnsgard, 1993). The plumage of shags and cormorants is supposedly wettable (Rijke, 1968) and the plumage air volume is reduced when compared with other aquatic birds (Wilson et al., 1992; Grémillet et al., 2005a), reducing buoyancy. Buoyancy is the dominant factor determining dive costs in lesser scaup ducks (Aythya affinis; Stephenson, 1994), hence, a reduction in buoyancy will tend to reduce dive costs. However, unlike in penguins, the sub-cutaneous fat layer of shags and cormorants is negligible and they have to rely on plumage air as an insulating layer when diving in cold water. A thinner insulating layer will make them prone to heat loss, hence, it is not surprising that cormorants and shags leave the water at the end of a foraging bout to rest on land.

Schmid et al. (1995) measured the diving metabolic rate of great cormorants (*P. c. sinensis*) as ~10-12 times their metabolic rate when resting in air (RMR). This is in strong contrast to the diving metabolic rates that have been reported for other diving birds, which typically range between 2–4 times basal metabolic rate (BMR) for wing-propelled divers and between 3–5 times BMR for foot-propelled divers (see Table 2.1). Schmid et al. (1995) attributed these exorbitant costs to the poor insulation of cormorants (supposedly wettable plumage) and the less efficient mode of propulsion (drag-based oscillations, generating thrust only during one phase of the cycle), when compared with wing-propelled divers (lift-based oscillations, generating thrust during both phases of the cycle; Lovvorn, 2001, Lovvorn et al., 2004). However, Johanssen and Norberg (2003) showed that instead of relying entirely on drag-based propulsion, great cormorants (and probably most foot-propelled divers) use a combination of drag-based and lift-based propulsion during diving, increasing hydrodynamic and, hence, energetic efficiency. Similarly, Grémillet et al. (2001) used a model integrating the effect of water temperature and dive depth on energy expenditure during diving to estimate the energetic costs of foraging great cormorants (*P. c. carbo*) in Greenland and France. They calculated that dive costs will vary between 9 and 21 times RMR (Schmid et al., 1995) when diving in shallow/warm water and deep/cold water, respectively.

These high energy costs during foraging contrast with the finding by Grémillet et al. (2003) who showed that daily food requirements in cormorants are normal for a seabird of its mass. Hence, it was suggested that cormorants might employ a behavioural strategy, whereby birds will minimize the amount of time spent in the water to reduce daily energy expenditure, especially when wintering in thermally challenging climates (Grémillet et al., 2001). Great cormorants in Greenland were observed to reduce their time spent in water from about 50 min day^{-1} in the summer to about 9 min day^{-1} in the winter (Grémillet et al., 2001). Such a strategy has not been observed in other species within the Phalacrocoracidae family. European shags wintering in Scotland for example spend up to 7 h day^{-1} diving in water of around 5-6 ^{o}C (Daunt et al., in press). Since European shags typically dive to much greater depth and for longer durations than great cormorants, the energetic challenge might be even more pronounced for them. Could it be that the energetic costs associated with foraging in Phalacrocorax are overestimated? Grémillet et al. (2005a) demonstrated that the plumage of cormorants is only partially wettable (while the outer feather part is wettable, the central part is highly waterproof) and that birds maintain a thin insulating layer of air within their plumage. Hence, insulation during diving might be better, and heat loss lower, than previously expected assuming an entirely wettable plumage. In both Bank cormorants (*P. neglectus*) and South-Georgian shags (*P. georgianus*) there is a progressive reduction in abdominal temperature throughout dive bouts (Wilson and Grémillet, 1996; Bevan et al., 1997). This abdominal temperature drop, supposedly reflecting a temperature decline in other tissues as well, was suggested as a mechanism to reduce metabolic rate during diving and increase aerobic dive duration. Given the paucity of data on the energetic costs associated with diving in foot-propelled pursuit divers and the exorbitant costs suggested by previous studies, we felt it was important to investigate the energetic costs associated with diving in another

Phalacrocorax species, the European shag. Such an investigation is especially important in light of the contrasting foraging strategies pursued by shags and cormorants during winter. The purpose of this study was: (1) to study the energetic costs associated with diving in European shags and any modifying effects of temperature and food, and (2) to assess abdominal temperature changes during diving as a potential mechanism to extend dive duration and save energy.

Materials and Methods

Three adult European shags (*Phalacrocorax aristotelis* Linnaeus), one male, two females, with a mean mass of 1.67 ± 0.28 kg (mean ± S.D.) were used in this study. Birds were captured from the Runde colony off the west coast of central Norway in June 2001. They were housed in a sheltered outdoor pen (6m long x 4m wide x 2.5 m high) with water tank access, which was part of a larger facility built alongside Hopavågen lagoon, Agdenes community, on the west coast of central Norway. Birds were fed approximately 10–20 % of their body mass daily with a mixed diet consisting of Atlantic herring (*Clupea harengus*) and saithe (*Pollachius virens*), supplemented with vitamins and minerals (‘Sea Tabs’, Pacific Research Laboratories, El Cajon, CA, USA). Body mass was determined to the nearest 25 g when birds were post-absorptive and dry, if possible every morning, using a spring balance (Salter Abbey, West Bromwich, UK). Birds maintained a stable body mass throughout most of the study (July–Oct. 2001). However, daily food intake and body mass increased in mid October, coinciding with a decline in ambient temperature. Bird capture and all experimental procedures were conducted under permission of the Directorate for Nature Management (reference number 2001/77 ARTS/VI/IDA, 446.7), the County Governor of Møre og Romsdal (reference number 1997/09618/432.41/ME), and the Norwegian Animal Research Authority (reference number 7/01).

Training protocol

Within the first week of capture, the shags were introduced to a v-shaped shallow dive trench (17.5 m long x 2 m wide x 1 m deep) that had been dug, lined with thick PVC sheeting and filled with seawater. Two submersible water pumps (ITT Flygt, Oslo, Norway) provided a continuous exchange with seawater from the adjacent lagoon (approx. 200 l min^{-1}). Over the course of 4 weeks the surface of the trench was progressively covered with transparent PVC sheets until only a small section remained open at one end. Birds that submerged here swam to the opposite end of the trench where a fish was placed, swallowed the fish underwater and returned to the uncovered section. Eventually the open section was covered by a floating platform with a metal frame in its centre which allowed placement of a plexiglass dome, serving as a respiration chamber. Starting 2 weeks before data collection birds were captured every day, weighed and placed inside the dome. Birds dived continuously, while the respirometry system was running. Training trials lasted between 10 and 30 min and ended when a bird stopped diving voluntarily for more than 5 min. At the end of a trial the bird was released from the chamber and returned to its pen.

Respirometry system

Oxygen consumption was measured using an open-circuit respirometry system (Sable Systems, Henderson, NV, USA). To measure the metabolic rate during shallow diving, we used a transparent plexiglass dome in the shape of a truncated pyramid as the respiration chamber (0.6 m long x 0.6 m wide x 0.4 m high; volume: 50 l) which was partially immersed and received outside air through small holes on its 4 sides just above the waterline. Similarly, to measure resting metabolic rate in air we used a 55 litre bucket (0.35 m diameter x 0.65 m height) with an airtight plexiglass lid where air was drawn in via 4 small side holes near its bottom. Air from the respiration chambers was fed directly into the laboratory, which was set up inside a hut adjacent to the dive trench (Fig. 2.1). Airflow from the respiration chamber was dried using silica gel before being led into a mass-flowmeter (Sierra Instruments Inc., Monterrey, CA, USA) which automatically corrected the measured flow to STPD (273 K and 101.3 kPa). A sub-sample of 10 $l \cdot min^{-1}$ was bled into a manifold from which an oxygen (paramagnetic O_2-analyser PA-1B, Sable Systems; resolution: 0.0001 %) and CO_2 analyser (Beckman LB2 Medical CO_2-analyser, Schiller Park, IL, USA; resolution: 0.01 %) sampled in parallel. All connections between the various components of the respirometry system were made with gas-impermeable Tygon tubing.

Air flow through the respiration chamber was maintained at about 10 $l \cdot min^{-1}$ during the resting in air trials and at about 80 $l \cdot min^{-1}$ during the dive trials (Piston pump, Gast Manufacturing Inc., Benton Harbour, MI, USA). Oxygen concentration inside the respiration chamber was above 20.5 % and CO_2 concentration was below 0.4 % during all trials. The gas analysers were calibrated before each trial using pure N_2, 1.03 % CO_2 (AGA, Trondheim, Norway) and outside air (set to 20.95 % O_2 and 0.03 % CO_2). Analyser drift was minimal nevertheless any drift was corrected. Before a trial the entire system was tested for leaks by infusing pure N_2 gas. Time delay between air leaving the respiration chamber and arriving at the gas-analysers was calculated by dividing the total volume of the tubing and drying columns by the corresponding flow rate. The delay was found to be 27.0 s (resting in air) and 16.8 s (diving) for the oxygen analyser and 17.8 s (resting in air) and 7.65 s (diving) for the CO_2 analyser respectively. These delay times were taken into account when calculating oxygen consumption rates ($\dot{V}o_2$) and CO_2 production rates ($\dot{V}co_2$) and relating them to diving events. The time constant of the respiration chambers was calculated to be 5.5 min for resting in air and 0.6 min for diving, respectively.

Data from the flowmeter and the gas analysers were fed into a universal interface (16 bits resolution, Sable Systems) and mean values were recorded every 1 s (dive measurements) or 5 s (BMR measurements) onto a desktop computer using Datacan (Sable Systems).

Resting metabolism

Basal metabolic rate (BMR) was measured during the night (22.00–06.00 h) and day (08.00–18.00 h) while birds were resting, post-absorptive and presumably within their thermo-neutral zone (measurements between 10 and 19 ^{o}C air temperature; using the equation given by Ellis and Gabrielsen, 2002 reveals a lower critical temperature for our birds of ~6 ^{o}C). Birds were fasted overnight or for at least 7 h before being placed inside the respiration chamber. After the initial disturbance birds calmed down quickly and sat quietly in the darkened chamber for the remainder of the trial. A stable $\dot{V}o_2$ was typically reached within the first hour of these 3 to 5 h long trials. Air temperature in the respiration chamber was monitored using a digital thermometer (Oregon Scientific, Portland, OR, USA) and usually did not differ from outside air temperature by more than ± 2 ^{o}C. Birds were familiarized with the procedure on at least two occasions before data collection began. BMR was determined from at least three trials per bird during September 2001.

Diving metabolism

Diving metabolic rate was measured in all birds during September and October 2001 in water temperatures ranging from 4.9-12.6 ^{o}C. Water temperature was measured after each set of trials 10 cm below the surface. At the beginning of a trial a bird was captured, weighed and placed inside the respiration chamber, from which it dived continuously. Through the window in the laboratory hut (Fig. 2.1) it was possible to observe the undisturbed bird. All relevant behaviour of the birds was marked onto the respirometry traces, so that behaviour as well as dive and surface events could be related to the respirometry recordings. In a subset of trials swim speed was recorded. For this an observer with a digital stopwatch was placed on a ladder 2 m above ground at the 10 m mark of the dive trench. Swim speed ($m \cdot s^{-1}$) was calculated by dividing the distance swum (10 m) by the time taken. Only dives in which birds swam in a straight line were included in the analysis. The majority of trials lasted ~20 min (range: 10–50 min) during which birds dived voluntarily and without any interference. A trial was terminated when a bird remained at the surface for more than 10 min. A maximum of 2 dive trials per bird per day were conducted.

To investigate the effect that feeding might have on diving metabolic rate birds were diving in both the post-absorptive and absorptive state. For the post-absorptive trials birds were fasted overnight for at least 15 h. For the absorptive trials birds were fed various amounts of herring (40–160 g) at various times before a trial (0.5–5 h) and/or ingested herring during a trial.

During some trials birds would dive very little or not at all but rest at the surface. Stable resting periods from these trials were selected to calculate the metabolic rate during resting on water for both the post-absorptive and the absorptive state. Only resting periods that were separated from any diving activity by at least 5 min were included in the analysis.

Stomach temperature

In parallel with the respirometry measurements, temperature loggers (MiniTemp-xl, length: 70 mm, diameter: 16 mm, weight: 25 g, resolution: 0.03 K; earth&OCEAN Technologies, Kiel, Germany) were employed with all birds to measure stomach temperature during the dive trials. Stomach temperature should reflect abdominal body temperature during post-absorptive dive trials if no food is ingested. Temperature loggers were programmed to record stomach temperature every 5 s and were fed to the birds inside a herring. The loggers were equipped with a spring crown and were not regurgitated by the birds but retrieved when the memory was filled, after about 5 days (Wilson and Kierspel, 1998). After retrieval the data were downloaded onto a laptop computer, the logger was cleaned, re-programmed and re-fed to the bird.

Data analysis and statistics

Oxygen consumption rates ($\dot{V}o_2$) were calculated using equation 3b given by Withers (1977). BMR was calculated from the lowest 15-min running average value of $\dot{V}o_2$. Although our respirometry system was sufficiently fast to allow separation of individual dive and surface events, we were interested in obtaining an estimate of the overall energetic costs associated with foraging activity. Hence, we decided to calculate diving metabolic rate (MR_d) as the mean value of $\dot{V}O_2$ during a dive bout from its start until 30 s after the last dive in a bout (i.e. MR_d = oxygen consumption during the entire dive bout divided by the sum of all dive and surface durations within that bout). A dive bout was characterised by continuous diving activity and ended by definition when the bird started other activities (e.g. wing-flapping, see Fig. 2.2) or remained at the surface for longer than 2 min (using a log-survivorship plot as bout ending criterion; Slater and Lester, 1982). Birds typically started to dive from the moment they were introduced into the respirometry chamber. Because of the intrinsic time constant of our system, however, it took approximately 1 min before our system stabilised at an equilibrium point (see Fig. 2.2). Dives performed during this time were excluded from analysis. Oxygen consumption rates (ml $O_2 \cdot min^{-1}$) were transformed to kJ using the caloric equivalent corresponding to the respiratory exchange ratio (RER) of the birds. The RER was calculated by dividing $\dot{V}CO_2$ by $\dot{V}O_2$ and averaged 0.72 ± 0.09 (mean ± S.D.) during resting in air, 0.74 ± 0.07 during post-absorptive diving and 0.76 ± 0.03 during absorptive diving. Hence, a conversion factor of 19.7 $kJ \cdot l^{-1} O_2$ (Schmidt-Nielsen, 1997) was used to transform these values to Watts (W). Mass-specific metabolic rate (in $W \cdot kg^{-1}$) is given by: $\frac{19.7 \cdot \dot{V}O_2}{60 \cdot M_b}$, where M_b is body mass in kg and $\dot{V}O_2$ the oxygen consumption rate (ml $O_2 \cdot min^{-1}$).

Cost of transport (COT in $J \cdot kg^{-1} \cdot m^{-1}$) is defined as the amount of energy required to move one unit of body mass (1 kg) over one unit of distance (1 m). We calculated COT as the energy expenditure during a dive trial ($W \cdot kg^{-1}$) divided by the mean swim speed ($m \cdot s^{-1}$) during that trial. We included only post-absorptive dive trials in the COT analysis, which spanned a temperature range of 5-13 °C.

Insight into the insulative properties of birds can be gained by calculating their thermal conductance (TC). We calculated TC for our shags (post-absorptive trials) when resting in air and water, and during diving using the following equation:

$$TC = \frac{MR}{(T_b - T_a) \cdot SA}$$

where TC is in $W \cdot m^{-2} \cdot {}^{o}C^{-1}$ and MR (metabolic rate) in W; T_b is the body temperature (mean stomach temperature during a trial) in °C, T_a is the ambient temperature in °C, and SA is the surface area in m^2, which was estimated using Meeh's formula: $SA = 10 \cdot M_b^{0.67}$ (Drent and Stonehouse, 1971), where M_b is in g and SA is in cm^2.

Stomach temperatures were analysed using Multitrace (Jensen Software Systems, Laboe, Germany). Resting values during the night and day were established from periods when birds were calm. Temperature recordings were averaged over a period of 6 h during the night (between 23.00 h and 05.00 h) and over periods of at least 2 h during the day (between 08.00 h and 18.00 h). Temperature recordings from the entire period of experimentation were included in the analysis.

Stomach temperatures during the various phases of a dive trial were taken as averages from the first and last minute of a trial ('diving start' and 'diving end' respectively), and as the single highest value during a trial ('diving peak'). Only stomach temperature recordings from birds which had not ingested food for at least 3 h were included in the analysis to exclude periods of decreased stomach temperature after food ingestion.

One-way repeated measures analysis of variance (ANOVA) with Tukey pairwise multiple comparisons was used for comparison of metabolic rate during different activities and feeding status and for comparing stomach temperatures during various phases. When single comparisons were made, as in comparing BMR measured during the day and during the night, Student's paired t-test was used. Significance was accepted at $P < 0.05$. The relationship between energy expenditure and water temperature that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz and Slinker, 1990). All mean values are presented with standard deviation (± 1 S.D.).

Results

BMR measured at night and during the day was not significantly different ($t = 0.71$; $p = 0.55$), hence the data were pooled. When resting in air (10–19 ^{o}C) BMR was 4.73 ± 0.31 $W \cdot kg^{-1}$ (Fig. 2.3). Repeated measures ANOVA comparisons of shag metabolic rate during different activities and feeding status showed that resting in water, diving, and feeding significantly elevated metabolic rates above resting rates in air ($F = 58.98$, $p < 0.001$; Fig. 2.3). Resting in water significantly elevated metabolic rate (when compared with resting in air) to 19.37 ± 0.73 $W \cdot kg^{-1}$ and 22.23 ± 3.25 $W \cdot kg^{-1}$ in the post-absorptive and absorptive state respectively. During diving metabolic rate increased further to 22.66 ± 2.81 $W \cdot kg^{-1}$ in the post-absorptive state and 25.55 ± 3.57 $W \cdot kg^{-1}$ in the absorptive state (Fig. 2.3). Metabolic rate during diving was not significantly different, however, from birds resting at the surface ($t = 1.68$, $p = 0.23$). Feeding before a trial increased the metabolic rate during diving and when resting in water by an average of 13 % and 15 % respectively (Fig. 2.3). Diving metabolic rate remained elevated for up to 5 h after feeding, which was the maximum period tested. Preening and flapping (wing flapping in preparation for take off at the end of a dive bout) was the most costly activity averaging 39.41 ± 3.09 $W \cdot kg^{-1}$ in one of the birds displaying this behaviour (Fig. 2.3).

Water temperature had a significant effect on post-absorptive diving metabolic rate, so that metabolic rate increased with a decrease in water temperature (Fig. 2.4). The equation relating post-absorptive diving metabolic rate to water temperature (T_W) was:

$$MR = 28.461 - 0.671T_W,$$

where T_W is in °C and MR is in $W \cdot kg^{-1}$ ($p < 0.01$, $t = -3.52$, $r^2 = 0.69$).

However, when diving in the absorptive state this relationship was not significant ($p = 0.45$, $t = -0.76$) most likely because of confounding factors. For these dive trials birds were fed different amounts of food at different times before diving, which could have masked the effect of water temperature on diving metabolic rate. Declining water temperatures also increased the metabolic rate of shags resting on the water surface. Resting in water of 5 °C increased the metabolic rate of shags by 17 % when compared with resting in 10 °C water. This was similar to the 16 % increase observed in metabolic rate when water temperatures declined during post-absorptive diving.

Shags swam with a mean speed of 1.1 ± 0.1 $m \cdot s^{-1}$ (range: 0.9–1.3 $m \cdot s^{-1}$) and remained submerged for a mean duration of 23.7 ± 2.9 s (max: 57 s). The mean surface interval following a dive was 31.5 ± 6.7 s and the resulting dive to pause ratio was 1.32 ± 0.40. On average 46 % of each dive cycle (dive and subsequent surface interval) was spent underwater. When plotting COT against swim speed the relationship was best described by an inverse first order polynomial regression with a minimum COT value of 17.8 $J \cdot kg^{-1} \cdot m^{-1}$ at a swim speed of 1.3 $m \cdot s^{-1}$ ($r^2 = 0.48$, $p = 0.018$).

Thermal conductance when resting in air of 10–19 °C was 2.05 ± 0.16 $W \cdot m^{-2} \cdot {}^{o}C^{-1}$ and tripled when floating on water of 5–13 °C (6.64 ± 0.28 $W \cdot m^{-2} \cdot {}^{o}C^{-1}$). Diving within the same temperature range increased thermal conductance even further to 7.88 ± 0.5 $W \cdot m^{-2} \cdot {}^{o}C^{-1}$, almost 4 times the value when resting in air. There was no detectable change in TC with a decrease in water temperature within the range tested ($p = 0.62$, $t = -0.50$).

Mean stomach temperature when resting during the day was 40.6 ± 0.2 ^{o}C which declined significantly during the night to 39.2 ± 0.1 ^{o}C (Fig. 2.5). At the start of a dive trial temperature was significantly elevated from the daytime resting value and continued to rise during diving. After about 5–10 min of diving, however, a peak was reached after which temperature started to decline (Fig. 2.2). Stomach temperature at the end of a dive trial was significantly lower than the peak value reached during diving but this drop was not significant when compared with the temperature at the start of a dive trial (Fig. 2.5). The mean temperature increase early in a dive trial was about 0.3 ^{o}C, while temperature at the end of a trial was on average about 0.6 ^{o}C below the temperature at the start. Stomach temperature changes during a dive trial and the cooling rate (^{o}C min^{-1} in water) were not affected by the water temperature during a trial. Temperature drop and cooling rate were similar during trials in warm and cold water (range: 5-13 ^{o}C).

Discussion

Diving metabolic rate

Our study shows that the energetic costs associated with shallow diving in European shags are considerably lower than in great cormorants. During post-absorptive diving in water of 5–13 ^{o}C, the mean energy consumption of shags (22.66 ± 2.81 W·kg^{-1}) was about 25 % less than in great cormorants diving under similar conditions (31.4 W·kg^{-1}, Schmid et al., 1995; 29.1 ± 3.1 W·kg^{-1}, Grémillet et al., 2003). Based on our measurement of BMR for the shags (4.73 ± 0.31 W·kg^{-1}), this would correspond to a diving metabolic rate of 4.8 times BMR, which is about half of what has been suggested for great cormorants diving in shallow and moderately warm water (9–12 times BMR; Schmid et al., 1995; Grémillet et al., 2003). This discrepancy can be partly explained by the very low resting metabolic rate (RMR) that was measured in great cormorants (3.1 W·kg^{-1} for 2.43 kg birds; Schmid et al., 1995), so that diving metabolic rates expressed as multiples of RMR become exorbitant. While this value has been used widely in the literature, it is well below the predicted BMR of 4.14 W·kg^{-1} for a seabird of its mass (Ellis and Gabrielsen, 2002) and the measured value for the japanese sub-species, *P. c. hanedae* (4.28 W·kg^{-1}, Sato et al., 1988). Using the latter value would result in a diving metabolic rate for great cormorants of between 7.3 and 6.8 times BMR.

The BMR we measured in European shags is almost identical to the predicted BMR of 4.60 W·kg^{-1}, again using the allometric equation given by Ellis and Gabrielsen (2002), which is based on 77 seabird species. It is slightly lower, however, than the BMR value for European shags measured by Bryant and Furness (1995; 5.28 ± 0.22W·kg^{-1}).

The energetic costs of diving in European shags (expressed as multiples of BMR) are thus comparable to dive costs of other foot-propelled divers that have been investigated (Table 2.1). They are, however, considerably higher than dive costs observed in most wing-propelled divers. The energetic costs associated with diving are generally higher in foot-propelled than wing-propelled divers, with diving metabolic rates ranging between 3-5 and 2-4 times BMR respectively (Table 2.1). This general difference might be the consequence of an inherently lower efficiency of foot-propulsion, which is mostly drag-based, when compared to wing-propulsion, which is mostly lift-based. (Lovvorn and Liggins, 2002). Wing propulsion allows thrust on both upstroke and downstroke, whereas foot propulsion in most species has little or no thrust on the upstroke (but see Johanssen and Norberg, 2003). While some foot-propelled divers (e.g. South Georgian shags, Bevan et al., 1997) achieve dive performances (in terms of dive depth and swim speed) that are comparable to that of wing-propelled divers, Lovvorn and Liggins (2002) suggested that they might do so at great locomotor cost.

Cormorants and shags are both foot-propelled divers, so the propulsive mechanism alone is not likely to explain the observed difference in their diving metabolic costs. However, European shags are considerably smaller in size than great cormorants and their body shape is slimmer and more streamlined when compared with the more bulky great cormorant. Hydrodynamic drag is the most important mechanical cost during steady swimming in birds that dive to depth, where work against buoyancy will be reduced. Lovvorn et al. (2001) showed that the hydrodynamic drag experienced by diving birds strongly depends on body size and shape. Hence, the drag experienced by European shags during diving might be reduced when compared with the great cormorant in turn lowering energetic costs.

Another important factor to consider is buoyancy. In fact, the high diving costs observed in foot-propelled benthivore ducks (as indicated by Table 2.1) are mostly caused by the large amount of air trapped within their respiratory system and plumage (Lovvorn and Jones, 1991). Stephenson (1994) found that buoyancy was the dominant factor determining dive costs in lesser scaups diving to the bottom of a 1.5 m deep tank. Buoyancy accounted for ~75 % of the mechanical cost of underwater locomotion in these ducks. In foot-propelled pursuit divers, such as cormorants and shags, overall buoyancy is reduced, when compared with diving ducks (Lovvorn and Jones, 1991). While this would tend to decrease diving costs, it should be stressed that cormorants and shags are still highly buoyant, answering to the demands of aerial flight. Double-crested cormorants (*P. auritus*) have a specific buoyancy of 2.7 $N \cdot kg^{-1}$ (Lovvorn and Jones, 1991) and ascend passively by means of positive buoyancy from dives to 10 m depth (Enstipp et al., 2001). Hence, work against buoyancy might still contribute heavily to the overall dive costs in cormorants and shags, especially when diving in shallow tanks. In this context it is interesting to note that cormorants evolved a dynamic buoyancy control mechanism that enables them to counter the destabilizing effects of buoyancy at shallow depth simply by tilting their body and tail (Ribak et al., 2004). While this tilting behaviour would tend to increase drag and, hence, energetic costs, the authors speculated that this might be at least partly offset by the fact that cormorants use a burst-and-glide pattern during diving. When diving in the wild, great cormorants typically descend to shallow depths, where work against buoyancy might still be substantial (mean dive depth: 3-7 m; Grémillet et al., 2001). European shags, on the other hand, dive to depths where costs associated with overcoming buoyancy will be greatly reduced (mean dive depth: 26 m, range: 4-61 m; Wanless et al., 1997), decreasing the overall dive costs in European shags when compared with great cormorants. However, since shags in our study dived within a 1m deep trench this cannot explain the measured difference in diving metabolic rate between both species.

The relatively high diving costs observed in cormorants and shags might also be the result of their poor insulation, increasing thermoregulatory costs. In support of this, Table 2.1 shows that the metabolic rates of ducks resting on water are similar to their resting rates in air, indicating a good insulation and low thermoregulatory costs. In contrast, metabolic rate in great cormorants and European shags is greatly increased when floating on water (4.5 and 4.1 times BMR respectively), indicating greater heat loss and thermoregulatory costs when compared with resting in air. Similarly, Ancel et al. (2000) reported a metabolic rate for Brandt's cormorants of 10.9 $W \cdot kg^{-1}$ when resting in warm water (20 ^{o}C) during the day. This would correspond to 2.5 times BMR (BMR predicted from the allometric equation provided by Ellis and Gabrielsen, 2002). Heat loss will be further increased during diving, when the insulating plumage air layer will be compressed by the increase in hydrostatic pressure and when movement through the water will disturb the boundary layer. De Vries and van Erden (1995) found that the thermal conductance of aquatic bird carcasses increased by a factor of 4.8 during diving when compared with air. In our study the thermal conductance of European shags increased by a factor of 3.8 during diving. In great cormorants (using data from Grémillet et al., 2003) thermal conductance was not only higher in absolute terms but it also increased by a greater factor (4.4) during diving, indicating better insulative properties in

European shags. We used the heat loss model developed by Grémillet et al. (1998) and our measurements of energy expenditure during diving to estimate the minimal insulating plumage air volume in European shags. The value of 0.38 x 10^{-3} m^3 at a depth of 1 m corresponds to a 2.71 mm air layer, which is about 60 % greater than the calculated value for great cormorants. Hence, a thicker plumage air layer in shags will provide a better insulation, reducing heat loss during diving. This will be especially important for shags during winter, when they spend extended periods foraging in cold water. Heat generated by muscular activity during diving will also help to reduce thermoregulatory costs.

Factors modifying diving metabolic rate

Water temperature had a marked effect on metabolic rate of shags during diving and when resting in water, so that metabolic rate increased when water temperature decreased (Fig. 2.4). Relatively few studies have investigated the effect that water temperature has on the metabolic rate of unrestrained birds resting in water or diving. In tufted ducks (*Aythya fuligula*), common eiders (*Somateria mollissima*), common murres (*Uria aalge*), thick-billed murres (*Uria lomvia*), and little penguins (*Eudyptula minor*) that rest in water, metabolic rate increased with a decrease in water temperature, which was especially drastic at water temperatures below the point of thermal neutrality (Bevan and Butler, 1992; de Leeuw, 1996; Jenssen et al., 1989; Croll and McLaren, 1993; Stahel and Nicol, 1982). To our knowledge the effect of water temperature on diving metabolic rate has only been investigated in tufted ducks (Bevan and Butler, 1992; de Leeuw, 1996) and great cormorants (Grémillet et al., 2003). The increase in metabolic rate with a decrease in water temperature observed in our study during diving and when resting in water (16 % and 17 % respectively) was similar to what has been found in other aquatic birds. The following comparisons are all based on calculations covering the same temperature range investigated in our study (4.9-12.6 ^{o}C). Metabolic rate of tufted ducks resting in water and diving increased with a decline in water temperature by 12 % and 8.5 % respectively (de Leeuw, 1996). Similarly, in diving great cormorants metabolic rate increased by 17 % when water temperature declined (Grémillet et al., 2003). The greatest increase observed, however, was in common and thick-billed murres when resting in water (28 % and 30 % respectively; Croll and McLaren, 1993). It is not intuitively obvious why this temperature effect on metabolic rate should be the strongest in two species that, outside the breeding season, spend their entire time at sea with water temperatures below their lower critical temperature (15 ^{o}C; Croll and McLaren, 1993). The increase in metabolic rate of shags with declining water temperature was linear throughout the temperature range tested. This suggests that the point of thermal neutrality for European shags in water is above 12.6 °C, the highest temperature tested in our study.

The increase in metabolic rate that accompanies the process of digestion, assimilation of food and nutrient interconversion by animals is known as the 'heat increment of feeding' (HIF; Brody, 1945). Heating ingested cold food to body temperature also requires energy and will elevate metabolic rate further. Feeding before a trial elevated metabolic rate in shags during diving and when resting in water by an average of 13 % and 15 % above the post-absorptive rate respectively (Fig. 2.3). This is similar to the increase observed in common and thick-billed murres when diving after food ingestion (Fig. 1 in Croll and McLaren, 1993). An increased metabolic rate during diving would tend to reduce dive duration, as the available oxygen during a dive would be used up at a faster rate. Birds diving in the wild might therefore structure their foraging bouts accordingly. The increase in metabolic rate that we observed in our shags is lower than the increase observed in thick-billed murres after food ingestion when resting in air (40 %; Hawkins et al., 1997) or in sea otters (*Enhydra lutris*), when fed while resting in water (54 %; Costa and Kooyman, 1984). The latter authors suggested that otters might use the heat produced from the HIF to substitute for heat that otherwise has to be generated by activity or through shivering and, hence, reduce thermoregulatory costs. This could be an important energy saving mechanism especially for aquatic animals where foraging is often interspersed with long resting bouts on the water surface. However, European shags typically do not spend extended periods of rest on the water surface after a foraging bout but rather leave the water to rest on land. During chick rearing European shags in Scotland spent about 85 % of their daily time resting at the colony (Enstipp et al., in press). Cool air temperatures, wet and windy conditions are often prevalent and might require heat production which could be augmented by the HIF. Furthermore, stomach temperature of shags in our study remained elevated throughout dive trials even in 5 °C water. If this holds true also for their extended dive bouts during winter (up to 7 h; Daunt et al., in press) the additional heat generated by the HIF could be important in offsetting thermoregulatory costs during these dives. If, on the other hand, European shags, like South Georgian shags, allow body temperature to fall during these long dive bouts, the HIF might be an energetically inexpensive way of replacing heat lost during diving at the end of a foraging bout (Bevan et al., 1997). Heat generated during flight, when shags leave the foraging area might contribute even stronger to this end.

Stomach temperature

The stomach temperature patterns of diving European shags recorded in our study are similar to patterns observed in wild shags (Grémillet et al., 1998). Stomach temperature of shags in our study remained elevated throughout dive trials lasting up to 50 min in water as cold as 5 ^{o}C (Figs 2.2, 2.5). This is similar to the situation observed in great cormorants diving under comparable conditions (Schmid et al., 1995; Grémillet et al., 2001). Hence, unlike in South Georgian shags or Bank cormorants, there is no evidence that European shags or great cormorants might employ a strategy of regional hypothermia to potentially lower energetic costs and increase aerobic dive duration (Bevan et al., 1997).

Our study has shown that the energetic costs during shallow diving in European shags are considerably lower than in great cormorants and are comparable to other foot-propelled divers. This difference might be partially explained by lower hydrodynamic costs during diving in the shags, owing to their smaller size and more streamlined body shape. It might also be explained by a better thermal insulation in shags, reducing thermoregulatory costs during diving. Water temperature and feeding status had a strong impact on diving energetics in shags, so that metabolic rate increased with declining water temperatures and remained elevated after food ingestion for up to 5 h. We found no evidence that European shags might employ a strategy of regional hypothermia, since stomach temperature remained elevated throughout dive trials. Shags in this study were diving within a shallow dive trench. Hence, the effects that depth might have on the energetic costs during diving could not be evaluated. The increase in ambient pressure when diving to depth will decrease the amount of air trapped within the plumage and hence thermal insulation. The resulting increase in heat loss might outweigh any energetic advantages that a decreased buoyancy at greater depth might produce, especially if water temperature is low. However, the energetic consequences of diving to depth remain to be investigated.

Acknowledgements

Research was conducted and funded within the framework of the European Commission project ‘Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864).We wish to thank Claus Bech, Dept. of Zoology, Norwegian University of Science and Technology (NTNU) in Trondheim, Norway for help and advice with setting up the captive work with the shags at Sletvik Feltstasjon in Norway. Thanks to Geir Håvard Nymoen and Hans Jakob Runde for their help with the bird collection at Runde colony. We are indebted to Magali Grantham for her enthusiastic help with the experimental work and to Sissel Smistad who provided space for our research facility. Francis Daunt and Jean-Yves Georges are thanked for statistical advice. Francis Daunt also kindly provided the stomach temperature loggers, while Gerrit Peters was always available for advice on how to fix them. The Directorate for Nature Management, the County Governor of Møre og Romsdal, and the Norwegian Animal Research Authority granted capture and research permits for this study. We would also like to thank Olaf Vadstein and Vera Sandlund of NTNU in Trondheim for giving us unlimited access to the facilities at Sletvik Feltstasjon. Thanks to Gunna Weingartner and Dave Jones for reviewing an earlier version of this manuscript.

