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Jérôme Fort

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par Jérôme FORT

**REPONSES DES OISEAUX MARINS DE L'ARCTIQUE AUX
CONTRAINTES ENVIRONNEMENTALES HIVERNALES
DANS LE CONTEXTE DES CHANGEMENTS CLIMATIQUES**



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Fort J, Porter WP & Grémillet D. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *Journal of Experimental Biology* **212**:2483-2490.

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Fort J, Cherel Y, Harding AMA, Welker J, Jakubas D, Steen H, Karnovsky NJ & Grémillet D. Geographical and seasonal changes in isotopic niche of little auks. *In revision for Marine Ecology Progress Series*.

Fort J, Porter WP & Grémillet D. Modelling the energetics of seabirds using the first principles of thermodynamics. In preparation. *To be submitted to the Journal of Comparative Physiology A*.

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Note aux lecteurs

Croyez-vous vraiment pouvoir survivre en plein hiver au beau milieu de l'Atlantique Nord ? Imaginez, des vents d'une force inouïe dépassant régulièrement les 100 km h⁻¹, des températures pouvant descendre jusqu'à -20 °C, une eau autour de 0 °C et une luminosité extrêmement faible pendant seulement quelques heures par jour. Honnêtement, cela paraît impossible !

Pourtant, des millions d'oiseaux marins, endothermes comme vous et moi et donc sujets aux mêmes contraintes de thermorégulation, s'y retrouvent chaque année et y survivent. Entre deux migrations de parfois plusieurs milliers de kilomètres, ils hivernent au large pendant quelques mois, à des dizaines de kilomètres des côtes, dans des conditions qui seraient pour nous cauchemardesques. Et chaque année ils y retournent, inlassablement, comme attirés par ces contrées hostiles.

Mais que sait-on vraiment de ce qu'il se passe pendant cette période : que font les oiseaux, où sont-ils exactement, de quoi se nourrissent-ils et surtout comment font-ils face à ces conditions extrêmes ? Une seule chose est sûre, cela n'est pas sans risque puisque chaque année des centaines, parfois des milliers d'oiseaux sont retrouvés morts, échoués sur les côtes américaines, canadiennes et nord-européennes. Pour le reste : on ne sait pas grand-chose, pour ne pas dire rien. C'est la raison pour laquelle l'étude de l'écologie hivernale des oiseaux marins est désormais une priorité afin que l'on puisse connaître et comprendre les raisons de cette mortalité, ainsi que le rôle de ces organismes marins dans un écosystème hivernal encore mal connu.

Chapitre 1

Introduction générale



I) Cadre théorique : endothermie et évènements climatiques extrêmes

Déterminer l'impact des évènements climatiques extrêmes sur les populations animales est depuis longtemps un axe majeur de recherche visant à comprendre comment les animaux les prévoient, y font face et y répondent. Il permet ainsi d'évaluer les conséquences de ces évènements sur la survie et la dynamique des populations animales (e.g. Mysterud et al. 2001, Stenseth et al. 2002, Grosbois & Thompson 2005, Frederiksen et al. 2008). Cet enjeu est renforcé par l'impact des changements climatiques auxquels est souvent associée une augmentation de la fréquence et de l'intensité de ces évènements extrêmes (Stenseth et al. 2004). Dans ce contexte, l'étude des oiseaux marins est essentielle, et ce pour différentes raisons. En premier lieu, elle permet de mieux définir leur rôle au sein des écosystèmes aquatiques. Il s'agit par exemple de déterminer leur pression de prédation et l'ampleur du contrôle vertical descendant (top-down control) qu'ils exercent sur les niveaux trophiques sous-jacents (e.g. Barrett et al. 2002), ou bien d'estimer les transferts d'énergies dont ils sont responsables entre les différents milieux occupés (e.g. Hunt et al. 2005). D'autre part, l'étude des oiseaux marins et de leur écologie permet de mieux comprendre comment ces vertébrés, inféodés à un milieu difficile, réagissent aux fluctuations et parfois aux dégradations de leur environnement (e.g. Karnovsky et al. 2003, Grémillet & Boulinier 2009). Une telle connaissance permet ainsi, dans une perspective de conservation de la biodiversité aviaire, de mettre en évidence les mécanismes régissant la survie de ces espèces. Elle permet également, à plus long terme, d'évaluer quels seront les impacts potentiels des futurs changements climatiques sur les populations, les espèces et les communautés d'oiseaux marins. Enfin, en tant que prédateurs supérieurs, les oiseaux marins se trouvent par définition en bout de chaîne trophique, ce qui signifie qu'ils intègrent et reflètent l'état de l'ensemble du réseau trophique dont ils dépendent. Ils sont ainsi souvent considérés comme de puissants indicateurs écologiques des écosystèmes marins (Furness & Camphuysen 1997, Piatt et al. 2007), leur étude permettant alors d'observer de manière indirecte les niveaux trophiques inférieurs (e.g. Cherel & Hobson 2005). Ce rôle de bioindicateur est particulièrement intéressant dans cet environnement où les études écosystémiques en mer sont souvent très coûteuses et logistiquement impossibles à mettre en place, notamment dans les régions les plus isolées comme les milieux polaires.

Cependant, les oiseaux marins ne sont généralement accessibles aux scientifiques qu'au cours d'une période restreinte, celle de leur reproduction estivale. Par conséquent, la très grande

majorité des études se sont focalisées sur cette saison particulière, excluant presque totalement la période hivernale qui représente pourtant 2/3 de leur cycle annuel et au cours de laquelle ils ont à faire face à un environnement et des conditions climatiques extrêmement difficiles.

II) L'écosystème Nord Atlantique¹ en hiver : un milieu impitoyable

L'Atlantique Nord et son écosystème² suscitent depuis longtemps la curiosité des scientifiques (Hensen 1892). Aujourd'hui encore, la compréhension et la conservation de ce territoire gigantesque d'une superficie de 74 millions de km² sont une priorité d'ordre mondial (ACIA 2004). En effet, il détient entre autres un écosystème capital mais fragile dont dépendent les plus importantes zones de pêcheries mondiales, de vastes ressources pétrolifères et gazières et de nombreuses populations animales et humaines qui en tirent leurs ressources. D'un point de vue physique, cette zone est également le siège d'un des principaux moteurs de la circulation profonde des courants océaniques dont le régime conditionne une très grande partie des phénomènes climatiques terrestres. Cependant, la forte hétérogénéité et variabilité des conditions biotiques et abiotiques, ainsi que la rigueur climatique de ce milieu, font de ces objectifs de véritables défis.

II-1 Conditions climatiques en Atlantique Nord

II-1-1 Conditions climatiques hivernales

L'arrivée de l'hiver dans les eaux de l'Atlantique Nord s'accompagne de conditions climatiques particulièrement drastiques. Comme sur l'ensemble de la planète, cette saison est en effet associée à une forte diminution de la luminosité et de la durée des périodes d'ensoleillement qui iront jusqu'à disparaître totalement sous les latitudes extrêmes, au delà du cercle arctique en hémisphère nord. Cette diminution du rayonnement solaire atteignant le

¹ Au cours de cette thèse, l'Atlantique Nord sera défini comme l'ensemble des eaux océaniques se trouvant au delà de 40° de latitude nord. De par son immense superficie et l'hétérogénéité de sa topographie, il existe au sein de ce territoire une forte variabilité géographique des conditions physiques et biologiques. Au cours de cette partie, nous considérerons cependant l'Atlantique Nord comme un ensemble, depuis les zones englacées subarctiques aux eaux plus chaudes de la limite sud, des plateaux continentaux aux zones abyssales. Nous nous efforcerons cependant de mettre en exergue et de décrire les variations géographiques les plus importantes.

² Un écosystème est un système formé par un environnement et ses caractéristiques propres (le biotope), par les espèces qui y vivent (la biocénose) et par l'ensemble de leurs interactions.

substrat a pour conséquence directe une baisse importante des températures de l'air et de l'eau. Ainsi, les températures de l'air peuvent diminuer de plus de 30°C dans certaines régions pour atteindre les -20°C (Fig. 1.1). De la même façon, les températures de l'eau à la surface de l'océan atteignent -1.4°C, à la limite du point de congélation (Fig. 1.2). A cela s'ajoute également une augmentation générale de la vitesse des vents et de l'humidité relative de l'air.

Ces conditions climatiques de l'Atlantique Nord, caractéristiques des milieux polaires et subpolaires, et les contraintes qui y sont associées jouent ainsi un rôle majeur sur l'ensemble de l'écosystème marin. Cependant, cet environnement est loin d'être figé, avec de fortes variations spatio-temporelles, principalement sous l'effet de l'Oscillation Nord Atlantique.

II-1-2 L'importance de l'Oscillation Nord Atlantique

L'Oscillation Nord Atlantique (NAO) correspond à des modifications des masses atmosphériques entre l'Arctique (associées à de faibles pressions atmosphériques au dessus de l'Islande) et l'Atlantique subtropical (associées à de hautes pressions centrées sur les Açores) (Walker & Bliss 1932, voir Ottersen et al. 2004b). Cette oscillation se mesure par le biais d'un indice basé sur le rapport des pressions arctiques et subtropicales : lorsque les pressions arctiques sont inférieures à la normale et que les pressions subtropicales sont supérieures à la normale, alors la NAO est positive. Dans le cas contraire, la NAO est négative (Hurrell & Dickson 2004).

Les tendances de la NAO jouent un rôle très important en Atlantique Nord puisqu'elles y influencent directement les variations climatiques, et cela particulièrement pendant l'hiver. Variant fortement dans le temps et dans l'espace, elles ne suivent cependant pas de cycle temporel, avec de grands changements d'un hiver à l'autre et au sein d'un même hiver (Nakamura 1996).

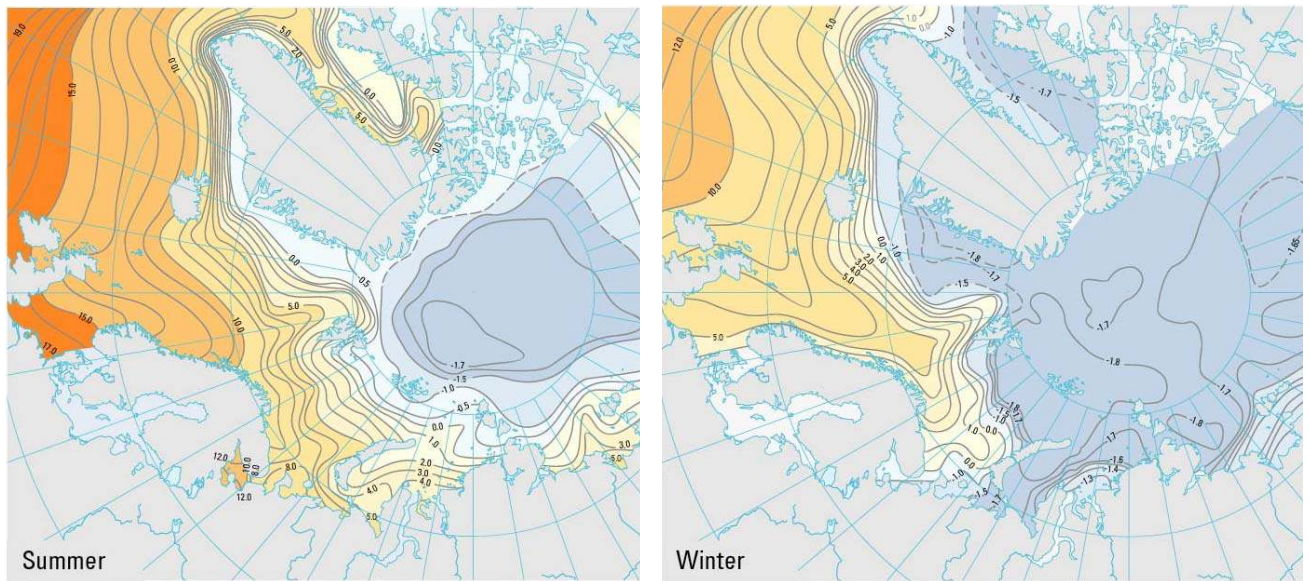


Fig. 1.1 Températures moyennes à la surface de l’océan en été (summer) et en hiver (winter) en Atlantique Nord. (Source : AMAP 1998)

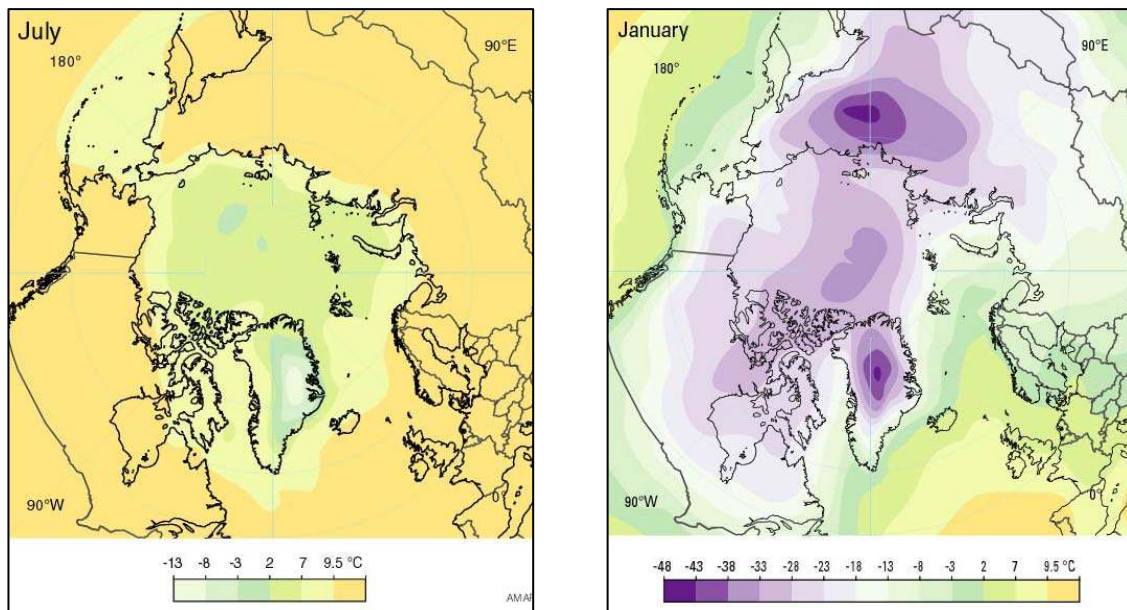


Fig. 1.2 Températures moyennes de l’air en été (juillet) et en hiver (janvier) dans l’Atlantique Nord. (Source : AMAP 1998)

En premier lieu, on sait que la NAO influence de manière importante les températures hivernales, que ce soit les températures de l'air ou celles mesurées à la surface de l'océan (Bjerknes 1964, Hurrell & Dickson 2004). Ainsi, on considère par exemple que la variabilité de la NAO explique environ 1/3 des changements interannuels de températures de l'hémisphère nord au cours de l'hiver (voir Hurrell & Dickson 2004). De manière simplifiée, lors des années où la NAO est positive, les températures rencontrées dans les eaux subarctiques sont froides, alors que les années où la NAO est négative, les conditions de température y sont plus clémentes (Fig. 1.3).

La NAO régie également l'intensité et la direction des vents (Fig. 1.3). De ce fait, les variations de cet indice vont être accompagnées par d'importants changements de l'intensité et de la fréquence des tempêtes, ainsi que des conditions climatiques associées. De manière générale, lors des hivers présentant une NAO positive, on observe une augmentation du nombre de tempêtes et de leur intensité en Atlantique Nord (Rogers 1990, Serreze et al. 1997). Cette recrudescence des tempêtes conduit également à des changements dans la distribution et l'intensité des précipitations (Dickson et al. 2000), ainsi qu'à des modifications des courants de surface (Hurrell & Dickson 2004).

Notons enfin que ces variations des conditions de vents et de températures créent indirectement des changements des conditions d'englacement dans la zone la plus boréale de l'Atlantique Nord (e.g. Prinsenbergh 1997 ; Fig. 1.3).

L'Atlantique Nord semble donc être un environnement particulièrement contraignant pour la vie animale, à la fois par ses conditions climatiques très difficiles, mais aussi par sa forte variabilité et imprévisibilité.

II-2 Réseau trophique

II-2-1 Un écosystème parfois complexe

Le système marin de l'Atlantique Nord dans sa partie la plus boréale est unique de par la combinaison de différents facteurs physiques. Ses caractéristiques sont une superficie proportionnellement importante de plateaux continentaux et d'eaux peu profondes, une forte saisonnalité, une faible intensité lumineuse et des températures extrêmement basses en hiver, l'abondance des zones englacées (permanentes ou semi-permanentes), ainsi qu'une forte influence de l'eau douce provenant des rivières ou de la fonte des glaces.

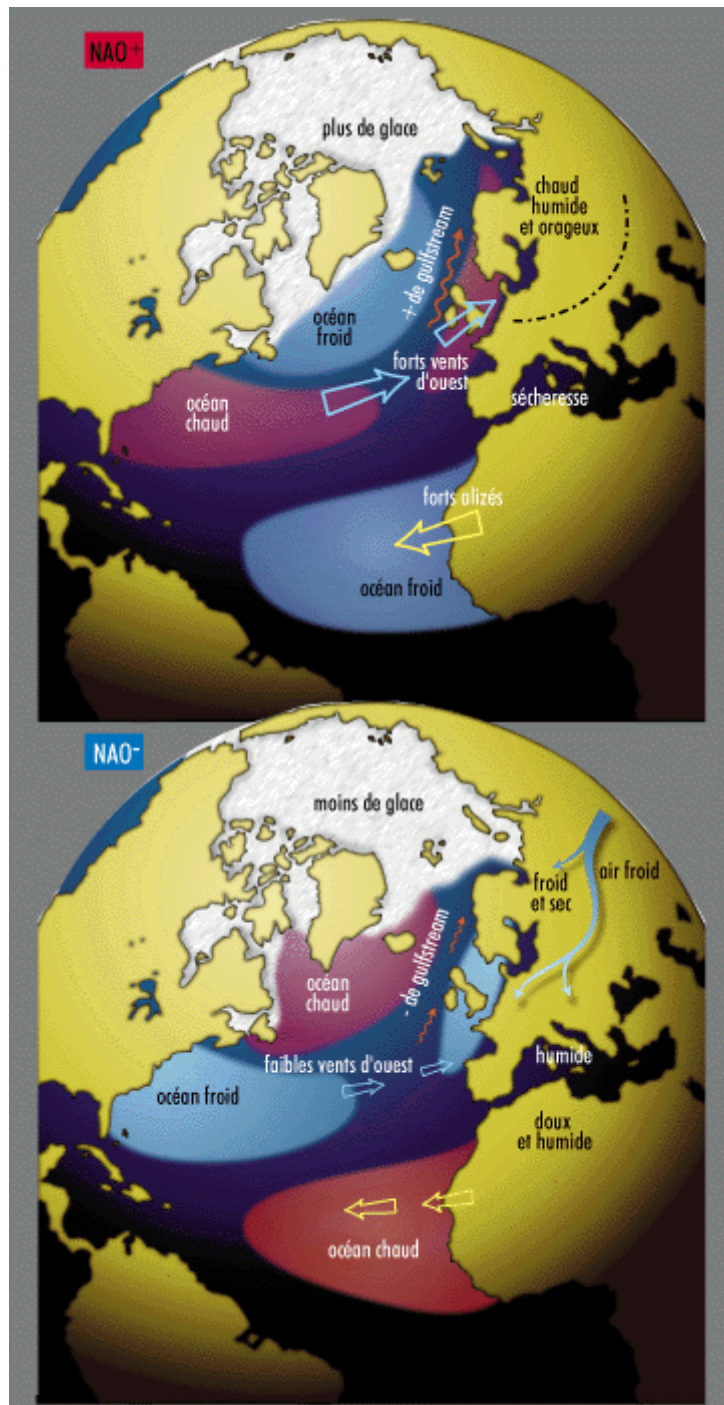


Fig. 1.3 Schéma des conditions climatiques associées à l'Oscillation Nord Atlantique selon que l'indice mesuré soit positif ou négatif. (Source : Heinz Wanner, Institut de géographie climatologie et météorologie, Université de Berne)

La plupart de ces facteurs représentent comme nous l'avons vu précédemment des conditions particulièrement austères pour la vie animale, résultant en un système composé en majorité d'espèces spécialistes qui ont été capables de s'adapter à ces conditions extrêmes. La conséquence est une diversité spécifique globalement faible, composée d'une faune récente d'un point de vue géologique (Loeng et al. 2005), ce qui a longtemps laissé penser qu'il s'agissait d'un écosystème relativement simple, composé de quelques espèces dominantes et formé d'un petit nombre de chaînes trophiques majeures et linéaires (voir Ciannelli et al. 2005 ; Fig. 1.4).

Cependant, une inspection plus détaillée de ce milieu Nord Atlantique, en particulier dans sa partie la plus boréale, montre que les réseaux trophiques de certaines zones peuvent être beaucoup plus complexes (Grémillet & Le Maho 2003 ; Fig. 1.5). Cette complexité s'explique notamment par des variations de préférence alimentaire entre individus d'une même espèce, mais également par une augmentation de la diversité biologique liée à la richesse spécifique de certaines régions particulières que sont les upwellings et les polynies (voir ci-dessous).

L'écosystème marin de l'Atlantique Nord se compose à sa base de nombreuses espèces de phytoplancton. Ce sont de microscopiques algues planctoniques unicellulaires résidant dans les masses d'eaux océaniques ou au contact de la glace de mer. Elles dépendent, pour se développer, des nutriments présents dans le milieu ainsi que de la luminosité disponible permettant la photosynthèse. Il existe de nombreuses espèces de phytoplancton en Atlantique Nord parmi lesquelles les diatomées et les dinoflagellés sont majoritaires.

Le niveau trophique supérieur est composé de zooplancton. Celui-ci joue un rôle clé dans le réseau trophique Nord Atlantique puisque le mesozooplancton (espèces de zooplancton dont la taille est comprise entre 0.2 et 20 mm) représente plus de 50 % de la biomasse³ pélagique de cet écosystème. Parmi ces espèces, les copépodes de la famille des *Calanidae*⁴ sont largement prépondérants, ces copépodes herbivores représentant dans certaines zones 70 à 90 % de la biomasse de mesozooplancton (Loeng et al. 2005, Ciannelli et al. 2005). Les copépodes les plus abondants en Atlantique Nord et qui, nous le verrons, sont aussi particulièrement importants pour certaines espèces d'oiseaux marins, sont *Calanus finmarchicus*, prédominant dans les eaux atlantiques, *Calanus hyperboreus* qui occupe à la fois les eaux atlantiques et arctiques, et *Calanus glacialis* que l'on retrouve exclusivement

³ La biomasse correspond à la masse totale des organismes vivants dans une zone considérée.

⁴ Dans la suite de ce manuscrit, les copépodes appartenant à la famille des *Calanidae* seront nommés **copépodes calanoïdes**.

dans les eaux arctiques. Au cours de l'hiver, les copépodes calanoïdes effectuent une importante migration verticale pour atteindre des profondeurs supérieures à 400 mètres, profondeurs qu'ils ne quittent qu'au début du printemps pour remonter vers les eaux de surface (< 50m) lors de l'émergence du phytoplancton (Falk-Petersen et al. 2009).

Le niveau trophique suivant est composé de poissons dont la composition spécifique est très variable selon les zones considérées. On retrouve environ 150 espèces de poissons dans les eaux les plus au nord de l'Atlantique Nord (Murray 1998, Froese & Pauly 2009), espèces qui pour la plupart entretiennent le niveau trophique supérieur. Les principales espèces de poissons présentes qui jouent également un rôle important dans l'alimentation des prédateurs supérieurs sont le capelan atlantique (*Mallotus villosus*), le hareng de l'Atlantique (*Clupea harengus*), le lançon (*Ammodytes spp.*), le sprat (*Sprattus sprattus*), le maquereau de l'Atlantique (*Scomber scombrus*), l'anchois d'Europe (*Engraulis encrasicolus*), la morue polaire (*Boreogadus saida*) et la morue de l'Atlantique (*Gadus morhua*).

Enfin, le dernier niveau trophique est représenté par les prédateurs supérieurs parmi lesquels se retrouvent les grands poissons prédateurs tels que les flétans (*Hippoglossus hippoglossus* et *Reinhardtius hippoglossoides*), les mammifères marins comme les phoques, les baleines ou les ours polaires, et enfin de nombreuses espèces d'oiseaux marins.

Ce réseau trophique est donc composé dans son ensemble d'une grande variété d'espèces toutes directement ou indirectement dépendantes les unes des autres. Cependant, la diversité et la biomasse représentées par ce réseau trophique sont très hétérogènes dans le temps, mais surtout dans l'espace, avec des zones particulièrement riches et attractives pour les prédateurs.

II-2-2 Hétérogénéité temporelle : le phénomène de saisonnalité

La période qui nous intéresse dans cette étude est l'hiver. Cependant, il apparaît important ici de replacer cette saison dans le cycle annuel, afin de mieux comprendre son rôle dans la dynamique du réseau trophique. En effet, le phénomène de saisonnalité, particulièrement prononcé dans les écosystèmes tempérés et subpolaires, permet à l'Atlantique Nord d'être une des zones océaniques les plus productives de la planète (Grémillet & Le Maho 2003). Ce phénomène joue donc un rôle très important pour la structuration saisonnière de l'ensemble du réseau trophique nord-atlantique. Ainsi en hiver, les vents intenses ont tendance à mélanger les eaux de surface avec celles plus profondes, homogénéisant alors la colonne

d'eau. Cela va permettre d'augmenter la quantité de nutriments présents dans la zone euphotique⁵, ainsi que d'homogénéiser leur distribution. Ces nutriments ne sont alors que peu utilisés par le phytoplancton présent, le manque de lumière limitant la croissance de ce dernier. En revanche, à l'arrivée du printemps, l'augmentation de la luminosité combinée à l'abondance de nutriments permet un développement extrêmement rapide du phytoplancton qui se retrouve en abondance dans le milieu (c'est le phénomène du « spring bloom »). Cette biomasse extrêmement importante joue de ce fait un rôle majeur sur le reste du réseau trophique, la distribution et l'abondance des espèces. A l'inverse en été, la stratification de la colonne d'eau est importante, et lorsque les nutriments des eaux de surface plus chaudes ont été consommés, ils ne sont plus renouvelés. L'été correspond donc à une période de faible productivité primaire.

II-2-3 Hétérogénéité spatiale et richesse alimentaire : les zones d'upwelling et les polynies

Upwelling

L'upwelling est un phénomène océanographique se développant sous l'influence première du vent. Il correspond à une remontée des eaux plus profondes vers la surface entraînant avec elles d'importantes quantités de nutriments. Ces derniers vont alors stimuler une forte productivité primaire qui supportera à son tour le développement de chacun des niveaux trophiques supérieurs et donc d'une quantité de biomasse considérable. Ces upwellings peuvent être côtiers ou apparaître au large, dans les zones de fronts océaniques (zones qui séparent les différentes masses d'eau). Il existe ainsi de nombreuses zones d'upwellings plus ou moins importantes en Atlantique Nord. Au cours de l'hiver cependant, ces phénomènes d'upwelling, bien que toujours présents, perdent de leur intensité. En effet, pendant les épisodes de tempêtes, les vents puissants, de vitesses et de directions très variables, ont tendance à brasser les masses d'eaux créant ainsi un milieu plus homogène (voir ci-dessus).

Polynie

Les polynies sont de vastes étendues d'eau libre, ou dont la couverture de glace est réduite. Elles se forment soit grâce à la présence d'upwellings localisés qui empêchent la formation de glace, soit grâce aux vents et courants qui chassent la glace présente. D'une superficie

⁵ La zone euphotique se définit comme la couche superficielle des océans qui reçoit suffisamment de lumière solaire pour que la production végétale y excède les pertes.

atteignant parfois plusieurs milliers de km², elles sont situées au cœur des zones fortement englacées des océans polaires et fournissent ainsi une zone propice au développement de la vie animale au sein d'un milieu beaucoup plus austère. Ces polynies sont en effet des zones permettant aux rayons solaires d'atteindre les eaux de surface, créant ainsi un milieu riche en phytoplancton et en algues planctoniques et épontiques⁶. Elles deviennent alors le foyer d'intenses productions du zooplancton herbivore, qui assure lui-même le développement de l'ensemble des maillons de la chaîne trophique.

En Atlantique Nord, différentes zones de polynie apparaissent comme très importantes pour les oiseaux marins en hiver. C'est le cas par exemple de la polynie des eaux du Nord qui est active pendant la majeure partie du cycle annuel (Karnovsky & Hunt 2002, Egevang et al. 2003). Zone de près de 50 000 km² située dans la partie nord de la baie de Baffin entre l'île d'Ellesmere au Canada et la côte ouest du Groenland, elle est parmi les régions les plus productives au nord du cercle arctique (Barber et al. 2001). C'est également le cas des côtes sud-ouest du Groenland qui constituent une zone d'hivernage pour un très grand nombre d'oiseaux marins (Boertmann et al. 2004)

Ces zones d'upwelling et de polynie sont par conséquent les endroits où l'on retrouve la plus forte concentration d'êtres vivants dans l'écosystème Nord-Atlantique, depuis la production primaire jusqu'aux prédateurs supérieurs, dont les oiseaux marins.

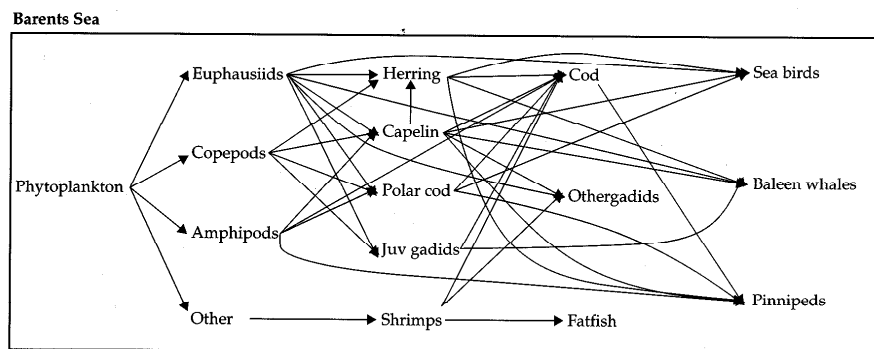


Fig. 1.4 Représentation schématique du réseau trophique Nord Atlantique rencontré en Mer de Barents. (Source : Ciannelli et al. 2005)

⁶ On dit d'une espèce qu'elle est **épontique** lorsqu'elle vie en relation avec la glace de mer et s'est adaptée à cet habitat. Son association avec cette glace de mer n'est cependant pas indispensable à sa survie (auquel cas l'espèce est dite sympagique) (voir Horner et al. 1988, 1992).