Table 2.1. Metabolic rates of foot-propelled and wing-propelled avian divers when resting in air and water and during diving

Species	Mass	Water temp.	BMR	Resting in water		Diving		Source
	(kg)	(°C)	(W·kg^{-1})	(W·kg^{-1})	(x BMR)	(W·kg^{-1})	(x BMR)	
Foot-propelled divers								
Aythya fuligula (Af)	0.597	13.6	4.80	5.38	1.1	18.68	3.9	Woakes and Butler, 1983
	0.578	23.0	4.80	5.96	1.2	13.53	2.8	Bevan and Butler, 1992
	0.571	14.4	4.80	7.52	1.6	15.21	3.2	Bevan et al., 1992
	0.605	7.4	4.80	10.84	2.3	18.50	3.8	Bevan and Butler, 1992
	0.600	22.0	4.80	5.83	1.2	19.00	4.0	De Leeuw, 1996
	0.600	8.0	4.80	8.33	1.7	24.50	5.1	De Leeuw, 1996
Aythya affinis (Aa)	0.591	13.0	4.80	7.90	1.6	21.00	4.4	Stephenson, 1994
Somateria mollissima (Sm)	1.79	13.7-19.0	4.20	10.05	2.4	16.09	3.8	Hawkins et al., 2000
Phalacrocorax carbo (Pc)	2.40	12.6	3.10	14.10	4.5	31.40	10.1	Schmid et al., 1995
Phalacrocorax carbo (Pc)	2.54	5.1	3.10	14.10	4.5	29.10	9.4	Grémillet et al., 2003
Phalacrocorax aristotelis (Pa)	1.67	9.0	4.73	19.37	4.1	22.66	4.8	This study
Wing-propelled divers								
Uria lomvia (Ul)	0.803	20.0	8.59	8.84	1.0	21.17	2.5	Croll and McLaren, 1993
Uria aalge (Ua)	0.836	20.0	7.18	7.30	1.0	16.51	2.3	Croll and McLaren, 1993
Eudyptula minor (Em)	1.20	21.0	3.30	6.40	1.9	7.28	2.2	Baudinette and Gill, 1985
Eudyptula minor (Em)	1.20	10.0	3.30	8.50	2.6	12.90	3.9	Bethge et al., 1997
Spheniscus humboldti (Sh)	4.60	18.0	2.45	4.25	1.7	7.24	3.0	Butler and Woakes, 1984
Spheniscus humboldti (Sh)	3.60	19.0	2.45	5.95	2.4	10.20	4.2	Luna-Jorquera and Culik, 2000
Pygoscelis antarctica (Pan)	3.80	4.0	3.72	8.75	2.3	8.90	2.4	Culik et al., 1994
Pygoscelis adeliae (Pad)	4.00	4.0	3.72	8.36	2.2	10.80	2.9	Culik et al., 1994
Pygoscelis papua (Pp)	5.50	4.0	3.89	8.19	2.1	13.70	3.5	Culik et al., 1994
Aptenodytes patagonicus (Ap)	11.50	9.1	3.50	4.65	1.3	8.40	2.4	Culik et al., 1996
Aptenodytes forsteri (Afo)	23.30	1.5-6.1	1.98	2.14	1.1	6.57	3.3	Kooyman and Ponganis, 1994

Only respirometry studies were included in Table 2.1. An energetic equivalent of 19.7 kJ·l^{-1} O$_2$ was assumed when transforming oxygen consumption to Watts. BMR values were taken from the following sources: Af and Aa: Daan, S. et al., 1990; Pc: Schmid et al., 1995; Em: Stahel and Nicol, 1988; Sh: Drent and Stonehouse, 1971; Pan and Pad: Chappell and Souza, 1988; Pp: Bevan et al., 1995b; Ap: Cherel et al., 1988; Afo: Le Maho et al., 1976. Resting in water rates were taken from Schmid et al., 1995 for Pc and from Culik et al., 1991 for Pan, Pad, and Pp.

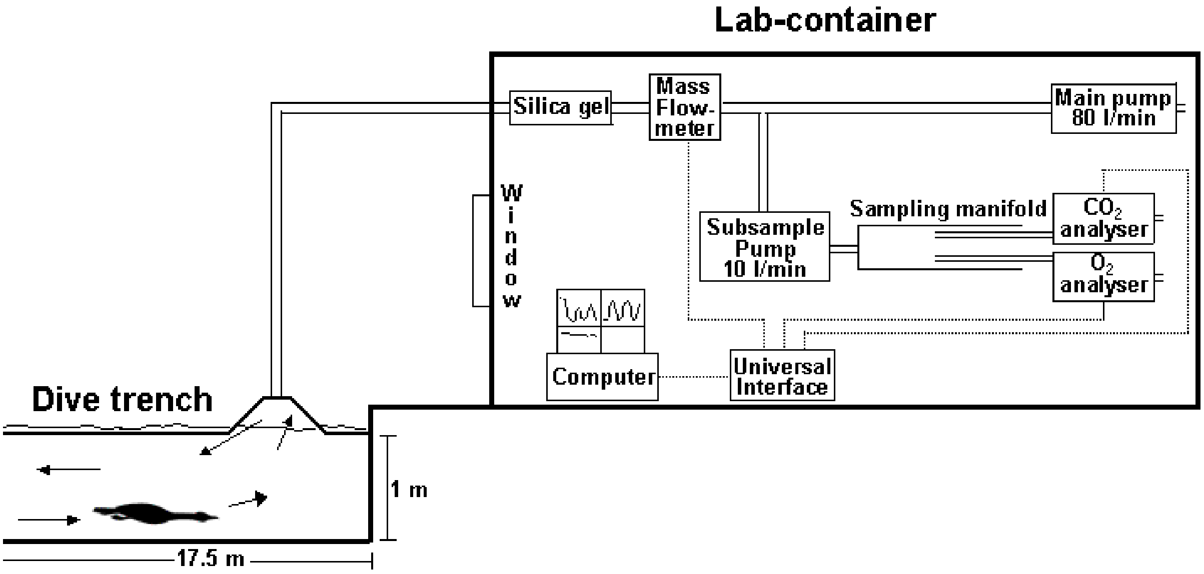


Fig. 2.1. Side view and dimensions of the dive trench and the set-up of the respirometry system within the laboratory container. The approximate underwater routes taken by the birds are indicated by the arrows, with arrowheads indicating the direction of locomotion.

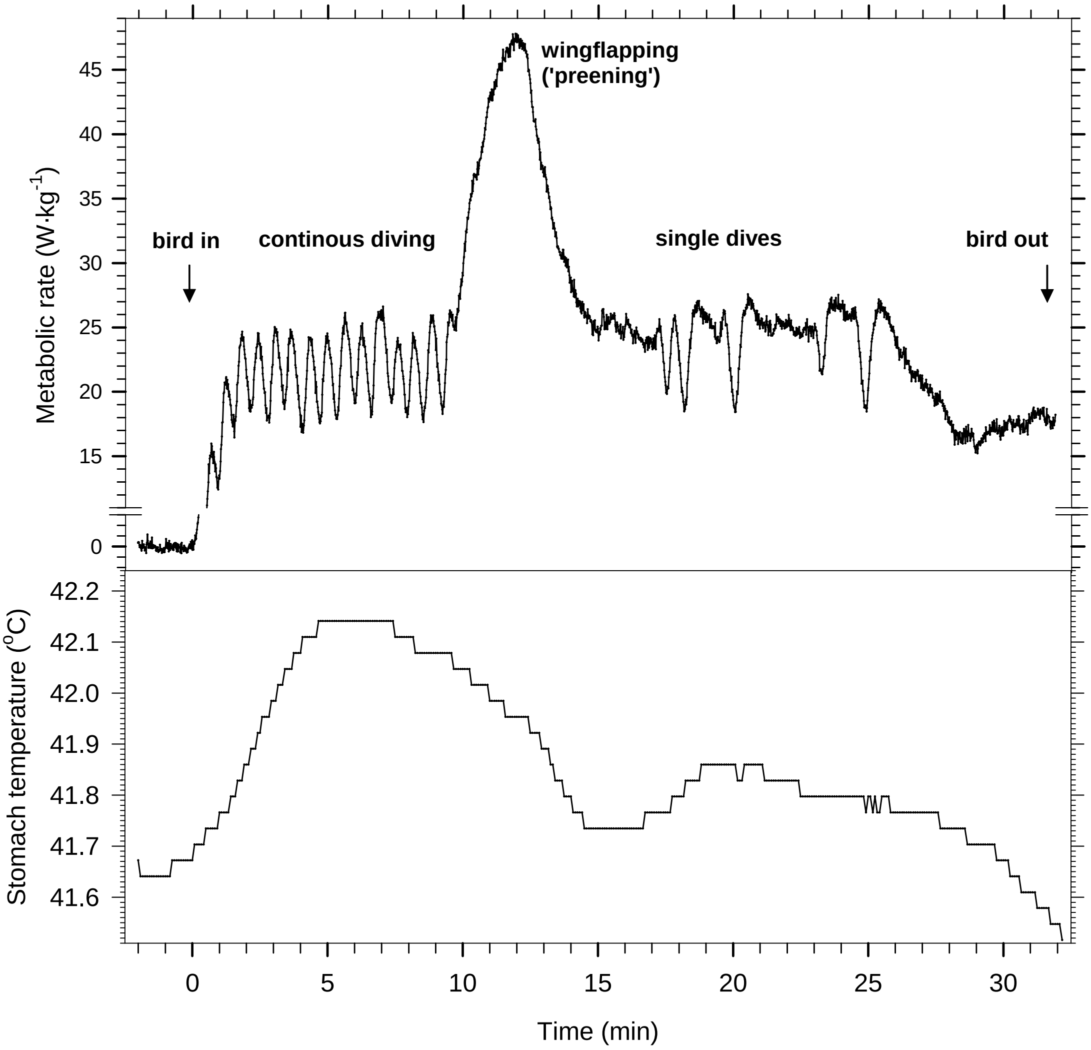


Fig. 2.2. Respirometry trace (top) and stomach temperature (bottom) of a European shag during a dive trial (post-absorptive). Arrows indicate when the bird entered and left the respirometry set-up. The trial lasted 32 min in water of 10.1 °C. Note, the upper trace does not represent instantaneous metabolic rate but gives an indication of metabolic rate during a dive trial. See 'Materials and Methods' for details on how diving metabolic rate was calculated.

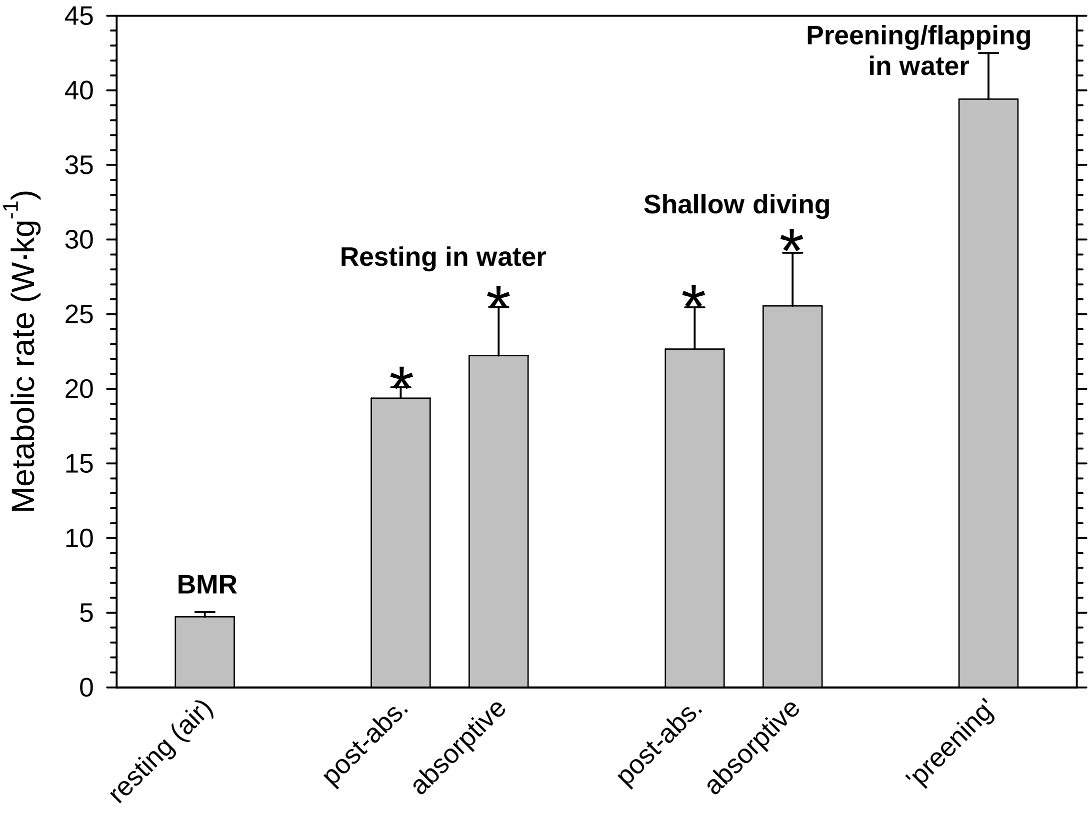


Fig. 2.3. Metabolic rate of European shags during various activities. BMR was measured in air temperatures between 10 and 19 °C. All measurements in water were made at water temperatures between 5 and 13 °C. Values are grand means ± 1 S.D., which were established from individual bird means. N = 3 birds for all activities except ‘preening’ where N = 1 bird. Asterisks indicate a significant difference from BMR.

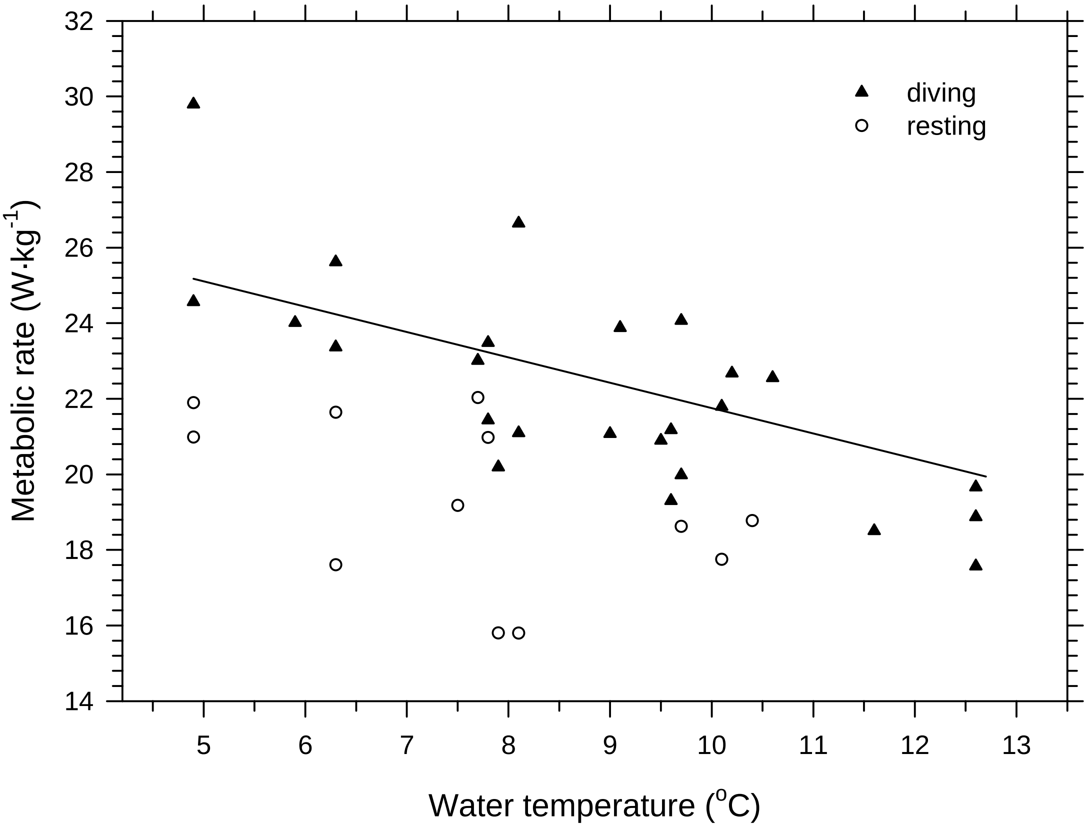


Fig. 2.4. Metabolic rate of post-absorptive European shags during diving (triangles) and when resting on the water surface (circles) at various water temperatures. There was a significant negative relationship between metabolic rate and water temperature during diving. The regression line shows the average relationship for all shags, which takes into account variability between subjects. It is best described by $y = 28.461 - 0.671x$, ($r^2 = 0.69$; N = 3 birds; n = 25 trials), where y is metabolic rate during diving and x is water temperature. During resting there was a non-significant trend for metabolic rate to increase with a decrease in water temperature (N = 3 birds, n = 12 trials).

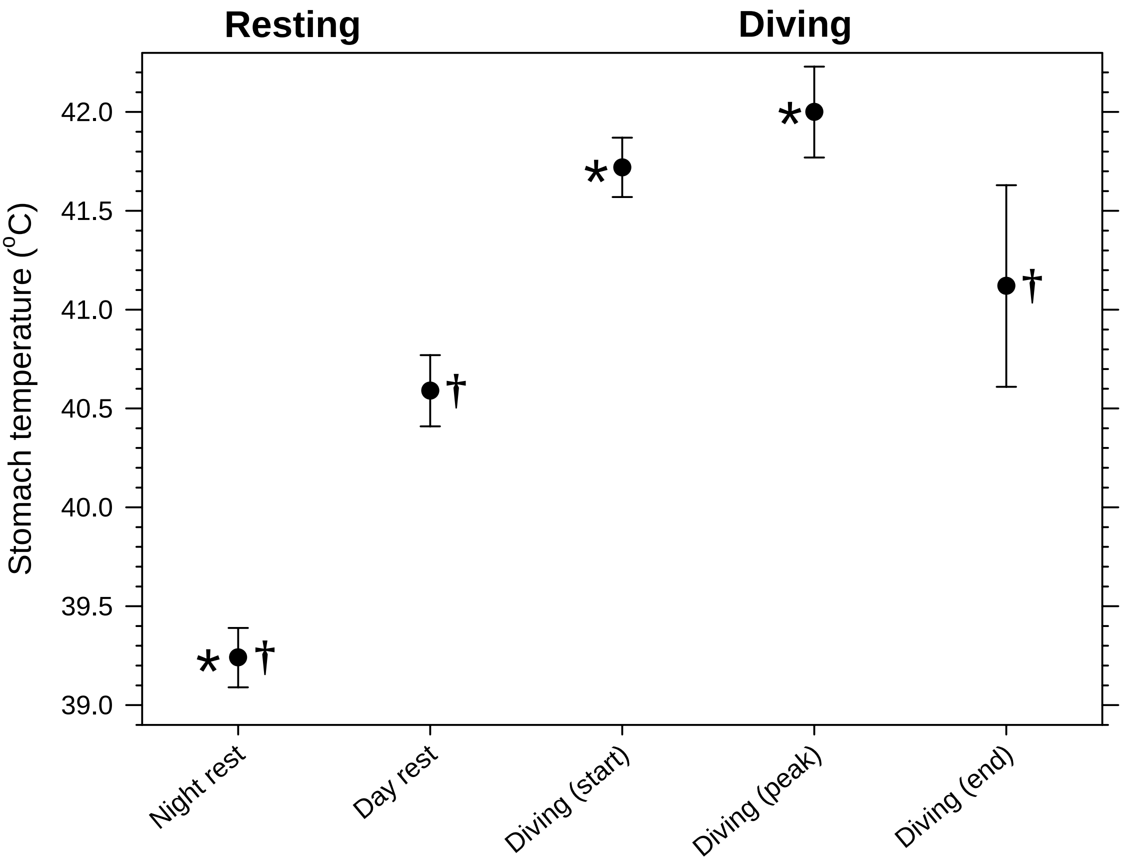


Fig. 2.5. Stomach temperatures of European shags during rest at night and during the day, and during diving. Values are grand means ±1 S.D., which were established from individual bird means. N = 3 birds. *Significantly different from day (rest) value. †Significantly different from diving (peak) value.

Chapter 3

The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*)

Note: this article has been submitted to the *Journal of Experimental Biology*.

Enstipp, M.R., Grémillet, D. and Jones, D.R. (*submitted*). The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*).

S. Taylor

Abstract

Avian divers are confronted with a number of physiological challenges when foraging in cold water, especially at depth. Besides the obvious constraint imposed by the necessity to return to the surface for gas exchange, cold water temperatures and a reduction in body insulation due to the increase in pressure with dive depth will elevate the energetic costs of foraging in these endotherm divers. The complex effect that depth has on the diving energetics of aquatic birds has largely been ignored. To date, no study has assessed the impact of depth on diving energetics over a significant depth range, naturally encountered by the diver. We used open-circuit respirometry to study the energetic requirements of a foot-propelled pursuit diver, the double-crested cormorant (*Phalacrocorax auritus albociliatus*), when diving in a shallow (1 m) and deep (10 m) dive tank, and when resting in air and water. We also investigated the modifying effects of air or water temperature and feeding status on the costs associated with diving and resting. Of all factors investigated, dive depth exercised the strongest influence on diving metabolic rate. Diving to 10 m depth increased metabolic rate on average by 22 % when compared with shallow diving. Declining temperatures in air and water significantly elevated metabolic rate of cormorants resting in air and water as well as during diving. Feeding before resting in water or diving increased metabolic rate by 5-8 % for at least 2 h. Cormorants maintained an elevated stomach temperature (> 42 ^{o}C) when resting in water and during diving, showing no signs of regional hypothermia. The elevated dive costs during deep diving, when compared with shallow diving, are most likely a consequence of the increased thermoregulatory costs associated with a greater heat loss to the water at depth. Nevertheless, our study shows that dive costs in double-crested cormorants are similar to those of other foot-propelled avian divers.

Keywords: diving energetics, depth, double-crested cormorant, temperature, HIF, heat loss.

Introduction

Avian divers take advantage of rich food sources within a variety of productive aquatic ecosystems. However, when pursuing prey underwater, they face a number of physiological challenges. As air breathers they have to return to the water surface frequently to reload their oxygen stores and unload accumulated CO_2. Therefore, a central aspect of their diving behaviour is the economic use of finite oxygen stores during submergence to maximise underwater foraging time. Anaerobic metabolism routinely contributes very little to energy production during diving (Butler, 2004) and it appears that the majority of dives under natural conditions are predominantly aerobic in nature (Butler and Jones, 1997). Aerobic dive duration is governed by two factors: (1) the amount of oxygen stored in tissues, and (2) the rate at which these stores are used. Modulation of aerobic metabolic rate will influence diving performance, so that the higher the rate of aerobic metabolism, the shorter will be the aerobic dive duration (Butler and Jones, 1997). Biotic and abiotic factors influence the metabolic rate of endotherms foraging underwater, mostly by affecting the domains of hydrodynamics and thermoregulation. In pursuit divers for example, required changes in swim speed when pursuing fast moving prey will affect metabolic rate. Since the physical work load to overcome hydrodynamic resistance increases directly with swim speed, so will the metabolic work performed by the diver (Fish, 2000). Decreasing water temperatures, on the other hand, will increase thermoregulatory costs, while metabolic rate will be further increased after food ingestion via the heat increment of feeding (HIF).

One factor, however, that has been largely ignored in most studies investigating the energetic costs of diving in endotherms is dive depth. In avian divers, the increase in ambient pressure when diving to depth will decrease the amount of air trapped within the plumage. The consequences are twofold: (1) a decrease in buoyancy and, in turn, lower mechanical costs of underwater locomotion and (2) a reduction in thermal insulation. At 10 m depth all air spaces will be reduced to half the surface volume, reducing insulation from air trapped within the plumage. The resulting increase in heat loss might outweigh any energetic advantages that might accrue from a decreased buoyancy at greater depth, especially if water temperature is low. We are only aware of one study to date that investigated the energetic consequences of diving to depth. De Leeuw (1996) found that dives to 2.2 m and 5.5 m depth were equally costly in tufted ducks (*Aythya fuligula*). One possible explanation could be that since the depth range covered in the study was rather small, the energetic savings in mechanical costs with an increase in depth (reduced buoyancy) were balanced by an increase in thermoregulatory costs. Hence, how depth shapes the energetic costs associated with diving still remains unclear.

Double-crested cormorants (*Phalacrocorax auritus*) are foot-propelled pursuit divers that forage on benthic and pelagic fish. They target their prey in the upper part of the water column (depth range observed by Ross, 1974: 1.5-7.9 m) in coastal and freshwater ecosystems. Owing to a partially wettable plumage (Grémillet et al., 2005a) buoyancy is reduced in cormorants when compared with many other avian divers (2.7 $N \cdot kg^{-1}$ at the surface for *P. auritus*; Lovvorn and Jones, 1991a), lowering mechanical costs during diving. The accompanying reduction in thermal insulation makes cormorants susceptible to substantial heat loss, especially when diving in cold water. Hence, it is generally believed that diving is very costly in cormorants when compared with other avian divers (see Table 1 in Enstipp et al., 2005). Grémillet et al. (2001) used a model integrating the effects of water temperature and dive depth on energy expenditure during diving to estimate the energetic costs of great cormorants (*Phalacrocorax carbo carbo*) during foraging. They calculated that dive costs will vary between 28 and 64 $W \cdot kg^{-1}$ (i.e. 9 to 21 times RMR; Schmid et al., 1995) when diving in shallow/warm water and deep/cold water, respectively. This has led to the suggestion that poor insulating properties of their plumage and the resulting high foraging costs might be a limiting factor for the geographic distribution of cormorants (Gaston, 2004). However, great cormorants winter in the Arctic and spend considerable time foraging in almost freezing water (Grémillet et al., 2005b). Similarly, European shags (*Phalacrocorax aristotelis*) spend up to 7 h per day foraging in water temperatures of about 5-6 ^{o}C in Scotland (Daunt et al., in press). If foraging costs are as high as expected in cormorants, then their required daily food intake (DFI) should be high compared with other seabirds. However, Grémillet et al. (1999) estimated the DFI for great cormorants to be similar to the required intake of other, well insulated seabirds, of comparable mass. Moreover, dive costs of European shags diving in a shallow trench have recently been measured and were considerably lower than previous measurements for great cormorants. Dive costs of shags were in fact similar to other foot-propelled divers and this has led to the suggestion that dive costs might be overestimated in cormorants (Enstipp et al., 2005). Given the depth range exploited by cormorants in the wild and their unique morphological features (partially wettable plumage, which reduces buoyancy but also reduces plumage insulation), makes the cormorant an ideal model to investigate the energetic consequences of diving to depth within the constraints of a captive setting.

Beyond these physiological considerations, measurements of activity specific metabolic rates and the evaluation of modifying factors are of great importance for the calculation of time-energy budgets. These allow detailed estimates of individual and population energetic requirements of seabirds, which are urgently needed for management purposes (Enstipp et al., in press). Hence, to gain a detailed understanding of cormorant energetics we studied the energetic costs of double-crested cormorants associated with (a) resting in air and (b) water and (c) during diving. To study the importance of modifying factors, we altered air temperature, water temperature, diving depth and feeding status. The hypothesis that diving to depth will increase dive costs in cormorants compared with shallow diving was tested. Also, since mechanical and thermoregulatory costs evolve in opposite directions during deep diving, we predicted that the increase in dive costs during deep diving will be less than expected from heat loss considerations alone.

Materials and Methods

Twelve adult or sub-adult double-crested cormorants (*Phalacrocorax auritus albociliatus*; minimum age 2 years) with a mean body mass of 2.10 ± 0.16 kg (mean ± S.D., range 1.81–2.47 kg) were used in this study. Ten of the birds were captured as chicks (5-6 weeks of age) from the Mandarte Island breeding colony, BC, Canada. Two birds were bred in our captive setting. All birds were well established in captivity and were housed communally in sheltered outdoor pens (8 m long x 4 m wide x 5 m high) with water tank access at the South Campus Animal Care Facility of the University of British Columbia (UBC), Vancouver, Canada. Birds were fed approximately 10 % of their body mass daily with a mixed diet consisting of Pacific herring (*Clupea pallasi*) and rainbow smelt (*Osmerus mordax*), supplemented with vitamin B1 tablets (thiamine hydrochloride, Stanley Pharmaceuticals Ltd., North Vancouver, Canada). Body mass was determined to the nearest 10 g when birds were post-absorptive and dry, usually every morning, using a digital spring balance (UWE HS-15K; Universal Weight Enterprise Co., Taipei Hsien, Taiwan). All birds maintained a stable body mass throughout the study. All experimental procedures were approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care.

Diving facilities and training protocol

Birds were split into groups of 4 individuals which were housed either within the shallow dive setting, the deep dive setting or in their outdoor pen. In the shallow dive setting, the entire surface of the tank (16.5 m long, 2 m wide, 1.5 m deep) was covered with flexible PVC mesh with the exception of a small area at the one end of the tank, that held a plexiglass dome inside a frame, which served as a respiration chamber. Birds were trained to submerge from within this plexiglass dome, swim to the opposite end of the tank to pick up a chopped herring piece and return to the dome to swallow their prey (‘shallow horizontal dives’, Fig. 3.1a). Similarly, in the deep dive setting the surface of the tank (5 m in diameter, 10 m water depth) was covered and birds were trained to dive from within the dome. Birds dived to the bottom of the tank where they picked up chopped herring pieces from a suspended feeding platform (‘deep vertical dives’, Fig. 3.1b) before surfacing into the respiration dome. Cormorants were rotated between the various settings throughout the experimental period. They were trained for a period of at least 2 weeks in a particular setting before data collection started. Double-crested cormorants in British Columbia forage in both saltwater and freshwater and the consequences for their buoyancy are negligible (see Fig 7 in Lovvorn and Jones, 1991b). Hence, both tanks were filled with freshwater which was continuously replaced at a water turnover rate of approximately 30 $l \cdot min^{-1}$ for the shallow dive tank and 100 $l \cdot min^{-1}$ for the deep dive tank. Because of this continuous mixing, water temperature in both tanks was homogenous (no stratification) and this was checked by running temperature profiles for both tanks throughout the seasons (max temperature difference between top and bottom in the deep dive tank was ± 2 ^{o}C).

Respirometry system

Oxygen consumption rates ($\dot{V}o_2$) were measured using an open-circuit respirometry system (Sable Systems, Henderson, NV, USA). To measure the metabolic rate during diving, we used a transparent plexiglass dome in the shape of a truncated pyramid as a respiration chamber (0.6 m long x 0.6 m wide x 0.4 m high; volume: 50 l) which was partially immersed and received outside air through small holes on its 4 sides just above the waterline. Similarly, to measure resting metabolic rate we used a 55 litre bucket (0.35 m in diameter x 0.65 m high) with an airtight plexiglass lid, and air was drawn in via 4 small side holes near its bottom. Air from the respiration chambers was fed directly into the laboratory, which was set up inside a hut adjacent to the dive tanks (Fig. 3.1). The main airflow from the respiration chamber was dried using silica gel before being led into a mass-flowmeter (Sierra Instruments Inc., Monterrey, CA, USA) which automatically corrected the measured flow to STPD (273 K and 101.3 kPa). A sub-sample of 10 $l \cdot min^{-1}$ was bled into a manifold from which an oxygen (paramagnetic O_2-analyser PA-1B, Sable Systems; resolution: 0.0001 %) and CO_2 analyser (Beckman LB2 Medical CO_2-analyser, Schiller Park, IL, USA; resolution: 0.01 %) sampled in parallel. All connections between the various components of the respirometry system were made with gas-impermeable Tygon tubing.

Air flow through the respiration chamber was maintained at about 10 $l \cdot min^{-1}$ during the resting in air trials, at about 45 $l \cdot min^{-1}$ during the resting in water trials and at about 80 $l \cdot min^{-1}$ during the dive trials using a vacuum pump (Piston pump, Gast Manufacturing Inc., Benton Harbour, MI, USA). Oxygen concentration inside the respiration chamber was above 20.5 % and CO_2 concentration was below 0.4 % during all trials. The gas analysers were calibrated before each trial using 99.995 % pure N_2, 1.03 % CO_2 (PraxAir, Richmond, BC, Canada) and outside air (set to 20.95 % O_2 and 0.03 % CO_2). Analyser drift was minimal but, if any occurred, it was corrected for during data analysis. Before a trial the entire system was tested for leaks by infusing pure N_2 gas. Time delay between air leaving the respiration chamber and arriving at the gas-analysers was calculated by dividing the total volume of the tubing and drying columns by the flow rate. The delay was found to be 18 s ('resting in air') and 11 s ('resting in water' and 'diving') for the oxygen analyser and 21 s ('resting in air') and 11 s ('resting in water' and 'diving') for the CO_2 analyser respectively. These delay times were taken into account when calculating $\dot{V}o_2$ and $\dot{V}co_2$ and relating them to diving events. The time constants of the respiration chambers were calculated to be 5.5 min for resting in air, 67 s for resting in water, and 37.5 s for diving. Data from the flowmeter and the gas analysers were fed into a universal interface (16 bits resolution, Sable Systems) and average values were recorded every 1 s ('resting in water' and 'diving') or 5 s ('resting in air') onto a desktop computer using Datacan (Sable Systems).

Resting metabolism

Basal metabolic rate (BMR) was measured during the day (08.00–18.00 h) while birds were resting, post-absorptive and within their thermo-neutral zone (mean air temperature was 22.1 ± 1.7 °C; range: 18.3–25.4 °C; lower critical temperature for our birds, calculated after the equation given by Ellis and Gabrielsen, 2002 should be 8-9 °C). Birds were fasted overnight (for at least 15 h) before being placed inside the metabolic chamber. After the initial disturbance birds calmed down quickly and sat quietly in the darkened chamber for the remainder of the trial. A stable $\dot{V}o_2$ was typically reached within the first hour of these 3 to 5 h long trials. Air temperature in the respiration chamber was monitored using a digital thermometer (Oregon Scientific, Portland, OR, USA) and usually did not differ from outside air temperature by more than ± 2 °C. Birds were familiarized with the procedure on at least three occasions before data collection began. BMR was determined from at least three trials per bird. To investigate the effect of air temperature on resting metabolism and to determine the lower critical temperature (below which thermoregulatory costs should increase) measurements were also conducted at various temperatures, ranging from 5 to 25 ^{o}C.

Resting in water

The metabolic costs associated with resting in water were measured in separate trials during which birds floated calmly inside the dome, on the water surface of the shallow dive tank. A metal grid mounted about 30 cm below the base of the respiration chamber prevented birds from submerging. After the initial disturbance, when introduced into the chamber, birds calmed down quickly and a stable $\dot{V}_{O_2}$ was typically established within 10 min. Trials lasted 30 min during which undisturbed birds were observed from inside a hut through a tinted glass window (Fig. 3.1a). Birds were familiarized with the procedure on at least three occasions before data collection started. To investigate the effect of water temperature on metabolic rate when resting in water, we conducted trials in water temperatures ranging from 7.8 to 15.6 ^{o}C. The effect of feeding (heat increment of feeding, HIF) on the metabolic rate during resting in water was investigated in specific trials when birds were fed a known amount of food (60 g of herring) at various times (30–120 min) before a trial. Mean water temperature during these trials was 14.6 ^{o}C (range: 13.5–15.8 ^{o}C).

Diving metabolism

Diving metabolic rate was measured in all birds during shallow and deep diving at water temperatures ranging from 6.1 to 17.5 ^{o}C. Water temperature was measured after each set of trials 10 cm below the surface. At the beginning of a trial a bird was captured, weighed and placed inside the respiration chamber. A trap door at the bottom of the dome prevented the bird from submerging directly. When the bird floated calmly and a stable $\dot{V}_{O_2}$ was established (usually within 5–10 min) the trap door was opened through a remote pulley system and diving activity began. During a trial birds dived continuously to the opposite end of the shallow dive tank or to the bottom of the deep dive tank. Through the tinted glass window in the laboratory hut (Fig. 3.1) it was possible to observe the surface behaviour of the birds without causing any disturbance. To monitor the behaviour of birds underwater, submersible cameras (Lorex, MBrands, Scarborough, ON, Canada) were positioned within the tanks and connected to a multiplexer (EverFocus Electronics Corp., Taipei, Taiwan) and a video monitor inside the hut. This was especially important in the deep dive setting where dives were classified as deep (diving to the bottom) or shallow (diving to less than 3 m of depth). Birds typically started a dive bout with an exploratory shallow dive before performing a series of deep dives to the bottom of the tank. Similarly, they terminated a deep diving bout by either remaining at the surface or by switching back to shallow diving. To avoid a mixture of shallow and deep dives within a deep dive trial as much as possible, the trap door was closed, preventing birds from submerging, as soon as it became apparent that birds had no intention to return to depth. Deep dive trials during which birds spent more than 30 % of the overall time spent submerged at shallow depths were excluded from the analysis. All relevant behaviour of the birds was marked onto the respirometry traces, so that behaviour as well as dive and surface events could be related to the respirometry recordings. The majority of shallow dive trials lasted about 20–30 min during which birds dived voluntarily and without any interference. Here a trial was terminated by remotely closing the trap door when a bird remained at the surface for more than 10 min. In the deep dive setting birds were not motivated to dive to the bottom of the tank unless food was placed there. Hence, birds ingested small herring pieces during all deep dive trials. Preliminary results from experiments during which cormorants were fed a similar amount of herring while resting in air, showed that metabolic rate was not increased during the first 10 min after ingestion (Enstipp et al., unpubl. data). Consequently the duration of deep dive trials was kept within this time frame. Therefore, 'post-absorptive deep dive trials' refers to trials where birds had been fasted overnight (at least 15 h) beforehand but ingested small amounts of herring during the trial.