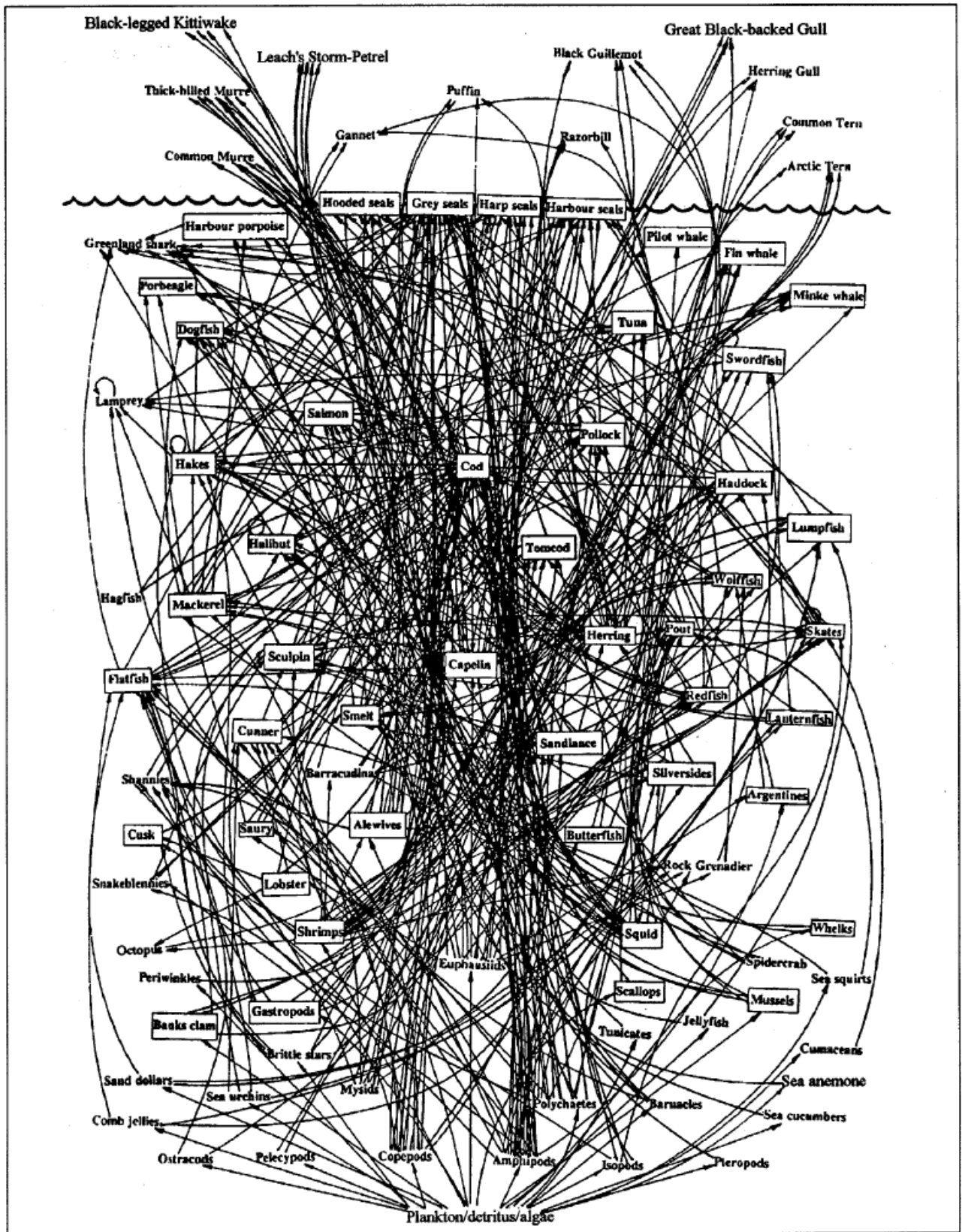


Fig. 1.5 Représentation schématique d'une partie du réseau trophique marin rencontré dans l'Atlantique Nord-Ouest, au large du Canada. (Source : Lavigne 1991)

III) Les oiseaux marins face à cet environnement

III-1 Les oiseaux marins

III-1-1 Quelques généralités

Les oiseaux marins représentent environ 300 espèces réunies en 4 grands groupes (Charadriiformes, Péléciformes, Procellariiformes and Sphénisciformes) et comprennent 15 familles (Gaston 2004). Ils sont répartis sur l'ensemble du globe et ont su coloniser toutes les zones marines, de l'équateur aux pôles. Comme leur nom l'indique, ils passent la majeure partie de leur vie en mer. Seule leur reproduction, par la nécessité de pondre leur(s) œuf(s) sur un substrat dur et protégé, les force quelques mois par an à se retrouver à terre. Pendant cette période, les oiseaux se regroupent pour la plupart au sein de colonies parfois immenses. C'est ainsi une période propice aux scientifiques qui une fois à terre ont un accès relativement facile aux oiseaux, ce qui permet aujourd'hui d'avoir une très bonne connaissance de l'écologie de ces espèces pendant la saison de reproduction.

La communauté des oiseaux marins est très diverse, que ce soit en termes de morphologie, de comportement ou de régime alimentaire. Par exemple, les plus petites espèces telles que l'océanite de Wilson (*Oceanites oceanicus*) ou la starique minuscule (*Aethia pusilla*), qui pèsent respectivement 40 et 85 g environ, s'alimentent essentiellement de zooplancton (del Hoyo et al. 1992, 1996). Les plus grosses telles que le fou de bassan (*Morus bassanus*) ou l'albatros hurleur (*Diomedea exulans*), qui eux atteignent respectivement des poids de 3 et 11 kg, s'alimentent de poissons ou de céphalopodes (del Hoyo et al. 1992). Pour se nourrir, certaines espèces plongent à de grandes profondeurs de plusieurs dizaines voire centaines de mètres (e.g. Wienecke et al. 2007), alors que d'autres s'alimentent à la surface de l'eau. Ces espèces ont cependant des points communs associés à leur vie marine. Ainsi, toutes présentent une importante longévité (parfois plusieurs dizaines d'années). La très grande majorité de ces espèces possèdent également des caractéristiques communes de plumage garantissant entre autres leur étanchéité et leur isolation. Enfin, les espèces plongeuses partagent des adaptations morphologiques favorisant leur déplacement sous l'eau (Schreiber & Burger 2002, Gaston 2004).

III-1-2. Ecologie hivernale

Si la période de reproduction est bien connue, l'écologie hivernale des oiseaux marins de l'Atlantique Nord est encore aujourd'hui un grand mystère. En effet, pendant cette saison, la plupart des espèces sont pélagiques et se trouvent au large des côtes dans un environnement défavorable à l'homme, où elles sont difficiles d'accès et par conséquent particulièrement compliquées à étudier. Cependant, c'est au cours de cette période qu'ont lieu des événements cruciaux tels que les migrations leur permettant de faire le lien entre leur zone de reproduction et leur site d'hivernage libre de glace, ou encore leurs périodes de mue leur assurant un nouveau plumage essentiel à leur efficacité de thermorégulation, de prédation sous-marine et de vol pendant les migrations. De plus, l'hiver est une période qui influence le succès de la prochaine reproduction des oiseaux en conditionnant notamment la condition corporelle d'un individu (Daunt et al. 2006). Enfin, l'hiver joue également un rôle clé dans la survie des oiseaux marins et donc indirectement sur la dynamique de leurs populations (Barbraud & Weimerskirch 2003 ; Grosbois & Thomson 2005). En effet, chaque année de grandes quantités d'oiseaux morts échoués, sont retrouvées sur les côtes canadiennes, nord-américaines et européennes (Gaston 2004, Camphuysen *pers. com.*). Ces échouages massifs sont la plupart du temps considérés comme associés à de violentes tempêtes qui chassent les oiseaux vers les côtes, les privant ainsi de leurs proies et entraînant la mort des plus faibles. Cependant, cette hypothèse n'a jamais été validée et les mécanismes et réelles causes de ces échouages massifs restent flous.

L'hiver est donc une période cruciale pour les oiseaux marins. Aujourd'hui, ce que l'on connaît durant cette période concerne (1) les zones d'hivernage de certaines espèces définies grâce au déploiement intensif de bagues pendant la saison de reproduction et retrouvées sur les oiseaux en hiver, et grâce à des observations en mer à proximité des côtes (Donaldson et al. 1997 ; Boertmann et al. 2004) (2) le régime alimentaire des quelques espèces légalement chassées sur les côtes groenlandaises et canadiennes telles que les guillemots de Brünnich (*Uria lomvia*) (Lilliendahl 2009 ; Rowe et al. 2000) (3) les mouvements et routes de migration d'une poignée d'individus en Atlantique Nord définis grâce aux nouvelles technologies telles que les GLS⁷ permettant de localiser et suivre les déplacements d'un oiseau sans l'observer directement (e.g. Shaffer et al. 2006, Guilford et al. 2009).

⁷ Les GLS (Global Location Sensors) sont des enregistreurs miniaturisés qui s'attachent à la patte des oiseaux (fixés sur leur bague d'identification). Ils enregistrent et stockent pendant plusieurs mois/années des informations sur les niveaux de lumières ambiantes. A partir de ces informations, il est ensuite possible de retracer quotidiennement la position géographique à laquelle se trouvait l'oiseau, avec cependant une incertitude d'environ 185 km.

Une meilleure compréhension de leur écologie durant cette période est aujourd'hui nécessaire, notamment pour déterminer comment les oiseaux marins font faces aux conditions climatiques extrêmes rencontrées durant cette saison, et ainsi comprendre quels sont les mécanismes sous-jacents à la forte mortalité hivernale observée. Parmi tous les oiseaux marins de l'Atlantique Nord, une famille regroupant quelques unes des espèces les plus abondantes mais aussi les plus frappées par cette mortalité hivernale attire l'attention : celle des alcidés.

III-2 Les Alcidés

La famille des alcidés regroupe 25 espèces (dont 1 éteinte : le grand pingouin (*Pinguinus impennis*)) qui se répartissent sur l'ensemble des eaux de l'hémisphère nord où elles occupent des habitats extrêmement différents. Ces espèces jouent un rôle prépondérant dans l'écosystème marin de l'Atlantique Nord où elles représentent plus de 69 % de la biomasse d'oiseaux marins, incluant probablement plus de 90 % de la population nicheuse des zones arctiques et boréales (Gaston & Jones 1998).

Tous les oiseaux de cette famille sont dit 'plongeurs', ce qui signifie qu'ils capturent leurs proies sous l'eau, souvent à plusieurs dizaines de mètres de profondeurs (Gaston & Jones 1998). Ce comportement de plongée soutenu est devenu possible grâce à de nombreuses adaptations physiologiques et morphologiques. Ainsi, au niveau physiologique, on retrouve chez ces espèces un important volume sanguin (jusqu'à 12 % de la masse corporelle chez les guillemots de Brünnich), de même que de forts taux de myoglobine, ce qui augmente la capacité de stockage de l'oxygène et donc le temps de plongée (Gaston & Jones 1998). La principale évolution morphologique est une réduction de la surface alaire, qui leur permet d'utiliser leurs ailes comme propulseurs au cours de leurs plongées et de véritablement voler sous l'eau. Mais cela a également un impact sur leur capacité de vol. En effet, le faible ratio surface alaire / masse corporelle entraîne chez les alcidés un vol difficile et coûteux en énergie, fait de battements d'ailes rapides et continus. Le grand pingouin, aujourd'hui éteint, présentait une telle adaptation morphologique à la vie aquatique que ses ailes, devenues trop petites, ne lui permettaient plus de voler. Notons également que de manière générale, les alcidés ont une isolation du plumage qui apparaît comme relativement faible au regard des conditions climatiques auxquelles ils font face (Gaston & Jones 1998). Cette caractéristique semble avoir été l'objet d'un compromis évolutif entre la nécessité d'être isolé du milieu

environnant (par un plumage dense emprisonnant une quantité d'air importante) et celle d'avoir un profil aérodynamique performant ainsi qu'une faible flottabilité favorisant les performances en plongée (en minimisant le volume d'air emprisonné dans le plumage). D'un point de vue énergétique, ce compromis a d'importantes conséquences puisque les alcidés ont un métabolisme de repos (RMR) très élevé comparé à des espèces de même taille, et donc une forte dépense énergétique associée aux coûts thermodynamiques (Birt-Friensen et al. 1989, Konarzewski et al. 1993).

Notons enfin que chez les alcidés, une mue complète du plumage a lieu chaque année, rapidement après la saison de reproduction (excepté chez les macareux où elle ne concerne que les plumes de couverture). Elle permet l'apparition du plumage hivernal ainsi que la disparition des ornements nuptiaux. Au cours de cette mue complète, toutes les rémiges tombent simultanément (excepté chez les stariques), ce qui entraîne une période d'incapacité au vol de plusieurs semaines pendant laquelle les espèces restent sur l'eau au large des côtes (Gaston & Jones 1998). Ce n'est qu'après cette période de mue que les oiseaux entament leur migration vers leur site d'hivernage. Après l'hiver, et chez la majorité des alcidés, une mue partielle se produit, au cours de laquelle seules quelques plumes de couverture situées au niveau de la tête, du cou et de la poitrine vont être remplacées (Nettleship & Birkhead 1985, Gaston & Jones 1998).

Au cours de cette thèse, trois espèces d'alcidés ont été étudiées. L'espèce principale, autour de laquelle elle s'articule est le mergule nain (*Alle alle*). Les autres espèces sont le guillemot de Brünnich (*Uria lomvia*) et le guillemot de Troil (*Uria aalge*).

Notons qu'il existe différents facteurs à la mortalité hivernale observée chez ces trois espèces. Parmi eux se trouve un facteur anthropique. Ainsi les guillemots, comme de nombreuses autres espèces, sont en compétition directe avec les pêcheries qui provoquent une importante déplétion de la ressource dans certaines zones et réduisent la quantité de proies disponibles aux oiseaux. Ces pêcheries sont également la cause de nombreuses prises accidentelles d'oiseaux dans les filets de pêche (Anker-Nilssen et al. 2000). De plus, les mergules nains et les guillemots sont les espèces les plus sensibles à la pollution en mer (notamment par les phénomènes de dégazage des bateaux) et sont parmi les plus touchées lors d'accidents et de marées noires (Anker-Nilssen et al. 2000). Enfin, la chasse est une cause importante de mortalité chez ces 3 espèces, consommées l'hiver par les populations de Terre-Neuve et du Groenland (e.g. Falk & Durinck 1992). Comme nous l'avons vu, il existe cependant un autre

facteur potentiel à cette mortalité hivernale, dont les conséquences sont moins connues ; il s'agit d'un facteur climatique. Au cours de ce mémoire, nous nous focaliserons uniquement sur cet aspect climatique en nous intéressant plus particulièrement à la variabilité environnementale décrite précédemment ainsi qu'aux changements climatiques (voir plus bas).

Avant tout, il paraît important de décrire de manière plus précise l'écologie générale de chacune de ces trois espèces.

III-2-1 Le mergule nain

Le mergule nain est l'un des plus petits alcidés (la plus petite espèce de l'Atlantique Nord) avec une masse corporelle moyenne de 150g (Stempniewicz 2001). Sa distribution englobe l'ensemble de l'Atlantique Nord, depuis les côtes canadiennes jusqu'au nord de la Russie, les oiseaux rencontrant ainsi des régimes océaniques et climatiques très variables. Les principales colonies se trouvent au Spitzberg ainsi qu'à l'est et au nord-ouest du Groenland (Gaston & Jones 1998, Stempniewicz 2001 ; Fig. 1.6). On trouve également quelques colonies de petite taille dans la région du Déroit de Béring du côté Pacifique.

Ces oiseaux sont aujourd'hui considérés comme les plus abondants de l'Atlantique Nord et parmi les plus abondants au monde, avec des estimations récentes faisant état de plus de 80 millions d'individus (Gaston & Jones 1998, Kampp et al. 2000, Isaksen & Gavriilo 2000, Egevang et al. 2003). Ils se nourrissent presque exclusivement de zooplancton, leurs principales proies au printemps comme en été étant les copépodes (e.g. Karnovsky et al. 2008, Harding et al. 2009a), alors qu'il semblerait que ces oiseaux se tournent vers une alimentation majoritairement constituée d'amphipodes au cours de l'automne (Karnovsky et al. 2008). Ils jouent ainsi un rôle particulièrement important au sein des écosystèmes arctique et nord-atlantique (Stempniewicz 2006), notamment en termes de transferts d'énergie. Par exemple, les populations nicheuses de la région de la polynie des eaux du nord sont responsables de 92 à 96 % des flux de carbone attribués aux oiseaux marins et consomment jusqu'à 24 % des stocks de copépodes présents dans cette région (Karnovsky & Hunt 2002). Comme tous les alcidés, les mergules nains capturent leurs proies lors de plongées sous-marines. Au cours de leur période de reproduction, ces plongées sont d'une profondeur moyenne de 10 m (maximum de 27 m) et d'une durée moyenne de 52 secondes (Harding et al. 2009a).

Les connaissances que l'on a aujourd'hui sur l'écologie des mergules nains au cours de l'hiver sont extrêmement parcellaires, voire inexistantes. Ainsi, nul ne sait de quoi s'alimentent ces oiseaux, quel est leur comportement, ni même où ils se trouvent pendant cette période. Seuls quelques indices nous laissent penser que la majorité des oiseaux nichant au Groenland et au Svalbard migrent vers le sud pour hiverner au large de Terre Neuve et des côtes sud et sud-ouest du Groenland (Stempniewicz 2001). On ne sait en revanche rien de l'origine des oiseaux hivernant en mer du Nord et au large des côtes européennes, ni des zones d'hivernage des populations nicheuses russes de l'Archipel François-Joseph, de Nouvelle Zemble et de Severnaya Zemlya (Fig. 1.6).

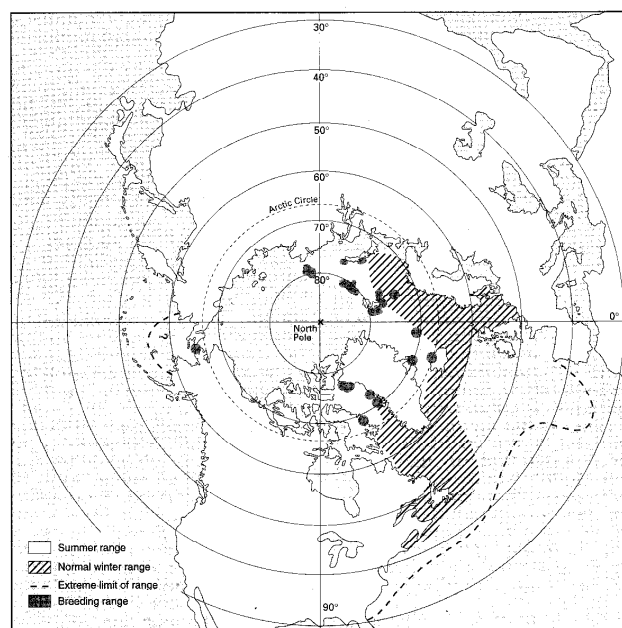


Fig. 1.6 Distribution des mergules nains au cours des différentes saisons (Source : Gaston & Jones 1998)

III-2-2 Les guillemots de Brünnich

Les guillemots de Brünnich sont, avec les guillemots de Troil, les plus grands des alcidés, avec une masse corporelle moyenne d'un kg (Gaston & Jones 1998). Leur distribution circumpolaire couvre l'ensemble des eaux arctiques et subarctiques. On les retrouve ainsi du côté pacifique dans le Golfe d'Alaska, la mer de Béring, les îles Aléoutiennes ou encore en mer de Tchoukotka. Cependant, les populations les plus importantes sont situées dans l'Atlantique Nord, notamment en baie de Huston, au Groenland ouest et au Spitzberg (Gaston & Jones 1998 ; Fig. 1.7). Au total, leur population en Atlantique est estimée entre 10 et 15

millions d'individus dispersés sur différentes colonies (Gaston & Jones 1998) et ils représentent ainsi l'espèce la plus importante en biomasse de l'Atlantique Nord. Décrits comme les 3^{èmes} consommateurs en termes de biomasse ingérée (1^{ers} de l'hémisphère nord), ils consomment presque 4 millions de tonne de nourriture par an (Brooke 2004) et jouent eux aussi un rôle essentiel dans les réseaux trophiques Nord Atlantiques et Arctiques. Cependant, et contrairement aux mergules nains, ces oiseaux ont un régime alimentaire généraliste, c'est-à-dire composé de types de proies variés. Ils se nourrissent de nombreuses espèces de poisson et de zooplancton, les morues arctiques (*Boreogadus saida*) étant leur proie favorite en été (Barrett et al. 1997, Gaston & Jones 1998). Les plongées pour capturer ces proies sont très profondes (entre 20 et 60 m) et peuvent régulièrement dépasser les 100 m (Melhum et al. 2001, Takahashi et al. 2008).

Les connaissances limitées de l'écologie hivernale des guillemots de Brünnich ont été permises par leur distribution plus côtière que les autres alcidés ainsi que par la forte pression de chasse à laquelle ils font face en hiver au large des côtes canadiennes et groenlandaises (voir Anker-Nilssen et al. 2000). Ainsi, différentes études basées sur l'analyse de contenus stomacaux ont montré que les populations atlantiques se nourrissent essentiellement de poissons pendant la première partie de l'hiver (capelans et morues arctiques) alors que les crustacés, et plus particulièrement les euphausiacés, dominent leur alimentation entre janvier et mars (Elliot et al. 1990, Rowe et al. 2000).

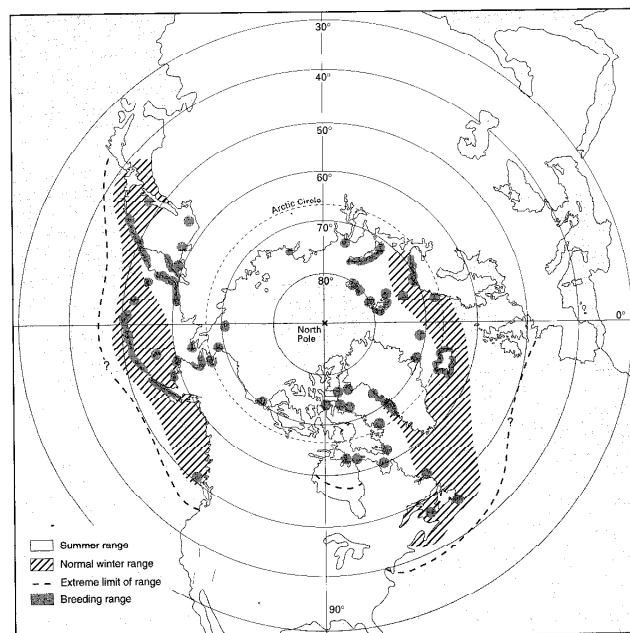


Fig. 1.7 Distribution des guillemots de Brünnich au cours des différentes saisons (Source : Gaston & Jones 1998)

III-2-3 Les guillemots de Troïl

Tout comme le guillemot de Brünnich, cette espèce à une distribution très vaste en Arctique, Atlantique Nord et Pacifique Nord (Gaston & Jones 1998 ; Fig. 1.8). La population atlantique est estimée entre 6 et 9 millions d'individus nicheurs, les colonies les plus importantes se situant en Islande, au Spitzberg et au Canada (Gaston & Jones 1998). Les guillemots de Troïl ont eux aussi un régime alimentaire généraliste, mais ils ne consomment cependant que des poissons, les crustacés et les calmars étant marginaux (Gaston & Jones 1998). Les principales espèces de poissons consommées par ces oiseaux en Atlantique Nord sont le hareng, le lançon et le sprat. Leur comportement de recherche alimentaire est similaire à celui des guillemots de Brünnich, avec des plongées moyennes comprises entre 20 et 50 m, mais pouvant atteindre 210 mètres (Piatt & Nettleship 1985).

Une fois encore, l'écologie hivernale de cette espèce est peu connue. Suite à leur mue complète post-reproduction, certaines populations de guillemots de Troïl n'effectuent pas de longues migrations, contrairement à la plupart des autres alcidés (Gaston & Jones 1998, Steen et al. *unpublished*), mais retournent aux alentours de leur site de reproduction où ils passent l'hiver. Seules les populations nichant dans des zones où l'eau est libre de glace tout au long de l'année semblent exercer ce comportement. Au cours de cette saison, les poissons restent les proies exclusives de ces oiseaux (Gaston & Jones 1998).

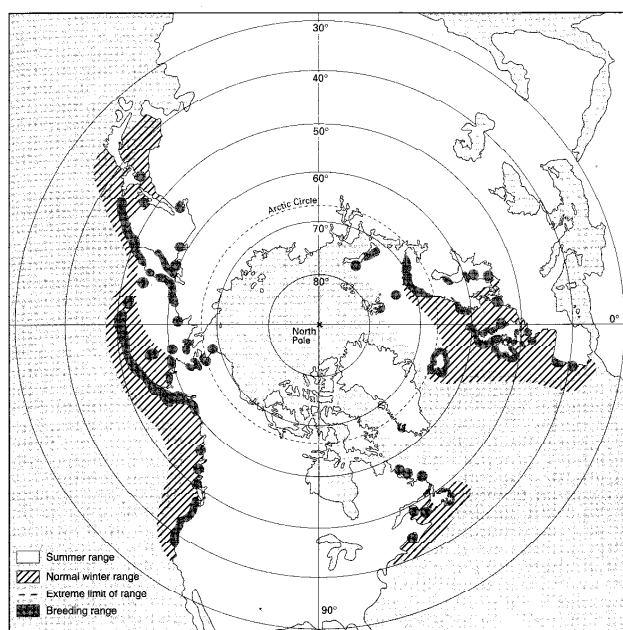


Fig. 1.8 Distribution des guillemots de Troïl au cours des différentes saisons (Source : Gaston & Jones 1998)

IV) Les changements climatiques : un facteur aggravant.

Ces trois espèces jouent donc un rôle majeur dans un environnement âpre, variable, mais auquel elles ont su s'adapter. Aujourd'hui, une autre source de variabilité beaucoup plus forte et rapide apparaît, risquant d'augmenter la mortalité observée et de modifier la dynamique des populations avant que les oiseaux n'aient eu le temps de s'y adapter : les changements climatiques.

IV-1 Océanographie physique et changements climatiques en Atlantique Nord

C'est indéniable, le climat sur Terre change, avec aujourd'hui une vitesse accrue (ACIA 2004, IPCC 2007). Ces changements climatiques touchent tous les écosystèmes, mais c'est dans les régions polaires et notamment en Arctique que l'on s'attend à observer les impacts les plus importants. En effet, contrairement à l'Antarctique isolé de la présence humaine par un vaste océan permettant une zone tampon, l'Arctique est un milieu en contact direct avec l'homme et les activités qui lui sont associées.

Cette sensibilité accrue de l'Arctique face aux changements climatiques par rapport à d'autres régions est due à différents processus physiques de rétrocontrôle bien définis :

- L'albédo⁸ de la glace de mer est élevé (entre 0.50 et 0.90). Cela crée une réflexion importante de la lumière solaire vers l'atmosphère, ce qui maintient ces zones « froides ». Un réchauffement du climat, et notamment la fonte des glaces associée (voir plus bas), va provoquer l'apparition de zones d'eaux libres avec une surface plus foncée et un albédo plus faible (environ 0.1). Ainsi, les rayons solaires vont être plus absorbés par le substrat, ce qui va créer un rétrocontrôle positif. En effet, cette plus grande absorption des rayons lumineux va entraîner un réchauffement du milieu, ce qui va augmenter la fonte des glaces, créant ainsi de nouvelles zones sombres qui à leur tour vont par l'absorption solaire augmenter le réchauffement du milieu et ainsi de suite.
- La fonte du permafrost (sol gelé de manière permanente) provoquée par l'augmentation des températures va entraîner une libération des gaz à effet de serre qu'il contient. Ces gaz étant une des principales causes du réchauffement climatique,

⁸ Dans notre cas, l'albédo se définit comme la proportion de l'énergie de rayonnement incidente qui sera réfléchi par le substrat considéré.

cette libération va donc contribuer à l'augmentation des températures, ce qui va encore augmenter la fonte du permafrost, la libération des gaz à effet de serre, l'augmentation des températures et ainsi de suite.

Dans le milieu marin et en Atlantique Nord, les changements climatiques correspondent essentiellement à une augmentation des températures de l'air, une augmentation locale des vitesses des vents, une couverture nuageuse plus importante de même que des précipitations accrues (Ottersen et al. 2004b). Ainsi, les nombreux modèles mis en place pour étudier ces phénomènes prévoient d'ici à 2080 une augmentation annuelle des températures de l'air d'en moyenne 4 à 5 °C en Atlantique Nord, augmentation accrue pendant la période hivernale (Fig. 1.9). La récurrence et l'amplitude croissantes des phases de NAO positives devraient tendre à une augmentation de la fréquence des tempêtes dans le futur (ACIA 2004). L'intensité de ces tempêtes devrait néanmoins baisser sous l'effet d'une diminution du gradient de température entre l'équateur et le pôle (Loeng et al. 2005), diminution qui n'aura cependant pas lieu dans toutes les zones (pas en mer du Labrador, ni en mer du Nord, par exemple). Enfin, on prévoit que la couverture nuageuse et les précipitations vont respectivement augmenter de 8 % et 10 % d'ici à 2080 (ACIA 2004).

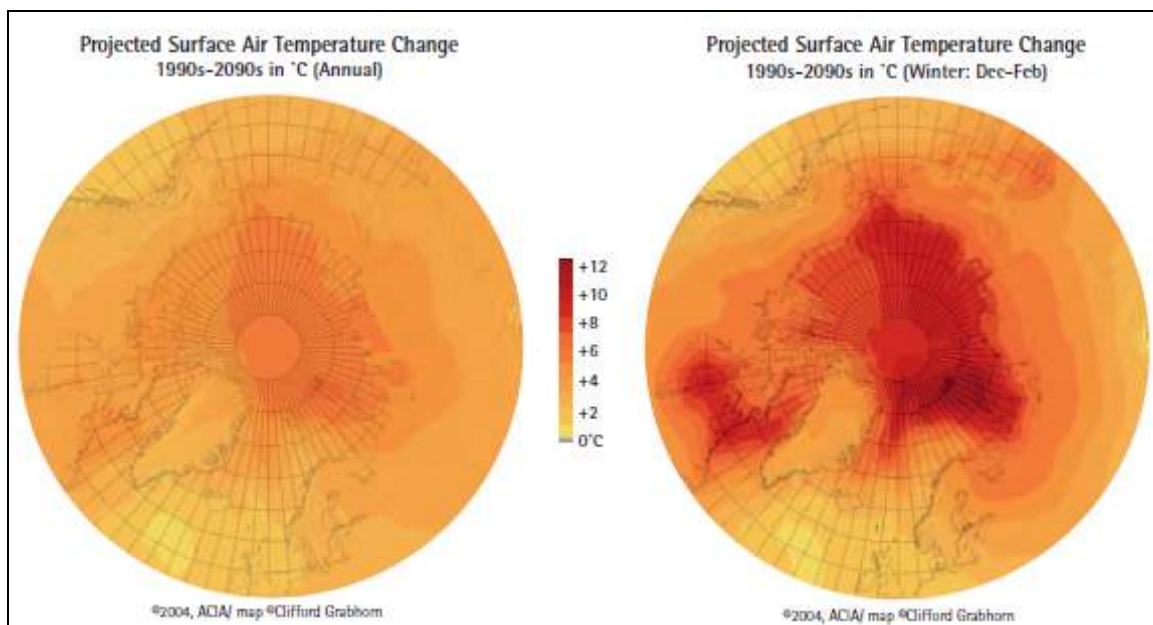


Fig. 1.9 Augmentation prédite des températures (annuelles et hivernales) entre 1990 et 2090.
(Source : ACIA 2004)

L'impact de ces changements environnementaux sur l'écosystème marin se fait essentiellement par le biais de mécanismes physiques. Les principales conséquences sur le milieu abiotique sont les suivantes :

- Dans les régions arctiques et subarctiques, l'étendue et l'épaisseur des zones océaniques englacées vont diminuer (ACIA 2004, Loeng et al. 2005). On estime déjà qu'au cours des 30 dernières années, la superficie de ces zones a diminué de 8 %, soit 1 million de km² (l'équivalent de la Norvège, de la Suède et du Danemark réunis).
- La fonte accélérée des glaces provenant à la fois des glaciers, de la glace de mer et de la couverture neigeuse, va entraîner une augmentation du volume d'eau douce libéré dans l'océan. Or, ce dernier régit directement l'intensité de la stratification de la colonne d'eau dans le milieu marin (l'augmentation de l'eau douce augmentant la stratification), dont dépendent de nombreux organismes et qui est à l'origine de la Circulation Thermohaline de l'Océan Atlantique⁹. Notons que l'eau provenant de la fonte des glaces de mer a pour origine l'eau de mer elle-même, cette fonte n'ayant donc pas d'incidence sur le niveau de l'océan contrairement à une idée répandue (seule la fonte des glaciers terrestres aura cette conséquence).
- L'intensité et la direction des vents océaniques sont connues pour affecter la circulation des courants dans certaines régions de l'Atlantique Nord (Jónsson 1991 ; Isachsen et al. 2003). Leur changement (lié à la NAO) pourrait donc modifier les masses d'eau associées aux différents courants, ainsi que la localisation et la force des fronts polaires. De plus, la rétraction des zones englacées devrait permettre l'apparition de nouvelles polynies et zones d'upwelling induites par le vent à la frontière glace / océan (ACIA 2004).
- Enfin, une augmentation des températures de surface de l'océan de la même intensité que la température de l'air est attendue dans les zones non-englacées. En revanche, les températures de surface des zones englacées devraient rester inchangées (Loeng et al. 2005).

⁹ La circulation thermohaline correspond à un phénomène de mouvements d'eau à l'échelle de la planète, dû à des différences de densités entre les eaux de surface et les eaux plus profondes. Ainsi en Atlantique Nord, les eaux de surface, plus froides et donc plus denses s'enfoncent en profondeur. Ces eaux profondes se répandent ensuite à travers tout l'océan et remontent progressivement vers la surface, dans le Pacifique Nord par exemple pour revenir à leur point de départ en Mer du Groenland. Cette circulation thermohaline joue un rôle climatique très important puisque c'est par exemple elle qui contrôle les transports océaniques de chaleur vers les hautes latitudes dans l'Atlantique Nord (voir Loeng et al. 2005, Ottersen et al. 2004b.)