To investigate the effect that feeding (HIF) might have on diving metabolic rate, dive trials were conducted in both the post-absorptive and absorptive state. For the absorptive trials birds were fed a known amount of food (60 g of herring) at various times (30–150 min) before a trial. Trials were conducted in the mornings and afternoons with a maximum of 2 dive trials per bird per day.

Stomach temperature

In parallel with the respirometry measurements, temperature loggers (MiniTemp-xl, length: 70 mm, diameter: 16 mm, weight: 25 g, resolution: 0.03 K; earth&OCEAN Technologies, Kiel, Germany) were employed with all birds to measure stomach temperature during the dive trials and when birds rested in water. Stomach temperature should reflect abdominal body temperature during post-absorptive trials if no food is ingested. Temperature loggers were programmed to record stomach temperature every 10 s and were fed to the birds inside a herring. The loggers were equipped with a spring crown and were not regurgitated by the birds but retrieved when the memory was filled, after about 10 days (Wilson and Kierspel, 1998). After retrieval the data were downloaded onto a laptop computer, the logger was cleaned, re-programmed and re-fed to the bird.

Data analysis and statistics

In a preliminary analysis oxygen consumption rates ($\dot{V}o_2$) were calculated using equation 3b given by Withers (1977), which indicated a respiratory exchange ratio (R_E) of 0.73 in post-absorptive birds resting in air. However, during some of the dive trials these values seemed unreasonably low, probably because CO_2 was absorbed by the water or because of non-pulmonary CO_2 loss by our birds (Walsberg and Wolf, 1995). Hence, for our analysis we assumed a R_E of 0.71 for all post-absorptive and 0.8 for all absorptive trials and used equation 3a from Withers (1977) to calculate oxygen consumption rates ($\dot{V}o_2$).

Metabolic rate during resting in air was calculated from the lowest 15-min running average value of $\dot{V}o_2$. Similarly, metabolic rate during resting in water was taken as the average from the lowest and stable 10 min section of $\dot{V}o_2$ from each 30 min trial. Our respirometry system was sufficiently fast to allow separation of individual dive and surface events. However, since we were interested in obtaining an estimate of the energetic costs associated with foraging activity, we decided to calculate diving metabolic rate (MR_d) as the average value of $\dot{V}o_2$ during a dive bout from its start until 30 s after the last dive in a bout:

$$\mathrm{MR_d}\ (\dot{V}o_{2\ \mathrm{dive}}) = \frac{Vo_{2\ total\ dive\ bout}}{\sum t_{dive} + \sum t_{surface}} \qquad (1)$$

where $\sum t_{\mathrm{dive}}$ and $\sum t_{\mathrm{surface}}$ are the sum of all dive and surface durations in a dive bout respectively. A dive bout was characterised by continuous diving activity and ended by definition when birds remained at the surface for longer than 100 s (using a log-survivorship plot as bout ending criterion; Slater and Lester, 1982) or when the trap door was closed (deep diving). Birds typically started to dive from the moment the trap door was opened. Because of the intrinsic time constant of our system, however, it took approximately 1 min before our system stabilised at an equilibrium point. Dives performed during this time were excluded from analysis. Oxygen consumption rates (ml $O_2 \cdot min^{-1}$) were transformed to kJ using the caloric equivalent corresponding to the assumed respiratory exchange ratio (RER). We used a conversion factor of 19.7 $kJ \cdot l^{-1} O_2$ for post-absorptive trials (RER = 0.71) and 20.1 $kJ \cdot l^{-1} O_2$ for absorptive trials (RER = 0.8; Schmidt-Nielsen, 1997) to transform these values to Watts (W). Mass-specific metabolic rate (MR in W·kg^{-1}) is given by: $\frac{19.7 \cdot \dot{V}o_2}{60 \cdot M_b}$ for post-absorptive and by $\frac{20.1 \cdot \dot{V}o_2}{60 \cdot M_b}$ for absorptive trials respectively, where M_b is body mass in kg and $\dot{V}o_2$ the oxygen consumption rate (ml O_2·min^{-1}).

Underwater filming allowed the calculation of stroke frequencies (strokes·s^{-1}) during diving as an indicator of locomotor effort. For deep diving we calculated stroke frequencies during descent (near top and near bottom) and bottom phase, while for shallow diving it was calculated for a position about halfway along the shallow dive tank. To this end we recorded the video signal together with the signal of a video date time generator (RCA, resolution: 0.1 s) onto VHS tape. Video analysis was performed on 10 sequences per bird for each category by counting the total number of strokes per sequence and dividing by the time elapsed. Duration of selected sequences ranged between 1 and 5 s.

Stomach temperatures were analysed using Multitrace (Jensen Software Systems, Laboe, Germany). Resting values during the night and day were established from periods when birds were calm. Temperature recordings were averaged over a period of 6 h during the night (between 23.00 h and 05.00 h) and over periods of at least 2 h during the day (between 08.00 h and 18.00 h). The average day temperature (‘day avg’) was taken as the mean stomach temperature during the hours of daylight (from sunrise to sunset). Stomach temperatures during the various phases of the dive and resting in water trials were taken as averages from the first and last minute of a trial (‘start’ and ‘end’ respectively), as the single highest value during a trial (‘peak’) and as the entire trial average. We included only stomach temperature recordings from birds that had not ingested food for at least 3 h in our analysis (with the exception of ‘day avg’ temperature), to exclude periods of decreased stomach temperature after food ingestion.

Thermal conductance (TC) was calculated when cormorants rested in air and water, and during shallow and deep diving (post-absorptive trials only) using the following equation:

$$\mathrm{TC} = \frac{MR}{(T_b - T_a) \cdot SA} \qquad (2)$$

where TC is in $W \cdot m^{-2} \cdot {}^{o}C^{-1}$ and MR (metabolic rate) in W; T_b is the body temperature (mean stomach temperature during a trial) in ^{o}C, T_a is the ambient temperature in ^{o}C, and SA is the surface area in m^2, which was estimated using Meeh's formula: $SA = 10 \cdot M_b^{0.67}$ (Drent and Stonehouse, 1971), where M_b is in g and SA in cm^2.

Two-way repeated measures analysis of variance (ANOVA) with Tukey pairwise multiple comparisons was used for comparison of metabolic rate during different activities at various temperatures. To investigate the effect of depth, water temperature and feeding status on cormorant diving metabolic rate we used a repeated measure ANOVA on three factors. When single comparisons were made, Student's paired t-test was used. Significance was accepted at $p < 0.05$. The relationship between energy expenditure/thermal conductance and air or water temperature that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz and Slinker, 1990). All mean values are presented with standard deviation (± 1 S.D.).

Results

BMR of double-crested cormorants was 4.56 ± 0.56 $W \cdot kg^{-1}$ (Table 3.1). Repeated measure ANOVA comparisons revealed that activity (resting in air/water, shallow/deep diving, $p < 0.001$, $F = 402.65$) and temperature (warm vs. cold; range: 5 to 25 ^{o}C in air and 6.1 to 17.5 ^{o}C in water; $p < 0.001$, $F = 96.24$) significantly affected metabolic rate (Fig. 3.2). Compared with the resting situation in air ('warm'), the metabolic rate of cormorants was significantly elevated when resting (2.5 x BMR) or diving (shallow, 4.5 x BMR and deep, 5.5 x BMR) in 'warm' water (Table 3.1).

Temperature had a significant effect on the metabolic rate of cormorants during all activities ($p < 0.001$, $F = 96.24$). Resting in air at an air temperature around or below their lower critical temperature significantly elevated metabolic rate (Figs 3.2, 3.3; mean air temperature during cold air trials: 8.6 ± 1.1 ^{o}C). When resting or diving in 'cold' water the metabolic rate of cormorants was significantly increased when compared with the respective 'warm' water trials (Table 3.1 and Figs 3.2, 3.3). In all cases there was a significant negative relationship between metabolic rates of double-crested cormorants during different activities and temperature, which allowed the calculation of linear regression equations (Table 3.2, Fig. 3.3).

Diving to depth was energetically more costly than performing shallow horizontal dives (Figs 3.2, 3.3). Again this difference was significant, when comparing shallow and deep diving while accounting for water temperature and feeding status ($p < 0.001$, $F = 83.36$).

While metabolic rate was increased after feeding this increase was not significant when the effects of temperature and activity were accounted for ($p = 0.072$, $F = 5.15$). In other words, metabolic rates in absorptive and post-absorptive trials during a particular activity (e.g. shallow diving) and at a particular temperature (e.g. warm) were not significantly different from each other (Fig. 3.2). However, metabolic rates during all absorptive trials were increased by about 5-8 % above the post-absorptive level within 30 min after feeding and remained elevated for at least 2 h.

The various factors investigated in our study (activity, temperature, depth, feeding status) were interactive and additive. While diving was more costly than resting (in water and air), descending to depth increased the energetic expenses even more. Ingesting food and decreasing water temperatures further increased the energy expenditure of cormorants. As can be seen in Table 3.1 and Fig. 3.2, the highest energy expenditure observed was during deep diving in cold water after food ingestion (absorptive), when metabolic rate increased by a factor of 6.4 x BMR.

Dive durations of birds were similar for shallow and deep diving. Surface duration, however, was significantly shorter during deep diving ($p = 0.019$, $t = 3.42$) resulting in a higher dive-pause ratio (Table 3.1). Similarly, the fraction of the dive cycle (dive and succeeding surface interval) spent underwater was higher during deep diving (60.4 %), when compared with shallow diving (53.2 %).

Stroke frequency during the early descent phase of deep dives (3.42 ± 0.25 strokes s^{-1}) was significantly elevated when compared with all other phases during deep and shallow diving ($p < 0.001$, $F = 98.98$; Fig. 3.4). Stroke frequency declined with increasing depth and reached values similar to the horizontal shallow dive situation at a depth of about 10 m (Fig. 3.4). In accordance with the changes in stroke frequency, glide duration between strokes increased with increasing depth.

Stomach temperature showed a clear diurnal pattern in which resting temperature declined significantly from $40.5 \pm 0.2\ ^{o}C$ during the day to $39.4 \pm 0.2\ ^{o}C$ during the night (Fig. 3.5). During activity temperature increased rapidly and remained at values significantly above resting. During all trials (resting in water, shallow diving) stomach temperature was elevated above 42 °C and did not decline throughout trials lasting up to 30 min in water temperatures ranging from 7.0-15.6 °C (Fig. 3.5).

With a decrease in water temperature, thermal conductance (TC) decreased significantly during deep ($p < 0.001$, $F = 19.62$) and shallow diving ($p < 0.001$, $F = 24.07$), while it changed little when birds rested in water (Fig. 3.6). Similarly, TC decreased significantly with a decrease in air temperature when birds rested in air ($p < 0.001$, $F = 5.91$).

Discussion

Our study is the first detailed investigation of the combined effects of dive depth, water temperature and feeding status on the energetic requirements of a diving endotherm. Activity-specific metabolic rates and the influence of modifying factors reported in this study will also be of great importance for estimating individual and population energetic requirements of diving seabirds.

Resting in water

Resting in water increased metabolic rate of double-crested cormorants by a factor of 2.3 and 3.2 x BMR for warm and cold water respectively (Table 3.1). This is considerably lower than what was previously reported for great cormorants (4.5 x Resting metabolic rate, RMR, Schmid et al., 1995) and European shags (4.1 x BMR, Enstipp et al., 2005) but similar to Brandt's cormorants (*Phalacrocorax penicillatus*) resting in 20 °C water during the day and at night (2.5 and 1.6 x BMR respectively; Ancel et al., 2000; BMR predicted from Ellis and Gabrielsen, 2002). When resting in water the temperature effect on metabolic rate was even stronger than during diving. Metabolic rate increased by almost 40 % within the temperature range tested (Table 3.1), resulting in the steepest regression slope (Table 3.2, Fig. 3.3). This indicates that birds might be able to use some of the heat generated by muscle activity during diving to compensate for the heat loss in cold water. Inactive birds floating at the surface, however, will have to spend additional energy for thermoregulation. Similar patterns have been observed in other avian divers, like tufted ducks (Bevan and Butler, 1992) and macaroni penguins (*Eudyptes chrysolophus*). In 6 °C water, body temperature of macaroni penguins dropped when birds remained inactive at the water surface but remained stable in birds that swam or dived (Barré and Roussel, 1986). While stomach temperature in our cormorants remained stable during both diving and resting in water, mean stomach temperature when resting in water was significantly lower than during diving (Fig. 3.5), indicating that overall heat production was greater during diving.

Dive behaviour

Dive patterns displayed by the cormorants in our study (Table 3.1) were similar to patterns observed in double-crested cormorants foraging in the wild. Ross (1974) reported mean dive and surface durations for double-crested cormorants of 25.1 s and 10.3 s, respectively, when foraging in water 1.5-7.9 m deep. In our study, surface durations between consecutive shallow dives were longer than after deep diving, resulting in a higher dive-pause ratio during deep diving. This would indicate that birds dived more efficiently during deep diving since potential underwater foraging time was increased.

Diving metabolic rate and modifying factors

Our study clearly illustrates the importance of a variety of factors (depth, temperature, feeding status) on shaping the energetic costs associated with foraging in cormorants. Dive depth had the strongest influence on dive costs. While metabolic rate increased on average by 22 % during deep diving (post-absorptive and absorptive trials) compared with shallow diving, a lower water temperature increased diving metabolic rate on average by 14 % and 17 % during post-absorptive and absorptive trials respectively (Table 3.1). Feeding before a trial increased metabolic rate during diving or when resting in water. However, the effect was small (5-8 %) when compared with the other factors investigated (Table 3.1). Since the amount of food ingested before a trial was relatively small (60 g of herring), it is conceivable that the HIF for cormorants in the wild is greater, when birds might ingest up to a few hundred grams of fish in quick succession.

Our study also shows that dive costs in double-crested cormorants are similar to other avian divers (Fig. 3.7). While dive costs in cormorants as a group tend to lie above the average relationship relating diving metabolic rate to body mass in avian divers (Fig. 3.7), this is most noticeable in the great cormorant. To allow comparison between dive cost measurements for different Phalacrocorax species, we removed the effect of water temperature on diving metabolic rate by recalculating the dive costs during shallow diving for a water temperature of 12.6 ^{o}C (the water temperature for *P. carbo sinensis* in Schmid et al., 1995). Our analysis revealed that mass-specific metabolic rates for all three cormorant species are very similar (*P. auritus*: 21.62 $W \cdot kg^{-1}$, this study, Table 3.2; *P. aristotelis*: 20.01 $W \cdot kg^{-1}$, Enstipp et al., 2005; *P. carbo carbo*: 22.85 $W \cdot kg^{-1}$, data from Grémillet et al., 2001). These mass-specific values are considerably below the dive costs previously reported for *P. carbo sinensis* by Schmid et al. (1995; 31.40 $W \cdot kg^{-1}$) and are similar to other foot-propelled divers (Table 1 in Enstipp et al., 2005).

The effect of dive depth on diving metabolic rate

The observed increase in metabolic rate during deep diving, when compared with shallow diving (Table 3.1, Fig. 3.2), might be caused (1) by the distinct increase in locomotor effort during early descent (Fig. 3.4) or (2) by an increase in heat loss as a consequence of the reduced insulative properties of the plumage.

(1) Mechanical costs

As indicated by stroke frequency, cormorants worked the hardest during the early descent phase of deep dives (Fig. 3.4). It is important here to consider the different body orientation of birds when descending in the deep dive tank or when diving in the shallow tank with no changes in depth. In the shallow tank, apart from the very short submergence and emergence to and from about 1 m depth, birds swam horizontally (with a body angle of about 0^o, i.e. parallel to the surface), comparable to the bottom phase of a deep dive (albeit at a greater buoyancy). In the deep dive tank, however, birds swam almost vertically during descent and ascent, with a body angle of about -70^o and 70^o, respectively. The higher stroke frequency we observed during descent to depth might therefore be explained by the greater mechanical work required to overcome buoyancy during vertical descent to depth, when compared with shallow horizontal diving (Lovvorn et al., 1991; Lovvorn et al., 2004). However, the increased stroke frequency could also indicate that birds submerged with a greater air volume within their respiratory system during deep diving than during shallow diving. Respiratory movements were clearly visible in preparation for deep dives, while this was not the case for shallow dives. Also, deep dives were typically initiated with a pre-dive leap (Wilson et al., 1992a), which rarely occurred at the onset of shallow dives. This could indicate that cormorants regulate their respiratory air volume in accordance with the anticipated dive depth, as has been suggested for other avian divers, namely penguins (Sato et al., 2002; Wilson, 2003).

In this context it is interesting to note that Enstipp et al. (2001) reported heart rates during deep dives of double-crested cormorants (same individuals, identical set-up) that were significantly higher than during shallow dives of similar duration. Similarly, Froget et al. (2004) found that heart rate during the first 6 s of submersion in king penguins (*Aptenodytes patagonicus*) was higher in long (deep) dives than in short (shallow) dives. For the cormorants it was argued that compression hyperoxia during descent and an assumed reduction in energetic costs associated with reduced buoyancy during deep dives would delay a chemoreceptor mediated decline in heart rate. However, based on the suggestion by Sato et al. (2002) that king penguins inhale more air prior to deep dives, Froget et al. (2004) argued that higher heart rates during the beginning of deep dives might be explained by the greater effort necessary to overcome an increase in buoyancy. The high stroke frequencies we observed during the early phase of deep dives would point in the same direction and might have contributed to the significantly higher energetic costs we measured during deep diving. Seen in this light, the observed higher heart rates during deep diving in cormorants (Enstipp et al., 2001) might be explained by the necessity to maintain a high blood flow to the hard working leg muscles, at least during early descent. On the other hand, submerging with a greater respiratory air volume and, hence, a larger oxygen store, might enable cormorants to maintain a higher arterial oxygen tension (Pa_{O_2}) in the deep diving situation despite a higher $\dot{V}o_2$ (when compared with shallow diving), delaying a chemoreceptor mediated heart rate decline.

However, the propulsive effort of cormorants was greatest during the initial descent phase of deep dives. Stroke frequency declined with increasing depth and was similar to the shallow dive frequency near the bottom of the 10 m tank. Furthermore, while birds had to continue stroking throughout shallow diving, they surfaced passively during deep diving, reducing mechanical costs. Watanuki et al. (2005) found that European shags foraging in the wild descend and ascend almost vertically (60-90° relative to sea surface). Stroke frequency during descent decreased with depth, while ascent from dives to 40 m depth was passive. Shags maintained the duration and strength of the power stroke during descent but changed glide duration between strokes (Watanuki et al., 2005). Hence, stroke frequency might be a good indicator of locomotor effort during diving in cormorants. To get a better understanding of locomotor effort during deep and shallow diving, we estimated the average stroke frequency during both modes by adding the number of strokes during the different phases of a 20 s dive and dividing by dive duration. The resulting avg stroke frequency of 1.8 and 2.1 strokes$\cdot s^{-1}$ for deep and shallow diving, respectively, indicates that overall stroke frequency and probably locomotor effort was reduced during deep diving.

(2) Thermoregulatory costs

As Wilson et al. (1992b) pointed out, if depth leads to an increase in diving metabolic rate as a direct consequence of a compromised insulative capacity will depend largely on peripheral heat conservation mechanisms such as vasoconstriction. In emperor penguins (*Aptenodytes forsteri*), among others, such a mechanism seems to be in place. During diving, birds maintain a high core temperature, while the outer body shell cools (Ponganis et al., 2003). The latter is probably a consequence of peripheral vasoconstriction and decreased plumage insulation, which increases conductive and convective heat loss to the water. The reduced thermal gradient between core and peripheral tissues will decrease heat loss to the water. Whether cormorants use a similar mechanism to reduce heat loss during diving, remains to be investigated. The fact that abdominal temperature (as measured by stomach temperature loggers) does not change significantly during post-absorptive shallow diving in double-crested cormorants (Fig. 3.5), great cormorants (Grémillet et al., 2001) and European shags (Enstipp et al., 2005), indicates that peripheral vasoconstriction is restricted to the skin or adjacent tissues. Hence, the size of the peripheral shell subjected to cooling might be smaller in these species than in South-Georgian shags (*Phalacrocorax georgianus*, Bevan et al., 1997) and possibly bank cormorants (*Phalacrocorax neglectus*, Wilson and Grémillet, 1996), in which abdominal temperature has been shown to decrease during dive bouts in the wild. Our stomach temperature recordings also suggest that double-crested cormorants do not develop a regional hypothermia during diving, a strategy supposedly pursued by expert avian divers to lower energetic costs and increase aerobic dive duration (Bevan et al., 1997; Handrich et al., 1997). We did not deploy stomach temperature loggers during deep diving, so we have no information on abdominal temperature during these dives. Previous recordings (using a thermistor positioned close to the heart alongside an ECG electrode; Enstipp, M.R., Andrews, R.A. and Jones, D.R., unpubl. data) showed that core temperature of double-crested cormorants remained stable during dives to a depth of 10 m (water temperature ~15 ^{o}C). An indication that some mechanisms for heat conservation are in place in double-crested cormorants, comes from the observation that thermal conductance (TC) declined significantly during both shallow and deep diving, when water temperature decreased (Fig. 3.6). The decrease in TC and, hence, increase in insulation did not completely prevent heat loss during diving, however, as can be seen by the increase in heat production with falling water temperature (Fig. 3.3).

The question remains, to what degree heat loss and consequently thermoregulatory costs might have contributed to the observed difference in diving metabolic rate between shallow and deep diving. De Leeuw (1996) argued that diving metabolic rate (MR_d), the way it is usually calculated in respirometry studies, only reflects the mechanical costs but not the thermoregulatory costs, which are largely paid after the end of a dive bout and, hence, are excluded from analysis. While this raises some interesting points, Fig. 3.3 clearly illustrates that thermoregulatory costs associated with diving in double-crested cormorants were included in our analysis. Furthermore, the almost identical slopes of the regression equations relating dive costs to water temperature (Table 3.2) suggest that thermoregulatory costs are similar during deep and shallow diving. However, to gain a better understanding of heat loss and potentially incurred thermoregulatory costs during diving, we conducted an analysis similar to de Leeuw (1996). To this end we calculated the 'excess diving costs' (EDC) of cormorants during deep and shallow diving in cold water (post-absorptive trials). EDC, the excess oxygen consumption over the resting rate, was calculated over the period from the first dive in a bout until metabolic rate returned to the resting level (see de Leeuw, 1996). Our analysis showed that EDC during shallow diving was about 1.5 times MR_d, whereas during deep diving it was about 2.6 times MR_d. This indicates that heat loss and thermoregulatory costs during deep diving are in fact substantially increased when compared with shallow diving. However, to study the effect of dive depth on heat loss and to evaluate how heat loss might shape diving costs in cormorants, heat flux measurements during diving, as have been conducted in marine mammals (Willis and Horning, 2005) are urgently needed. One should also keep in mind that in the wild, cormorants, like other avian divers, can potentially use a number of mechanisms to decrease thermoregulatory costs. For example, birds might be able to use the additional heat generated by the flight muscles when leaving the foraging area or they might be able to use heat generated from the HIF to substitute for thermoregulatory costs (Kaseloo and Lovvorn, 2003). These mechanisms might allow birds to make up for at least some of the incurred heat loss during diving without having to spend additional energy for thermoregulation by means of shivering or non-shivering thermogenesis. However, in our experimental set-up, capacity for these mechanisms was limited.

In former years, in lack of direct measurements, thermodynamic modelling was used to assess the impact of dive depth on the energetic costs of diving. Grémillet and Wilson (1999) for example used a theoretical relationship between dive depth and heat flux, to incorporate the increased heat loss experienced by great cormorants when diving to depth into their dive cost analysis. To compare our measurements with the model predictions, we adapted the depth-heat flux relationship from Grémillet et al. (1998) for double-crested cormorants and used the output values to calculate their energetic costs of diving to 10 m depth, as predicted by eqn. 10 in Grémillet and Wilson (1999). This modelling approach predicts a metabolic rate for double-crested cormorants diving to 10 m depth of 33.87 and 37.37 $W \cdot kg^{-1}$ when diving in warm and cold water, respectively. These values correspond to a 65 % increase in dive costs during dives to 10 m depth when compared with shallow dives (1 m). Our own measurements, however, indicate an increase of about 22 % (Table 3.1). The discrepancy between our measurements and the model predictions might be explained by the following considerations. The depth-heat flux relationship incorporated into the model is entirely based on physical properties and does not take into account any ability of birds to regulate heat flux to the environment. Furthermore, Grémillet and Wilson (1999) did not consider any effect that buoyancy changes might have on the energetic costs when diving to depth. As already pointed out, apart from the initial descent phase, the required amount of work against buoyancy in the deep diving situation is reduced and would tend to decrease mechanical costs, especially if the time spent at the bottom and during passive ascent is great compared with the descent phase. Consequently, the model of Grémillet and Wilson (1999) greatly overestimates the effect that depth has on the energetic costs of deep diving in cormorants. Hence, we confirm the hypothesis that the measured increase in dive costs during deep diving in cormorants reflects a composite of mechanical and thermoregulatory costs that evolve in opposite directions.

Our study shows that depth is an important factor to consider when assessing the energetic costs associated with underwater foraging in a diving endotherm. In contrast, most respirometry studies to date, investigating the energetic costs of diving in endotherms, have been conducted in shallow dive tanks because of logistic difficulties. When diving to depth, work against buoyancy will be greatly reduced beyond the initial 10 m, while heat loss will be greatly increased as body insulation decreases. Divers might employ morphological (e.g. subcutaneous fat layer) and/or physiological means (e.g. peripheral vasoconstriction) to reduce heat loss at depth. They might also try to counter heat loss through increased heat production or they might allow certain tissues to cool as a potential mechanism to prolong aerobic dive duration. However, thermoregulation during diving is a complex issue and still awaits its full scientific appreciation. Only recently has it become possible to record temperatures of various tissues in avian divers foraging in the wild (Bevan et al., 1997; Handrich et al., 1997; Schmidt et al., subm.) and these studies have started to shed some light into the different strategies employed by endotherm divers to maximise underwater foraging time.

The elevated dive costs we measured during deep diving in our cormorants are probably a consequence of the increased thermoregulatory costs associated with a greater heat loss to the water at depth. While we found some evidence that heat loss during deep diving might be substantially higher than during shallow diving, mechanisms of peripheral heat conservation in cormorants and other avian divers await further study. To this end, heat flux measurements, which would allow quantification of heat loss during diving, would be an important first step. Investigating further to what degree heat generated as a by-product of locomotion (diving, flying) or the HIF is used to make up for the heat loss incurred during diving, would allow the evaluation of how heat loss shapes diving costs in avian divers.

Acknowledgements

Research was conducted and funded within the framework of the European Commission project ‘Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864). Financial support was also provided by a ‘discovery grant’ and equipment grants from NSERC to D.R.J. The British Columbia Ministry of Environment granted holding permits for the double-crested cormorants. Arthur Vanderhorst and Sam Gopaul of the Animal Care Facility at UBC provided support in caring for the birds. We wish to thank Magali Grantham and Gunna Weingartner for help with the experiments and preliminary data analysis, and Dave Rosen for his advice with Datacan. Francis Daunt kindly provided the stomach temperature loggers, while Gerrit Peters was always available for advice on how to fix them. Thanks also to Jim Lovvorn and Brian Bostrom for fruitful discussions about the biomechanics of underwater locomotion and the thermoregulatory impact of deep diving.

Table 3.1. Dive patterns observed in double-crested cormorants and energy expenditures associated with different activities and feeding status

			Temperature (°C)	Energy expenditure (W·kg^{-1})	Factor (x BMR)	Dive duration (s)	Surface duration (s)	Dive/pause ratio	N$_o$ dives per bout	N	n
BMR			22.1 ± 1.0	4.56 ± 0.56						10	27
Resting in water											
	(post-absorptive)	warm	15.0 ± 0.7	10.65 ± 1.62	2.34					8	24
		cold	7.9 ± 0.0	14.76 ± 2.60	3.24					8	21
	(absorptive)	warm	14.6 ± 1.1	11.13 ± 1.80	2.44					7	36
Shallow diving											
	(post-absorptive)	warm	16.4 ± 1.1	20.16 ± 1.86	4.42	23.5 ± 2.6	20.0 ± 7.5	1.7 ± 0.6	17.3 ± 7.0	9	49
		cold	7.5 ± 0.1	23.23 ± 1.52	5.09	19.1 ± 3.2	21.3 ± 8.2	1.4 ± 0.3	9.7 ± 3.3	7	45
	(absorptive)	warm	15.5 ± 1.2	20.58 ± 2.10	4.51	23.9 ± 2.9	24.9 ± 9.8	1.5 ± 0.6	14.9 ± 5.2	9	62
		cold	7.3 ± 0.1	24.88 ± 1.96	5.46	23.1 ± 0.9	26.8 ± 9.8	1.3 ± 0.5	8.9 ± 3.4	7	23
Deep diving											
	(post-absorptive)	warm	13.9 ± 1.2	24.95 ± 0.94	5.47	21.2 ± 3.6	14.4 ± 4.3	1.7 ± 0.4	3.8 ± 0.7	7	55
		cold	7.6 ± 1.4	28.03 ± 1.37	6.15	19.1 ± 1.3	13.3 ± 2.7	1.7 ± 0.4	3.9 ± 0.4	7	77
	(absorptive)	warm	13.9 ± 1.2	25.96 ± 1.10	5.69	21.4 ± 3.9	14.6 ± 3.8	1.7 ± 0.3	4.5 ± 1.3	7	61
		cold	7.7 ± 1.3	29.20 ± 2.04	6.40	19.3 ± 1.8	12.9 ± 2.8	1.7 ± 0.4	4.7 ± 0.6	7	68

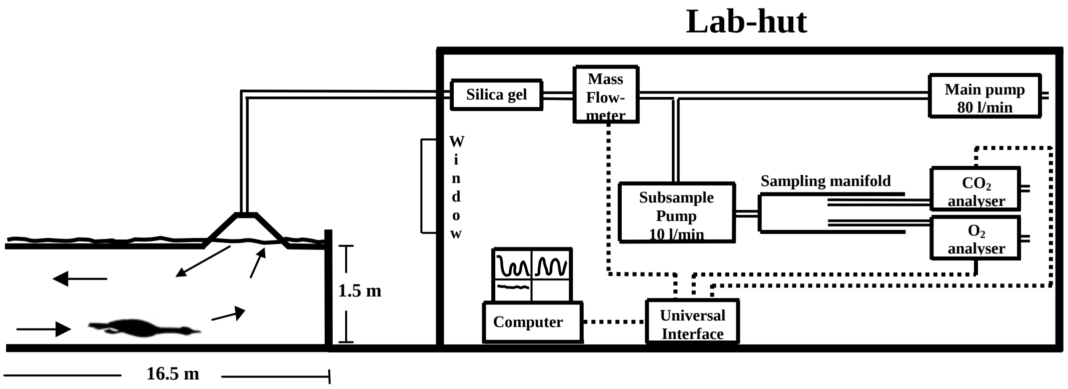
Values are grand means ± 1 S.D. which were established from individual bird means. Temperature refers to air temperature in case of 'BMR' and to water temperature in all other cases. 'Factor' is the energy expenditure of the respective activity expressed in multiples of BMR. All behavioural parameters given for 'deep diving' exclude individual shallow dives that birds might have performed during a deep dive trial. N gives the number of birds, while n refers to the number of trials.

Table 3.2. Equations for linear regressions of resting and diving metabolic rates (W·kg^{-1}) of double-crested cormorants against temperature (^{o}C)

	Temperature (^{o}C)	Intercept	Slope	N	n	r^2	P
Resting in air (post-absorptive)	16.6 (6.2–25.4)	6.994 ± 0.27	- 0.117 ± 0.015	10	62	0.73	< 0.001
Resting in water (post-absorptive)	11.7 (7.8–15.6)	19.880 ± 0.87	- 0.620 ± 0.072	9	45	0.78	< 0.001
Shallow diving (post-absorptive)	12.1 (7.1–17.5)	26.676 ± 0.46	- 0.401 ± 0.033	9	94	0.77	< 0.001
Shallow diving (absorptive)	13.1 (7.0–17.1)	28.953 ± 0.77	- 0.533 ± 0.054	9	85	0.70	< 0.001
Deep diving (post-absorptive)	10.2 (6.1–15.4)	30.920 ± 0.43	- 0.418 ± 0.038	8	132	0.60	< 0.001
Deep diving (absorptive)	10.7 (6.1–15.4)	32.409 ± 0.52	- 0.462 ± 0.045	8	129	0.62	< 0.001

Regressions were determined by multiple linear regression that takes into account variability between subjects (Glantz and Slinker, 1990). Values are means ± S.E. Temperature (mean and range) refers to air temperature in case of 'resting in air' and to water temperature in all other cases. N gives the number of birds, while n refers to the number of trials.

(a) Shallow dive tank



(b) Deep dive tank

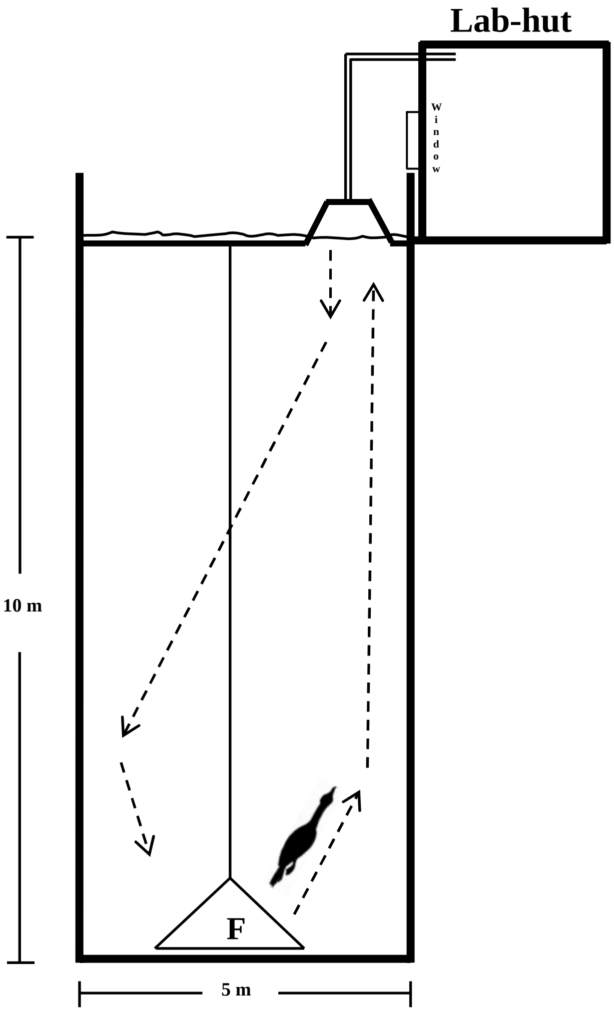


Fig. 3.1. Side view and dimensions of the shallow (a) and deep (b) dive tanks and the respirometry set-up in the laboratory hut. ‘F’ indicates the feeding spot, where birds picked up chopped herring pieces. The approximate underwater routes taken by the birds are indicated by the dashed lines, with arrowheads indicating the direction of locomotion.