Au travers de ces différents processus océanographiques, les changements climatiques se répercuteront ensuite sur l'ensemble du réseau trophique.

IV-2 Impacts sur la biocénose, et en particulier sur les oiseaux marins

Mise à part quelques rares cas de chauves-souris et de passereaux que l'on peut voir évoluer à proximité des côtes, les oiseaux marins sont aujourd'hui les seules espèces volantes à avoir véritablement colonisé les océans. Ils ont ainsi la particularité de se retrouver à l'interface de trois milieux différents : (1) **le milieu terrestre** qui leur permet de se reproduire et qu'ils fréquentent pendant une partie de leur cycle annuel, (2) **le milieu aérien** où ils effectuent la quasi-totalité de leurs déplacements par leur capacité de vol, et (3) **le milieu aquatique marin** dans lequel ils passent une grande partie de leur vie et dont ils tirent leurs ressources. Chacun de ces milieux joue un rôle primordial pour la survie et la pérennité de ces espèces. Mais cela signifie aussi que les oiseaux marins dépendent de ces trois milieux et donc qu'un changement dans un seul d'entre eux pourrait avoir des conséquences directes ou indirectes sur leurs populations.

(1) Milieu terrestre : les perturbations de ce milieu n'affecteront pas directement l'écologie hivernale des oiseaux marins, puisqu'elles ne concernent qu'une courte période estivale, celle de la reproduction. Notons tout de même qu'au travers d'une augmentation des pluies ou d'une fonte plus rapide des neiges au printemps, les changements climatiques pourraient provoquer des inondations plus fréquentes des nids (en particulier pour les espèces nichant dans des cavités telles que les mergules nains ou les macareux ; Rodway et al. 1998, Schreiber 2001). De plus, les pluies verglaçantes pourraient affecter négativement la balance thermique des poussins et donc leur survie (Burger & Gochfeld 1990). Ces perturbations terrestres pourraient ainsi avoir d'importantes conséquences sur le succès reproducteur des oiseaux marins concernés.

(2) Milieu aérien : deux principaux changements du milieu aérien pourraient affecter les oiseaux marins de l'Atlantique Nord. Il s'agit d'abord de l'augmentation de la température générale de l'air. Les oiseaux marins de ces régions sont morphologiquement et physiologiquement adaptés à des températures ambiantes froides. On s'attend ainsi, au cours de la période hivernale, à ce que cette augmentation ait un effet général positif sur la balance

thermique et l'énergétique de certaines espèces, excepté chez les individus distribués dans les régions les plus chaudes. Une des principales conséquences attendues est donc une remontée vers le nord des limites sud de distribution des espèces. Ensuite, un changement des vents pourrait avoir un impact non négligeable sur l'énergétique associée au comportement de vol des oiseaux, impact positif ou négatif en fonction des espèces considérées (Loeng et al. 2005).

(3) Milieu aquatique marin : il s'agit du milieu qui aura l'impact le plus fort sur les oiseaux marins qui intègrent l'ensemble des perturbations affectant chacun des maillons trophiques inférieurs dont ils dépendent. Ainsi, en plus d'avoir des conséquences directes sur les oiseaux comme les milieux précédents, ces perturbations auront des conséquences indirectes au travers l'ensemble du réseau trophique (phénomène de bottom-up control ; e.g. Frederiksen et al. 2006).

Voyons tour à tour comment les différents niveaux du réseau trophique de l'Atlantique Nord, et en bout de chaîne les oiseaux marins, vont être affectés par les futures variations de l'océanographie physique sous l'impact des changements climatiques.

- Le phytoplancton et la production primaire

La production biologique des océans est avant tout basée sur celle du phytoplancton. La présence de glace entraîne une diminution de la luminosité dans le milieu marin. Ainsi, la luminosité sous la glace est similaire à celle trouvée à 40 m de profondeur en eau libre. Cette lumière étant le facteur limitant au développement du phytoplancton, une diminution des étendues de glace devrait permettre une augmentation de la luminosité et donc une augmentation de la production (2 à 5 fois) et de la distribution du phytoplancton (ACIA 2004, Loeng et al. 2005). Cependant, cela ne sera possible que dans l'hypothèse où les vents (et le brassage des masses d'eau associé) permettraient un apport suffisant de nutriments. De plus, une augmentation des températures de surface va avoir en parallèle un impact direct sur l'abondance de ces espèces (Richardson & Schoeman 2004) ainsi que sur leur développement, en diminuant notamment le temps de croissance du phytoplancton, réduisant ainsi la durée du « spring bloom¹⁰ » et leur période de disponibilité pour leurs prédateurs.

¹⁰ Le « spring bloom » du phytoplancton est un phénomène de développement soudain d'une biomasse importante de phytoplancton au printemps dans les eaux tempérées et subpolaires. Cette émergence est notamment conditionnée par la luminosité (et donc la fonte des glaces dans certaines régions), la température et la disponibilité de nutriments.

- Le zooplancton

Les changements climatiques pourraient également avoir un impact négatif sur les populations de zooplancton. Par exemple, de nombreuses espèces vivent au dépend de la glace de mer qui leur offre un habitat ainsi que des proies comme les algues planctoniques. Une fonte accélérée de la glace de mer risque d'une part de détruire cet habitat, mais aussi d'accentuer la couche superficielle d'eau douce résultante, entraînant un remplacement des espèces d'algues aujourd'hui présentes et diminuant le stock de proies disponibles. De plus, de nombreuses espèces sont inféodées à des températures bien particulières (exemple des copépodes calanoïdes : Fig. 1.10). Un changement de quelques degrés pourrait profondément affecter leur reproduction et on s'attend ainsi à un déplacement de ces espèces vers le Nord (cf. Beaugrand et al. 2002b), remplacées par des espèces d'eaux tempérées. Enfin, la période de disponibilité avancée du phytoplancton (voir ci-dessus) pourrait entraîner une désynchronisation entre phytoplancton et zooplancton, menant à une diminution de la productivité du zooplancton (Loeng et al. 2005).

- Les poissons

Les poissons étant des organismes ectothermes (leur température corporelle suit celle de leur environnement) avec eux aussi des préférences thermiques, les zones de distribution spécifiques devraient se déplacer vers le nord sous l'effet direct de l'augmentation des températures de l'eau. Cette augmentation devrait aussi modifier les routes de migration des espèces ainsi que les périodes et zones de fraie, leur taux de fécondité et le taux de survie des larves (e.g. Loeng et al. 2005, Ottersen et al. 2004a). Enfin, une désynchronisation entre phytoplancton et zooplancton (voir ci-dessus) pourrait fortement diminuer la disponibilité des proies pour les poissons et donc leur survie (Loeng et al. 2005). Certaines espèces plus aptes à s'adapter pourraient profiter de ce changement de l'environnement. Ainsi, des espèces comme les morues de l'Atlantique ou les harengs vont se déplacer vers le nord et proliférer au dépend d'autres espèces comme le capelan ou la morue arctique dont l'abondance devrait diminuer (Loeng et al. 2005).

- Les oiseaux

Différentes études ont suggéré qu'en réponse aux changements de distribution et d'abondance de leurs proies, les oiseaux allaient se déplacer vers le nord (e.g. Brown 1991).

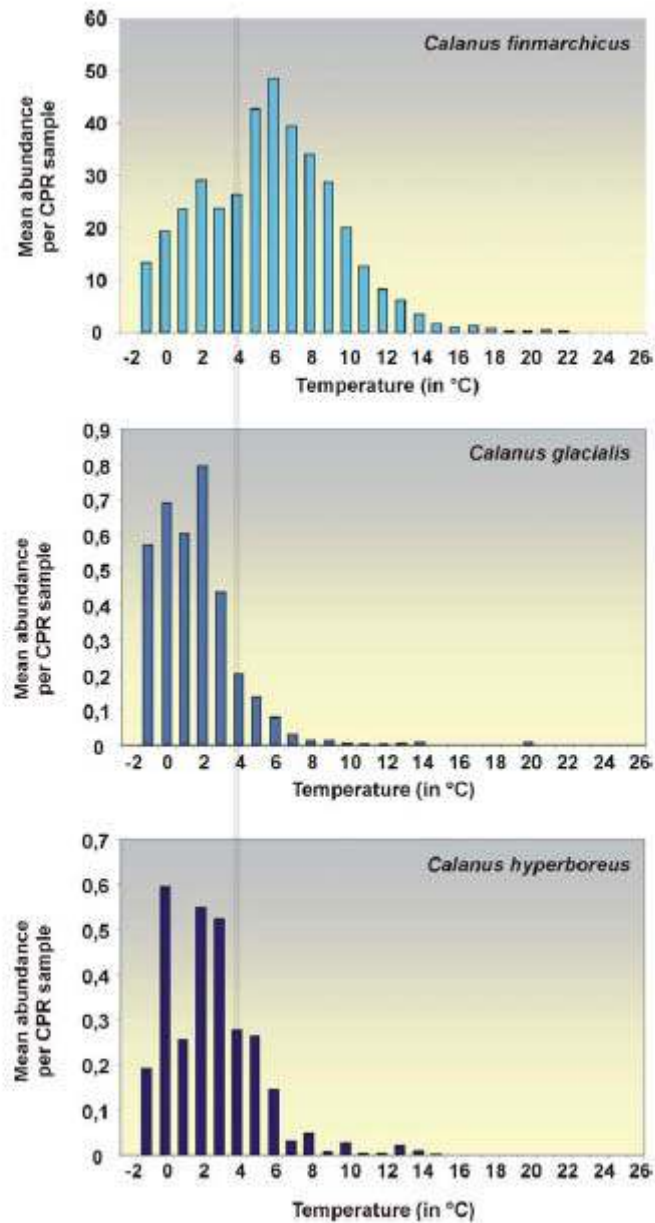


Fig. 1.10 Préférences thermiques de 3 espèces de copépodes calanoïdes de l’océan Nord Atlantique. L’abondance en axe des ordonnées est une moyenne d’abondance par prélèvement CPR¹¹ (soit environ 3m³ d’eau de mer filtrée ; Source : Beaugrand unpublished).

¹¹ L’étude « Continuous Plankton Recorder » est un large programme de suivi des communautés de zooplancton en Atlantique Nord et en Mer du Nord depuis 1931.

Pendant la saison de reproduction, les oiseaux marins sont contraints de revenir au nid pour alimenter leur poussin (« central place foragers » ; Orians & Pearson 1979), ce qui limite les distances qu'ils peuvent parcourir. On estime ainsi que la plupart des oiseaux marins de l'arctique s'alimentent dans un périmètre de 200 km autour de leur site de reproduction (Hunt et al. 1999). Que se passe-t-il alors si les conditions environnementales et les disponibilités de proies se dégradent ? La majorité des oiseaux marins ne pondent qu'un seul œuf et ne peuvent donc pas répondre aux conditions défavorables en modulant la taille de leur nichée. Ils doivent alors diminuer les soins parentaux afin d'assurer leur propre survie, ce qui affectera leur succès reproducteur (e.g. Harding 2009b). On peut ainsi penser que les sites de reproduction de certaines espèces pourraient changer en faveur de sites à proximité de zones plus productives comme des zones d'upwelling quand celles-ci seront disponibles. Cependant, la fidélité d'autres espèces à leur site de reproduction risque d'empêcher de tels déplacements et leur être particulièrement délétère (Pichegru et al. *unpublished*). Une autre solution possible serait un avancement de la période de reproduction permettant de faire face à des conditions climatiques plus favorables (Schreiber 2001). Cependant, la mise en place d'une telle réponse pourrait prendre du temps chez ces espèces longévives et n'a donc pas encore été observée chez les oiseaux marins (Thompson & Ollason 2001).

En hiver, les oiseaux sont libres d'évoluer au sein de l'océan et un changement de distribution leur permettant de continuer d'occuper les zones les plus profitables semble possible. Malgré tout, un déplacement des populations vers le nord est limité et les oiseaux ne pourront pas remonter indéfiniment vers des latitudes plus froides. En plus d'être géographique, cette limitation est due à un problème de luminosité (White et al. *unpublished*). En effet, la plupart des espèces plongeurs se servent, au moins en partie, de la vision pour capturer leurs proies sous l'eau et adaptent donc leurs périodes d'alimentation et leur comportement de plongée en fonction des niveaux de lumière (e.g. Wanless et al. 1999, Daunt et al. 2006, White et al. 2008). Or plus les oiseaux se trouvent sous de hautes latitudes, plus la luminosité rencontrée est faible, voire nulle pendant la nuit polaire, affectant ainsi leur efficacité prédatrice et leur acquisition d'énergie. Cette limitation de déplacement des espèces distribuées sous les plus hautes latitudes, couplée à la remontée vers le nord de celles dites « tempérées » sous l'effet de l'augmentation des températures, risque également d'augmenter la compétition interspécifique pour la ressource.

On voit donc bien que les changements climatiques à venir pourraient, en affectant le milieu et le réseau trophique, avoir un impact important sur la survie et la distribution des oiseaux marins, et il est urgent de mieux comprendre comment ces oiseaux vont réagir et si possible s'adapter. Pour cela, il nous faut dans un premier temps étudier comment ces espèces répondent à leur environnement à l'échelle de temps la plus courte, comment les événements climatiques extrêmes agissent sur leur écologie, leur survie et à long terme sur la dynamique de leurs populations.

V) Balance énergétique et plasticité comportementale

La balance énergétique d'un organisme correspond à la relation d'équilibre qu'il existe entre l'apport, la dépense et le stockage d'énergie. Sous l'effet de l'environnement, elle conditionne directement le budget énergétique des animaux et donc l'énergie qu'ils vont pouvoir allouer dans chacune de leurs activités, ainsi que dans leur propre condition et donc leur survie (Blem 2000). La balance énergétique est ainsi à la base des stratégies adoptées par l'animal. Lorsqu'il fait face à des changements environnementaux extrêmes, ou tout du moins à des changements à court terme, l'animal doit alors maintenir cette balance énergétique à l'équilibre afin d'assurer sa survie (Cuthill & Houston 1997).

Pour maintenir cet équilibre, différentes stratégies s'offrent à lui. Parmi elles, la plasticité comportementale joue un rôle essentiel. En effet, même si celle-ci apparaît parfois limitée tant d'un point de vue physiologique que morphologique, elle permet une réponse extrêmement rapide de l'animal face à son environnement en fonction des nouvelles conditions. Par exemple, lorsque les proies préférentielles d'un individu montrent un changement d'abondance ou de distribution, celui-ci peut (si sa physiologie et sa morphologie le lui permettent) se tourner vers des proies de substitution, permettant un maintien de l'énergie absorbée. C'est le cas des fous de bassan (*Morus bassanus*) qui sont capables de changer de proies pour s'adapter à la disponibilité du milieu et assurer leur survie ainsi que celle de leur poussin (Hamer et al. 2007). Lorsque, au cours de l'hiver, les conditions de luminosité sont altérées ou que le climat devient trop rude, les oiseaux marins peuvent également modifier leur budget temps (temps alloué à différentes activités). Cela leur permet de maximiser leur ingestion de proies et donc leur acquisition d'énergie, ou de diminuer leur activité et donc leur dépense énergétique. C'est le cas par exemple du grand cormoran (*Phalacrocorax carbo*) hivernant en Arctique qui durant cette période s'adapte aux conditions d'éclairement en

plongeant plus longtemps et de manière plus efficace (Grémillet et al. 2005a,b). Au contraire, les cormorans huppés (*Phalacrocorax aristotelis*) réduisent leur activité de recherche alimentaire sous-marine lors des périodes où la température de l'eau est la plus froide et la vitesse du vent la plus élevée, cela afin de diminuer leurs coûts énergétiques de thermorégulation (Daunt et al. 2006).

Balance énergétique et comportement sont donc intimement liés et jouent ainsi un rôle très important permettant aux oiseaux marins d'assurer leur survie dans un environnement hétérogène, variable et difficile. Dans ce contexte, étudier l'énergétique des oiseaux marins de l'Atlantique nord pendant leur saison hivernale apparaît donc comme particulièrement pertinent pour mieux comprendre les réponses et les adaptations de ces endothermes face aux événements climatiques extrêmes et aux perturbations de leur environnement, et ce dans le contexte des changements climatiques.