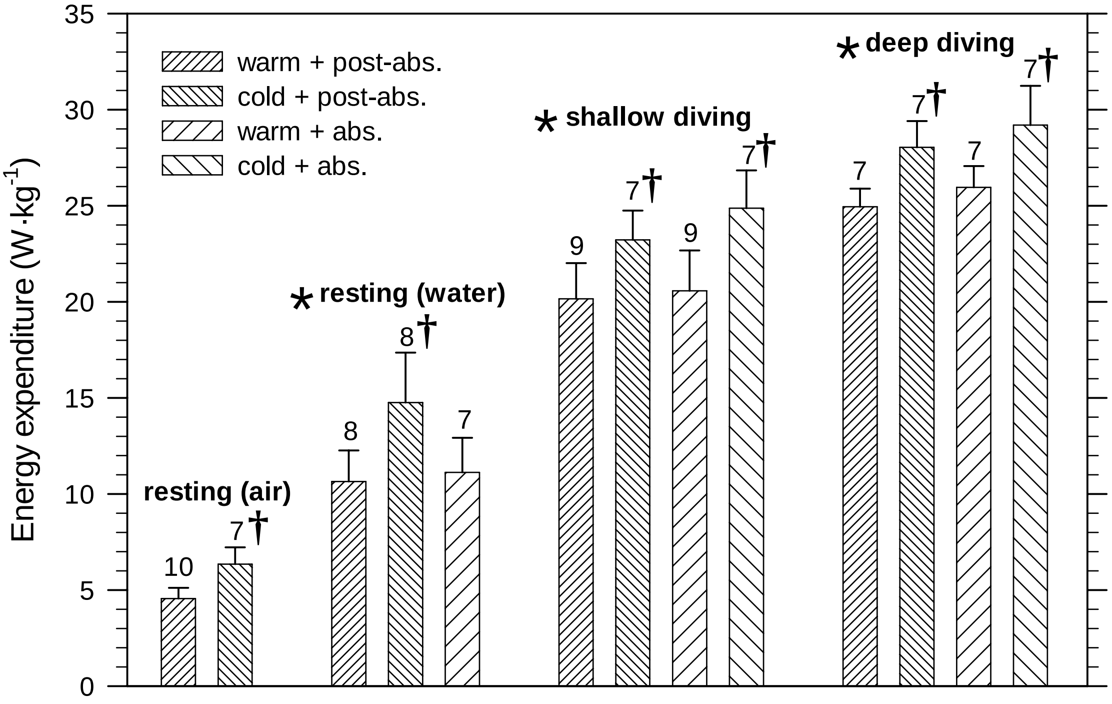


Fig. 3.2. Energy expenditure (W·kg^{-1}) of double-crested cormorants during various activities at different temperatures ('warm' and 'cold') and feeding status ('post-absorptive' and 'absorptive'). Mean temperatures when resting in air were 22.1 and 8.6 °C for 'warm' and 'cold' trials respectively. For temperature values during all other trials see Table 3.1. Energy expenditure during resting in air ('warm') was taken as BMR. Values are grand means ± 1 S.D. which were established from individual bird means. Values above the columns indicate the number of birds used. *Significantly different from resting (air) values. †Significantly different from respective 'warm' temperature values.

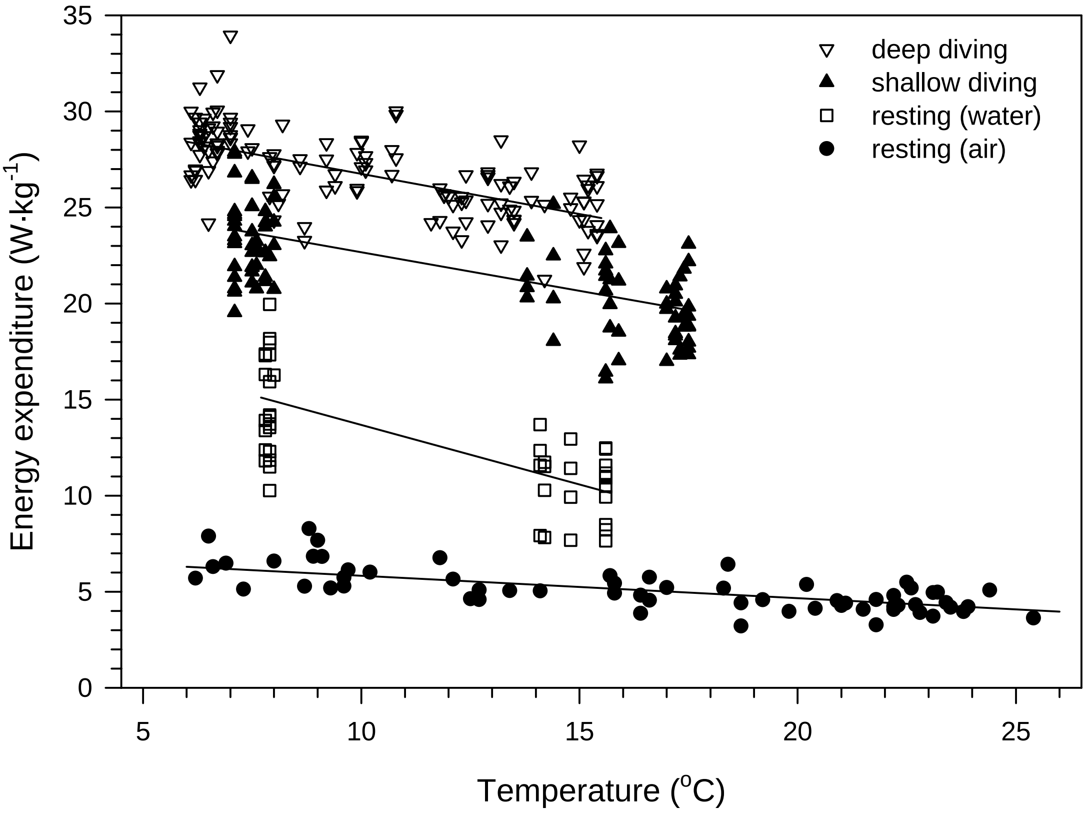


Fig. 3.3. Energy expenditures (W·kg^{-1}) of double-crested cormorants during various activities in relation to temperature (post-absorptive trials only). Temperature refers to air temperature in case of 'resting in air' and to water temperature in all other cases. See Table 3.2 for details about the regression equations and the number of trials and birds used for each category.

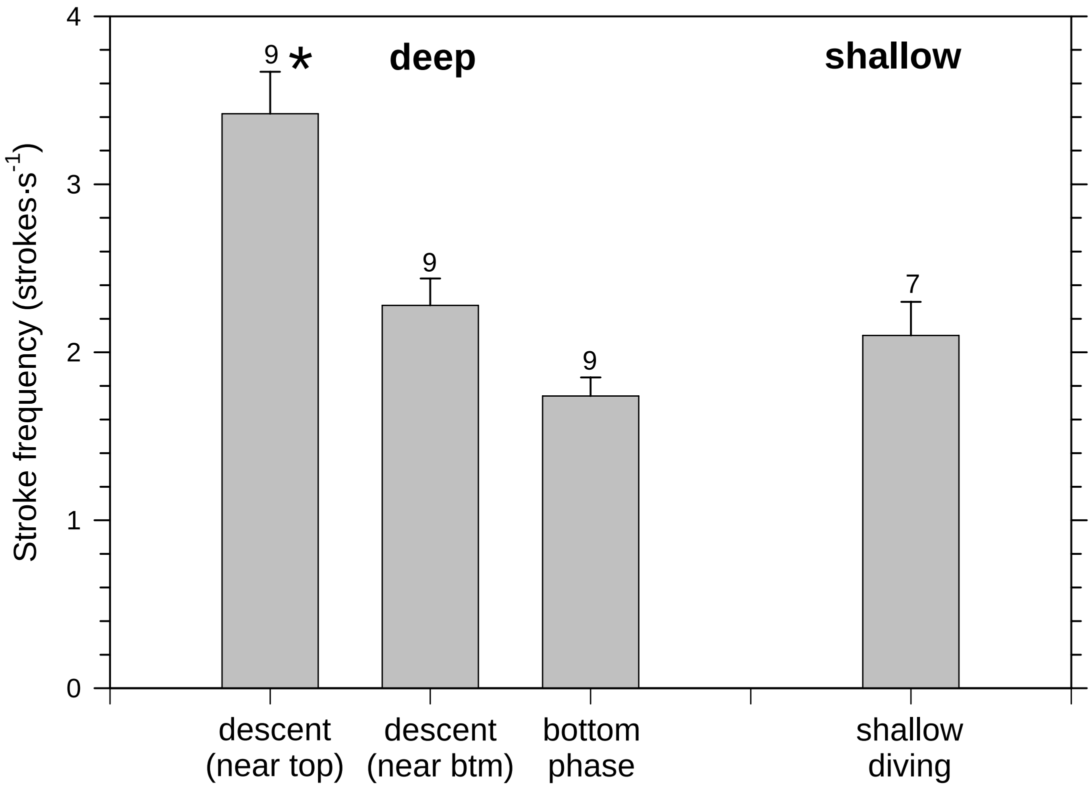


Fig. 3.4. Stroke frequencies (strokes·s^{-1})) during deep and shallow diving in double-crested cormorants. Values are grand means established from individual bird means ± 1 S.D (the number of birds used is indicated above each column) and are based on 10 observations per bird and category. Birds ascended passively during deep diving. *indicates a significant difference from shallow diving.

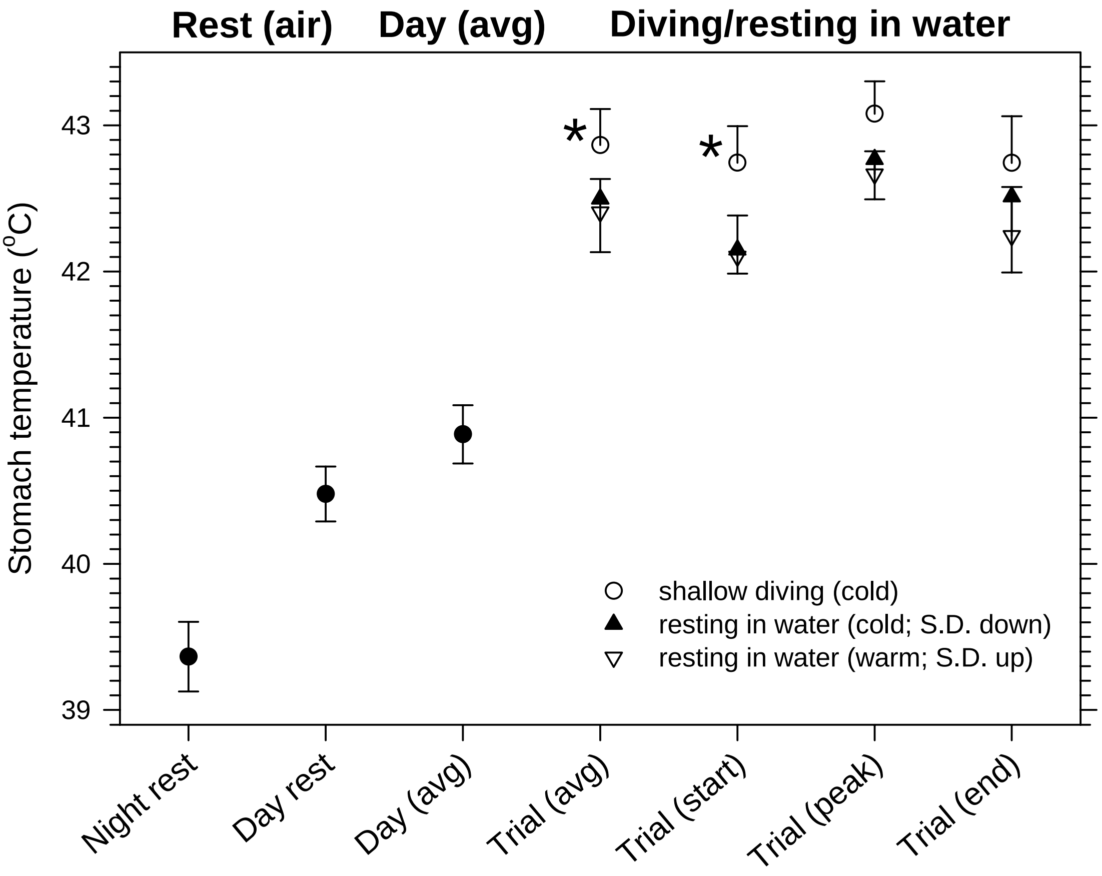


Fig. 3.5. Stomach temperatures (^{o}C) of double-crested cormorants during rest at night and during the day, during resting in 'warm' and 'cold' water (triangles), and during shallow diving in 'cold' water (circle; values are grand means ± 1 S.D.; N = 9 birds). 'Day (avg)' is the mean stomach temperature during the hours of daylight (from sunrise to sunset), which includes periods of food ingestion. Air temperatures ranged from 10-26 ^{o}C during the day and 0-11 ^{o}C during the night. All temperature values were significantly different from the 'day rest' value. *Significantly different from 'resting in water' values.

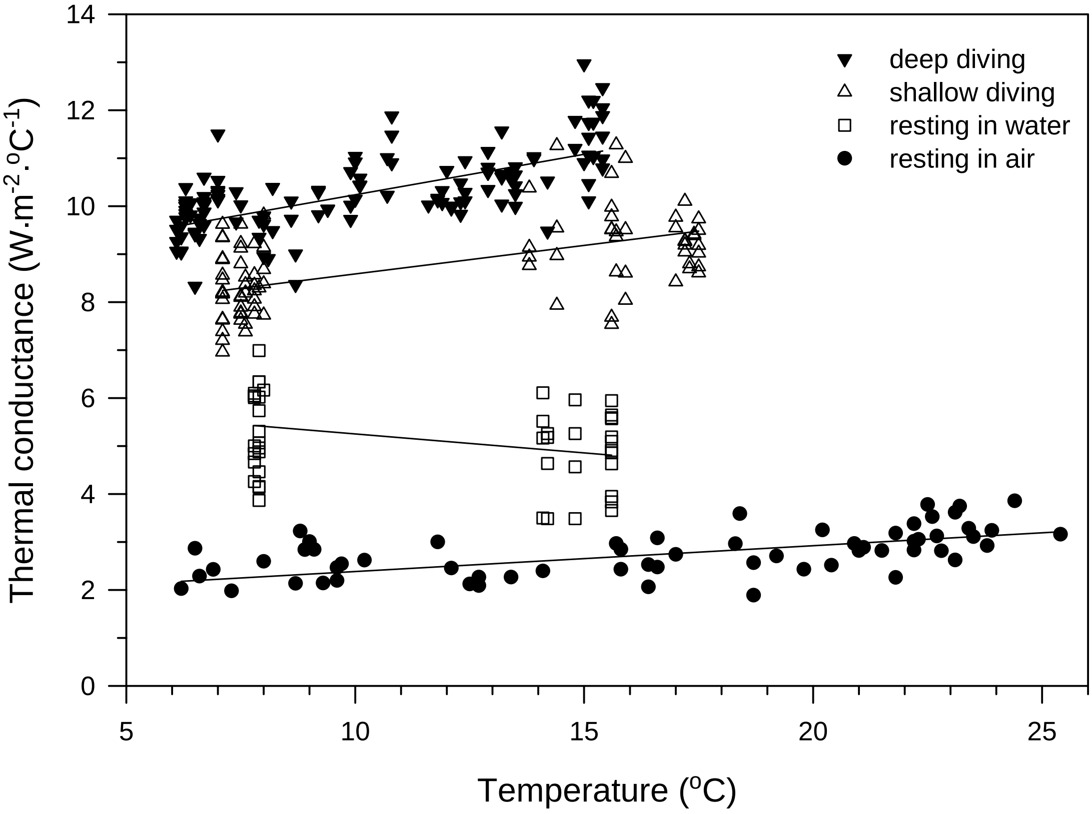


Fig. 3.6. Thermal conductance (W·m^{-2}·^{o}C^{-1}) of double-crested cormorants at various air and water temperatures during deep and shallow diving, when resting in water and when resting in air (post-absorptive trials only). Temperature refers to air temperature in case of 'resting in air' and to water temperature in all other cases. See Table 3.1 for details about the number of trials and birds used for each category.

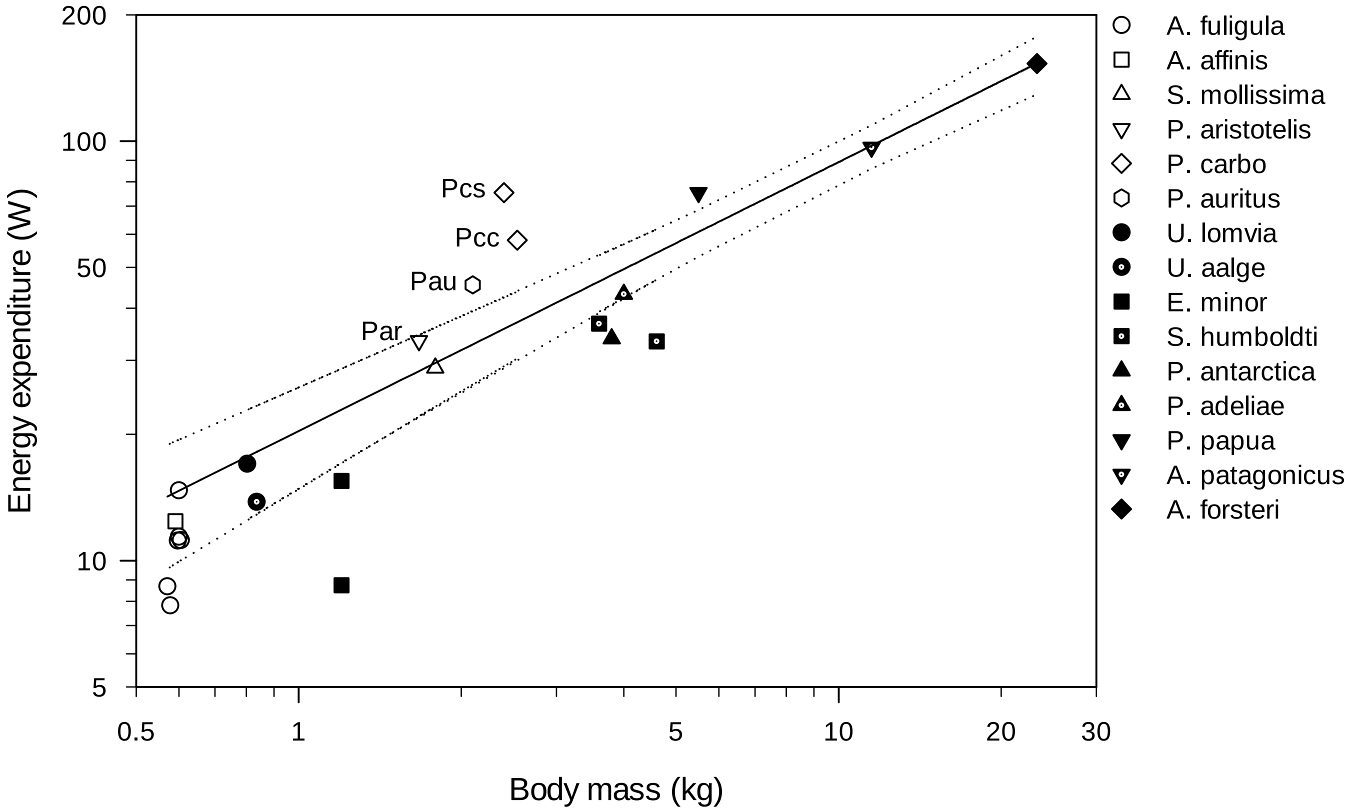


Fig. 3.7. Energy expenditure (W) of foot-propelled (open symbols) and wing-propelled (closed symbols) aquatic birds during diving. The relationship is best described by the following power function (2 varibles): Energy expenditure (W) = $20.36 \cdot M_b^{0.64}$; $r^2 = 0.87$, where M_b is body mass in kg. Note that values are plotted along a $\log_{10}$ scale. The dotted lines indicate the 95 % confidence interval. Values are based on Table 1 in Enstipp et al. (2005) and include only respirometry studies. With the exception of 2 values for *A. fuligula* (de Leeuw, 1996) and the values for *U. lomvia* and *U. aalge* (Croll and McLaren, 1993) all values are based on studies of birds diving in shallow tanks (for references see Enstipp et al., 2005). Values for the three cormorants species were recalculated for a water temperature of 12.6 °C (the water temperature for *P. carbo sinensis*, 'Pcs', in Schmid et al., 1995) by using established regression equations (*P. aristotelis*, 'Par', Enstipp et al., 2005; *P. auritus*, 'Pau', this study; *P. carbo carbo*, 'Pcc', data from Grémillet et al., 2001).

Chapter 4

Factors affecting the prey-capture behaviour of a diving predator, the double-crested cormorant (*Phalacrocorax auritus*)

Note: this article is currently in preparation.

Enstipp, M.R., Grémillet, D. and Jones, D.R. (*in prep.*). Factors affecting the prey-capture behaviour of a diving predator, the double-crested cormorant (*Phalacrocorax auritus*).

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Abstract

Seabirds are conspicuous top predators in marine ecosystems. Dramatic changes within many of these systems have been reported in recent years. Hence, it is of great importance to investigate the mechanisms operating within marine food chains. Studying the relationships linking marine top predators and their prey is therefore crucial. Unfortunately, direct and continuous observation of underwater prey-capture behaviour of diving endotherms in the wild is nearly impossible. However, in a captive setting predator-prey interactions can be studied under controlled conditions and in great detail. Using an underwater video-array, we investigated the prey-capture behaviour of a foot-propelled pursuit diver, the double-crested cormorant (*Phalacrocorax auritus*), targeting juvenile rainbow trout (*Oncorhynchus mykiss*). We tested the effects of prey density, prey size/mass, prey behaviour (shoaling vs. non-shoaling), light conditions, water temperature, and depth on the underwater foraging behaviour of cormorants. Our results show that prey density exerted the strongest influence on cormorant foraging success. While we found a linear relationship between prey density and prey capture rate, a prey density below the threshold of 2 $g \cdot m^{-3}$ resulted in proportionally lower CPUE values and this might have important implications for birds confronted with a decline in food abundance in their natural environment. Fish behaviour also strongly influenced predator-prey interactions in our study. When attacking shoaling trout rather than solitary trout, capture success of cormorants was significantly reduced, while pursuit duration was significantly increased. In contrast, prey size, light conditions, water temperature and depth did not have a measurable impact on cormorant prey-capture behaviour. This is the first in-depth experimental investigation of the underwater prey-capture behaviour of a diving endotherm. We provide input values essential for ecosystem modelling, which will help to understand predator requirements in a changing environment.

Keywords: foraging, prey-capture, CPUE, diving, prey density, functional relationship, double-crested cormorant, rainbow trout, light, shoaling.

Introduction

Predatory fish, seabirds and marine mammals are key players at the top of marine food chains and structure marine ecosystems across a wide range of spatial and temporal scales. To understand this complex system, it is essential to study the relationships linking these predators and their prey. How does prey abundance and behaviour affect predatory performance? The functional link between these variables is crucial if we want to model marine ecosystems and their response to environmental change. Unfortunately, direct observation of marine predators foraging underwater is a challenging task, which is hampered by numerous practical difficulties and is therefore rare (Axelsen et al., 2001; Similae and Ugarte, 1993). In the last two decades many of these difficulties have been overcome through the development of miniaturized electronic devices (data loggers), which can be attached to animals foraging in the wild. While this has enabled us to gather a great deal of information concerning the overall foraging patterns of marine predators (location, dive depth, dive duration, etc.), we still know little about predator-prey interactions on a fine scale. In fact, we have learnt a great deal about the behaviour of predators but little do we know about their behaviour in relation to that of their prey. Recently, animal mounted underwater cameras have been deployed (Davis et al., 1999; Takahashi et al., 2004; Grémillet et al., in press b) and allow us a glimpse into the underwater behaviour of these animals. However, currently most of these cameras are either relatively large, restricting deployment to larger species or allow only infrequent sampling. Hence, continuous direct observation of marine predators foraging in the wild is still not possible. In addition, there are a multitude of factors that have important consequences for the fine scale foraging behaviour of a predator that are impossible to control in the field. In a captive setting, however, logistic problems can be overcome and a variety of factors can be altered systematically, which allows the study of predator-prey interactions in great detail. The following introduces some of the factors constraining the fine scale foraging behaviour of diving endotherms.

Prey abundance (density)

Prey density is probably the most critical factor to predator foraging success. Holling (1959) predicted a functional link between the foraging success of vertebrate predators and prey density (functional response). For aquatic birds foraging on fish it has been shown that foraging success increases with prey density in form of a hyperbolic shaped curve, similar to the type II curve of Hollings model (Wood and Hand, 1985; Draulans, 1987; Ulenaers et al., 1992). This suggests that at high prey densities, the intake rate of a predator might be limited by its ability to handle and digest prey. In contrast, if prey density is low, a predator might have to spend an increased amount of time and energy to locate and capture prey in sufficient amounts. Predators might also be restrained in terms of prey choice and might not be able to switch to different prey items if their preferred prey is in low supply. A threshold density might exist, below which sustainable foraging might become impossible.

Prey size/mass

While there are obvious limitations on the size of prey that a predator can swallow, size has also implications for the locomotor performance of a prey species and its ability to escape a predator. Larger fish of a given species can reach higher steady speeds than smaller individuals (Beamish, 1978). It might therefore be easier for a predator to intercept a smaller fish of a given species, rather than a larger fish after a prolonged chase. In contrast, the speed achieved by fish within a given time is size independent, while manoeuvrability decreases with body length (for review see Domenici and Blake, 1997). Hence, overall manoeuvrability and acceleration of small prey might be superior to that of a large predator and might make it easier for small prey to escape.

Light levels

Most marine mammals and birds are visual predators and rely on sight to locate and capture their prey. These divers experience a decrease in illumination with increasing depth because of scatter and absorption of light by water molecules and suspended particles (turbidity). Consequently, image brightness and contrast degrade rapidly with increasing depth and/or turbidity. The amount of light available during foraging is therefore likely to be an important factor that might constrain foraging to periods with sufficient light or areas with low turbidity.

Prey behaviour

A number of behavioural patterns evolved in prey species which decrease the likelihood of being eaten by a predator. Shoaling/schooling is such an important anti-predator behaviour that evolved in many fish species that form social groups (shoals). It provides protection from predators through a number of mechanisms (see Pitcher and Parrish, 1993 for review). Targeting shoaling prey might have important consequences for a predator since it might be more difficult to pursue and capture an individual within a shoal. Shoaling in prey species might, hence, decrease the foraging success (prey-capture rate) of a predator.

For practical reasons, experimental investigation of predator-prey interactions in the aquatic environment is mostly restricted to fish (Neil and Cullen, 1974; Turesson and Broenmark, 2004), while studies on diving birds or mammals are lacking. In the few studies that experimentally investigated the foraging behaviour of aquatic birds (Wood and Hand, 1985; Ulenaers et al., 1992; Fox, 1994), observation was restricted to surface behaviour, omitting all underwater activity (i.e. search, pursuit, capture, handling) from analysis. To investigate the importance of the above mentioned factors on predator performance, we studied the fine scale prey-capture behaviour of double-crested cormorants (*Phalacrocorax auritus albociliatus*) foraging on juvenile rainbow trout (*Oncorhynchus mykiss*) using an underwater video array. Double-crested cormorants are foot-propelled pursuit divers that forage on both benthic and pelagic fish. Along the pacific coast of North America they utilise a variety of marine and freshwater habitats, where they target their prey in the upper part of the water column (typically < 20 m). Diet composition strongly reflects habitat use and pelagic/schooling fish species (especially salmonids) make up a substantial part of the prey biomass ingested in estuarine areas (Collis et al., 2002; Anderson et al., 2004). Cormorants often target juvenile salmonids, such as rainbow trout, that are released from Hatcheries as part of salmonid enhancement programs in the Pacific North-West.

The purpose of our study was to investigate in detail the underwater foraging behaviour of double-crested cormorants targeting rainbow trout of different mass/size and at different prey densities. We also investigated the effects of fish behaviour (shoaling vs. non-shoaling), light conditions, water temperature, and depth on the prey-capture behaviour of cormorants.

Materials and Methods

Nine adult or sub-adult double-crested cormorants (minimum age 2 years) with a mean body mass of 2.10 ± 0.16 kg (mean ± S.D., range 1.81–2.47 kg) were used in this study. Eight of the birds had been captured as chicks (5-6 weeks of age) from the Mandarte Island breeding colony. One bird had been bred in our captive setting. All birds were well established in captivity and were housed communally in sheltered outdoor pens (8 m long x 4 m wide x 5 m high) with water tank access at the South Campus Animal Care Facility of the University of British Columbia (UBC), Vancouver, BC, Canada. Birds were fed approximately 10 % of their body mass daily with a mixed diet consisting of Pacific herring (*Clupea pallasi*) and rainbow smelt (*Osmerus mordax*), supplemented with vitamin B1 tablets (thiamine hydrochloride, Stanley Pharmaceuticals Ltd., North Vancouver, BC, Canada). Body mass was determined regularly to the nearest 10 g when birds were post-absorptive and dry, using a digital spring balance (UWE, HS-15K; Universal Weight Enterprise Co., Taipei Hsien, Taiwan). All birds maintained a stable body mass throughout our study (June–Nov 2003). All experimental procedures were approved by the UBC Animal Care Committee

(Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care.

Video set-up

An underwater video array was set-up within a deep dive tank (5 m in diameter, 10 m water depth), consisting of 8 b/w video cameras (Model CVC6990, a light sensitive, submersible camera with a 3.6 mm wide angle lens; minimum illumination 0.01 lux; Lorex, MBrands, Scarborough, ON, Canada), 2 multiplexer (EverFocus Electronics Corp., Taipei, Taiwan), a video date time generator (RCA), 2 video recorders (Sony) and 2 video monitors (Citizen). The cameras were mounted at various positions within the deep dive tank (Fig. 4.1), which allowed for a complete visual coverage. Three cameras were mounted on tripods outside the tank, while the underwater cameras were suspended from a rope, positioned in the centre of the tank. The visual field of most cameras was overlapped, so that foraging activity could be observed from different positions. The video signals of the cameras were fed into 2 multiplexer, which projected the images onto 2 video monitors (4 cameras per monitor). One multiplexer was equipped with an internal clock (resolution: 1 s) while the signal of the other multiplexer was fed into a video date time generator (resolution: 0.1 s). Both clocks were synchronized before a series of trials started and were recorded together with the images on VHS tape. All recording equipment was kept inside a small observation hut on top of the dive tank, from which additional observations were carried out during the trials.

Fish

Juvenile rainbow trout (total length:15–22 cm, body mass: 23–92 g) were obtained from the Fraser Valley Trout Hatchery (British Columbia Ministry of Water, Land and Air Protection) in June 2002 and kept in de-chlorinated, fully aerated Vancouver city tapwater. Upon arrival fish were caught, weighed (to the nearest g), measured (to the nearest 0.5 cm) and sorted into 2 weight/size classes ('small fish' with a mass < 50 g and a total length < 18.5 cm, and 'large fish' with a mass ≥ 50 g and a total length ≥ 18.5 cm) which were kept in separate holding tanks. A linear relationship was found between fish body mass (M_b) and total body length (TL) and was best described by '$TL = 0.11 (M_b) + 12.93$' ($r^2 = 0.85$), where TL is in cm and M_b in g. Water temperature in the tanks varied according to season and ranged between 6 ^{o}C in winter and 15 ^{o}C in summer. Fish were fed commercial trout food daily (Jamiesons Feed, Richmond, BC, Canada) until used in the experiments.

At least 3 days before conducting trials, the deep dive tank was filled with chlorinated Vancouver city tapwater. To eliminate the chlorine, air was bubbled through the tank for at least 2 days before any fish were introduced into the tank. Chlorine levels were checked before fish introduction and were always less than 0.05 $\mathrm{mg \cdot l^{-1}}$, well below a level that might have affected the fish and no adverse effects were observed. Because water inside the dive tank was standing, its water temperature fluctuated more widely than the water temperature inside the fish holding tanks, where water ran through at a constant rate. However, the temperature difference between the fish holding tanks and the deep dive tank rarely exceeded 5 ^{o}C. Every morning, before a set of trials, 15–20 'small' or 'large' trout were caught, weighed (to ensure proper classification and to calculate the mean fish mass/size inside the dive tank) and introduced to the bottom of the dive tank by means of a PVC tube and a plunger. To allow fish to accommodate to the new environment, they were introduced at least 2 hrs before the start of the trials. A variety of structures (concrete blocks, PVC tubes, etc.) had been placed at the bottom of the tank to provide hiding places for the fish. While fish made use of these structures, they were generally very mobile and roamed throughout the tank after initial introduction to the bottom.

Training protocol and trials

All birds were familiar with the set-up and were used to dive to the bottom of the tank to pick up chopped herring pieces. Birds were trained to dive for live juvenile rainbow trout of varying size and density within this set-up for at least 3 weeks before data collection began. Each bird participated in one trial per day. At the beginning of a trial a bird was caught in its holding pen and introduced into the dive tank. Here the bird usually started to dive immediately. All underwater and surface activity during the trial was filmed with the video set-up. After the capture of a number of fish the bird usually left the water and wingspread for some time, often starting another foraging bout towards the end of the 30 min trial. At the end of a trial the bird was caught and returned to its holding pen.

One important factor to consider when conducting foraging behaviour experiments with captive animals is motivation. If the motivation of an animal to forage and capture prey fluctuates too much between trials, this might obscure results. In an attempt to keep bird motivation during the trials similar over the course of data collection, we kept the daily amount of food ingested by a bird constant. The amount needed for each bird to maintain motivation was established during the training trials. When the daily trials were completed, birds were handfed their remaining daily allotment. Birds were then kept post-absorptive for at least 17 hrs before a new set of trials started. Consequently, all birds cooperated well during the period of data collection and seemed highly motivated to capture live fish.

Concurrent with filming we recorded the following parameters for each trial: air temperature, water temperature, illumination, fish density in tank and mean mass/size of fish in tank. Air temperature was measured at the start of each trial, while water temperature was measured at the end of a set of trials just below the water surface and at the bottom. A light attenuation profile (at 1 m, 5 m, and 10 m water depth) was taken at the end of every single foraging trial using the GeoLT data logger (earth&OCEAN Technologies, Kiel, Germany) which recorded illuminance (lx; resolution at 100 lx was 0.03 lx). Fish density ($g \cdot m^{-3}$ or number of $fish \cdot m^{-3}$) was calculated as the overall fish mass (or number of fish) inside the dive tank at the start of a trial divided by water volume (196 m^3). Mean mass/size of fish for each trial day was calculated as the mean mass/size of the trout introduced into the dive tank in the morning. Occasionally birds did not eat all the fish that had been introduced into the dive tank in the morning. The exact number of fish left over was counted via the video set-up the following morning and checked against our records. Fish density in the dive tank was then balanced by introducing relatively fewer fish of the same weight/size class for that day. Weight/size of the individuals left over was taken as the mean weight/size from the day before.

Video analysis

Videotapes were viewed and all dive and surface times within a 30 min trial were marked down to the nearest second. Each dive cycle (dive and subsequent surface interval) was split into the following behavioural categories: searching, prey pursuit, prey handling, rest at surface. For each behavioural category observed, start and end time as well as duration was noted to the nearest second. By definition a bird was ‘searching’ during a dive until it started a ‘prey pursuit’ or surfaced. ‘Prey pursuit’ was taken as an interaction between a bird and a fish (or shoal of fish) and its initiation was typically accompanied by a change in swim direction or speed (as indicated by an increase in stroke frequency) on the birds side. ‘Prey pursuit’ ended either when the bird caught a fish or when it ‘gave up’, as indicated by a change in swim direction or speed (slowing of stroke frequency). After an unsuccessful ‘prey pursuit’ the bird, by definition, continued ‘searching’ until it either initiated a new ‘prey pursuit’ or surfaced. ‘Prey handling’ was taken as the time between prey capture and prey ingestion.