VI) Problématique et objectifs de l'étude

Centré sur l'étude de la balance énergétique des oiseaux, ce travail a donc eu pour objectif de répondre à la problématique suivante :

« Quelles sont les réponses des oiseaux marins hivernants en Atlantique Nord aux contraintes environnementales pour maximiser leur survie ? »

Après une rapide description des méthodes utilisées (Chapitre 2), la suite de cette thèse sera divisée en quatre chapitres principaux, chacun d'entre eux étant constitué de publications ou de travaux en cours de soumission.

- Un premier chapitre (Chapitre 3) aura pour objectif de confirmer, dans notre contexte d'étude, que l'environnement marin en Atlantique Nord en hiver est complexe et encore largement méconnu malgré son importance.
- Un second chapitre (Chapitre 4) s'attachera à étudier les impacts des conditions abiotiques hivernales, et plus particulièrement des facteurs climatiques, sur la survie des oiseaux marins. Pour cela, nous étudierons le lien entre conditions climatiques et dépense énergétique.

- Dans un troisième chapitre (Chapitre 5), nous étudierons comment les oiseaux répondent aux conditions biotiques de l'environnement au cours de l'hiver, notamment en termes de disponibilité alimentaire. Pour cela, nous étudierons l'acquisition d'énergie par les oiseaux marins, et donc leur écologie alimentaire.
- Enfin, nous élargirons notre étude en étudiant dans le chapitre suivant (Chapitre 6) comment les conditions environnementales rencontrées au cours de la période de reproduction peuvent, elles aussi, affecter la mortalité hivernale des oiseaux.

Pour finir, une synthèse des résultats obtenus au cours de cette thèse sera présentée et discutée et des perspectives de recherche découlant de ces travaux seront proposées (Chapitre 7).

Chapitre 2

Etudier l'hiver en expérimentant l'été...



...les méthodes utilisées

Comme nous venons de le voir, les réponses aux différents objectifs de cette thèse nécessitent toutes une étude approfondie de l'écologie, plus spécifiquement de l'écophysiologie et du comportement des oiseaux marins pendant la période hivernale. Or ces oiseaux ne sont observables et manipulables que pendant leur période de reproduction passée à terre. Cette contrainte nous a par conséquent obligé à utiliser de nouvelles méthodes pour répondre à nos questions.

La réalisation de cette thèse et de ce mémoire repose en grande partie sur du travail de terrain et de collecte de données. Dans un premier temps, ce chapitre s'attache donc à résumer les différentes missions de terrain qui ont permis la récolte des données utilisées, ainsi que les programmes de recherche dans lesquelles elles s'inscrivaient. Il présente ensuite les différentes méthodes utilisées ayant rendu possible une étude hivernale par le biais de manipulations estivales.

I) Récolte des données

I-1 Les mergules nains et le programme ADACLIM

L'ensemble des données ayant permis l'étude des mergules nains ont été récoltées au cours de trois saisons de terrains menées en 2007, 2008 et 2009 auxquelles j'ai participé sur une période totale de 4 mois. Elles ont eu lieu sur une colonie du Groenland Est (Kap Höegh, 70°44'N 21°35'W, Fig. 5.D.1). Cette colonie se situe sur l'un des plus importants sites de reproduction de cette espèce en Atlantique Nord. Les missions s'inscrivaient dans un programme de recherche (ADACLIM) soutenu par l'Institut Polaire Français Paul-Emile Victor (IPEV). L'objectif scientifique de ce programme est d'étudier les adaptations des oiseaux marins de l'Atlantique Nord face aux variations de leur environnement.

Par le biais de nombreuses collaborations internationales, des échantillons supplémentaires ayant permis une étude comparative (Chapitre 5) ont également été prélevés en 2006 sur différentes populations du Spitzberg (Magdalenefjorden (79°35'N, 11°05'E), Kongfjorden (79°01'N, 12°25'E), Longyearbyen (78°13'N, 15°19'E) et Hornsund (77°00'N, 15°22'E) ; Fig. 5.D.1).

I-2 Les guillemots et le programme BarentsBirds

La récolte des données sur les guillemots de Brünnich et les guillemots de Troil a été permise par une collaboration franco-norvégienne dans le cadre du projet BarentsBird (www.barentsbirds.com) financé par la Fondation Total et Total Norvège. Ce projet vise à étudier les mouvements saisonniers et la biologie hivernale des populations de guillemots de la mer de Barents. Les données utilisées au cours de cette thèse ont été acquises au cours de deux saisons de reproduction en 2007 et 2008.

II) Les méthodes utilisées

II-1 Un nouveau modèle de thermodynamique : Niche Mapper™

Comme nous l'avons vu précédemment, l'étude de la balance énergétique chez les êtres vivants et des facteurs la gouvernant est particulièrement importante. En effet, celle-ci conditionne directement leur condition corporelle et régie donc indirectement leurs décisions et stratégies de vie.

Il existe diverses méthodes permettant d'estimer la dépense énergétique d'un animal dans son milieu naturel ou en semi-captivité (e.g. Duffy & Jackson 1986, Gabrielsen et al. 1991, Wilson et al. 1995a, Grémillet et al. 1996). Cependant, la plupart d'entre elles nécessite de pouvoir observer et même manipuler les individus étudiés. Or en hiver, période qui nous intéresse, les oiseaux marins se trouvent en pleine mer, quasiment inaccessibles à toute manipulation, rendant donc ces techniques inutilisables. Récemment, de nouvelles technologies et le développement de la miniaturisation ont permis des mesures de la fréquence cardiaque d'oiseaux au cours de l'hiver, permettant ainsi d'estimer indirectement leur dépense énergétique pendant cette saison (Green et al. 2009). Pour cela, les appareils sont posés sur les oiseaux pendant la saison de reproduction et permettent ensuite un enregistrement hivernal sans qu'un accès aux oiseaux ne soit nécessaire. Cependant, ces dernières technologies restent logistiquement très contraignantes et la taille de tels enregistreurs implique une utilisation sur des espèces de grande taille uniquement (> 1kg), telles que les manchots ou les albatros. Par conséquent, une nouvelle méthode alternative et complémentaire est nécessaire à l'étude de l'énergétique des oiseaux marins hivernants.

Niche Mapper™ est un modèle basé sur les principes premiers de la thermodynamique, incluant la physiologie, la morphologie et le comportement de l'animal étudié. Son objectif est de calculer le métabolisme nécessaire à un animal pour maintenir une homéothermie dans un environnement donné et avec un comportement particulier. Pour cela, Niche Mapper™ s'appuie sur 2 sous-modèles :

- (1) le premier sous-modèle est un modèle climatique (Micro2006c). Il utilise différents paramètres environnementaux (température de l'air, température de l'eau, humidité relative, vitesse du vent, latitude et longitude) afin de calculer, pour chaque heure du jour et pour chaque localisation préalablement définie, les conditions les plus froides et les plus chaudes que pourrait rencontrer l'animal.
- (2) Le deuxième sous-modèle est un modèle animal (Endo2007d). Il intègre tour à tour les paramètres environnementaux générés par le sous-modèle climatique, les paramètres physiologiques, morphologiques et comportementaux (tous décrits dans la Table 4.B.1), ainsi que le milieu dans lequel évolue l'organisme étudié (dans l'eau, l'air ou à la surface de l'eau dans le cas des oiseaux plongeurs). Ce modèle animal va alors résoudre un système couplé de transferts de chaleur et de masse entre l'organisme et son environnement, représenté par les équations suivantes :

$$\text{Equilibre de chaleur (W): } Q_{in} + Q_{gen} = Q_{out} + Q_{st}$$

$$\text{Equilibre de masse (g/d): } m_{in} = m_{out} + m_{st}$$

Où Q_{in} correspond à l'acquisition de chaleur par l'organisme (due aux rayons solaires atteignant l'animal), Q_{gen} à la chaleur produite par l'organisme, Q_{out} à la perte de chaleur de l'organisme vers l'environnement par convection, conduction et radiation et Q_{st} à la chaleur emmagasinée par l'organisme. m_{in} correspond à l'entrée de matière dans l'organisme (nourriture entrant dans l'appareil digestif ou air entrant dans l'appareil respiratoire), m_{out} à la sortie de matière (par les fèces ou l'air expirée), et m_{st} à la quantité de matière stockée (correspondant à la masse de nourriture qui doit être absorbée par l'animal pour compenser sa demande énergétique quotidienne).

Les différents composants de ce système sont schématiquement représentés en figure 2.1.

Le sous-modèle animal va alors nous renseigner sur différents paramètres et besoins de l'organisme étudié que sont 1) les périodes d'activités de l'animal (basé sur le fait que celui-ci est diurne, nocturne et/ou crépusculaire, mais aussi sur le fait qu'un individu va maximiser ses activités lorsque les conditions seront les plus favorables), 2) ses pertes ainsi que ses besoins quotidiens en eau, 3) sa demande énergétique quotidienne, ainsi que 4) la quantité de nourriture dont il a besoin pour faire face à cette dépense énergétique, pour une alimentation donnée.

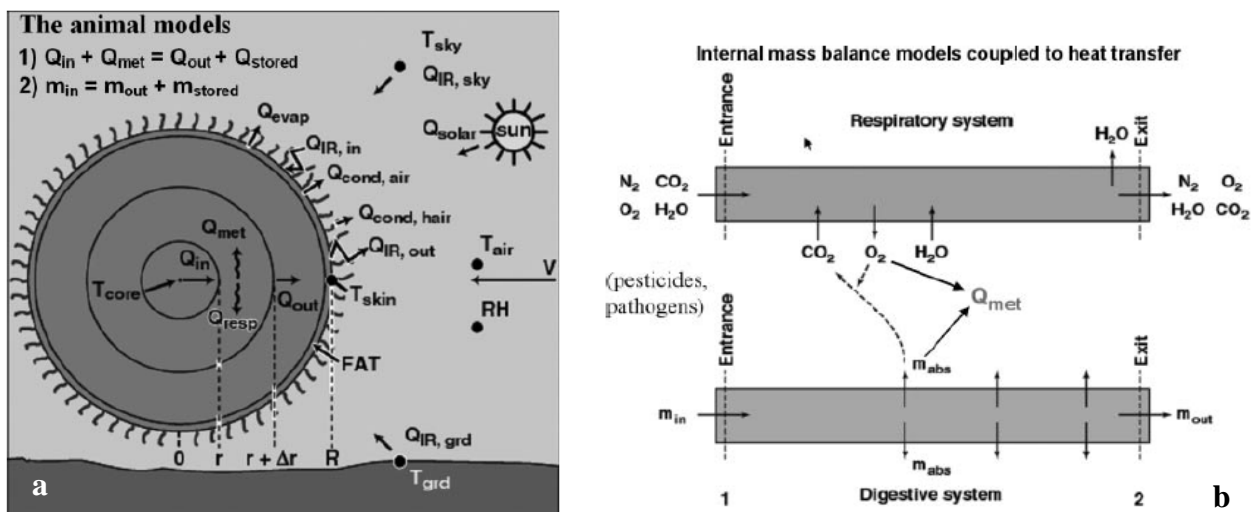


Fig. 2.1 Représentations schématiques du sous-modèle animal ainsi que des différents échanges de chaleur (a) et de masse (b) existants entre l'organisme et son environnement (Source : Porter et al. 2006).

II-2 L'analyse des isotopes stables

On définit les isotopes comme des atomes qui possèdent le même nombre de protons et d'électrons, mais un nombre variable de neutrons. Lorsque ces isotopes sont énergétiquement stables, qu'ils ne se détériorent pas et sont donc non-radioactifs, on dit qu'ils sont stables (Michener & Lajtha 2007). Ainsi, un isotope est stable lorsque le nombre de neutrons (N) et le nombre de protons (Z) qui le constitue tendent à être similaires ($N/Z \leq 1.5$). Ces atomes particuliers constituent, entre autres, l'ensemble des molécules d'un organisme parmi lesquelles se trouvent les acides aminés, unité structurale de base des protéines. Chaque

protéine d'un organisme possède ainsi une signature isotopique propre en fonction de la nature de ses acides aminés et donc de ses isotopes stables.

Lorsqu'un prédateur ingère une proie, il ingère aussi les protéines qui la composent. Une fois dans son intestin, ces protéines se décomposent, libérant les acides aminés les constituant. Ces acides aminés pénètrent ensuite la paroi intestinale et sont, en partie, réutilisés par le prédateur pour synthétiser ses propres protéines. C'est ainsi que les acides aminés d'une proie et leur signature isotopique sont transférés dans les tissus de son prédateur.

En écologie alimentaire, la technique des isotopes stables est donc basée sur le fait que nous sommes ce que nous mangeons. C'est-à-dire que la composition biochimique de nos tissus reflète de manière prévisible la composition biochimique de notre alimentation. En d'autres termes, lorsque le prédateur mange sa proie, la signature isotopique de ses tissus représente la signature isotopique de cette alimentation particulière. Chaque individu possède donc une signature isotopique qui lui est propre et qui évolue à chaque renouvellement de ses protéines. Dans le milieu marin, deux éléments sont classiquement utilisés : le Carbone (C) et l'Azote (N). Chacun d'entre eux possède deux formes isotopiquement stables : $^{12}_6\text{C}$ et $^{13}_6\text{C}$ pour le carbone, $^{14}_7\text{N}$ et $^{15}_7\text{N}$ pour l'azote. Dans chacun des cas, le rapport entre l'élément le plus lourd et le plus léger, c'est-à-dire $^{15}\text{N}/^{14}\text{N}$ (noté $\delta^{15}\text{N}$) et $^{13}\text{C}/^{12}\text{C}$ (noté $\delta^{13}\text{C}$), est calculé. Ces deux rapports offrent chacun un avantage particulier dans l'étude de l'écologie trophique en milieu marin. En effet, le rapport $\delta^{15}\text{N}$ s'enrichit d'environ 3‰ entre chaque niveau trophique (Fig. 2.2). Il nous apporte ainsi une information sur le niveau trophique du prédateur au sein de son écosystème (Michener & Kaufman 2007). Plus celui-ci occupe une position trophique élevée dans la chaîne alimentaire, plus il présentera un $\delta^{15}\text{N}$ élevé (Kelly 2000). Le rapport $\delta^{13}\text{C}$ lui, varie très peu le long de la chaîne alimentaire (Fig. 2.2). En revanche, ce rapport nous renseigne sur la source de carbone à la base de cette chaîne et permet donc de différencier dans le milieu marin les apports benthiques et néritiques des apports pélagiques et océaniques (Kelly 2000). De plus, ce rapport varie aussi dépendamment de la température de l'eau et est donc différent en fonction des masses d'eau (Rau et al. 1982). Ces informations combinées permettent donc d'utiliser le rapport $\delta^{13}\text{C}$ comme indicateur des zones d'alimentation des prédateurs (Hobson et al. 1994). Dans l'océan austral, il existe une variation importante et progressive des températures de l'eau, entraînant ainsi une variation latitudinale du rapport $\delta^{13}\text{C}$ (Rau et al. 1982 ; Fig. 2.3). De nombreuses études se sont appuyées sur cette particularité pour déterminer les zones d'alimentation des prédateurs marins dans l'hémisphère sud (e.g. Cherel et al. 2006, 2007). En revanche, il est important de

noter qu'à cause d'une plus grande hétérogénéité de températures océaniques, un tel gradient n'existe pas dans l'hémisphère nord, empêchant toute étude corrélative de ce type (Rau et al. 1982 ; Fig. 2.3).