'Rest at surface' marked the time spent at the surface between consecutive dives. Additionally, we recorded a variety of observations regarding fish and bird behaviour (e.g. fish distribution within the dive tank; are fish shoaling? do single fish remain stationary or move away from an approaching bird? do birds pursue individuals or a shoal? number of fish caught, etc.).

Assessing effects on prey-capture behaviour

We investigated the effect of the following parameters on cormorant prey-capture behaviour:

(1) Prey abundance (fish density)

Fish density at the beginning of a series of daily trials was kept relatively constant (about 7 $g \cdot m^{-3}$). The fish density that a bird encountered during a trial, however, was altered by randomly changing the bird's position within the daily trial order. Fish density was highest at the beginning of the first trial of the day and declined as successive birds caught and ingested fish, so that fish density was lowest during the last trial of the day. The effect of fish density on cormorant foraging success was assessed by computing prey capture rates during a trial ('catch per unit effort', CPUE, in g fish caught$\cdot s^{-1}$ submerged) versus fish density ($g \cdot m^{-3}$) at the beginning of that trial. We also assessed the effect of fish density on search time and prey encounter rate.

(2) Prey size

We investigated the effect that fish size might have on predator performance. To this end we systematically altered the size/mass of trout introduced into the dive tank, while choosing trial days with 'small' (< 50 g, TL < 18.5 cm) or 'large' (≥ 50 g, TL ≥ 18.5 cm) fish at random. Predatory performance was assessed by computing CPUE values for trials of both size classes with similar fish densities. We also computed the success rate of initiated prey pursuits and the duration of successful pursuits (as an indication of foraging effort) for both fish size classes.

(3) Light conditions

To investigate if the predatory performance of cormorants might be limited by the available light, we altered light conditions encountered by the birds underwater. This was achieved by conducting trials either around midday, when light conditions were best (max

120 lx at 10 m depth, comparable with workspace lighting), or in the late afternoon, when light conditions deteriorated (min 1.8 lx at 10 m depth, corresponding to full moon lighting). Water inside the tank was clear with a turbidity of about 0.5 NTU (nephlometric turbidity units) during all trials.

(4) Fish behaviour (shoaling versus non-shoaling fish)

During the training trials we observed that fish often started to form shoals inside the dive tank and this appeared to affect predator behaviour and success. Hence, in our video analysis we distinguished between a ‘shoaling’ and a ‘non-shoaling’ situation when birds attacked prey. By definition, in a non-shoaling situation the bird targeted an individual fish that was not part of a shoal (although a shoal might have existed elsewhere within the tank). In contrast, in a shoaling situation the bird targeted the shoal or an individual that was part of the shoal. Predatory performance was assessed by computing success rate (% successful pursuits and dives) and the duration of successful pursuits (as an indication of foraging effort), contrasting a shoaling and non-shoaling situation.

(5) Water temperature

It has been suggested that cormorants might reduce the amount of time spend foraging in cold water to a minimum (Grémillet et al., 2001). By conducting trials at various water temperatures ranging from 5 to 22 ^{o}C, we investigated the effect that water temperature might have on cormorant foraging behaviour.

(6) Dive depth

We compared predator-prey interactions occurring at shallow depth ($\leq$ 3 m) with interactions occurring at greater depth (> 3 m) to assess the effect of depth on cormorant foraging behaviour. In our analysis we included dive and surface durations as well as the success rate of prey pursuits initiated at shallow and greater depth.

Statistical analysis

All statistical analysis was performed using SigmaStat software (Jandel Scientific, San Rafael, CA, USA). When single comparisons were made, as in comparing the success rate of pursuits attacking shoaling or non-shoaling fish, Student’s paired t-test was used. All percentage values were normalised by arcsine transformation beforehand. Significance was accepted at $P < 0.05$. The relationship between fish density and prey capture rate (CPUE) that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz and Slinker, 1990). Regression lines for Figs. 4.2-4.4 were fitted using custom made software (J. Lignon and J.L. Rodeau, CEPE, Strasbourg, France). Values given are grand means established from individual bird means and are presented with standard deviation (± 1 S.D.).

Results

Between late August and early November 2003 we conducted a total of 100 foraging trials with 9 birds of which 82 trials were included in the current analysis. During these 82 trials birds conducted a total of 624 dives, lasting between 3 s to 49 s in duration. During a trial a bird would typically start diving within 30 s of introduction into the set-up. If prey was encountered, the bird usually started a pursuit which ended either with the capture of the trout, a switch to attacking/pursuing another trout, or with the return to the surface, when the bird 'gave up'. A bird typically dived until either satiated (after multiple prey ingestions) or 'frustrated' (if no prey was encountered or caught) and left the water afterwards to wingspread. In the first situation a bird typically started another dive bout towards the end of the 30 min trial. In the latter situation a bird would usually reassess the situation frequently during the first half of a trial by performing a few exploratory dives, before finally giving up (and remaining outside the water), if no prey was encountered or caught.

We observed 518 prey pursuits of which 275 ended in the successful capture and ingestion of a trout. Mean success rate of all initiated pursuits by 9 birds was 58.3 ± 21.0 % (range: 31.0–92.9 %). Since birds often initiated more than one prey pursuit per dive, success rate was higher when expressed on a per dive basis, with a mean of 77.7 ± 14.5 % of all dives during which prey was encountered and pursued being successful. Mean duration of pursuits that ended with prey capture was 6.77 ± 1.48 s (range: 1–28 s). After prey capture, birds typically surfaced with the fish and manipulated it so as to swallow it headfirst. Double-crested cormorants are certainly capable of swallowing 'small' fish underwater (Enstipp, pers. observ.). In the current study, however, this was only observed in 9 cases (out of 275 prey captures) and mostly concerned the two largest birds. Handling times at the surface (from surfacing to prey ingestion) were short (mean: 3.8 ± 1.5 s, range: 1–12 s). If handling time was calculated as the time from prey capture to prey ingestion (hence, including the time underwater from capture to surfacing), it became largely a function of the depth at which prey was caught.

Most fish that were attacked by a bird seemed to be well aware of the predator early on, as they were actively moving away from it. However, in 18 % of all bird attacks a fish remained stationary until a very late stage and was captured in 73 % of these attacks.

Prey abundance (fish density)

The total number of fish inside the dive tank during a trial ranged from 1 to 23, which corresponded to a fish density of 0.005 to 0.12 fish·m^{-3} (0.17 to 7.27 g·m^{-3}). Fish density within the dive tank had a strong effect on the various aspects of cormorant prey-capture behaviour investigated (Figs 4.2–4.4). The total amount of time that cormorants spent searching underwater during a foraging trial increased with a decline in fish density (Fig. 4.2). While cormorants searched on average less than 2 min during a trial when prey density was above 2 g·m^{-3} (about 0.04 fish m^{-3} or 7 fish within the tank), search time quadrupled when prey density fell below this threshold. Similarly, the time that birds spent submerged at the beginning of a trial before the first fish was encountered increased with a decline in fish density, while the proportion of dives in a trial during which prey was encountered declined with a reduction in fish density (Fig 4.3). In all cases the relationship between fish density and the variable of bird foraging performance (search time, prey encounter rate) was not simply linear. It was rather characterised by a breaking point at a fish density of 2-3 g·m^{-3}, below which the change was accelerated (Figs 4.2, 4.3). There was also a significant linear relationship relating fish density to prey capture rate (CPUE). As fish density increased, so did the prey capture rate of cormorants (Fig. 4.4). However, at prey densities below 2 g·m^{-3} the prey capture rate of cormorants was below average and in some trials no fish were caught. We computed prey intake rates by combining the underwater foraging part with the handling time of fish at the surface. Fig. 4.5 illustrates that the overall foraging process of cormorants feeding on trout resembles the sigmoid type III curve of Hollings model.

Prey size

Body mass and length of the introduced trout ranged from 23 to 108 g and 15.5 to 25 cm, respectively. Within the size range of trout that we investigated, there was no significant effect of fish size on cormorant predatory performance. The likelihood of getting caught was similar for ‘large’ (≥ 18.5 cm) and ‘small fish’ (< 18.5 cm). In trials with a similar mean fish density (0.06 fish·m^{-3}) prey capture rates achieved by the birds were comparable for ‘small fish’ (115 ± 67 g·min^{-1} submerged or 2.2 ± 1.2 fish·min^{-1} submerged) and ‘large fish’ (100 ± 25 g·min^{-1} submerged or 1.5 ± 0.3 fish·min^{-1} submerged). While individual pursuits tended to be more successful in trials with small fish (67 % versus 61 % for large fish), this difference was not significant ($p = 0.95$, $t = 0.07$). Similarly, foraging effort, as indicated by the duration of successful pursuits, was similar for both size classes (6.3 s versus 6.8 s for small and large fish respectively).

Light conditions

Light conditions did not limit the predatory performance of cormorants within the illuminance range tested (1.8–120 lx at 10 m depth). Cormorants achieved high prey capture rates even under low light conditions (Fig. 4.5). While we recorded some low CPUE values especially at the lower end of the illuminance scale (Fig. 4.6), these were also trials with a low fish density ($< 2\ g\cdot m^{-3}$). Removing the effect of fish density on foraging success (i.e. excluding trials with a fish density below $2\ g\cdot m^{-3}$) shows that light conditions did not have a significant influence on cormorant foraging success.

Fish behaviour

Fish often started to form shoals, especially when the overall number of fish within the dive tank was large (> 10 individuals). This shoaling behaviour had consequences for the predatory performance of the cormorants. In 55.8 % of all pursuits initiated, birds targeted individual fish that were not part of a shoal. 70.8 ± 22.1 % of these pursuits were successful. 44.2 % of all pursuits recorded were directed towards a shoal or an individual that was part of a shoal. However, the success rate of these pursuits was significantly lower, with only 40.5 ± 14.5 % of pursuits culminating in prey capture ($p = 0.003$, $t = -4.14$). A similar picture emerged when we looked at the prey capture success of cormorants on a per dive basis (Fig. 4.7). Cormorants succeeded in 86.9 ± 12.9 % of dives during which prey was encountered and pursued when non-shoaling prey was targeted, but prey capture success was reduced to 63.3 ± 20.2 % when the target was part of a shoal ($p = 0.002$, $t = -4.72$). Besides reducing predator success rate, shoaling also significantly increased the amount of time birds had to spend in prey pursuit in order to succeed. When successfully attacking a non-shoaling fish, birds spent on average 5.2 ± 1.4 s in prey pursuit. In contrast, a bird spent on average 10.2 ± 2.9 s in prey pursuit when it attacked and captured a fish that was part of a shoal ($p < 0.001$, $t = -5.78$). In a few cases we observed birds seemingly ignoring a shoal close to the surface, diving to the bottom of the 10 m tank instead, where a few non-shoaling fish were present.

Water temperature

Water temperature within the dive tank did not affect cormorant foraging behaviour within the range of temperatures tested (5–22 ^{o}C). While birds seemed to spend less time in water as water temperature declined, this trend was not significant (Fig. 4.8).

Dive depth

Dive duration was significantly shorter in shallow dives ($\leq$ 3 m, 12.1 ± 1.7 s) than in deep dives ($>$ 3 m, 27.2 ± 2.4 s; $p < 0.001$, $t = -12.56$). The duration of the succeeding surface interval, however, was not significantly different between shallow and deep dives (18.0 ± 9.6 s versus 25.9 ± 5.6 s), which was true also for the resulting dive to pause ratio (1.11 ± 0.37 versus 1.36 ± 0.33). 73.7 ± 14.6 % of all shallow dives during which prey was encountered and pursued were successful, compared with 81.0 ± 17.9 % of deep dives. While this difference was not significant ($p = 0.11$, $t = -1.83$), the difference in success rate of individual pursuits during shallow and deep diving was. 68.2 ± 15.8 % of all initiated pursuits were successful during shallow diving, compared with 53.5 ± 21.1 % during deep diving ($p = 0.027$, $t = 2.71$).

Discussion

Our study is the first detailed investigation of the combined effects of a multitude of biotic and abiotic factors on the prey-capture behaviour of a diving endotherm. The functional links between these factors and cormorant foraging performance established in our study will be essential when trying to estimate minimum requirements for these avian divers within changing marine ecosystems.

Our experiments were conducted within the confined space of a tank, with walls potentially restricting the movements of both predator and prey. However, tank dimensions were large in comparison with the size of the animals swimming inside. The width of the tank (5 m) was 26 times the average length of our rainbow trout (19 cm) and the overall volume of the tank (196 m^3) was gigantic in relation to fish size. Still, it is difficult to judge to what degree the confined space might have worked in favour of the predator. However, cormorants captured fish at any position within this tank, at its side, as well as in its centre. Similarly, fish escape movements were directed in the horizontal as well as in the vertical plane. Fish also had the possibility to hide within structures provided at the bottom of the tank. We therefore believe that we minimised the effects of a confined space on predator-prey interactions.

Prey density

How do the prey densities we used in our study compare with prey abundances that birds would encounter in the wild? Abundance estimates for fish species not commercially exploited by humans are rare. Besides the intrinsic methodological problems with accurately assessing fish abundance, densities are usually expressed on a per square meter basis. While this might be appropriate for bottom dwelling species, it becomes more problematic for pelagic species that occupy the water column, a three-dimensional space. If we express the fish densities in our study on a per square meter basis, then birds dived in water with fish densities of between 0-70 $g \cdot m^{-2}$, which corresponds to 0-2.1 $trout \cdot m^{-2}$. Grémillet et al. (2004) estimated the abundance of benthic fish in a foraging area frequented by great cormorants in Greenland to be 0.09 prey $items \cdot m^{-2}$. This was considered to be rather low and estimates of between 0.5-2.3 $fish \cdot m^{-2}$ are more typical for comparable habitats throughout Europe (see Grémillet et al., 2004). Hence, the fish densities encountered by the cormorants in our study might be a good approximation of the natural situation within coastal, temperate habitats.

Prey density strongly affected the foraging behaviour and success of double-crested cormorants. While a decline in fish density increased the time cormorants spent searching during a trial (Fig. 4.2), it decreased both prey encounter rate (Fig 4.3) and prey capture rate (Fig. 4.4). In all cases the effect was most noticeable below a fish density of 2-3 $g \cdot m^{-3}$, when cormorant foraging performance was significantly altered. Hence, 2-3 $g \cdot m^{-3}$ might represent a threshold density below which sustainable foraging in cormorants is compromised. It should be noted, however, that fish behaviour could have contributed to the observed shift in predator performance. (1) An intrinsic difference between fish in their ability to avoid being caught by a predator might exist. At the beginning of a trial day fish density was high and gradually decreased throughout successive trials, as birds removed fish. Birds might have preferentially removed fish that were easy to catch, leaving the harder to catch individuals for the later, low density trials. (2) The ability of a fish to avoid a predator might improve through repeated exposure to a predator. Hence, fish in the later, low density trials, could have been more experienced than in the early, high density trials of that day. Wood and Hand (1985) reported that juvenile coho salmon (*Oncorhynchus kisutch*) with previous predator exposure were captured less frequently by common mergansers (*Mergus merganser*) than individuals without previous exposure.

Few studies investigated the effect of prey density on the foraging success of avian divers. Two studies investigated the foraging behaviour of common mergansers (*Mergus merganser*; Wood and Hand, 1985) and great crested grebes (*Podiceps cristatus*; Ulenaers et al., 1992) but both were restricted to shallow ponds or streams. Both studies found a significant increase in prey capture rate with an increase in fish density. Wood and Hand (1985) reported a success rate for mergansers during pursuits initiated from the surface of about 36 %. This is well below the overall success rate of pursuits initiated by cormorants in our study (58 %). Analysis in these studies was restricted to surface observations, so that little conclusions can be drawn upon the underwater behaviour of avian predators. Capture success is usually expressed as the proportion of successful dives, based on the observation of prey handling at the surface. No information on the frequency of prey encounter, nor the frequency and outcome of predator attacks can be conveyed from these studies. The reported proportion of successful dives for avian predators is consequently low with 3.1 % for great crested grebes (Ulenaers et al., 1992) and between 3 to 8 % for little grebes (*Tachybaptus ruficollis*) foraging in 1-2.5 m deep water (Fox, 1994). In our study 48 % of all dives conducted by the cormorants ended in the successful capture and ingestion of a trout, while 78 % of all dives during which prey was encountered and pursued were successful. Prey densities in the study by Ulenaers et al. (1992) ranged between 0.1-2.09 fish·m^{-2} or 8-58 g·m^{-2} for roach/rudd. These density values are similar to our study, while effective fish density was even lower in our study because of the depth factor. Hence, density cannot explain the observed difference in prey-capture success between grebes and cormorants. It might simply be that the prey capture capabilities of cormorants are exceptional amongst avian divers that have been investigated so far. Grémillet et al. (2001) reported CPUE values for great cormorants foraging in Greenland during winter of up to 60 g fish·min^{-1} underwater. At the highest fish density tested in our study (7 g·m^{-3}) cormorants reached CPUE values in the order of 190 g fish·min^{-1} underwater. This density was most likely considerably higher than what cormorants typically encounter in Greenland (see Grémillet et al., 2004). However, it also demonstrates that cormorants are able to achieve a higher foraging yield than suggested by field studies, if fish densities are sufficiently high.

The underwater part of the foraging process in cormorants showed a linear relationship with fish density (Fig. 4.4), and, hence, resembles a type I curve in Hollings model (Holling, 1959). However, the relationship between overall feeding rate (including the handling time at the surface) and fish density (Fig. 4.5) was characterized by a sigmoid-shaped curve (type III curve in Hollings model). This would indicate that at higher fish densities prey handling limits the further increase in feeding rate in double-crested cormorants. A levelling off at higher prey densities has also been reported for other piscivorous birds, albeit in a hyperbolic shaped curve (type II curve in Hollings model; Wood and Hand, 1985; Draulans, 1987; Ulenaers et al., 1992).

Prey size

Size/mass of trout did not affect cormorant foraging behaviour in our study. Prey capture rates were similar for both size classes ('small' and 'large') and so were the durations of successful pursuits, indicating that capture effort was comparable. In contrast, Ulenaers et al. (1992) found a significant effect of fish size/mass on the foraging behaviour of great crested grebes. In their study, the proportion of successful dives increased as fish weight decreased, while the duration of successful dives increased with fish weight (range: 8-40 g for roach/rudd), suggesting a longer underwater handling time for larger fish. The size/mass range covered in our study is probably close to the typical range exploited by double-crested cormorants in the wild. While rainbow trout of the size/mass range offered in our study did not constrain cormorant foraging behaviour, this could be different for other prey species exploited by the cormorants.

Light conditions

The light conditions encountered by cormorants in our study did not limit their prey capture capabilities. Birds achieved high capture rates even at light levels below 5 lx (measured at 10 m depth; Fig. 4.6). However, we were unable to run trials at even lower light levels and it is conceivable that light levels below the ones tested in our study would soon have limited cormorant predatory performance. Nevertheless, the range of light conditions tested in our study compares well with conditions naturally encountered by avian divers during foraging. Wanless et al. (1999) recorded light levels that European shags (*P. aristotelis*) and South-Georgian shags (*P. georgianus*) encountered during diurnal foraging. Illumination at depth during diving ranged from 0.5 to 100 lx for the deeper diving South-Georgian shags (mean depth: 3-73 m), while European shags (mean depth: 8-35 m) dived at light levels of between 7.9 to 100 lx. Both species feed predominantly near the sea bottom, hence, prey search and presumably capture must have taken place at the lower range of light levels encountered. Recently Grémillet et al. (in press a) found that great cormorants wintering in Greenland conducted 46 % of their foraging dives during the polar night in the dark (< 1 lx at the surface). Hence, they suggested that cormorants might switch from visual cues to tactile and/or acoustic cues to capture their prey at these low light conditions. While this might be a realistic scenario for benthic prey (e.g. sculpins), it seems highly unlikely for pelagic/schooling prey like the trout in our study. In little penguins (*Eudyptula minor*) foraging activity within a shallow dive tank (1.3 m depth) declined with decreasing light levels (Cannell and Cullen, 1998). As light levels decreased, penguins reduced the time spent in search for live fish, while prey pursuits were also initiated less frequently. No fish were caught at light levels below 0.01 $\mu e \cdot m^{-2} \cdot s^{-1}$ (equivalent to about 0.6 lx; using the conversion cited in Cannel and Cullen, 1998: 1000 lx = 16.5 $\mu e \cdot m^{-2} \cdot s^{-1}$). The visual resolution of great cormorants (*P. carbo*) underwater is exceptionally good (Strod et al., 2004). It is better than in most fishes and marine mammals, despite the challenge of living in two different media (air/water) that require compensatory mechanisms. However, water turbidity strongly affects the visual environment of cormorants underwater and decreases image resolution (Strod et al., 2004). Turbidity also reduces the visual distance between predator and prey and it is not known, who benefits from greater turbidity. On the one hand, prey might be able to hide better from predators in turbid water but turbidity also reduces the distance at which prey will be able to detect a predator and, hence, decreases the amount of time available to react and escape the predator. In this context it is interesting to note that great cormorants at Lake Ijsselmeer in Holland switched from a solitary foraging habit to mass fishing as visibility declined during the 1970's (van Eerden and Voslamber, 1995). However, the effects of very low light levels and turbidity on the prey-capture performance of avian divers remain to be investigated.

Fish behaviour

Shoaling/schooling is an important anti-predator behaviour in many fish species that form social groups (shoals). It provides protection from predators through a number of mechanisms, such as early predator warning, the encounter-dilution effect, and the predator confusion effect (see Pitcher and Parrish, 1993 for review). Vigilance will be increased in shoals, allowing earlier detection of a predator, increasing the likelihood of a successful escape. The likelihood for an individual of being detected and attacked is diluted in a shoal and decreases with increasing group size. An attacking predator will be confused because of the many moving targets within a shoal that cause a sensory overload, making it difficult for the predator to single out and track an individual prey. The effectiveness of these mechanisms has been demonstrated in experimental studies. Neill and Cullen (1974) for example showed that the success rate of cephalopod and fish predators attacking schooling fish decreased significantly with an increase in shoal size. Attacks were much more likely to be successful if single prey was targeted. Furthermore, attacks on larger shoals lasted longer. Similarly, Krause and Godin (1995) found that hunting success of cichlid predators attacking free-swimming guppy shoals decreased significantly with increasing shoal size. Zheng et al. (2005) developed a model to investigate the most efficient behaviour pattern for individuals within a shoal to avoid being caught by a predator. They found that in shoals of increasing size the confusion effect resulted in an increase in the number of attacks before capture. The predator also changed its target more often in larger shoals, illustrating how difficult it was for the predator to continuously pursue a single fish within the shoal. Hence, the significant decrease in foraging success (Fig. 4.7) and the significant increase in pursuit duration that we observed when cormorants targeted shoaling trout rather than individual trout is in accordance with the findings of the above studies on fish predators. When cormorants attacked a shoal they deployed a strategy similar to the anti-confusion tactics described by Zheng et al. (2005). Birds either charged into a shoal in an attempt to split the shoal into smaller groups and/or they tried to isolate a single fish from the group, which was then pursued and in most cases captured. Birds were also more likely to switch the target when they attacked a shoal rather than a single fish. 18 % of all bird attacks were directed towards an individual that remained stationary until a very late stage, rather than trying to maintain the distance to the predator. Since in most cases fish seemed to be well aware of the predator, this behaviour might represent a different strategy, whereby a fish might have tried to rely on camouflage rather than actively swimming away. This behaviour was most often observed when fish were near the bottom of the tank, where added structural elements could have provided some shelter from the predator. However, 73 % of these attacks resulted in prey capture, while the average success for all pursuits was only 58 %, which should question the effectiveness of this strategy.

Water temperature

Cormorants seemed to reduce the amount of time spent in water during a trial when water temperature declined (Fig. 4.8). While this trend was not significant in our study, it could have become significant if we would have been able to extend water temperature to lower levels. Cormorants have a partially wettable plumage (Grémillet et al., 2005a) so that heat loss to the water might be extensive when foraging in cold water, increasing the energetic costs of foraging. Dive costs in European shags and double-crested cormorants increase significantly with a decrease in water temperature (Enstipp et al., 2005; Enstipp et al., subm.). Hence, Grémillet et al. (2001) suggested that cormorants might employ a behavioural strategy, whereby birds will minimize the amount of time spent in water to reduce daily energy expenditure, especially when wintering in thermally challenging climates. The following observations could lend support to this idea. One strategy of our birds, which seemed to be more exploited as water temperatures dropped, was to ‘monitor’ fish from a platform outside the water and start a pursuit when fish were close to the surface. Another strategy, more prevalent at cold temperatures was to leave the water after each dive.

Depth

Little is known about the effect of depth on foraging success in avian divers. Fox (1994) studied the foraging behaviour of wintering little grebes in a tidal river and found that feeding success of grebes declined significantly when water depth increased from 1 to 2.8 m. Since depth changes were the result of tidal movements, feeding success could have been strongly influenced by a difference in prey abundance with different tidal stages. However, Fox (1994) attributed the decline in foraging success mostly to the greater energetic challenge when diving in deeper water. Certainly, diving to depth has important energetic consequences for avian divers. The reduced insulative air layer within the plumage at depth will increase heat loss to the water, which in turn will increase thermoregulatory and, hence, overall dive costs when compared with shallow diving (Enstipp et al., subm.). From an energetic point of view, grebes and cormorants should therefore forage at a shallow depth if possible, especially in cold water. The strategy mentioned above that at colder water temperatures some cormorants ‘monitored’ fish from outside the water and started a pursuit when fish came close to the surface would point in that direction. Interestingly, cormorants evolved a dynamic buoyancy control mechanism that allows them to counter the destabilising effects of buoyancy at shallow depth (Ribak et al., 2004), enabling them to effectively exploit shallow waters. However, the depth range investigated in our study does certainly not present a physiological or energetic challenge to the cormorants and did not constrain their foraging behaviour. Foraging success (% success in dives during which prey was encountered and pursued) of cormorants was identical during shallow ($\leq$ 3 m) and deep dives ($>$ 3 m), while individual pursuits were more likely to be successful at shallow depth. This could indicate that birds at greater depth were more willing to end a so far unsuccessful pursuit in order to initiate another (i.e. switch fish) than when they stayed at shallow depth.

In summary, our study illustrates the importance of a variety of factors in shaping the fine scale foraging behaviour of cormorants. Prey density exerted the strongest influence on foraging success. While there was a linear relationship between prey density and prey capture rate (Fig. 4.4), a prey density below the threshold of about 2 g·m^{-3} resulted in proportionally lower CPUE values and this might have important implications for birds in the wild confronted with a decline in food abundance. Fish behaviour also significantly altered predator success and might force birds to spend more time and energy when targeting shoaling fish rather than solitary fish. In contrast, prey size, light conditions, water temperature and depth did not have a measurable impact on cormorant prey-capture behaviour within the range investigated in our study.

Our study is also the first in-depth experimental investigation of the underwater prey-capture behaviour of a diving endotherm. We provide input values for ecosystem modelling which are urgently needed. The prey capture rates of cormorants and their modulation by various factors reported in this study will form the basis for feeding models of piscivorous diving birds, which in turn will help to understand predator requirements in a changing environment.

Acknowledgements

Research was conducted and funded within the framework of the European Commission project 'Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864). Financial support was also provided by a 'discovery grant' and equipment grants from NSERC to D.R.J. The British Columbia Ministry of Environment granted holding permits for the double-crested cormorants. Arthur Vanderhorst and Sam Gopaul of the Animal Care Facility at UBC provided support in caring for the birds. Bruce Gillespie and Don Brandies of the UBC Zoology Mechanical Workshop were of great help for technical questions. Thanks to Ken Scheer from the Fraser Valley Trout Hatchery for generously providing us with live rainbow trout and to Andrew Lotto (UBC Forestry) for his fish transportation tank. Tom Hoeg was indispensable in setting up the Underwater Camera System within the deep dive tank and generously donated knowledge, expertise and time. Magali Grantham helped with animal care, experimentation and preliminary data analysis. Thanks to John Gosline (UBC Zoology) for providing the video date time generator and to Robin Liley (UBC Zoology) for tolerating the takeover of his fish holding tanks and access to video equipment. Gerrit Peters kindly provided the GeoLT data logger and was always available for advice on how to fix it. Lovena Toolsy is thanked for help during the long hours of video analysis and J.-P. Robin for help with the line fitting procedure. Thanks to Gunna Weingartner for reviewing an earlier version of this manuscript.

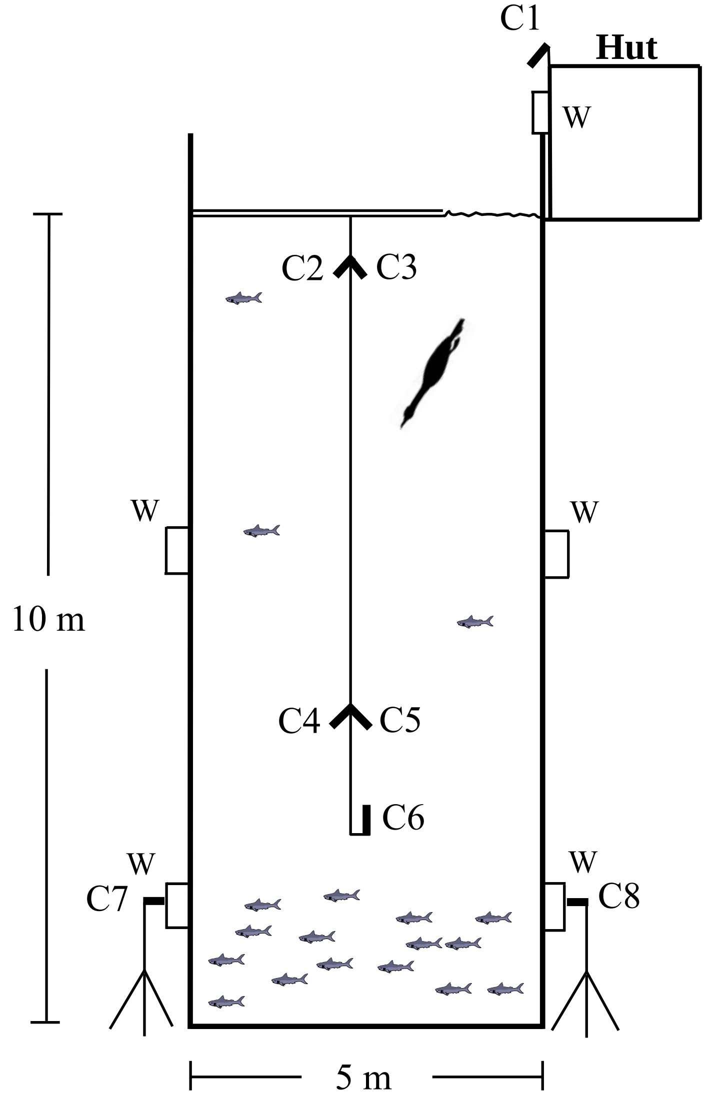

Fig. 4.1. Video camera set-up in the deep dive tank indicating the position of the 8 b/w video cameras (C1-C8), which allowed for a complete visual coverage. Tank dimensions (with a total water volume of 196 m^3), underwater windows (W) and a typical fish distribution at the beginning of a series of trials (when fish density was highest) are also indicated.

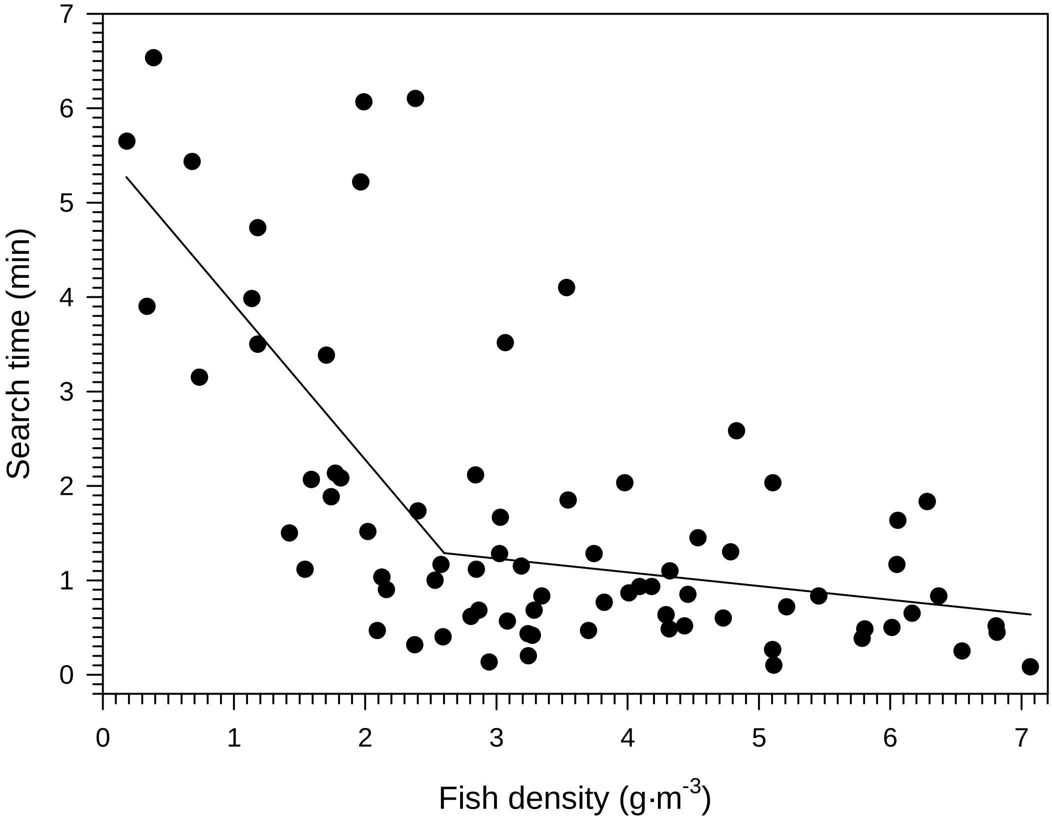

Fig. 4.2. Time spent searching underwater during a trial (min) in relation to fish density (g·m^{-3}). A threshold fish density seems to exist between 2-3 g·m^{-3} below which the amount of time a cormorant spent searching during a trial increased drastically. The indicated relationship is best described by:

$y = -1.64(x-t)-0.15t+1.67$ for $x<t$ and $y = -0.15x+1.67$ for $x>t$, where t is the breaking point, calculated to be at 2.92 g·m^{-3}, y is the search time and x is fish density ($F = 48.84$, $p < 0.0001$, $r^2 = 0.49$, N = 9 birds, n = 77 trials).