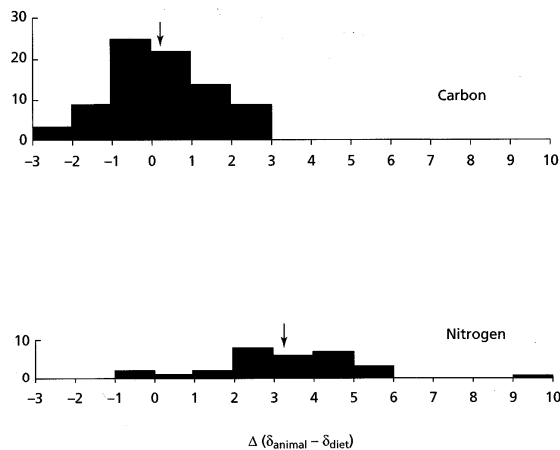


Fig. 2.2 Facteur d'enrichissement trophique entre un prédateur et sa proie pour le carbone et l'azote. L'axe des ordonnées représente la taille d'échantillons observés pour chaque classe (Source : Michener & Kaufman 2007)

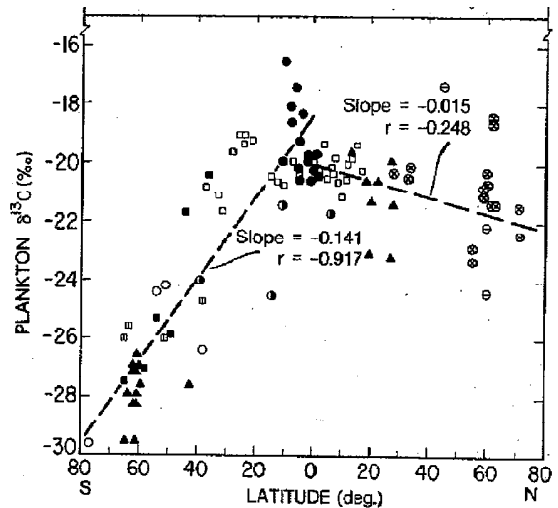


Fig. 2.3 Relations existantes dans les hémisphères nord et sud entre la latitude et le rapport $\delta^{13}C$ du phytoplancton (Source : Rau et al. 1982).

Une autre notion particulièrement importante dans l'étude des isotopes stables est celle d'intégration temporelle. Comme nous l'avons vu, la composition isotopique des protéines d'un tissu reflète de manière prévisible l'alimentation du consommateur. Or ces protéines vont se renouveler, nous permettant ainsi de suivre l'évolution de régime alimentaire du prédateur. Cependant, ce temps de renouvellement protéique diffère en fonction des tissus, créant alors une variabilité quant à l'information obtenue. Ainsi, le renouvellement protéique dans le sang total¹² permet d'obtenir une information sur l'alimentation du prédateur quelques semaines plus tôt (Hobson & Clark 1992, Evans-Ogden et al. 2004). Celui du plasma permet quant-à-lui une information sur l'alimentation quelques jours plus tôt (Hobson & Clark 1992,

¹² Le sang total correspond au sang dans son ensemble, avec tous les éléments qui le constituent (plasma, globules blancs, globules rouges, plaquettes...)

Evans-Ogden et al. 2004). Les plumes étant un tissu mort, les protéines ne s'y renouvellent pas et sont donc les mêmes que celles qui composaient la plume lorsque celle-ci a poussé. Elles reflètent donc l'alimentation du consommateur au moment de la croissance de cette plume (Bearhop et al. 2002). Cette intégration temporelle des protéines permet donc, par l'analyse de différents tissus d'un même animal, de suivre son écologie alimentaire à différentes échelles temporelles et donc différentes périodes de son cycle biologique (Hobson 1993, Cherel et al. 2008).

II-3 Miniaturisation électronique et études du comportement de plongée

La première étude à s'être intéressée au comportement de plongée des oiseaux marins remonte à la fin des années 1960 (Kooyman et al. 1971). Grâce à l'utilisation d'enregistreurs pesant 700 g chacun, elle avait alors permis d'étudier de manière précise le nombre, la durée et la profondeur des plongées effectuées par les manchots empereurs (*Aptenodytes forsteri* ; 25 kg) de l'île de Ross en Antarctique. La nouveauté de cette méthode et les nombreux champs d'investigations qu'elle ouvrait ont alors rapidement entraîné un nouvel engouement et une multiplication des études utilisant ces enregistreurs (e.g. Kooyman 1982, Wilson et al. 1984, 1991). A la fin des années 1980, les nouvelles technologies, la miniaturisation de l'électronique et l'apparition de nouveaux capteurs de pression ont permis de diminuer considérablement la taille et le poids des enregistreurs utilisés, autorisant ainsi l'étude d'espèces de plus en plus petites telles que les guillemots pesant environ 1 kg (Croll et al. 1992). Malgré tout, ces enregistreurs restaient relativement gros (6x2.5x1.5 cm ; 35 g) et de nombreuses améliorations étaient nécessaires pour permettre l'étude d'espèces encore plus petites, ainsi qu'une meilleure précision et une plus grande autonomie.

Aujourd'hui, les enregistreurs utilisés dans ces études de comportement chez les oiseaux plongeurs (« Time Depth Recorder » : TDR) permettent de mesurer les mêmes paramètres qu'avant. Ils sont toutefois devenus beaucoup plus petits (les plus petits TDR ne mesurent que 12 x 6 x 5 mm et pèsent 1 g dans l'air), sont équipés de capteurs plus précis et possèdent une mémoire et des batteries beaucoup plus performantes. Ces caractéristiques autorisent ainsi des déploiements de longues durées et sur de petites espèces. Ces TDR, une fois posés sur l'oiseau, peuvent enregistrer le comportement de plongée d'un individu pendant 2 ou 3 ans avant d'être récupérés. En effet, après son déploiement, chaque enregistreur stocke les

données enregistrées sur une mémoire interne qui ne pourra être déchargée qu'une fois l'oiseau recapturé et l'enregistreur récupéré.

Le capteur de pression permet une mesure précise de ce paramètre au cours du temps (en déci-bar ; dBar). Lorsque l'oiseau plonge sous l'eau pour rechercher ses proies et s'alimenter, les pressions auxquelles est soumis le capteur sont enregistrées à un intervalle de temps défini. Sous l'eau, la pression varie de 1dBar tous les mètres (1 dBar = 1.0197 m dans une eau à 4°C) et les deux unités (dBar et mètre) sont donc considérées comme équivalentes. Il devient alors facile de convertir les enregistrements de pressions en profondeurs de plongée avec une précision de 0.1m et au minimum une mesure par seconde, permettant le calcul de nombreux paramètres comportementaux tels que le temps passé en plongée, la durée d'une plongée, la durée d'une phase de recherche alimentaire, les profondeurs d'alimentation ou les profils de plongée (Fig. 2.4; Harding et al. 2009a).

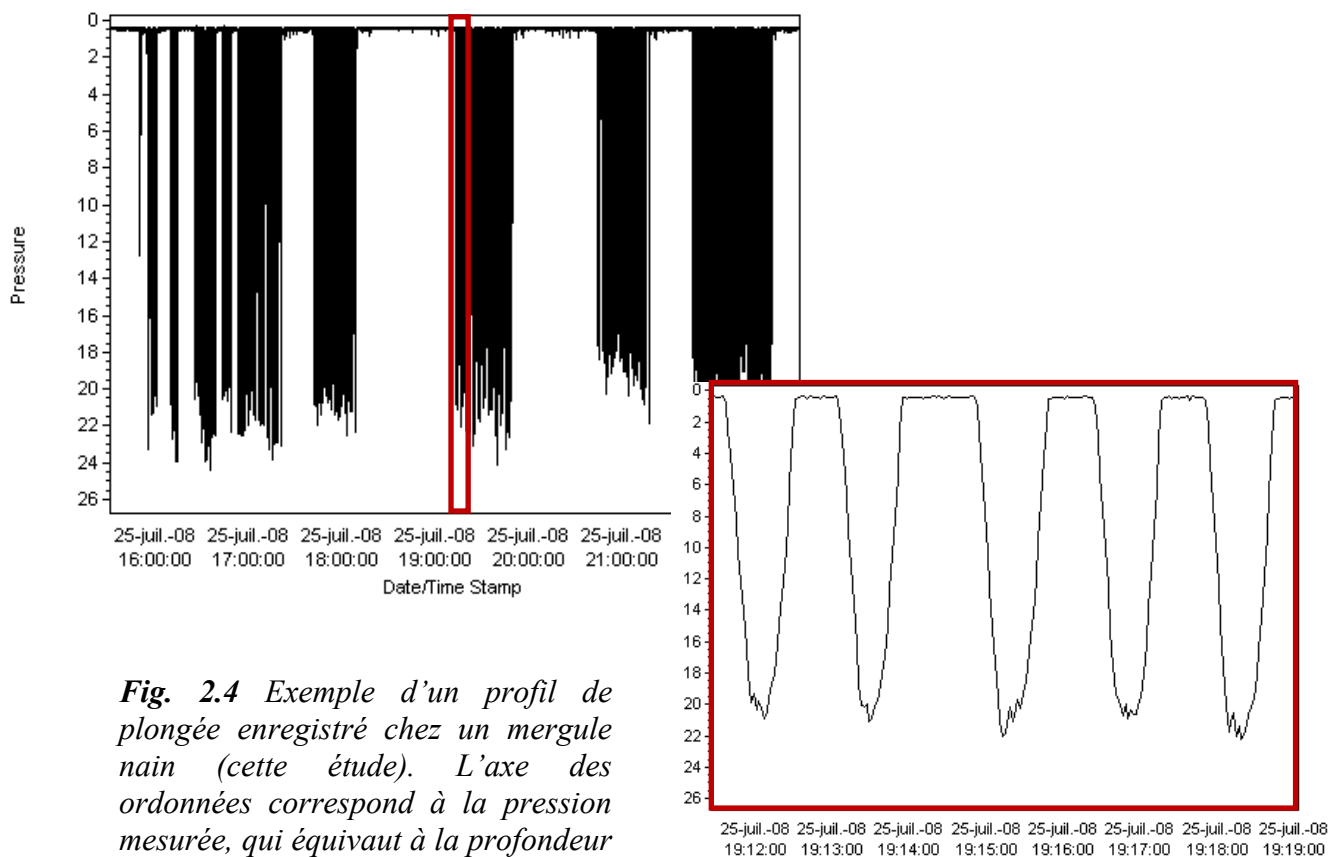


Fig. 2.4 Exemple d'un profil de plongée enregistré chez un mergule nain (cette étude). L'axe des ordonnées correspond à la pression mesurée, qui équivaut à la profondeur de plongé.

La majorité des TDR est également équipée d'un capteur de température. Lorsque le TDR est attaché à l'animal, il peut donc enregistrer la température du milieu environnant (eau ou air). Seule surface corporelle dépourvue de plumes durant l'hiver arctique, les pattes des oiseaux marins sont, avec la tête, la première source de perte de chaleur, entraînant ainsi d'importants coûts de thermorégulation. Différentes adaptations physiologiques et comportementales sont apparues chez les oiseaux marins (comme chez de nombreux autres organismes) pour maintenir leurs pattes dans une zone thermique acceptable, limitant ainsi ces coûts et permettant une survie dans les environnements les plus froids. Parmi ces adaptations comportementales, on retrouve chez la majorité des oiseaux marins un comportement qui consiste à rentrer les pattes dans le plumage lorsqu'ils sont en vol, les isolant ainsi de l'environnement extérieur et les maintenant à une température proche de leur température corporelle (Schreiber & Burger 2002). Lorsque les TDR sont déployés sur la patte d'un l'oiseau (Fig. 2.5), ils enregistrent donc les fluctuations de températures ambiantes auxquelles sont soumises ces pattes (Fig. 2.4). Par conséquent, lorsque l'oiseau est en vol avec les pattes rentrées dans le plumage, le TDR enregistre une température similaire à la température corporelle périphérique de l'oiseau (entre 30 et 42 °C selon les espèces ; e.g. Gabrielsen 1988, Grémillet et al. 2005a, Niizuma et al. 2007). En revanche, lorsque l'oiseau se trouve à la surface de l'eau ou en plongée, ces pattes sont sorties et le TDR enregistre la température de l'eau (généralement comprise entre -1 et 10°C en Atlantique Nord en hiver).

Une étude de l'évolution de la température enregistrée au cours du temps permet donc de déterminer avec précision à quelles périodes l'oiseau est en phase de vol, la durée de ces phases, ou encore le temps passé en vol par jour.

Grâce aux TDR et à la combinaison des données enregistrées par les capteurs de pression et de température, il devient donc possible de déterminer le budget-temps précis des oiseaux, c'est-à-dire le temps alloué à différentes activités : en plongée, en vol, au repos à la surface de l'eau (période où l'oiseau ne vole ni ne plonge). La connaissance de ce budget-temps est essentielle pour étudier la balance énergétique des animaux puisque chaque comportement est associé à un effort et une thermorégulation différents, et donc à une consommation d'oxygène et une dépense énergétique très variables (Pennycuick et al. 1990, Ellis & Gabrielsen 2002, Enstipp et al. 2006)

Notons enfin que ces TDR peuvent également être implantés dans la cavité abdominale des oiseaux plutôt que d'être attachés sur leur bague d'identification. Cette méthode ne modifie en

rien le principe d'enregistrement de la pression et donc l'étude du comportement de plongée. En revanche, elle permet d'une part d'éviter une gêne hydrodynamique pour l'oiseau, mais également d'enregistrer la température interne de l'animal au cours du temps. De tels enregistrements sont particulièrement importants pour étudier l'écophysiologie et l'énergétique de la plongée chez les oiseaux marins. Ils permettront notamment d'appréhender les contraintes de thermorégulation et de pertes de chaleur de l'organisme dans le temps, et au cours de cette activité.

L'implantation de TDR dans la cavité abdominale se fait sur des oiseaux reproducteurs et sous anesthésie générale. Le protocole de chirurgie est celui décrit par Stephenson et al. (1986). Une fois capturé dans son nid, l'oiseau est transporté le plus rapidement possible dans un environnement stérile où a lieu l'opération. Dans notre étude, il s'agissait d'une tente installée à moins de 200 m de la colonie. L'oiseau y est immédiatement endormi par anesthésie gazeuse (mélange O₂-isoflurane) puis l'enregistreur est implanté dans la cavité abdominale. L'utilisation d'antibiotiques (oxytétracycline, Terramycine® LA) et d'anti-inflammatoires (Kétoprofène, Ketofen® 1%) est systématique lors de chaque chirurgie. Une fois l'oiseau opéré, celui-ci est redéposé encore endormi dans son nid, afin de diminuer son stress au maximum. Notons que l'enregistreur, avant d'être implanté, est enrobé dans une fine couche de silicone puis stérilisé dans un mélange d'éthanol 70% (90%) et de chlorhexidine 5% (10%). Cela permet de limiter au maximum les risques d'infection dus à l'implant.

Cette méthode a été utilisée avec succès chez plusieurs espèces d'oiseaux marins telles que les grands cormorans (Grémillet et al. 2005a,b) ou les fous du Cap (*Morus capensis*) (Grémillet et al. 2008).



Fig. 2.5 Exemple d'un enregistreur TDR de pression et température (LTD 2400; Lotek Wireless, St. Johns, NF, Canada) attaché sur la bague d'un guillemot de Brünnich.
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Chapitre 3

**L'écosystème marin en hiver :
une exploration inachevée ?**



Introduction du chapitre

Comme nous avons pu le voir précédemment, l'écosystème marin en Atlantique Nord a été intensivement étudié depuis le 19^{ème} siècle, et est aujourd'hui considéré comme globalement bien compris. Cependant, les conditions hivernales très rudes dans certaines zones ont toujours rendues les études difficiles d'un point de vue logistique, et nos connaissances du réseau trophique durant l'hiver sont souvent basées sur des études ponctuelles et géographiquement restreintes. Tout laisse donc penser que l'immensité de cette zone et sa forte hétérogénéité spatiale et temporelle font que de nombreux aspects de cet écosystème restent encore à explorer. Une bonne connaissance de ce milieu est cependant indispensable à l'étude de chacun des niveaux trophiques, et notamment des oiseaux marins, prédateurs supérieurs qui dépendent de chaque maillon de ce réseau.

Nous avons ainsi voulu montrer dans cette première partie que de nombreuses zones d'ombres existent encore dans nos connaissances de l'écosystème marin de l'Atlantique Nord en hiver, ce qui complique d'avantage les études des oiseaux marins. Pour cela, nous nous sommes focalisé sur un maillon essentiel de cet écosystème : les copépodes ainsi qu'un de leurs prédateurs : le mergule nain. Au cours de l'hiver, les copépodes sont connus pour effectuer dans leur grande majorité une longue diapause de plusieurs mois à des profondeurs supérieures à 400 m, profondeurs qu'ils ne quittent qu'au début du printemps pour remonter vers les eaux de surfaces (< 50 m). Cependant, une étude récente a remis en cause ce résultat, laissant supposer que ces copépodes continuent de remonter quotidiennement à la surface pendant l'hiver à hautes latitudes, et cela malgré une absence permanente de luminosité (Berge et al. 2009).