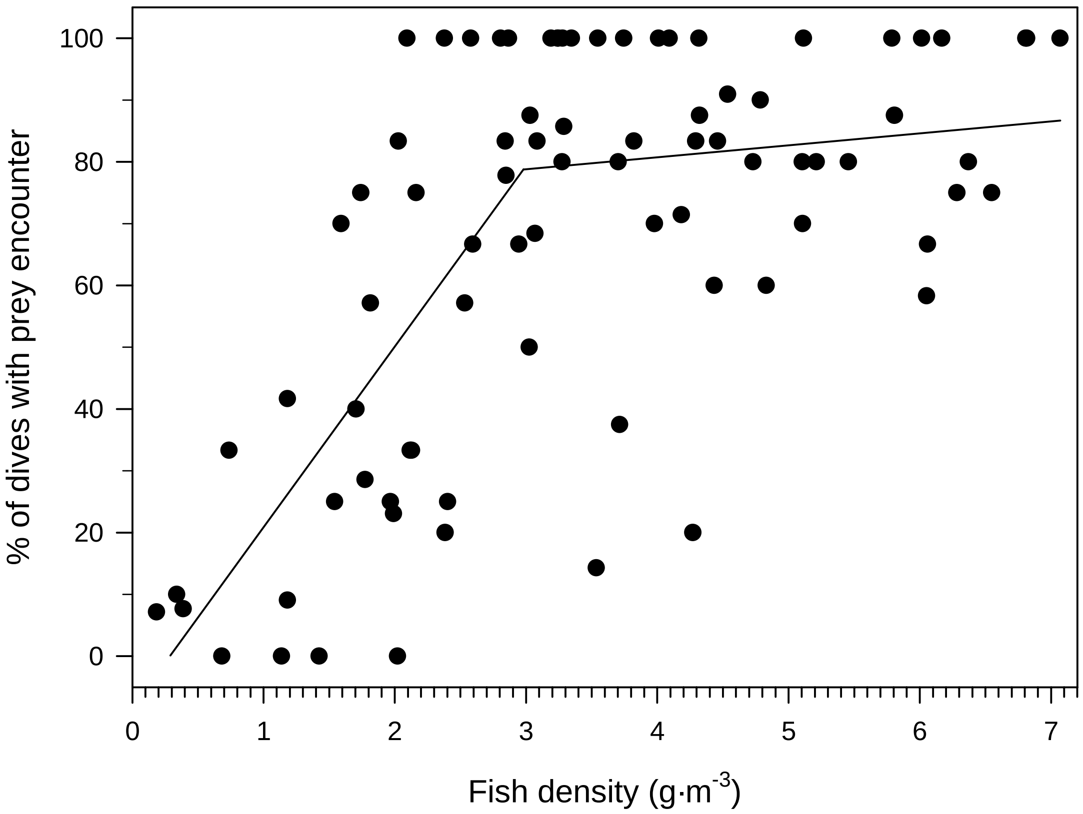

Fig. 4.3. Prey encounter rate (proportion of dives within a trial when prey was encountered) in relation to fish density (g·m^{-3}). A threshold fish density seems to exist between 2-3 g·m^{-3} below which the likelihood for a bird to encounter a fish during a dive decreased drastically. The indicated relationship is best described by:

$y = 29.22(x-t)+1.94t+72.98$ for $x<t$ and $y = 1.94x+72.98$ for $x>t$, where t is the breaking point, calculated to be at 2.98 g·m^{-3}, y is the % of dives with prey encounter and x is fish density ($F = 27.68$, $p < 0.0001$, $r^2 = 0.52$, N = 9 birds, n = 82 trials).

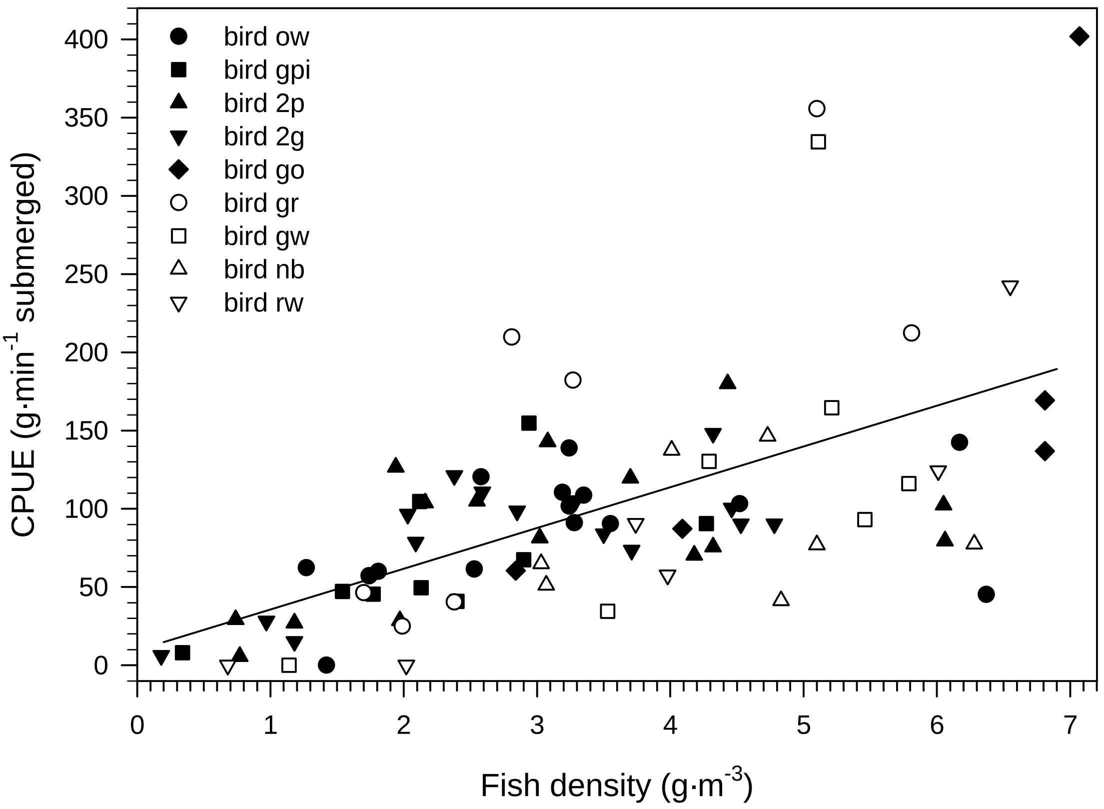

Fig. 4.4. Prey capture rate (CPUE in g·min^{-1} submerged) of double-crested cormorants versus fish density (g·m^{-3}). CPUE increased significantly with an increase in fish density. The regression line is the average relationship for all cormorants that takes into account variability between subjects and is described by $y = 26.04x+9.6$, where y is CPUE and x is fish density ($F = 6.84$, $p < 0.0001$, $r^2 = 0.45$, N = 9 birds, n = 82 trials).

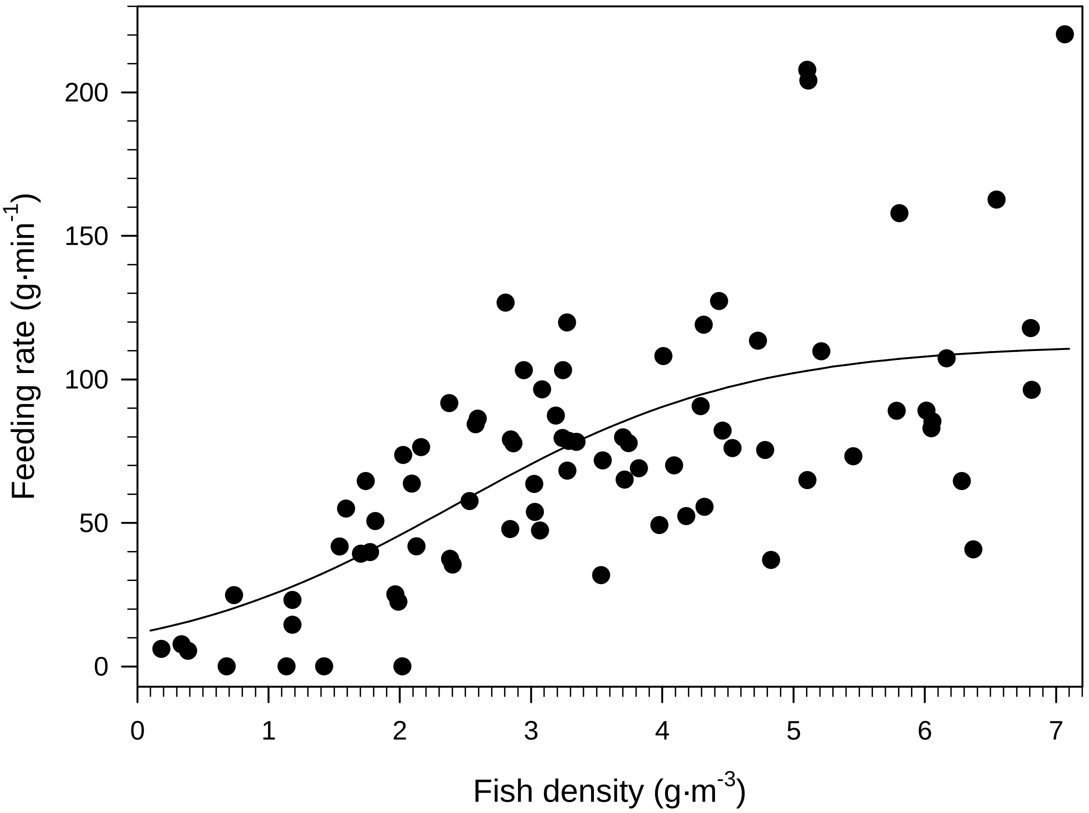

Fig. 4.5. Feeding rate (g·min^{-1}) of double-crested cormorants versus fish density (g·m^{-3}). Feeding rate includes the underwater part of the foraging process as well as the food handling time at the surface. The relationship is best described by:

$y=\frac{112.32}{1+e^{-\left(\frac{x-2.42}{1.11}\right)}}$, where y is the feeding rate and x is fish density ($F = 30.83$, $p < 0.0001$, $r^2 = 0.44$, $N = 9$ birds, $n = 82$ trials).

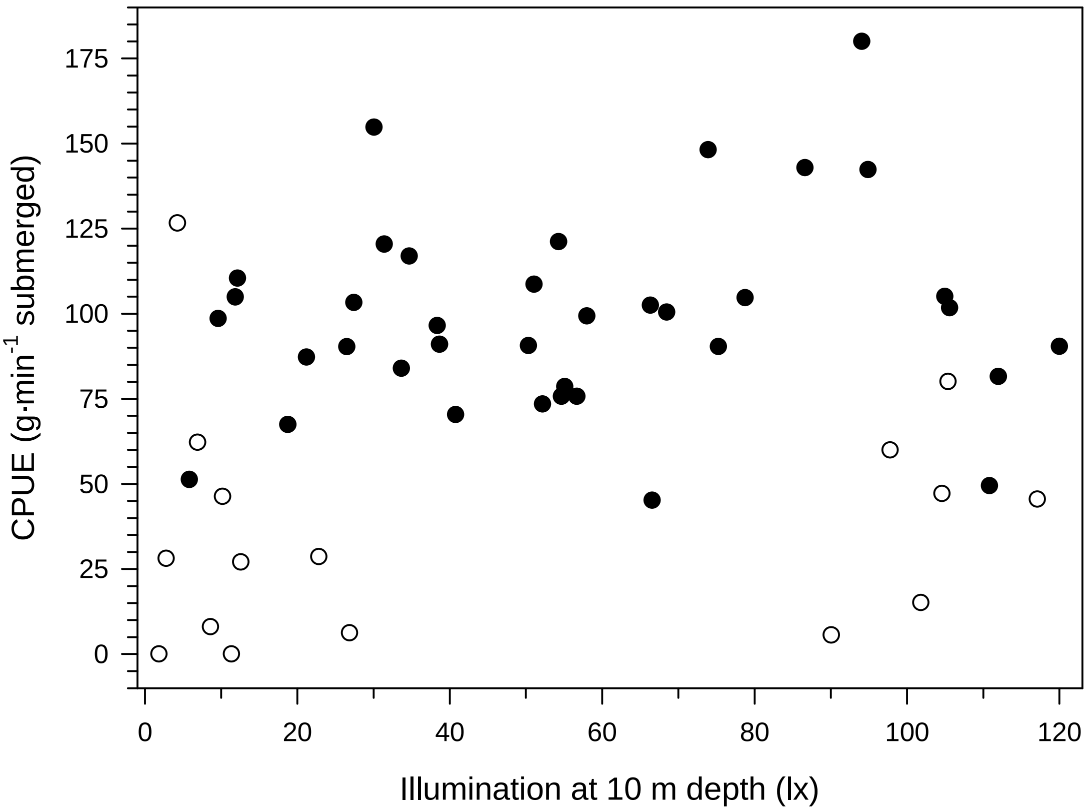

Fig. 4.6. Prey capture rate of cormorants (CPUE in g·min^{-1} submerged) in relation to illumination (lx) measured at the bottom of the deep dive tank. Open circles indicate trials when prey density was below 2 g·m^{-3}. No clear trend is apparent but cormorants achieved high prey capture rates even at the lower illumination range, indicating that light conditions encountered did not limit their prey capture capabilities. N = 9 birds; n = 54 trials.

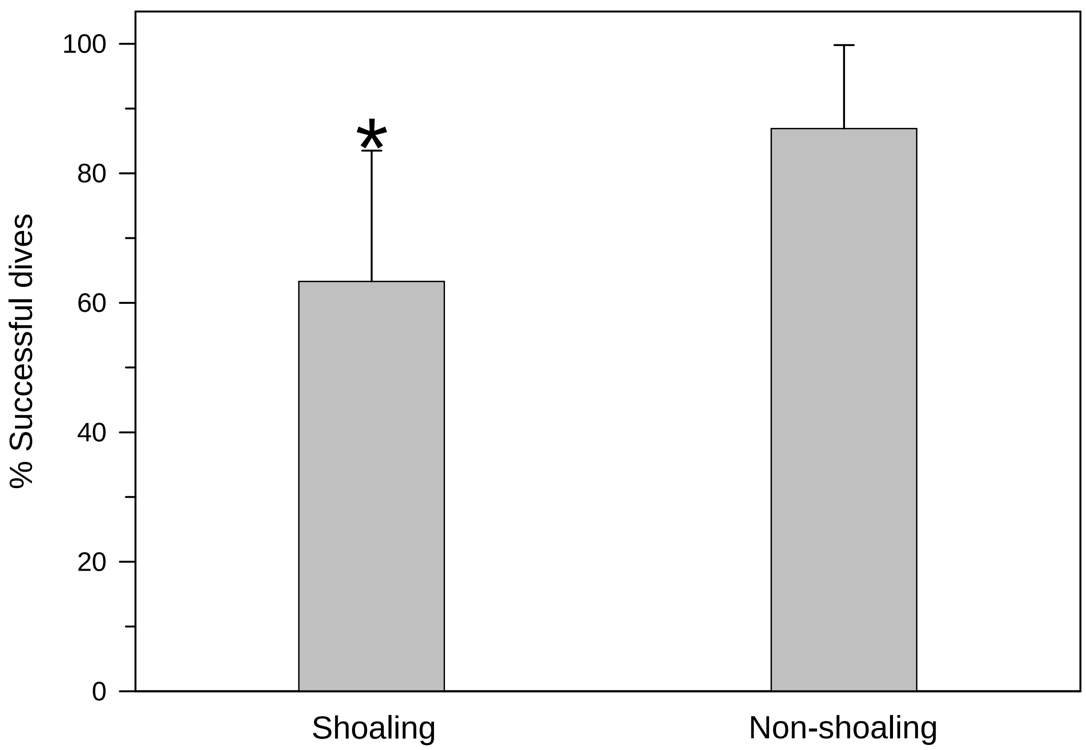

Fig. 4.7. Prey capture success of cormorants (mean ± S.D.) when individual or shoaling prey was pursued. In a non-shoaling situation the bird targeted an individual fish that was not part of a shoal (n = 209 observations), while in a shoaling situation the bird targeted a shoal or an individual that was part of a shoal (n = 148 observations). There was a significant difference between the two situations encountered (indicated by the asterisk), with a much higher success rate when birds targeted individual fish that were not part of a shoal (p = 0.002, t = -4.72, N = 9 birds, n = 82 trials).

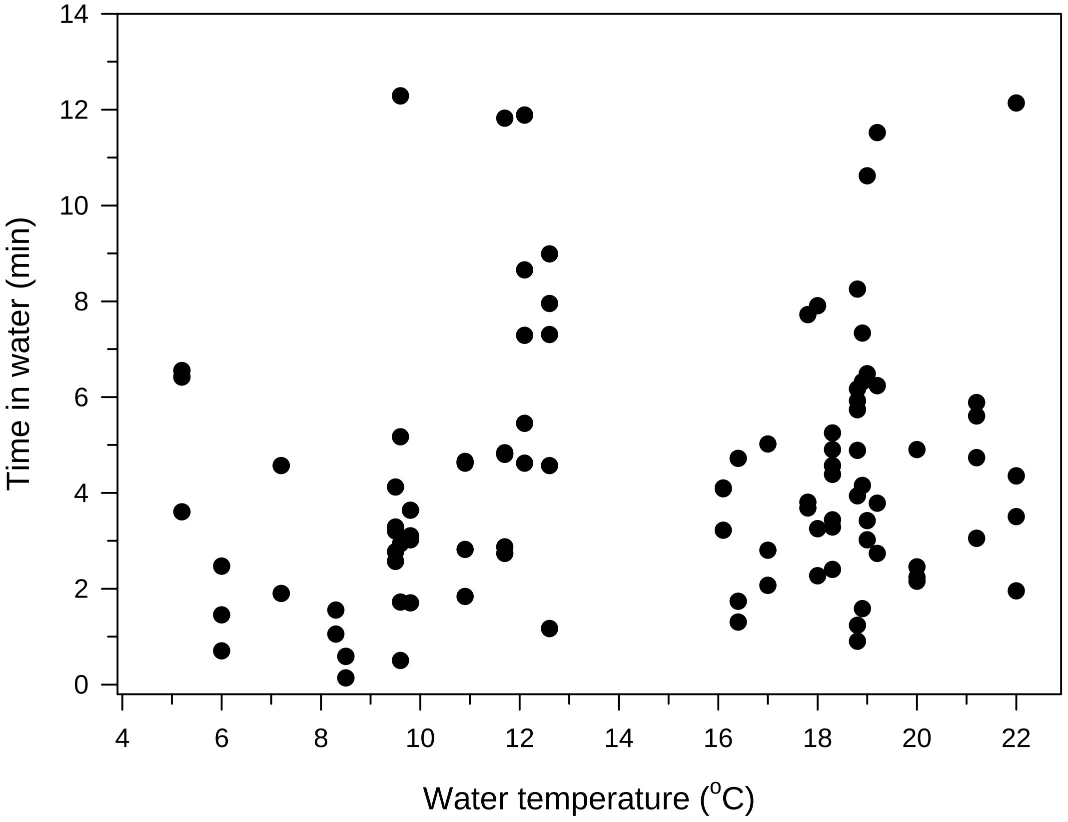

Fig. 4.8. Amount of time spent in water (min) during a 30 min trial versus water temperature within the tank (^{o}C). Shown is the accumulative time spent submerged and resting at the surface during a trial. Birds seemed to reduce the amount of time spent in water as water temperature declined but this trend was not significant within the range of temperatures tested (5–22 ^{o}C). N = 9 birds, n = 100 trials.

Chapter 5

Do cormorants injure fish without eating them? An underwater video study

Note: this article is currently in press in *Marine Biology*.

Grémillet, D., Enstipp, M.R., Boudiffa, M. and Liu, H. (*in press*). Do cormorants injure fish without eating them? An underwater video study. *Marine Biology*.

Abstract

The populations of European great cormorants (*Phalacrocorax carbo*) and North American double-crested cormorants (*Phalacrocorax auritus*) have increased sharply over the last decades and these piscivorous birds are suspected to deplete valuable fish stocks and compete with human fisheries. Beyond direct consumption of fish, cormorants are accused of injuring vast numbers of prey without eating them. Using underwater video systems, one of them mounted onto the back of tame Chinese cormorants, we evaluated the proportion of successful pursuits of cormorants on live fish. Trials were conducted with 6 great cormorants and 9 double-crested cormorants and involved a total of 676 prey pursuits. We show that, although they are regarded as highly efficient predators, cormorants aborted about half of their pursuits. However, detailed analysis of prey-capture behaviour in double-crested cormorants revealed that only 0.4% of the prey pursued was injured without being ingested. Further studies using miniature video systems deployed on free-ranging cormorants are required to complement our knowledge of their hunting tactics.

Keywords: Foraging performance, bird-borne camera, tame Chinese cormorants, prey capture techniques, sub-optimal foraging.

Introduction

Humans act as consumers within the higher trophic levels of numerous food webs and exert substantial pressure on a large proportion of the world's resources. This is particularly true within aquatic ecosystems and there is a growing body of evidence showing that most natural marine and freshwater systems are unsustainably challenged by men (Jackson et al., 2001). Within these habitats humans share their ecological niche with a series of other top predators, such as large predatory fish, aquatic mammals and birds. These three groups are also exploited by humans to various degrees and species that are not targeted directly are often perceived as competitors. Cormorants, which are diving, fish-eating birds are a classic example of such perceived 'pest species'. The cormorant family is present on all continents and comprises over thirty species. Among them, two are accused of depleting valuable fish stocks and affecting the profitability of human fisheries: (1) great cormorants (*Phalacrocorax carbo*) which occur in Australia, Asia, Europe, Africa, and North America, and (2) double-crested cormorants (*Phalacrocorax auritus*) which are present throughout North America and the Caribbean. Both species feed on fish, which they target in shallow water (usually < 10 m depth, max 35 m) within coastal and freshwater ecosystems.

European great cormorant populations and North American double-crested cormorant populations are considered a threat to human fisheries because their numbers grew rapidly during the past twenty years. In Europe the annual population growth rate for great cormorants was at least 15 % during that period, with a total of ca. 200,000 pairs in the late 1990s (Carss et al., 2003). In North America double-crested cormorant populations also increased enormously since the 1970's, with annual growth rates for the Atlantic breeding population of about 14 % (Hatch, 1995). The combined total for all breeding birds in six regional populations (Atlantic, Interior, Florida, San Salvador, Alaska and West Coast) was more than 360,000 pairs in the early 1990's and the total population was estimated between 1 and 2 million birds at that point (Hatch, 1995). The likely causes of such population growth were: (1) the (anthropogenic) eutrophication of freshwater ecosystems throughout Europe and North America, which boosted their productivity and the abundance of cormorant prey (mainly cyprinids; de Nie, 1995); (2) the disuse of certain pesticides which used to greatly reduce cormorant fecundity (Hatch, 1995); and (3) new legislations ensuring the protection of both species ('Blue Listing'; Hatch, 1995; Carss et al., 2003). Recent population studies indicate that the great cormorant population in Europe might have reached its carrying capacity (Frederiksen and Bregnballe, 2000) but such population numbers are considered unsustainably high by fisheries representatives (Carss et al., 2003). Cormorant numbers are being regulated by destruction of eggs and/or adult birds in several European and US American states and in some Canadian provinces (Carss et al., 2003; Trapp et al., 1995; Keith, 1995).

Great and double-crested cormorants are perceived as a threat to fish communities because their food requirements are thought to be abnormally high. Cormorant plumage was believed wettable, so that birds would lose substantial amounts of heat to the water when diving for fish. High food intake rates were thought to compensate for these very high foraging costs. We showed that the great cormorant plumage is actually well adapted to its foraging environment (Grémillet et al., 2005a), and that its food requirements are perfectly normal for an aquatic bird of its size (Grémillet et al., 2003). This is also likely to be the case for double-crested cormorants, which have foraging costs similar to other foot-propelled divers (Enstipp et al., subm.). However, fishermen from Europe and North America claim that cormorants are a threat to their livelihood not only because their growing populations consume unsustainably large amounts of prey but also, because these predators supposedly injure numerous fish without eating them. Injured fish lose market value and can spread diseases (Carss et al., 2003). However, cormorants injuring fish had never been observed directly.

To address these concerns we studied the prey-capture techniques and the predatory performance of great cormorants and double-crested cormorants using underwater video systems. We tested the hypothesis that cormorants injure fish without eating them.

Materials and Methods

Great cormorants

We studied the underwater predatory behaviour of tame great cormorants in China using a bird-borne digital camera. Great cormorants (*Phalacrocorax carbo sinensis*) are widespread in China, where they are being used as fishery helpers throughout the Eastern provinces. Chinese fishermen have raised tame great cormorants and fished with them for at least 2000 years. We collaborated with Zhang Shiyuan, a fisherman from Anxin (Hebei province) and his six tame great cormorants in April 2004. The birds were in breeding plumage, with an average body mass of 2.75 ± 0.25 kg, and were fed approximately 10 % of their body mass daily. Prior to the experiments they were trained for two weeks to dive for fish while carrying a harness. During the experiments the birds were equipped with a digital camera (modified Sanyo Xacti C1; 10 x 5 x 4 cm, 240 g, including underwater housing; Earth & Ocean Technologies, Kiel, Germany), which was attached to the back of the birds using a harness. Camera and housing were neutrally buoyant at the water surface. This set-up allowed us to record video footages showing the neck and the head of the birds while foraging for fish underwater (Video format Mpeg-4, 640 x 480 pixels SHQ, 30 frames/s, ISO400 high sensitivity, lens: f = 5,8-33,8 mm, viewing angle ca. 120° underwater, running time 20 min). Birds equipped with the camera were observed from above water while hunting for fish and the start/end of each dive was recorded. Chinese tame cormorants are traditionally fitted with a neck collar (in our case a simple grass blade), which prevents them from swallowing captured prey. The tame cormorants used in this study therefore kept prey-items in their extensible gular pouch and brought them back to the fisherman and an observer, who followed them on a punt. The size and mass of each prey item caught was recorded. The study zone was an aquaculture area within which prey size and density could be manipulated. Trials were organized so that birds foraged in waters harbouring cyprinid fish of three distinct mass classes: fish mass < 100 g, fish mass 100-500 g, and fish mass > 500 g

In order to assess the impact of the back-mounted camera on the behaviour of the birds we also recorded the foraging performance (g of fish caught per unit time spent underwater) of pairs of birds foraging simultaneously. One bird was fitted with the camera, while the other foraged without the camera.

Digital footage was analysed using Apple Quick Time Player 6.5.1 and Ulead Video Studio 7.0 to determine (1) the beginning and the end of each dive, and (2) the number and the outcome of prey pursuits. The beginning of a dive was defined as the moment when both head of the bird and the camera submerged, while the end was defined as the moment when both head of the bird and the camera emerged. Detailed analysis of the footage revealed that prey pursuits started with a rapid (< 1 s) retraction of head and neck, followed by a forward movement (Fig. 5.1). This was confirmed by direct observation of birds catching fish conducted from the water surface. We therefore used this criterion to count the number of pursuits initiated. When pursuits were successful, the video recording showed that the fish was kept in the gular pouch or the bill (when the prey was too large to be swallowed) until it was brought back to the fisherman. This was also confirmed by direct observation of the birds' predatory performance (recording each capture). Due to the reduced viewing angle of the camera underwater we could only record the initial head movement at the beginning of a pursuit and its outcome, while prey-items were mainly seized outside the viewing field of the camera. Pursuits were therefore classified as successful when a prey was caught or unsuccessful when no prey was caught. However, we could not determine the proportion of fish, which might have been touched by the cormorants but could not be held.

Double-crested cormorants

All experiments were carried out at the South Campus Animal Care Facility of the University of British Columbia (UBC), Vancouver, Canada. The procedures were approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care. Nine adult or sub-adult double-crested cormorants (minimum age 2 years) with a mean body mass of 2.10 ± 0.16 kg (mean ± S.D., range 1.81–2.47 kg) participated in this study. The cormorants had been captured as chicks (5-6 weeks of age) from the nearby Mandarte Island breeding colony and were well established in captivity. They were housed communally in sheltered outdoor pens (8 m long x 4 m wide x 5 m high) with water tank access. All birds were taking part in a study investigating the fine scale foraging behaviour of cormorants and had been trained to forage within a dive tank (5 m in diameter, 10 m water depth) on live rainbow trout (*Oncorhynchus mykiss*), which are part of their natural diet. In addition to the trout that birds caught during the daily 30 min trials, they were fed previously frozen Pacific herring (*Clupea pallasi*) and rainbow smelt (*Osmerus mordax*), supplemented with vitamin B1 tablets (thiamine hydrochloride, Stanley Pharmaceuticals Ltd., North Vancouver, Canada).

An underwater video array was set up within the dive tank, consisting of 8 b/w video cameras (Model CVC6990, a light sensitive, submersible camera with a 3.6 mm wide angle lens; minimum illumination 0.01 lux; Lorex), 2 multiplexer (EverFocus Electronics Corp., Taipei, Taiwan), a video date time generator (RCA), 2 video recorders (Sony) and 2 video monitors (Citizen). The cameras were mounted at various positions within the dive tank, which allowed for a complete visual coverage. The video signal of the cameras was fed into 2 multiplexer, which projected the images onto 2 video monitors (4 cameras per monitor) and was recorded on VHS tape.

Juvenile rainbow trout (total length (TL):15–22 cm, body mass: 24–92 g) were obtained from the Fraser Valley Trout Hatchery (British Columbia Ministry of Water, Land and Air Protection) in June 2002 and kept in dechlorinated, fully aerated Vancouver city tapwater. Every morning, 15-20 trout of a particular size class were caught, weighed and/or measured, to make sure they all fitted a specific size class. They were then introduced into the tank (at least 2 hrs before any trials with the cormorants). A variety of structures (concrete blocks, PVC tubes, etc.) had been placed at the bottom of the tank to provide hiding places for the fish. While fish made use of these structures, they were generally very mobile and roamed throughout the tank after initial introduction to the bottom.

Birds were trained to dive for live juvenile rainbow trout of varying size and density within this set-up for at least 3 weeks before data collection began. Each bird participated in one trial per day. We conducted trials between July and Oct. 2003. At the beginning of a trial a bird was caught in its holding pen and introduced into the dive tank. Here the bird usually started to dive immediately. All underwater and surface activity during the trial was filmed with the video set-up. After the capture of a number of fish the bird usually left the water and wingspread for some time, often starting another foraging bout towards the end of the 30 min trial. At the end of a trial the bird was caught and returned to its holding pen.

Videotapes were viewed and all dive and surface times within a 30 min trial were marked down to the nearest second. Each dive was split into 'searching' and 'prey pursuit'. By definition a bird was 'searching' during a dive until it started a 'prey pursuit' or surfaced. 'Prey pursuit' was taken as an interaction between a bird and a fish (or shoal of fish) and its initiation was typically accompanied by a change in swim direction (towards the prey) or speed (as indicated by an increase in stroke frequency) on the birds' side. 'Prey pursuit' ended either when the bird caught a fish or when it 'gave up', as indicated by a change in swim direction or speed (slowing of stroke frequency). After an unsuccessful 'prey pursuit' the bird, by definition, continued 'searching' until it either initiated a new 'prey pursuit' or surfaced. From video analysis it was therefore possible to (1) assess the success of individual pursuits initiated by the cormorants, and (2) quantify the number of attacks in which cormorants caught a fish but lost it subsequently, therefore injuring the fish.

All values given are grand means established from individual bird means and are presented with standard deviation (± 1 S.D.).

Results

Great cormorants

We conducted 36 trials during which one bird was foraging while carrying a back-mounted camera (6 trials for each of the 6 birds). Birds conducted an average of 24 ± 13 dives per trial, which lasted for 11 ± 2 s, followed by recovery periods of 9 ± 1 s at the water surface. The water depth of the foraging zone was 1-2 m. Before starting a dive bout cormorants repeatedly submerged their head and neck, probably to search for potential prey (Johnsgard, 1993). They initiated dives with characteristic half jumps and submerged head first (Wilson et al., 1992a). When birds searched for fish underwater, the neck was fully stretched and propulsion was provided by simultaneous kicking of the legs. The regular forward strokes resulted in small body undulations, which could be detected clearly in the video recordings.

Analysis of the video footage revealed the initiation of 158 pursuits, which were characterized by sudden and rapid movements of the head and neck (Fig. 5.1). 81 of these pursuits occurred while birds chased small prey-items (mass 58 ± 21 g, TL 14 ± 2 cm), 21 while chasing intermediate prey-items (mass 370 ± 92 g, TL 26 ± 2 cm) and 56 while chasing large prey-items (mass 638 ± 121 g, TL 32 ± 2 cm). Birds initiated an average of 4.4 ± 2.8 pursuits per trial, i.e. 1.7 ± 1.9 pursuits per min underwater. On average only 63 ± 17 % (range 48–92 %) of these pursuits were successful. Because of the reduced viewing angle of the camera we could not distinguish between pursuits that were abandoned before birds reached their prey and cases when they physically touched their prey but did not manage to subdue it. However, during 2 of the 70 unsuccessful pursuits we could witness that a bird seized a fish, which subsequently escaped. Both prey items were heavier than 500 g.

The average success of pursuits was 72 ± 15 % for small prey-items, 31 ± 40 % for middle-sized prey-items, and 50 ± 29 % for large prey-items (Fig. 5.2). Foraging success was not significantly different between trials in which birds targeted small and large fish respectively ($\chi^2 = 9.7$; d.f. = 1,5; $p < 0.001$; H_0: there is no significant difference between samples). The sample size for middle-size fish was too small to allow statistical testing.

A total of 18 trials were performed during which the prey-capture rate of a bird equipped with the camera and that of a control bird were recorded in parallel. Cormorants foraging without camera caught 55 ± 35 g fish per minute spent underwater (1.2 ± 0.8 fish min^{-1} underwater), while cormorants foraging with camera caught 64 ± 28 g min^{-1} underwater (1.1 ± 0.5 fish min^{-1} underwater). The average foraging performance of equipped versus non-equipped birds was therefore not significantly different ($t = 0.48$; $p = 0.64$). Average dive durations were also very similar for the two groups (11 ± 2 s for instrumented birds and 13 ± 4 s for control birds, $t = 0.93$, $p = 0.37$).

Double-crested cormorants

In 82 trials the 9 double-crested cormorants conducted a total of 624 dives, lasting from a few seconds to about 1 min. During a trial a bird would typically start diving within 30 s of introduction into the dive tank. If prey was encountered, the bird usually started a pursuit which ended either with the capture of the trout, a switch to attacking/pursuing another trout, or with the return to the surface, when the bird ‘gave up’. A bird typically dived until either satiated (after multiple prey ingestions) or ‘frustrated’ (if no prey was encountered or caught) and left the water afterwards to wingspread. During these 624 dives, birds caught a total of 277 trout with an average mass of 56 ± 14 g. We observed 518 prey pursuits of which 275 ended in the successful capture and ingestion of a trout. Mean foraging success during all initiated pursuits by 9 birds was 58 ± 21 % (Fig. 5.2; range: 31–93 %). Since birds often initiated more than one prey pursuit per dive, foraging success was higher when expressed on a per dive basis, with a mean of 78 ± 14 % of all dives during which prey was encountered and pursued being successful. In 8 out of 518 initiated prey pursuits (1.5 %) a cormorant successfully caught a fish but lost it subsequently, potentially injuring it. However, in 6 out of these 8 cases the bird successfully recaptured and ingested the fish. Only in 2 cases (out of 518 pursuits, i.e. 0.4 %) did a bird not recapture the fish. Additionally, in none of the other observed 241 unsuccessful pursuits did a bird physically touch the fish. These pursuits were abandoned well before the bird was able to reach the targeted fish.

Discussion

Studies of aquatic predators are technically challenging because prey capture typically occurs underwater and is difficult to observe. Recent technological developments have enabled the assessment of prey capture rates in these organisms (Wilson et al., 1992b, Wilson et al., 1995, Ancel et al., 1997, Grémillet et al., 2000) using miniature data logging devices, which has led to a better understanding of their role within marine and freshwater food webs. Additionally, the use of underwater cameras has proven a useful tool to document their prey-capture techniques (Davis et al., 1999; Ponganis et al., 2000; Takahashi et al., 2004). We used two underwater video systems, one fixed, one animal mounted, to assess the predatory efficiency of cormorants and the proportion of prey that they injure but do not ingest.

The techniques used within our studies have two limitations. First, the back-mounted camera deployed in tame Chinese cormorants is large, disrupts the streamlining properties of the birds' bodies during underwater swimming, and potentially handicaps them during foraging. Interestingly, we found no difference in the foraging performance of birds with or without the camera. This might be due to the facts that birds had been trained to wear the equipment for two weeks before trials started and that trials lasted for less than ten minutes. Powerful swimmers such as cormorants therefore seem to be able to compensate for the handicap caused by large back-mounted devices, at least in the short term. Moreover, the proportion of successful versus aborted prey captures were similar in great cormorants wearing cameras and in double-crested cormorants without cameras, adding weight to the assumption that back-mounted cameras did not substantially affect the predatory performance of great cormorants, at least not within the framework of our investigations.

The second potential bias is linked to the fact that our experiments were conducted within the confined space of a tank, with walls potentially restricting the movements of both predator and prey. However, tank dimensions were large in comparison with the size of the animals swimming inside. The width of the tank (5 m) was 26 times the average length of our rainbow trout (19 cm) and the overall volume of the tank (196 m^3) was gigantic in relation to fish size. Still, it is difficult to judge to what degree the confined space might have worked in favour of the predator. However, cormorants captured fish at any position within this tank, at its side, as well as in its centre. Similarly, fish escape movements were directed in the horizontal as well as in the vertical plane. Fish also had the possibility to hide within structures provided at the bottom of the tank. We therefore believe that we minimised the effects of a confined space on predator-prey interactions. Furthermore, if double-crested cormorants would have shown an artificially high predatory performance, and if great cormorants would have been significantly handicapped by back-mounted cameras, results for both species would have been markedly different for prey of similar size but they are not (Fig. 5.2). However, our results should be considered as a first step and further investigations, ideally on free-ranging individuals equipped with significantly smaller cameras and greater viewing angles are required for a detailed understanding of cormorant prey-capture behaviour.

Nevertheless, our study provides useful insights into the hunting techniques and the predatory performance of cormorants, with two major findings:

(I) Approximately half of the prey pursuits initiated by cormorants did not lead to prey capture (Fig.5.2).

This might seem somewhat surprising, since cormorants are generally considered as highly efficient predators. Great cormorants for example have a partly permeable plumage (Grémillet et al., 2005a), lose substantial amounts of heat to the water while diving and, as a consequence, supposedly reduce their foraging time to an absolute minimum (Grémillet et al., 2001). Such a strategy is supported by very high prey capture rates, which are presumably achieved by a broad dietary choice and opportunistic foraging techniques (Grémillet et al., 1999). Moreover, recent measurements of great cormorant swim speeds indicate that they are fast enough to catch most prey items encountered in freshwater and coastal habitats, with the exception of large salmonids (Ropert-Coudert et al., unpubl data). However, we suggest that the behavioural pattern observed in this study might allow birds to optimise foraging efficiency: Cormorants swim towards a potential prey item, yet, the pursuit is only maintained and the final capture attempt initiated, if the fish concerned is rated as sufficiently rewarding. Birds must also possess some means of judging the likelihood of capture. This strategy allows birds to save time and energy by avoiding prey items perceived as energetically less rewarding or difficult to catch. Little is known, however, about the multitude of factors governing prey choice in cormorants (e.g. nutritional status, prey type, perceived likelihood of capture).

We can attempt to explain the surprisingly high percentage of unsuccessful pursuits by considering the following. Double-crested cormorants were foraging on juvenile rainbow trout, which were highly mobile and able to out swim cormorants during short bursts, especially if fish reacted early on. In this case a cormorant sometimes gave up on the previously pursued fish and switched to another fish within closer reach. Furthermore, trout often formed shoals, which proved to be an effective predator avoidance strategy, confusing the birds (Enstipp et al., unpubl. data). An important factor to consider in the case of the great cormorants foraging within shallow aquaculture ponds is turbidity. Van Eerden and Voslamber (1995) and Strod et al. (2004) illustrated the importance of water turbidity on cormorant foraging behaviour and it is possible that the greater turbidity in the ponds (when compared with the dive tank) facilitated greater escape opportunities for the cyprinid fish.

(II) Only 0.4 % of fish pursued by double-crested cormorants were injured without being ingested.

Our observations of double-crested cormorants foraging on live trout validate the hypothesis that cormorants might injure fish without ingesting them. However, this phenomenon was extremely rare, and our current knowledge does not support the claim that cormorant populations injure more fish than they actually ingest, thereby threatening entire prey populations in freshwater and coastal habitats. Nevertheless, it is important to stress that these results are based upon investigations of double-crested cormorants foraging on relatively small prey-items (TL 15–22 cm, 24–92 g) at low densities (0.2–7 g fish·m^{-3}). Further studies of free-ranging birds foraging on larger fish within dense aquaculture areas are required. Indeed, our study of Chinese tame cormorants indicates that the rate of prey loss (and potential injury) might increase with fish size (Fig. 5.2).

Acknowledgements

This study was funded by the K C Wong Foundation, the DRI of the CNRS, the CNRS headquarters in Beijing, the British Council Paris and the European Union (IMPRESS Project; QRRS 2000-30864). For the Chinese part of the study grateful thanks are due to Marie-Pierre van Hoecke, Florence Hesters, Thi-Ngeune Lo, Bruno Ormile-dautel, Céline Le Bohec, Jean-Yves Georges and Yvon le Maho for their support at different stages of our project. Many thanks also to Zhang shiyuan and his family for hosting us in Anxin, and to Gerrit Peters (Earth & Ocean Technologies, Kiel, Germany) for tuning the cormo-cam. For the Canadian part of the study we would like to thank Dave Jones (UBC Zoology) for access to the Animal Care and diving facilities at South Campus. Arthur Vanderhorst and Sam Gopaul provided excellent support in caring for the birds. Bruce Gillespie and Don Brandies (UBC Zoology Mechanical Workshop) were of great help for technical questions. Ken Scheer from the Fraser Valley Trout Hatchery is thanked for generously providing us with live rainbow trout. Tom Hoeg was indispensable in setting up the Underwater Camera System within the dive tank and generously donated knowledge, expertise and time. Thanks also to Robin Liley (UBC Zoology) for tolerating the takeover of his fish holding tanks and access to video equipment. We are indebted to Magali Grantham for her enthusiastic help with animal care and experimentation and to Lovena Toolsy who helped with the video analysis. The British Columbia Ministry of Environment granted holding permits for the double-crested cormorants. All experimental procedures were approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care. Two anonymous referees provided very useful comments.

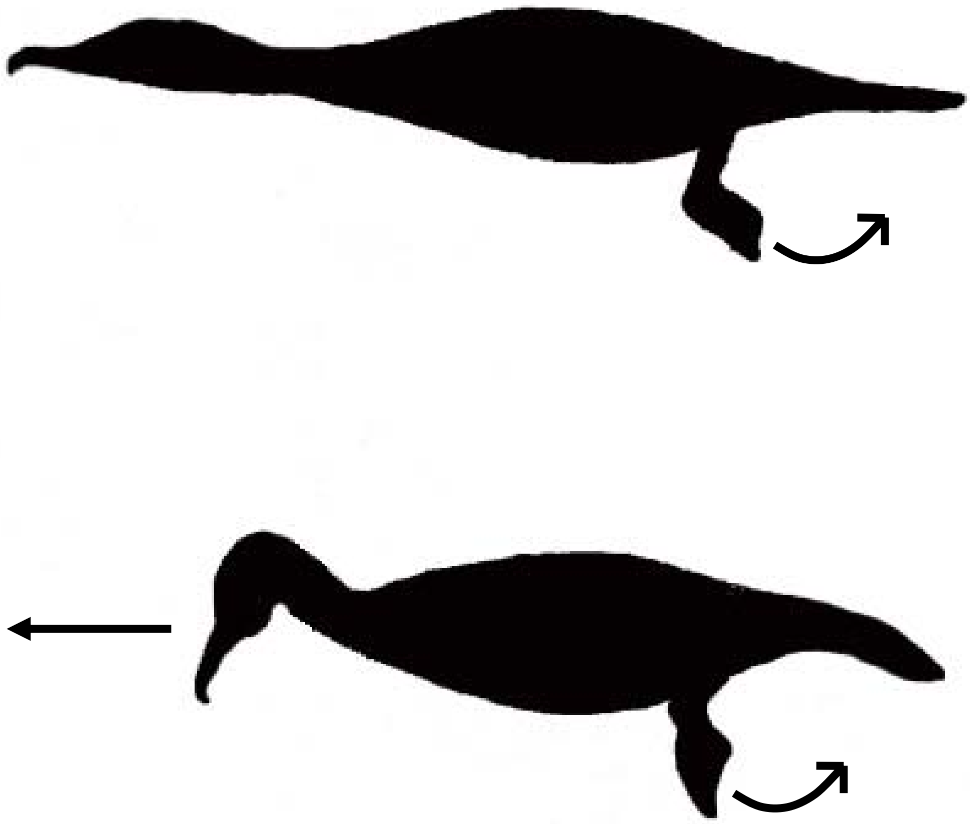

Fig. 5.1. Body position of great cormorants while searching for prey underwater (top), and prior to a pursuit (bottom). Cormorants use the synchronous movement of their webbed feet for underwater propulsion (Johnsgard, 1993). Just before initiating a pursuit they withdraw their head and neck slightly, and shoot towards their prey (bottom).

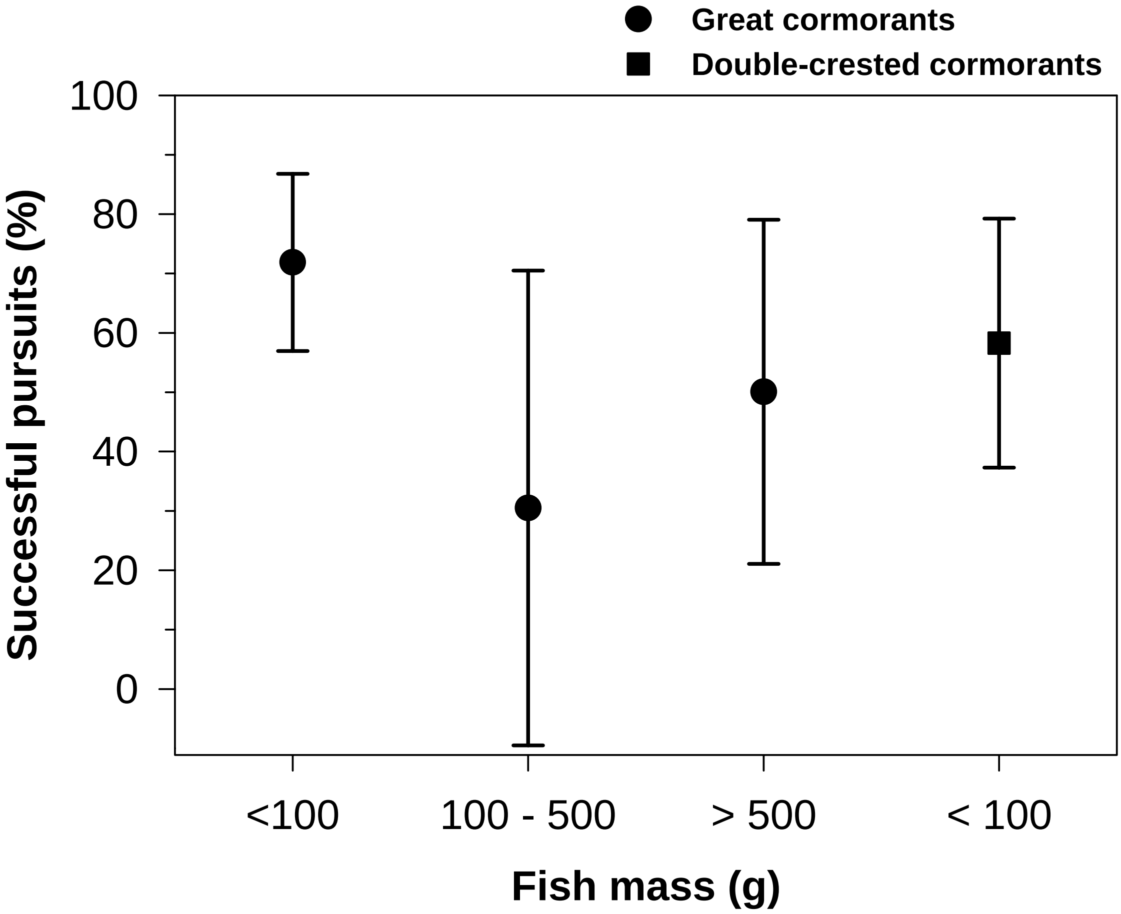

Fig. 5.2. Proportion of successful pursuits of 6 great cormorants (circles, 81 pursuits of prey items < 100 g, 21 pursuits of prey items between 100 – 500 g, 56 pursuits of prey items > 500 g) and 9 double-crested cormorants (square, 518 prey pursuits of prey items < 100 g) on fish of different mass. Error bars give the standard deviation of the mean.

Chapter 6

Foraging energetics of North Sea birds confronted with fluctuating prey availability

Note: this article is currently in press.

Enstipp, M.R., Daunt, F., Wanless, S., Humphreys, E.M., Hamer, K.C., Benvenuti, S. and Grémillet, D. (*in press*). Foraging energetics of North Sea birds confronted with fluctuating prey availability. In *Management of marine ecosystems: monitoring change in upper trophic levels* (Symposium of the Zoological Society London; ed. I.L. Boyd and S. Wanless). Cambridge: Cambridge Univ. Press.

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Abstract

In the western North Sea a large seabird assemblage exploits a limited number of fish species. Sandeels are particularly important prey items in this system, with populations that show strong spatial and temporal variability. This variability might be triggered by oceanic climatic features but could also be influenced by human activities, especially fisheries. In order to assess how different sandeel consumers are buffered against fluctuations in prey availability, we studied the foraging energetics of common guillemots, black-legged kittiwakes, European shags and northern gannets at two major colonies in southeast Scotland. Our analysis was based on: 1) time budgets recorded with data loggers attached to breeding adults foraging at sea; 2) metabolic measurements of captive and free-ranging individuals; and 3) information on diet and parental effort. We calculated daily food intake and feeding rates of chick-rearing adults and examined a number of hypothetical scenarios, to investigate how birds might be buffered against reduced sandeel availability. Our results suggest that under the conditions currently operating in this region, shags and guillemots may have sufficient time and energy available to increase their foraging effort considerably, whereas kittiwakes and gannets are more constrained by time and energy respectively. Of the species considered here, gannets are working at the highest metabolic level during chick-rearing, and hence have the least physiological capacity to increase foraging effort. However, to compensate for their energetically costly life, gannets might make use of a highly profitable foraging niche.

Keywords: Foraging energetics, seabirds, North Sea, sandeel fishery, prey availability, European shag, common guillemot, black-legged kittiwake, northern gannet.

Introduction

Human activities, such as commercial fisheries, have produced major changes in the structure of marine food webs (Pauly et al., 1998) but we know very little about the mechanisms involved. Species at intermediate trophic levels in such webs undergo strong spatial and temporal fluctuations, making it difficult to assess and monitor their populations. Conversely, predators at upper trophic levels, such as seabirds, are very conspicuous and potentially reliable indicators of the state of marine systems (Cairns, 1987; Montevecchi, 1993; Furness and Camphuysen, 1997). Thus, studying higher marine predators can provide insights into the mechanisms structuring marine food webs.

In the western North Sea, a large seabird assemblage exploits a small number of fish species. Sandeels, especially the lesser sandeel (*Ammodytes marinus*), are important prey items in this system and comprise a major component of the diet of seabirds, marine mammals, and predatory fish (see Furness and Tasker, 2000). Sandeel populations show strong spatial and temporal variability, which is poorly understood. A marked decline in sandeels around Shetland in the mid 1980s had adverse effects on many seabird species. Surface feeders like Arctic terns (*Sterna paradisaea*) and black-legged kittiwakes (*Rissa tridactyla*) had greatly reduced breeding success, whilst diving species like common guillemots (*Uria aalge*) were able to compensate for the reduction in sandeel availability to some extent by increasing their foraging effort (Monaghan, 1992; Monaghan et al., 1996). In 1990 a sandeel fishery opened around the Firth of Forth area (south-east Scotland) and expanded rapidly coinciding with a decline in breeding performance of kittiwakes from nearby colonies (Tasker et al., 2000). Concern for the future of these predators culminated in the closure of the fishery in 2000.

Furness and Tasker (2000) found that small seabirds with high energetic costs during foraging and a limited ability to switch diet (e.g. many surface feeders) were most sensitive to a reduction in sandeel abundance. Larger species with less costly foraging modes and a greater ability to switch diet (e.g. many pursuit-diving species) were less sensitive. Furness and Tasker were, however, uncertain about the relative importance of some factors, such as foraging energetics. Hence, it is important to test the hypothesis that the impacts of reduced sandeel availability on seabirds depend on energetic and behavioural constraints during foraging.

The current study addresses these issues in four North Sea seabird species during the period of chick rearing in south-east Scotland. Our study included two pursuit-diving species, the common guillemot and the European shag (*Phalacrocorax aristotelis*), one surface feeding species, the black-legged kittiwake, and one plunge-diving species, the northern gannet (*Morus bassanus*). We calculated the daily food intake (DFI) from knowledge of time-activity budgets, energy expenditures and diet, allowing the estimation of required feeding rates (catch per unit effort, CPUE) under a number of scenarios that investigated the capacity of the four species to compensate for a reduction in sandeel availability by altering their foraging behaviour.

Materials and Methods

Time-activity budget

Shags and guillemots were equipped with compass loggers and/or precision temperature/depth recorders (PreciTD; both from Earth&Ocean Technologies, Kiel, Germany). These provided very fine scale activity data that distinguished between phases of rest on land or at sea from flight and diving. A flight activity sensor combined with a saltwater switch was deployed on kittiwakes (Instituto di Elaborazione dell'Informazione, C.N.R., Pisa, Italy) and this allowed us to distinguish between periods of flight associated with travelling or foraging, periods of rest on land and at sea. Satellite tags (PTT; Microwave Telemetry, Inc., Columbia, MD, USA) on gannets enabled us to distinguish between periods spent at the colony from periods at sea and PreciTD loggers allowed to distinguish between flight, time spent submerged and resting at sea. All field data for kittiwakes, shags and guillemots were collected during the early chick-rearing period (June to July) from 1999-2003 on the Isle of May, Firth of Forth, southeast Scotland. Field data for the gannets were collected from the nearby Bass Rock breeding colony during early to mid chick-rearing in 2003. Input values for our algorithm were generated from yearly mean values for the time that birds spent in various activities per day, weighted according to sample size.

Energetic costs

Activity-specific metabolic rates for shags were measured directly via respirometry. This included measurement of BMR, metabolic rate during resting on water and during diving, incorporating the effect of water temperature (Enstipp et al., 2005). All other values were compiled from the literature. For kittiwakes all metabolic rates except for flight were taken from Humphreys (2002). BMR for gannets was taken from Bryant and Furness (1995) and metabolic rate during resting at sea was taken from Birt-Friesen et al. (1989). For guillemots we used the BMR value given by Hilton et al. (2000a) who established a regression equation from all published BMR values. Metabolic rate during resting at sea and during diving (incorporating the effect of water temperature) was taken from Croll and McLaren (1993). To account for activities at the nest such as chick feeding and preening, which will increase metabolic rate above BMR, we assumed a metabolic rate at the nest that was twice the BMR for all species except for the kittiwake where we used the measured value from Humphreys (2002). To incorporate the effect of water temperature on metabolic rate during resting at sea for kittiwakes and gannets we used the slope given by Croll and McLaren (1993) for guillemots. In the absence of data we assumed that metabolic costs of travel-flight and forage-flight for the kittiwake are identical and the same assumption was made for flying and plunge-diving for the gannet. All estimates of energetic costs during flight were calculated using the aerodynamic model of Pennycuick (1989), using the latest version ‘Flight 1.13’. Wing morphology values were taken from Pennycuick (1987). We accounted for the presumably higher flight costs during the return trip, after birds have ingested food and carry food for their chicks. Estimates of the daily energy expenditure of chicks were based on those provided by Visser (2002) for all species except the guillemot, which was taken from Harris and Wanless (1985), corrected for assimilation efficiency.

Diet, energy content of prey and assimilation efficiencies

Diet samples were collected as regurgitations, observations of prey delivered to chicks or from food dropped at the ledge. A mean calorific value for prey taken was established for each species based on the biomass proportions of prey and its size. Calorific values of the various prey items were taken from the literature (Hislop et al., 1991; Pedersen and Hislop, 2001; Bennet and Hart, 1993), accounting for seasonal effects. We took assimilation efficiencies for the gannet from Cooper (1978) and for all other species from Hilton et al. (2000b). Assimilation efficiency for chicks was assumed to be the same as in adults except in kittiwakes, for which we took the value from Gabrielsen et al. (1992).

Body mass, breeding success and water temperature

Body masses were obtained from birds during routine handling associated with ringing. Breeding success was determined as the number of chicks fledged from surveyed nests where eggs had been laid. We took water temperatures from Daunt et al. (2003) who measured water temperatures in the same area directly from foraging shags and guillemots during chick-rearing.

The algorithm

The algorithm used to compile the time-energy budgets ('baseline situation', see Table 6.1 for key input values) and to investigate the different scenarios was based on Grémillet et al. (2003) but incorporated the energetic requirements of chicks. In brief, the durations of the various activities that the birds engaged in during chick rearing (time-activity budget) were multiplied by the respective energy costs of these activities, and the energy costs were summed to give an estimate of the daily energy expenditure (DEE). A number of factors (body mass, water temperature, costs of warming ingested food) modified this estimate. In the following step the model calculated the food mass required to pay off the energetic expenses incurred (DFI) by taking into consideration the assimilation efficiency and the calorific value of the fish ingested. Adding the food mass required by their chick(s) resulted in an estimate of the total amount of food required by the adult and its chick(s). The chick estimate was based on the breeding success of the respective species (number of chicks fledged per pair, see Table 6.2) and assumed that both parents provided equally. In a final step the CPUE was calculated by considering the amount of time spent foraging. CPUE values (Table 6.2) were based on the time spent underwater for shags and guillemots, the time spent in forage-flight for kittiwakes and the total time spent at sea for gannets (a CPUE value based on the active time spent at sea is included in brackets to allow comparison across species). We conducted a sensitivity analysis (Table 6.4) to test the robustness of our algorithm (Grémillet et al., 2003).

Results and Discussion

Time-activity/energy budgets

The daily time-activity budget indicated that all species except shags spent about 50% of their time at the colony and 50% at sea. Shags on the other hand allocated only about 15% of their time towards food acquisition, and stayed at the colony for the remainder of the time. Kittiwakes, gannets and guillemots spent a considerable amount of their time at sea resting (15-30%), but resting at sea was negligible in shags. Shags and guillemots spent a much smaller proportion of their time flying than kittiwakes and gannets, reflecting the use of prey patches closer to the colony. Daily energy expenditures (DEE) calculated for the four species considered (Table 6.2) compared well with reported energy expenditures measured in the field using doubly-labelled water (DLW), where available. The time-energy budget emphasised the relative importance of energetically expensive activities, especially flight, on the overall daily energy expenditure. While birds spent only between 13-34% of their day active at sea, this period accounted for 39-60% of their daily energy expenditure. Gannets worked the hardest with a field metabolic rate (FMR) of 3.9 x BMR (basal metabolic rate), while all other species worked at a level of around 3 x BMR (Table 6.2).

CPUE values (based on active time spent at sea; see Table 6.2) for shags and gannets were high compared to the other species, with shags foraging most efficiently (Table 6.3; foraging efficiency is defined as the ratio of metabolizable energy gained during foraging to energy used during foraging).

Sensitivity analysis

An assessment of the sensitivity of the calculation of prey requirements to each variable used in the calculation (Table 6.4) indicated that the time spent in each activity and the caloric density of the prey ingested had the strongest influence on the total energy expenditure. The calculations for shags and guillemots were particularly sensitive to variation of the amount of time spent flying per day. In contrast, kittiwakes were most sensitive to time spent resting at the colony, whereas gannets were equally sensitive to time spent flying, resting at sea and resting at the colony. These results emphasise the importance of measuring these variables as precisely and accurately as possible.

Potential responses to decreased sandeel availability

Seabirds foraging in the North Sea are constrained by a delicate balance of the following three components: (a) the time they can allocate towards food acquisition; (b) the energy demands associated with their activities and (c) the food they are able to acquire. Confronted with a decline in availability of a particular prey species (e.g. sandeel), seabirds have a number of potential options to maintain their DFI at a sustainable level. For some it might be possible to switch to other prey species (e.g. clupeids, gadids) or to make greater use of fish discarded as bycatch in certain fisheries. Alternatively, they might be able to increase their foraging effort in a number of ways. In the following scenarios we explored the capacity of the four species to increase their foraging effort within the constraints imposed upon them by time, energy, and food. In all scenarios the increased amount of time allocated towards prey acquisition was balanced by reducing the time spent resting at sea and at the colony. While decreasing resting time at sea to zero we decreased resting time at the colony only to a minimum of 50% of the daily total, assuming that chicks were not left unattended. We also took into consideration that all species were inactive for some part of the night, during which no foraging activity occurred (shags: 8 hrs, Wanless et al., 1999; guillemots: 1 hr, Daunt unpubl.; kittiwakes: 3 hrs, Daunt et al., 2002; gannets: 5 hrs, Humphreys unpubl.). Assuming that partners shared the available time equally, the total time that could potentially be allocated towards foraging activity by an adult per day ranged from 8 hrs for shags to 11.5 hrs for guillemots.

Energy expenditure of endotherms sustained over a longer time period is limited by physiological constraints (e.g. digestive capacities; Weiner, 1992). Hence, if energy expenditure of animals in the wild approaches such a ceiling, fitness costs may be incurred (e.g. reduced survival). Here we assumed the metabolic ceiling of 4 x BMR as suggested by Drent and Daan (1980) for birds raising chicks. In scenario 1, birds increased their foraging time spent within a prey patch. In scenario 2, birds made use of a prey patch at a further distance from the colony, increasing the amount of time spent flying. Birds flew to a further prey patch and foraged for a longer time within the prey patch in scenario 3 (both variables raised equally). Finally, we investigated the effect that feeding on a diet of lower caloric density (4.0 kJ g^{-1} wet mass) had in combination with the above scenarios.

(1) Time and energy

If seabirds are to increase their foraging effort in response to a reduction in sandeel availability, the first constraint encountered is likely to be the availability of spare time. Time-activity budget analysis illustrated that, with the exception of the shag, no species could reduce their resting time at the colony much further, unless they left their chicks unattended. Doing so could potentially reduce their breeding success drastically, especially when the chicks are small. While non-attendance of chicks has been recorded in all four species (Harris and Wanless, 1997; Daunt, 2000; Lewis et al., 2004), we assumed that birds normally avoided this. All species except the shag, however, spent a considerable amount of time resting at sea. In a first step then, birds are predicted to reduce their resting time at sea to a minimum before starting to reduce their resting time at the colony. Based on the time-activity budgets birds could potentially reallocate between 10% (kittiwake) and 22% (guillemot) of their daily time towards an increase in foraging effort.

Increasing foraging effort in these scenarios led to an increase in the amount of required daily food (lower portion of Figs 6.1 to 6.3). This was especially drastic in scenario 2, where birds made use of a prey patch at a greater distance from the colony, requiring longer flight times. The exact relationship depended on the strategy being pursued (commuting to a further prey patch, foraging for longer in a particular prey patch or a combination of both) and on the specific costs of the associated activities (e.g. flight vs. diving). It also depended on the benefits accruing as a result of the increased effort. Figs 6.1 to 6.3 clearly underline the limited possibilities for gannets to increase their foraging effort because of energetic constraints. Gannets spent about 30% of their daily time resting at sea, of which 17% could potentially be allocated towards increasing their foraging effort (taking into account the inactive period at night). Since gannets already worked close to the presumed maximal energetic capacity, however, they could only do so in very small increments before reaching the assumed metabolic ceiling in any of the three scenarios. Birt-Friesen et al. (1989) also reported high metabolic rates for northern gannets during chick rearing and attributed these to the high costs of thermoregulation and flapping flight. The gannets in our study were already working at a much higher level than the other birds considered here, hence their physiological limitation to increase foraging effort was not surprising. One possible strategy for gannets, which is not explored in this analysis, since it assumes a balanced energy budget, could be that they incur an energy debt over a short period that is paid off at a later time. In fact, Nelson (1978) suggested that body condition declines in gannets over the course of the breeding season. A possible explanation for the high FMR values we calculated for the gannets could be the large size of the colony from which our data were collected. Foraging trip duration and foraging range of gannets nesting at the Bass Rock colony are high when compared to a colony of smaller size (see Hamer et al., in press), resulting in higher energy expenditures per foraging trip. Hence, gannets breeding at a smaller colony might not experience the same energetic constraint as the gannets in our study. The other three species had much more scope (in terms of time and energy) to increase their foraging effort. While in all three scenarios kittiwakes were ultimately limited by the amount of time they could reallocate towards an increase in foraging effort (Figs 6.1 to 6.3), shags and guillemots were mostly constrained by the energetic demand that accompanied such an increase. This difference can be attributed to the relatively high costs of flapping flight in the latter two species. However, the overall capacity to increase foraging effort in shags and guillemots was quite considerable. Shags could potentially increase their foraging time by about 222%, their flight time by about 106% and their total active time at sea by about 112%. Comparable values for guillemots were 111%, 190% and 65% respectively. Increased flight times in scenario 2 potentially doubled the foraging range of shags while it tripled that of guillemots (Table 6.3). A substantial increase in foraging range was prevented by time and energetic constraints in the case of kittiwakes (69%) and gannets (9%) respectively.

(2) Food

Birds are constrained by the amount of food available and by the rates at which they can acquire food. In many cases we know little about sandeel abundance in the North Sea but we know even less about the prey capture capacities of seabirds and the fish densities they require to forage effectively. Under conditions of reduced prey availability birds presumably have difficulties finding sufficient food to meet their energy requirements and those of their chicks. Any additional increase in foraging effort, as suggested by our scenarios, will lead to an even higher requirement for food. Foraging effort has to be even greater when birds are forced to feed on prey of lower energy density. Combining the above scenarios with a diet switch to prey of lower calorific value (4.0 kJ g^{-1} wet mass; Fig. 6.4) did not change the basic outcome of our calculations in terms of time and energy constraints. However, it drastically increased the food requirement and the associated feeding rates for all species. Fig 6.4a illustrates this for scenario 2 in the guillemot (foraging at a distant prey patch) and Fig 6.4b shows scenario 3 in the shag (foraging at a distant prey patch for a longer period).

How steep the increase in foraging effort will need to be depends on how energetically expensive the associated activities are. Making use of a prey patch at a greater distance from the colony, requiring longer flight times, greatly increased daily food requirements for most species considered here (Fig. 6.2). There will be a limit, imposed by the food availability, at which a further increase in foraging effort becomes unsustainable.

Feeding rates reported in the literature (6-12g fish min^{-1} underwater for shags, Wanless et al., 1998; 0.5-1.3g fish min^{-1} at sea for gannets, Garthe et al., 1999) are typically within the range or slightly lower than our estimates for the ‘baseline situation’ (before increasing foraging effort). The same holds true for DFI values reported for kittiwakes and guillemots. This could indicate that birds might not be able to achieve feeding rates that would be required in the above scenarios when foraging effort is drastically increased.

(3) Further potential responses

An alternative strategy to increasing foraging effort might be to switch to exploiting other prey types. Unlike the situation in Shetland where sandeels are the only small, shoaling forage fish, other prey species are present in the Firth of Forth area that are potentially available to seabirds (Daan, N. et al., 1990). Dietary information suggests that kittiwakes and shags may be less able to switch to alternative prey compared to guillemots and gannets. In the case of kittiwakes this might be exacerbated by its surface feeding habit that limits its foraging abilities to prey items at, or close to, the surface (Lewis et al., 2001).

In addition to switching to other live prey species, seabirds can also potentially exploit fishery discards. Most fisheries in the North Sea produce bycatch that is discarded and can be consumed by seabirds. While most pursuit-diving species tend to ignore these discards, many surface feeders readily feed on them. Of the four species considered here only the kittiwake and gannet are observed in substantial numbers at fishing boats (Garthe et al., 1996). However, with the volume of fishery discards in the North Sea potentially declining (see Votier et al., 2004), this might not be a sustainable option.

This chapter has highlighted the interactions between physiological and behavioural constraints that condition the different responses of seabirds in the Firth of Forth area to reduced sandeel availability. While shags and guillemots may have sufficient time and energy to allow them to increase their foraging effort considerably, kittiwakes and gannets appear more constrained by time and energy respectively. Our analysis was relatively restricted in time and space. Clearly, including activity data from a larger geographical area and over a longer time period to establish the time-energy budgets ('baseline situation') would be desirable and would minimise any bias that years of high or low prey availability might introduce. As previously recognised by Furness and Tasker (2000), consideration of energetic constraints is essential to fully evaluate the capacity of species to cope with food, particularly sandeel, shortages. Gannets scored low for the criteria used by Furness and Tasker to establish vulnerability and sensitivity indices for seabirds in the North Sea and the authors concluded that this species was generally well buffered against change. In contrast, our study suggests that during chick-rearing gannets are working at the highest metabolic level of all species considered and hence, have the least physiological capacity to increase foraging effort. This indicates that gannets could potentially be very sensitive to a reduction in sandeel availability. To compensate for their energetically costly life, however, gannets might make use of a highly profitable foraging niche.

Acknowledgements

Most of this work was funded by the European Commission project 'Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864). We thank Svein-Håkon Lorentsen, Claus Bech, Geir Håvard Nymoen, Hans Jakob Runde and Magali Grantham for help with the captive work on shags and guillemots. The Norwegian Animal Research Authority granted research permits for this study (ref no: 7/01 and 1997/09618/432.41/ME). Thanks also to the many people who helped with fieldwork particularly Stefan Garthe, Mike Harris, Janos Hennicke, Sue Lewis, Gerrit

Peters, and Linda Wilson. Scottish Natural Heritage and Sir Hew Hamilton-Dalrymple granted permission to work on the Isle of May and the Bass Rock respectively. Luigi dall'Antonia and Alberto Ribolini developed the flight activity sensors used on kittiwakes and provided software for data analysis. Thanks to Ian Boyd and two anonymous referees for improving the manuscript.

Table 6.1. Some of the input values (means ± SD) used to compile a time-energy budget (‘baseline situation’) for 4 North Sea seabirds during chick rearing (BMR = basal metabolic rate; DEE = daily energy expenditure).

	Black-legged kittiwake	European shag	Northern gannet	Common guillemot
Body mass (g)	361.64 ± 36.14	1780.43 ± 97.63	2998 ± 234	920.34 ± 57.44
Assimilation efficiency for chick (%)	80.00 ± 1.25			
Calorific value of fish (kJ/g wet)	5.0 ± 0.5	5.4 ± 0.5	5.8 ± 0.6	5.1 ± 0.5
Water temperature at surface (^{o}C)	11.1 ± 0.5	11.1 ± 0.5	11.1 ± 0.5	12.0 ± 0.5
Water temperature at bottom (^{o}C)		10.3 ± 0.4		8.8 ± 0.5
BMR (kJ day^{-1})	267.28	726.07 ± 46.15	1256.28 ± 227.94	584.48
Energy costs, resting at colony (W kg^{-1})	13.69 ± 1.20	9.44 ± 0.6	9.70 ± 1.76	14.70 ± 1.47
Energy costs, resting at sea (W kg^{-1})	12.82 ± 2.56	17.18 ± 2.02	12.46 ± 2.16	10.19 ± 1.02
Energy costs, flying (W kg^{-1})	44.83 ± 4.48	98.07 ± 9.81	43.69 ± 4.37	92.58 ± 9.26
Energy costs, foraging (W kg^{-1})	44.83 ± 4.48	20.58 ± 2.8	43.69 ± 4.37	23.83 ± 2.38
DEE of chick (kJ day^{-1})	525.71 ± 52.57	1203.98 ± 120.40	1593.30 ± 159.33	221.71 ± 22.17

Table 6.2: Daily energy expenditure (DEE), field metabolic rate (FMR expressed as xBMR), daily food intake (DFI) and feeding rate (catch per unit effort, CPUE) for 4 North Sea seabirds ('baseline situation'). CPUE values are based on the time spent underwater for shags and guillemots, the time spent in forage-flight for kittiwakes and the total time spent at sea for gannets. To allow comparison across species a CPUE value based on the active time spent at sea (excluding periods of rest at sea) is included in brackets.

	Black-legged kittiwake	European shag	Northern gannet	Common guillemot
Adult				
DEE (kJ day^{-1})	786.74	2249.25	4856.01	1641.01
FMR (xBMR)	2.9	3.1	3.9	2.8
DFI (g fish day^{-1})	211	514	1114	415
Chick				
DEE (kJ day^{-1})	525.71	1203.98	1593.30	221.71
DFI (g fish day^{-1})	131	275	366	56
No of chicks fledged/pair	0.71	1.51	0.67	0.69
DFI (g fish day^{-1}, portion/adult)	47	208	122	19
Total				
DFI (g fish day^{-1})	258	722	1237	434
CPUE (g fish min^{-1})	1.35 (0.50)	10.10 (3.84)	1.63 (3.89)	2.45 (1.18)

Table 6.3. Foraging efficiency (ratio of metabolizable energy gained during foraging to energy used during foraging) and foraging range of 4 North Sea seabirds.

Species	Energy acquired at sea per day to meet adult and chick requirements (kJ day^{-1})	Energy expenditure at sea per day		Foraging efficiency		Foraging range (km)	
		Total (kJ day^{-1})	Active[1](kJ day^{-1})	At sea	Active[1]	'Baseline situation'	Potential increase
Black-legged kittiwake	972.07	534.44	473.59	1.82	2.05	49.6	+ 34.0
European shag	3158.25	932.76	879.27	3.39	3.59	10.4	+ 11.1
Northern gannet	5389.76	3484.77	2500.13	1.55	2.16	282.4	+ 26.8
Common guillemot	1715.00	960.93	784.20	1.78	2.19	21.8	+ 41.5

[1] Excludes periods of rest at sea.

Table 6.4. Sensitivity analysis for the time-energy budget of 4 North Sea seabirds. Minimum and maximum input values for each parameter were used (see Table 6.1) to compute the individual variation in mean DFI (%). Minimum and maximum values for all parameters[1] combined were computed for the most and least demanding situation, which indicates the maximum range of potential DFI values for the birds.

	Black-legged kittiwake		European shag		Northern gannet		Common guillemot	
	Variation of mean DFI (%)	Range used	Variation of mean DFI (%)	Range used	Variation of mean DFI (%)	Range used	Variation of mean DFI (%)	Range used
Body mass (g)	± 8.1	S.D.	± 1.7	S.D.	± 5.2	S.D.	± 8.3	S.D.
Time resting at colony (min day^{-1})	± 10.8	S.D.	± 2.7	S.D.	± 9.9	S.D.	± 1.0	S.D.
Time resting at sea (min day^{-1})	± 2.3	S.D.	± 0.3	S.D.	± 9.4	S.D.	± 6.6	S.D.
Time spent flying (min day^{-1})	± 2.7	S.D.	± 5.3	S.D.	± 10.1	S.D.	± 18.5	S.D.
Time spent foraging (min day^{-1})	± 1.5	S.D.	± 2.0	S.D.	± 0.3	S.D.	± 5.9	S.D.
Assimilation efficiency (%)	± 1.5	S.D.	± 1.4	S.D.	± 5.9	S.D.	± 2.2	S.D.
Assimilation efficiency (%) for chick	± 0.4	S.D.						
Calorific value of fish (kJ g^{-1} wet)	± 10.5	10%	± 9.6	10%	± 10.8	10%	± 10.4	10%
Water temperature at surface (ºC)	± 0.4	S.D.	± 0.1	S.D.	± 0.5	S.D.	± 0.6	S.D.
Water temperature at bottom(ºC)			± 0.1	S.D.			± 0.1	S.D.
Energy costs, resting at colony (W kg^{-1})	± 1.9	S.D.	± 2.6	S.D.	± 4.2	S.D.	± 3.8	10%
Energy costs, resting at sea (W kg^{-1})	± 1.2	S.D.	± 0.2	S.D.	± 3.3	S.D.	± 1.0	10%
Energy costs, flying (W kg^{-1})	± 3.1	10%	± 1.9	10%	± 4.8	10%	± 2.4	10%
Energy costs, foraging (W kg^{-1})	± 1.9	10%	± 1.2	S.D.	± 0.1	10%	± 2.3	10%
Chick DEE (kJ day^{-1})	± 1.9	10%	± 2.9	10%	± 1.0	10%	± 0.5	10%

All parameters[1]	Black-legged kittiwake	European shag	Northern gannet	Common guillemot
Variation of mean DFI (%)	± 36.0	± 32.2	± 49.7	± 54.8
Absolute range of DFI (g fish day^{-1})	179-365	527-992	750-1979	245-721

Increasing foraging effort to buffer reduced sandeel availability: 3 scenarios

The upper portion of Figs 6.1 to 6.3 plots the daily energy expenditure for the four species (as multiples of BMR) against the increase in foraging effort considered in scenarios 1 to 3. The solid upper line indicates the presumed metabolic ceiling of 4 x BMR. Increases in foraging effort that lead to an increase in energy expenditure beyond this ceiling are assumed to be unsustainable, indicating a physiological constraint. The x-axis indicates the scope that the bird may have to reallocate time towards an increase in foraging effort, with zero being the 'baseline situation' before increasing foraging effort. If the plot for an individual bird stops before reaching the physiological ceiling it indicates a time constraint because birds have no time left to increase their foraging effort. The percentages given indicate the relative increase in foraging effort that is possible before a constraint is reached. The lower portion of Figs 6.1 to 6.3 indicates changes in the required DFI (g day^{-1}) which accompany the increase in foraging effort considered in scenarios 1 to 3.

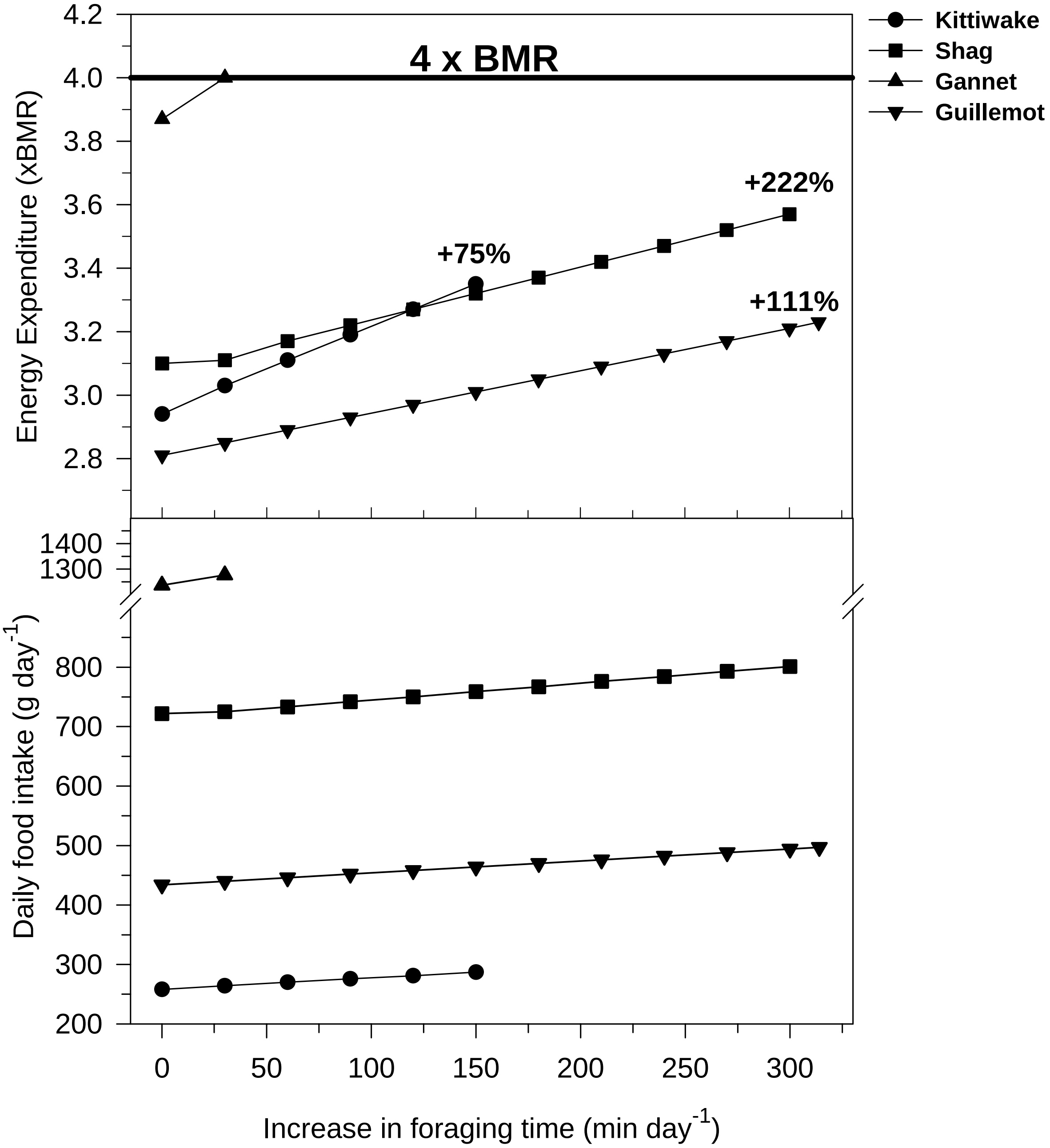

Fig. 6.1. Scenario 1: increasing foraging time within a prey patch. Zero indicates the ‘baseline situation’ (i.e. before increasing foraging time).

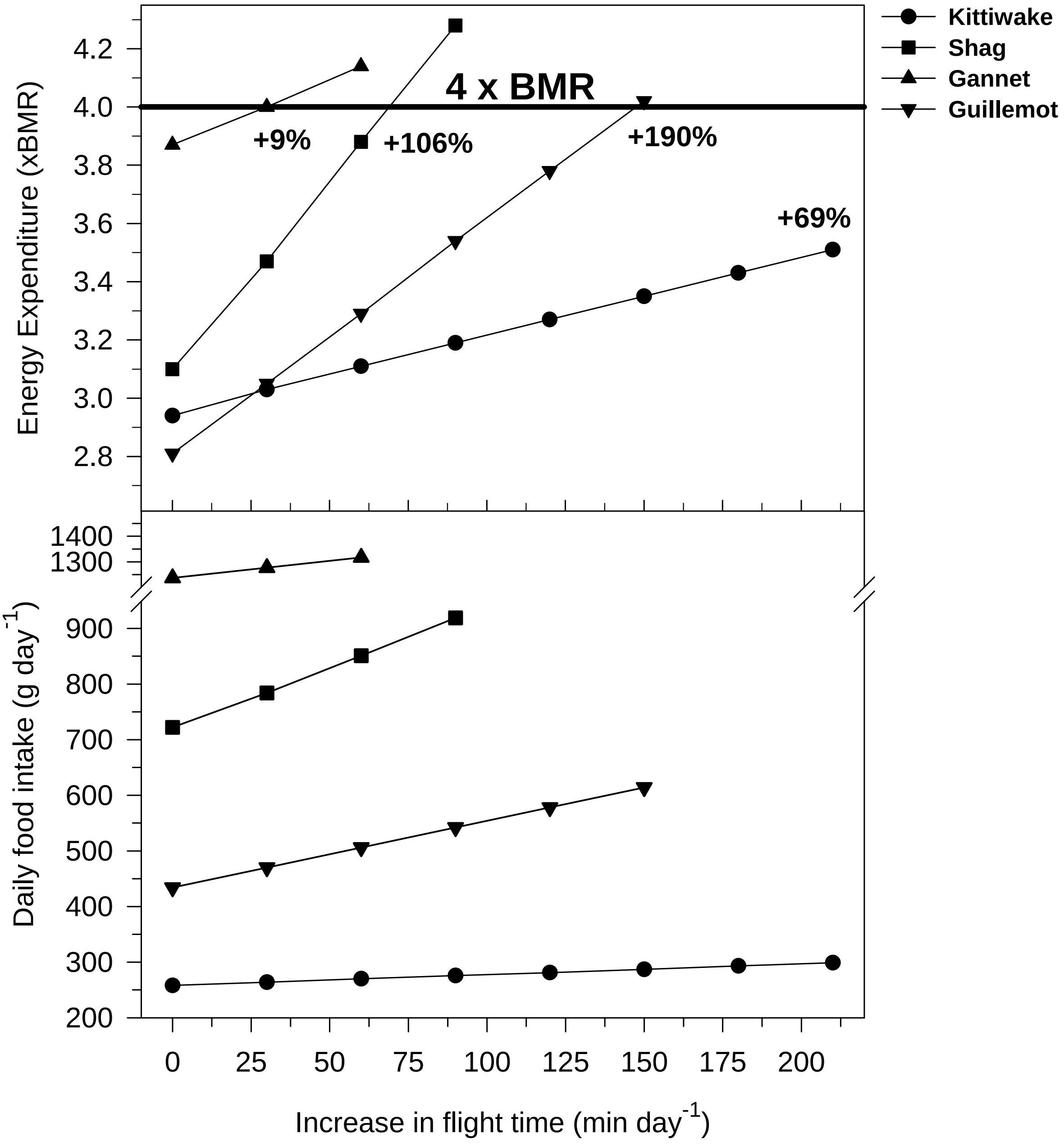

Fig. 6.2. Scenario 2: foraging at a more distant prey patch. Zero indicates the ‘baseline situation’ (i.e. before increasing flight time).

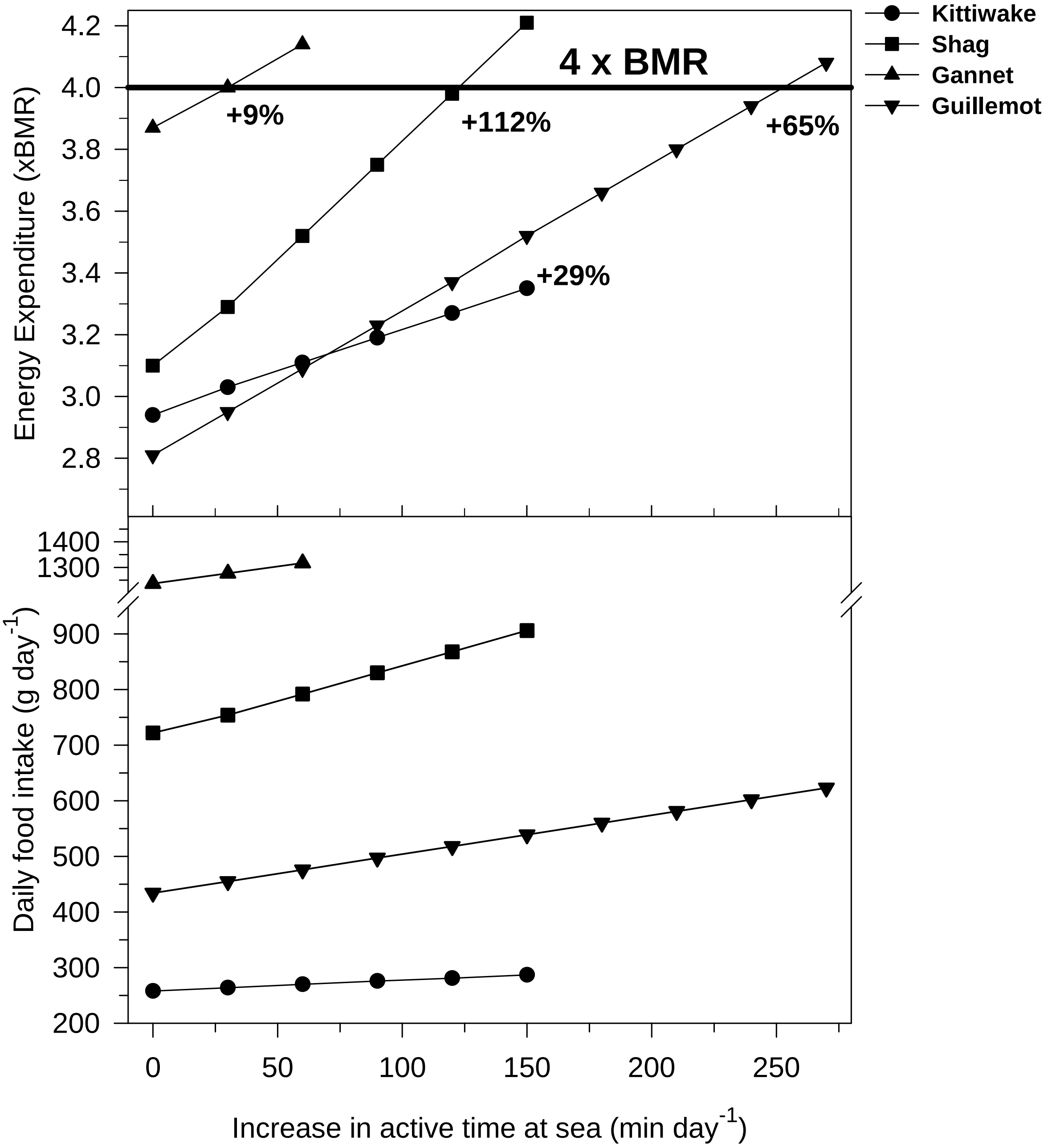

Fig. 6.3. Scenario 3: foraging at a more distant prey patch and for a longer time within that prey patch. Zero indicates the 'baseline situation' (i.e. before increasing flight and foraging time).

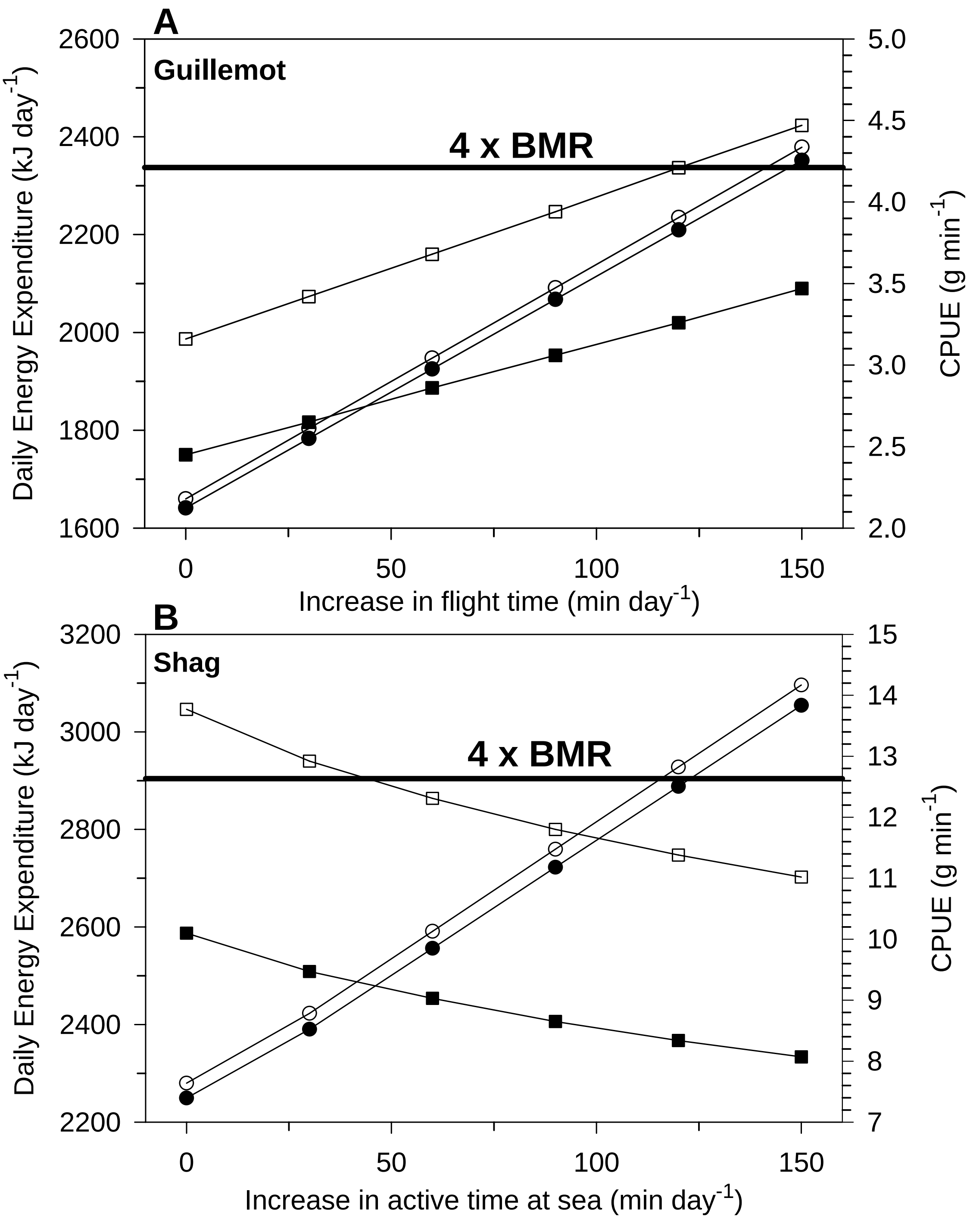

Fig. 6.4. (A) Scenario 2 (foraging at a more distant prey patch), and combined with feeding on prey of reduced caloric density for the guillemot. (B) Scenario 3 (foraging at a more distant prey patch and for a longer time within that prey patch), and combined with feeding on prey of reduced caloric density for the shag. Circles indicate DEE, while squares indicate CPUE. Filled symbols indicate scenario 2 and 3, while open symbols indicate combination of the respective scenario with feeding on less profitable prey. CPUE values are based on the time spent underwater.

Chapter 7

Conclusions and outlook

The central theme of this thesis has been the investigation of dive costs in avian divers and how these energetic considerations, in conjunction with aspects of their foraging behaviour, might constrain seabirds that are facing changes in food abundance.

I used an open-circuit respirometry system to study in detail the energetic costs of diving in European shags and double-crested cormorants in dependence of a variety of biotic and abiotic factors (chapters 2 and 3). Using both a shallow (1 m) and deep (10 m) dive tank, it was possible to investigate specifically the effect of depth on diving costs, a factor that has been largely ignored. I also used an experimental approach to investigate the importance of a variety of factors (prey density, prey size, light conditions, prey behaviour, water temperature, and depth) in shaping the prey-capture behaviour of cormorants foraging on live prey (chapter 4). These experiments further allowed me to test the hypothesis that cormorants capture fish without eating them in chapter 5. Finally, in a more theoretical approach in chapter 6, I developed an algorithm to predict daily energy expenditure (DEE), daily food intake (DFI) and required prey capture rates (catch per unit effort, CPUE) for four North Sea seabird species during chick-rearing in Scotland and tested their capacity to buffer a potential decline in food abundance through an increase in foraging effort.

Diving energetics

My thesis shows that the energetic costs of diving in European shags and double-crested cormorants are similar to those of other avian divers (chapters 2 and 3; Table 2.1, Fig. 3.7). While dive costs in cormorants as a group tend to lie above the average relationship relating diving metabolic rate to body mass in avian divers, this is most noticeable in the great cormorant (Fig. 3.7). However, when accounting for the effect of water temperature, it emerges that the mass-specific diving metabolic rates for European shags, double-crested cormorants, and the marine sub-species of the great cormorant (*P. carbo carbo*) are very similar and considerably below the value reported by Schmid et al. (1995) for the continental sub-species of the great cormorant (*P. carbo sinensis*).

Systematic alteration of a variety of factors (dive depth, water temperature, feeding status) in a captive dive setting demonstrated that all of these factors are important modulators of metabolic rate during diving (Figs 2.4, 3.2 and 3.3). Of all the factors examined, dive depth, which for the first time was investigated over a significant depth range naturally encounter by an avian diver, exercised the strongest influence on diving metabolic rate. However, the effect of depth was lower, than previously suggested based on thermodynamic modelling (Grémillet and Wilson, 1999). This discrepancy probably arises from the fact that the model did not take into account the ability of animals to regulate heat flux to the environment, nor did it account for the reduction in locomotor effort with increasing depth, as buoyancy decreases significantly (see p. 57).

Water temperature also had a significant influence on metabolic rate when resting in water and during diving, so that metabolic rate increased with declining water temperature (Figs 2.4 and 3.3). The strong effects of depth and water temperature on cormorant diving metabolic rate are probably a consequence of their partially wettable plumage and their reduced plumage air volume (Wilson et al., 1992b; Grémillet et al., 2005a; pers. observation), when compared with other avian divers (e.g. diving ducks). Given their plumage structure, cormorants and shags are prone to heat loss, which will be greatly increased when diving in cold water to depth. The trade off between reduced buoyancy (reducing mechanical costs of diving) and increased heat loss (increasing thermoregulatory costs) are discussed in detail in chapter 3. My study suggests that in double-crested cormorants the energetic savings accrued from reduced work against buoyancy when diving to 10 m depth is outweighed by the accompanying heat loss and the consequently increased thermoregulatory costs.

However, to study the effect of dive depth on heat loss in more detail and to evaluate how heat loss might shape diving costs in cormorants and shags, heat flux measurements during diving, as have been conducted in marine mammals (Willis and Horning, 2005) are urgently needed (but see Lovvorn, in press). One should also keep in mind that in the wild, cormorants and shags, like other avian divers, can potentially use a number of mechanisms to decrease thermoregulatory costs. For example, birds might be able to use the additional heat generated by the flight muscles when leaving the foraging area or they might be able to use heat generated from the heat increment of feeding (HIF) to substitute for thermoregulatory costs (Kaseloo and Lovvorn, 2003). These mechanisms might allow birds to make up for at least some of the heat loss incurred during diving without having to spend additional energy for thermoregulation by means of shivering or non-shivering thermogenesis. However, in my experimental set-up, capacity for these mechanisms was limited.

When diving after food ingestion, metabolic rate of both shags and cormorants was increased but this increase was not significant (chapters 2 and 3). While this would suggest that the scope for the HIF to substitute for thermoregulatory costs in cormorants and shags might be limited, the amount of food ingested by the birds before a trial was rather small. It is therefore conceivable that the HIF in the wild might be greater for these species, when birds ingest larger amounts of food in quick succession. This is supported by the finding that the increase in metabolic rate was greater and longer lasting in the shags that were fed larger amounts (up to 160 g) than the cormorants (60 g).

Stomach temperatures in both species were elevated when resting in water and during diving but remained stable during trials of up to 50 min in water temperatures as low as 5 ^{o}C (Figs. 2.5 and 3.5). Hence, it is suggested that neither species pursues a strategy of regional hypothermia during diving, a strategy that would lower energetic costs and therefore increase aerobic dive duration (Bevan et al., 1997; Handrich et al., 1997; Butler, 2004). However, appropriate investigation of such a strategy requires the study of birds implanted with temperature probes at various positions within their body that forage in their natural environment (e.g. Handrich et al., 1997).

Prey-capture behaviour

My study demonstrates the importance of taking into account prey density and behaviour when trying to evaluate seabird feeding requirements (chapter 4). When fish density within the tank declined, cormorants responded by increasing the amount of time spent searching during a trial (Fig. 4.2). A lower fish density also decreased both prey encounter rate (Fig 4.3) and prey capture rate (Fig. 4.4). In all cases the effect was most noticeable below a fish density of 2-3 $g \cdot m^{-3}$. I therefore suggest that this density represents a threshold prey density, below which cormorant foraging performance is significantly altered (see chapter 4, p. 83). As a consequence, birds might have to increase foraging effort, which in turn will increase energy expenditure, with potential effects on fitness (i.e. reduced reproductive success and/or survival; Drent and Daan, 1980; Daan et al., 1996). I also showed that fish behaviour might have important consequences for cormorant foraging success and required foraging effort. Shoaling behaviour of the rainbow trout proved an effective anti-predator behaviour during experimentation. It significantly decreased cormorant capture success (Fig. 4.7), while at the same time significantly increasing the amount of time birds had to spend in pursuit in order to succeed. Double-crested cormorants are opportunistic foragers that take the majority of their prey within the littoral-benthic zone (Robertson, 1974). However, in estuarine areas shoaling fish species (especially salmonids) make up a substantial part of the prey biomass ingested (Collis et al., 2002; Anderson et al., 2004). Hence, using rainbow trout as a prey species for my experiments was a realistic choice. Therefore my results suggest that there might be a cost attached for individually foraging cormorants to attack shoaling prey. A possible strategy could be to attack preferentially benthic, non-shoaling prey when foraging alone but to join groups (e.g. multi-species feeding flocks) when shoaling prey becomes available, since social foraging might facilitate easier prey-capture.

In chapter 4 I furthermore established a functional link between prey density and cormorant prey capture rates (Fig. 4.4; or feeding rates Fig. 4.5), which will be essential for feeding models of piscivorous diving birds and will help us to better understand predator requirements.

Cormorants are generally regarded as highly efficient predators (i.e. Grémillet et al., 2001). My foraging experiments, however, showed that double-crested cormorants aborted about half of their initiated pursuits on rainbow trout (chapter 5, Fig. 5.2). Pursuits were aborted well before birds reached a fish and, hence, fish were not injured in these incidents. Despite the claim by many interest groups that cormorants injure substantial amounts of fish without ingesting them (see Carss, 2003), I observed such behaviour in only 2 cases out of 518 prey attacks (i.e. 0.4 %), when fish managed to escape after being caught by a cormorant.

Bio-energetics modelling

Chapter 6 highlights the interactions between physiological and behavioural constraints that condition the different responses of seabirds in the Firth of Forth area of Scotland to reduced sandeel availability. This bio-energetic modelling exercise helped to visualize the differences in potential physiological (energetics), behavioural (prey-capture) and timely constraints between the four species investigated. It furthermore illustrated how a switch in diet (i.e. acquiring prey of lower caloric value) might interact with these constraints. Under the conditions currently operating in this area, shags (*Phalacrocorax aristotelis*) and guillemots (*Uria aalge*) may have sufficient time and energy to allow them to increase their foraging effort considerably in an attempt to buffer reduced sandeel abundance (Figs 6.1-6.4). Kittiwakes (*Rissa tridactyla*) and gannets (*Morus bassanus*) appear more constrained by time and energy respectively (Figs 6.1-6.3). These results seem somewhat surprising with respect to the gannet, since it is generally considered to be well buffered against sandeel decline (Furness and Tasker, 2000). In contrast, this study suggests that during chick-rearing gannets are working at the highest metabolic level of all species considered and hence, have the least physiological capacity to increase foraging effort. This indicates that gannets could potentially be very sensitive to a reduction in sandeel abundance.

Chapter 6 also illustrates the importance of accurate and detailed activity data as well as activity-specific metabolic rates in establishing time-energy budgets. When assembling activity-specific metabolic rates for the four seabird species, it became obvious how patchy our knowledge of seabird foraging energetics still is. Hence, further studies on activity-specific metabolic rates and their modification by biotic and abiotic factors are urgently needed as they are the centerpiece of any bio-energetic modelling. This is particularly true for estimates of flight costs. Besides a few DLW estimates that might be questionable (e.g. Birt-Friesen et al., 1989; see Wilson and Culik, 1993), few data are available. In the absence of measured data, we have to rely on aerodynamic models (e.g. Pennycuick, 1989). However, the validity of these models, especially for seabirds is disputable. For example, using morphological measurements from Pennycuick (1987) as input data into Pennycuick's 'Flight 1.13' aerodynamic model revealed shag flight metabolic rates in the range of 20 times BMR, which seems rather high. Hence, to improve the accuracy of time-energy budgets it is of great importance to investigate flight costs, which could be an important research field for the future. One promising avenue to estimate flight costs of seabirds in the field is the heart rate method (Butler, 1993), which I discussed in chapter 1 (p. 6).

My prey-capture experiments with the cormorants (chapter 4) emphasise the importance of taking prey density and behaviour into account, when developing management schemes for fisheries. In chapter 1 (p. 13), I briefly introduced the approach to calculate energetic requirements of particular seabird populations or colonies, and, based on this, to define a minimum prey abundance required within their foraging areas. However, this approach does not consider the full complexity of the situation. It does, for example, not take into account that seabirds might require particular prey densities for profitable foraging. For instance, Brown (1980) suggested that prey densities of at least 100 times the average are necessary for profitable foraging by some alcids (average being the even distribution of prey at sea). Hence, in order to be able to fully evaluate seabird requirements, we also need information about the functional relationship between prey abundance (density) and predator performance (prey-capture rates or feeding rates). However, investigating the link between prey abundance and predator performance in the marine environment remains challenging and field studies, especially at the higher trophic levels, are rare (Grémillet et al., 2004). In the absence of field studies, experimental investigation in a controlled, captive setting is crucial in our understanding of predator requirements. My experiments with the cormorants suggest that minimum prey densities exist, below which sustainable foraging might be impossible for a predator.

In chapter 1 (p 13), I already mentioned that it was not possible to incorporate aspects of cormorant prey-capture behaviour and sandeel abundance estimates in our model (chapter 6). I would like to return to this aspect now. In chapter 6, I calculated the required prey-capture rate (CPUE, based on estimates of DEE and activity data) for the European shag in the 'baseline situation' to be 10 $g{\cdot}min^{-1}$ submerged (Table 6.2). Using the relationship between prey density and prey-capture rate established for the cormorants in this study (Fig. 4.4, chapter 4), this would require a fish density of about 15 $mg{\cdot}m^{-3}$. Camphuysen (2005) estimated the density of 1+group sandeel (*Ammodytes marinus*), the principle prey for shags, to be 300 $mg{\cdot}m^{-3}$ for the relevant area (assuming an even distribution, which is of course an oversimplification). While this fish density would seem sufficient to satisfy the energetic requirements of shags in the 'baseline situation', it might not be, when considering that 200-300 $mg{\cdot}m^{-3}$ seemed to represent a behavioural threshold density during the prey-capture experiments with the cormorants (chapter 4). At densities below this threshold, prey-encounter rate was drastically reduced (Fig. 4.3), while birds increased their search time during a trial (Fig. 4.2). Hence, if shags are forced to increase their foraging effort, energy requirements will also increase. In the hypothetical scenarios of chapter 6, birds increased their foraging effort in various ways. For the shag, this increased the required prey-capture rate to ~18 $g{\cdot}min^{-1}$. The associated required fish density of about 323 $mg{\cdot}m^{-3}$ (Fig. 4.4) is above the fish density available in the relevant area, indicating that prey density could potentially be limiting for the shags within this system. This is of course a first approach, since the situation is more complex in reality. Given the patchiness of prey distribution in the marine environment, we have to also include the spatial component of seabird foraging, i.e. where do birds forage and what are the prey densities in these areas? Nevertheless, this basic approach illustrates some of the existing constraints for seabirds foraging within the North Sea ecosystem.

Outlook

In conclusion, my thesis has provided detailed information on some aspects of the diving energetics in European shags and double-crested cormorants. It also investigated the prey capture behaviour of double-crested cormorants and the various constraints experienced by seabirds in the North Sea during chick-rearing and their capacity to buffer environmental change (e.g. decreased prey abundance). As usual, this work also raises new questions. For example, as discussed in chapter 3, heat balance and thermoregulation during diving are complex issues that still await their full scientific appreciation. Also, the relevance of heat produced by exercise and/or the HIF in substituting for thermoregulatory costs incurred during diving is still largely unclear. Only recently has it become possible to record temperatures of various tissues in avian divers foraging in the wild (Bevan et al., 1997; Handrich et al., 1997; Schmidt et al., subm.) and these studies have started to shed some light into the different strategies employed by endotherm divers to maximise underwater foraging time. This is certainly a promising area for future research (see Lovvorn, in press).

The prey-capture experiments with the cormorants (chapter 4) provided some important insights into the behavioural constraints that might exist on a fine scale. However, there are limits to how far we can extrapolate from insights gained in captive studies, with their obvious constraints. One of the great challenges for future studies therefore is to obtain fine-scale measurements of food intake rates, prey density and the relevant environmental conditions simultaneously in the field.

To improve the bio-energetics model I developed in chapter 6, it is desirable to include more aspects, as data become available. Chapter 4 provided new information concerning the fine scale behavioural constraints of seabirds and should be incorporated in future models. Also, my model is focussing on individuals and we should proceed to the level of populations, combining the individual based modelling approach with demographic aspects of colonies or entire populations. Finally, we should also consider the spatial (i.e. where to birds forage?) and temporal components (expand model to cover annual cycle) in future bio-energetic models (e.g. Boyd, 2002).

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