Par conséquent, nous avons spécifiquement voulu tester l'hypothèse selon laquelle :

« Les copépodes calanoïdes restent présents en quantité importante dans les eaux de surface en hiver, étant ainsi disponibles à leurs prédateurs. »

Pour cela, nous avons utilisé une approche combinant l'utilisation de TDR et des analyses isotopiques. Cela nous a permis d'étudier le comportement de plongée et l'alimentation des mergules nains (oiseaux considérés comme se nourrissant essentiellement de copépodes) durant l'hiver.

The feeding ecology of little auks raises questions about winter zooplankton stocks in North Atlantic surface waters

Jérôme Fort, Yves Cherel, Ann M. A. Harding, Carsten Egevang, Harald Steen, Grégoire Kuntz, Warren P. Porter & David Grémillet

Abstract

Copepods are essential components of marine food webs worldwide. In the North Atlantic, they are thought to perform vertical migration and to remain at depths >500 m during winter. We challenge this concept through a study of the winter feeding ecology of little auks (*Alle alle*), a highly abundant planktivorous seabird from the North Atlantic. By combining stable isotope and behavioural analyses, we demonstrate that swarms of copepods are still available to their predators in water surface layers (< 20 m) during winter, even during short daylight periods. Using a new bioenergetic model, we show that the huge number (20-40 million birds) of little auks wintering off southwest Greenland consume 3900-7800 tonnes of copepods daily, strongly suggesting substantial zooplankton stocks in surface waters of the North Atlantic in winter.

Keywords: diving behaviour, energetic modelling, food requirements, marine food web, stable isotope, seabird

A-1. Introduction

Copepods are essential components of aquatic food webs and play an important role within marine ecosystems. Their life strategies have been extensively studied (e.g. Falk-Petersen 2009) and their ecology is considered well known. At high latitudes and during winter, copepods are thought to perform vertical migration to deeper water to undergo diapause, and to become unavailable to most predators (Falk-Petersen 2009). However, a recent study has shown that in high Arctic waters copepods maintain their synchronized diel vertical migration throughout the polar night (Berge et al. 2009), suggesting that further studies are necessary to yield a complete view of copepod winter ecology.

Seabirds are powerful indicators of marine food webs (e.g. Piatt et al. 2007) and here we used little auks (*Alle alle*) as biosamplers. Indeed, the little auk (*Alle alle*), a small Arctic seabird, is known to be the only seabird in the North Atlantic which feeds almost exclusively on zooplankton, essentially calanoid copepods (Stempniewicz 2001; Karnovsky et al. 2008).

We used isotopic tracers (Kelly 2000) and Time Depth Recorders to investigate little auk diet and foraging depths during winter. It is the first study to record the winter diving behaviour of such a small seabird. We tested the hypothesis that copepods are still available in upper surface layers and consumed by little auks, even during the short winter daylight period. We then used a bioenergetic model (Niche Mapper™) to estimate the daily food requirement of the population of little auks wintering off southwest Greenland, and to define the minimum amount of copepods that must be available to meet these requirements.

A-2. Materials and Methods

Little auks breed at high latitudes around the Arctic Ocean. The north-east Atlantic populations winter south of the ice edge (mainly off southwest Greenland and off Newfoundland) and in polynias (Stempniewicz 2001, Mosbech unpublished).

Breeding little auks were caught during the summer 2007 at Kap Hoëgh (East Greenland; 70°44'N 21°35'W). Blood samples (n=20; ~0.2ml) were collected from the brachial vein, as well as 16 chick meals transported in adult's sublingual pouch. A second set of 20 wintering birds was legally shot at sea off Nuuk (southwest Greenland; 64°10'N 51°45'W) by Greenlandic hunters in January 2007 and kept frozen until dissected in the laboratory, where blood samples were collected from the cardiac clot. Stomach contents were removed, but digestion precluded identifying prey items. Immediately after collection, blood and prey samples were added to 70% ethanol and kept frozen at -20°C until isotopic analysis.

To investigate copepods isotopic signatures, only chick meals containing >90% copepods were analysed. Samples preparation and stable isotope analyses were performed following Cherel et al. (2007), with blood $\delta^{15}\text{N}$ ($^{15}\text{N}/^{14}\text{N}$) values reflecting the trophic position / diet (Kelly 2000). Values are mean \pm S.D.

Eighteen breeding little auks from Longyearbyen (Spitsbergen; N78°13'N; 15°20'E) were equipped with a Time Depth Recorder archival tag (G5, CEFAS Technology Limited, Lowestoft, UK) during the summer 2007. This recorder was implanted into the abdominal cavity following Grémillet et al. (2005a,b) and was programmed to record pressure during 24 hour sessions at a sampling rate of 2 seconds every 12 days from 6th November 2007 to 22nd February 2008. Five birds were resighted the following year and three of those were recaptured. Unfortunately, only one logger successfully recorded pressure. Stored data were extracted using G5 Host software and analysed using MultiTrace-Dive software (Jensen Software Systems). To avoid artefacts due to waves, other bird activities or tag accuracy, only dives deeper than 1.5m were analyzed. To compare results from behavioural and isotopic analyses, only diving data recorded in January were used.

Individual daily energy and food requirements during January were calculated using Niche Mapper™ (Porter & Mitchell 2006). Based on the first principles of thermodynamics and on the physiological and behavioural responses of individual organisms to their environment, this model allows investigation of energy balance and energy transfers in a variety of animals. Niche Mapper™ has been previously validated and described in detail for seabirds in Fort et al. (2009). All input data to Niche Mapper™ are detailed in the electronic supplementary material (Table 3.A.2). Following isotopic results (see below), birds were assumed to feed on copepods during winter. We then estimated the minimum amount of copepods which should be present in southwest Greenland surface waters to meet the food requirements of the little auk population wintering there. This population is composed to a large extent of birds breeding in northwest Greenland, east Greenland and Svalbard (Stempniewicz 2001). The number of little auks wintering off southwest Greenland is therefore estimated between 20 and 40 million birds (Barrett et al. 2006, Karnovsky & Hunt 2002).

A-3. Results

During summer, the $\delta^{15}\text{N}$ value of chick meals (which correspond to copepod prey, Harding et al. 2009a) averaged $8.4 \pm 0.5\%$ (Fig. 3.A.1). Summer and winter bird blood $\delta^{15}\text{N}$ values were

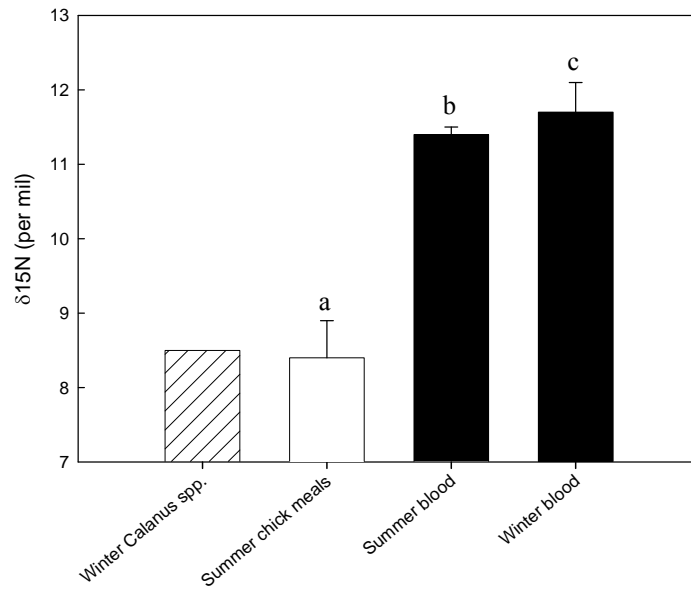


Fig. 3.A.1 Stable nitrogen isotope values for chick meals ($n=9$) and little auks whole blood samples ($n=20$) collected at Kap Hoëgh (East Greenland) during the summer, and for little auks whole blood samples ($n=21$) collected at sea off Nuuk (southwest Greenland) during winter. Values are means \pm SD. Values not sharing the same superscript letter are significantly different (see results). Winter value for *Calanus* spp. is from Sato et al. 2002.

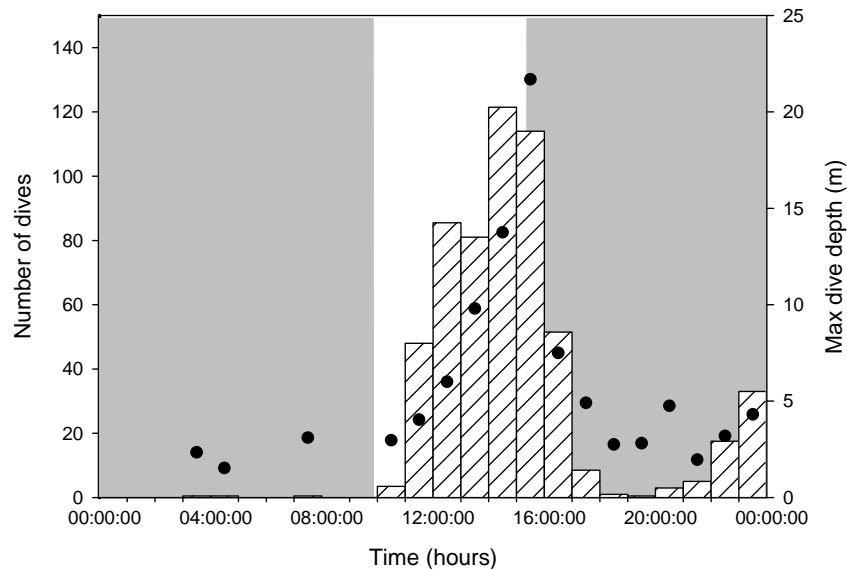


Fig. 3.A.2 Number of dives (▨) and maximum depth reach for any dive (●) at each hour of day during winter (January) 2008. The grey background represents the night/darkness period while the white background represents the daylight period off Nuuk, southwest Greenland ($64^{\circ}10'N$ $51^{\circ}45'W$).

almost identical (Fig. 3.1.A), yet statistically different (11.4 ± 0.1 and $11.7\pm 0.4\%$, respectively; t -test, $t=3.75$, $p<0.001$). During summer, adult bird blood was 3‰ enriched in $\delta^{15}\text{N}$ compared to copepod prey, as expected for an increase of one trophic level (Fig. 3.A.1).

During winter, measured bird blood was also 3‰ enriched in $\delta^{15}\text{N}$ compared to copepods (figure 1, Sato et al. 2002).

During winter (January), the mean depth of dives was $3.3\pm 2.0\text{m}$, with a maximum dive depth of 21.7m ($n=1151$ dives). The mean dive duration was $25.4\pm 9.9\text{s}$. On average, the bird spent 16.9% of its time diving. This diving activity was essentially concentrated during the daylight period (65.2% of dives, and 47.7% of the 5.5 hours daylight period spent diving) while 34.8% dives were performed at night (only 7.6% of the 18.5 hours night period) (Fig. 3.A.2). Following our recording protocol, these results for January are based on 2 recorded days. However, they are consistent with those obtained for November and December (see Table 3.A.1).

During January, Niche Mapper™ predicted an individual daily energy expenditure of 472 kJ day^{-1} , and a food requirement necessary to meet this expenditure of 195g zooplankton day^{-1} (wet mass). Consequently, we can estimate that the southwest Greenland wintering population of 20-40 millions birds has a daily prey intake between 3900-7800 tonnes of zooplankton per day (wet mass).

A-4. Discussion

Using a multidisciplinary-approach combining stable isotope analysis, diving behaviour and energetic modelling, this study presents indirect evidence that during winter daylight periods copepods are still numerous in surface waters <20m off southwest Greenland.

Little auks are known to feed almost exclusively on copepods in summer (e.g. Karnovsky et al. 2008), and blood $\delta^{15}\text{N}$ values found here are in agreement with birds preying upon *Calanus* spp. during this period (Karnovsky et al. 2008). Isotopic $\delta^{15}\text{N}$ signatures are similar for summer and winter copepods (Sato et al. 2002, Fig. 3.A.1), as well as for summer and winter adult blood samples (Fig. 3.A.1). This strongly suggests that little auks feed predominantly on *Calanus* spp. in winter. During this period, birds may also consume other prey, but in a minor proportion since these (e.g. amphipods or euphausiids) have higher isotopic signatures than copepods (e.g. Tamelander et al. 2008) and would thus lead to higher blood $\delta^{15}\text{N}$ values. Winter blood values slightly higher than those measured in summer might

reflect that amphipod/euphausiid effect, as well as the general food web enrichment between both periods (Rolff 2000).

Further, we infer from little auk diving behaviour that copepods remain abundant in winter surface water, even during the daylight period when they are supposed to perform vertical migration to greater depths (Fig. 3.A.2, Fortier et al. 2001, Berge et al. 2009). These first diving data obtained on such a small wintering seabird also indicate that little auks, as some other diving seabirds, increase their foraging effort (time spent diving and dive depth) during the daylight and dusk periods (e.g. Wanless et al. 1999, Jones et al. 2002, White et al. 2008). It suggests a visual predation, even during winter when daylight only lasts for a few hours, with very low overall luminance. The few nocturnal dives are shallow dives (<5m), performed at a depth at which prey might be still visible. However, even though our dive depth results are consistent with summer recordings (Harding et al. 2009a), further studies are needed to confirm this information. In any case the small size of little auks precludes diving to depths >500m where copepods are assumed to occur in winter (Burger 1991).

Copepods are classically thought to enter diapause in the fall and to spend all winter in deeper water (Falk-Petersen 2009). During early spring, and mostly synchronized with the phytoplankton spring bloom, they are supposed to migrate back to surface waters (Falk-Petersen 2009). However, a recent acoustic study has shown that even in winter and during the high-latitude polar night, some copepods perform a synchronized diel vertical migration in the epipelagic layer (Berge et al. 2009), whereby they migrate to the food-rich surface layers during darkness and move to deeper water during daylight where they are out of reach from predators (Fortier et al. 2001). Our study strongly suggests that during winter, swarms of copepods are still present in surface waters (*sensu* Berge et al. 2009) where they are targeted by little auks, essentially during the daylight period.

Using a bioenergetic model, we estimated that the amount of copepods available to birds was not negligible since the estimated daily intake of the little auk population wintering off southwest Greenland is 3900-7800 tonnes. This result based on a diet composed only of copepods might be slightly overestimated since little auks probably also consume a few other prey items such as amphipods or euphausiids. The standing stock of copepods is currently unknown and it is impossible to estimate the proportion of the population caught per day by wintering birds. However, a range of 3900-7800 tonnes of copepods caught per day during the winter off southwest Greenland is larger than the daily amount consumed during the summer by the breeding population of the North Water Polynya (i.e. 3450-6900 tonnes of wet food consumed per day, including 2340-4680 tonnes of copepods; Karnovsky & Hunt 2002).

Therefore, this suggests that the daily presence of copepods in the upper layer of the water column throughout the winter is much more important than usually assumed, with far-ranging consequences for regional food webs and energy flow.

Acknowledgements

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Table 3.A.1 *Electronic Supplementary 2 – Diving parameters recorded during each 24 hours session.*

	6-Nov	18-Nov	30-Nov	12-Dec	24-Dec	5-Jan	17-Jan
Total number of dives recorded	269	334	575	728	375	579	571
Mean Dive depth (m)	20.3	23.7	5.1	2.3	3.0	3.1	3.5
Max dive depth (m)	33.8	42.7	23.2	18.4	11.7	21.7	11.8
Mean Dive duration (sec)	54.8	60.1	25.8	20.8	25.9	29.4	21.3
Proportion of time spent diving per day (%)	17.1	23.2	17.2	17.3	11.3	19.7	14.1
Proportion of dives during daylight period (%)	78.3	62.6	58.4	38.4	15.3	70.8	57.3
Proportion of dives during night period (%)	21.7	37.4	41.6	61.6	84.7	29.2	42.7

Table 3.A.2 *Electronic Supplementary Material 1 – Parameters used in the bioenergetics model.*

	Input values	References
Morphological properties		
Body mass (kg) (max - min)	0.17	This study
Plumage depth (mm) (dorsal - ventral)	7.4 - 12.8	Fort et al. in press
Plumage reflectivity (%) (dorsal - ventral)	40.4 - 65.0	Fort et al. in press
Feather length (mm) (dorsal - ventral)	20.0 - 19.2	Fort et al. in press
Feather diameter (μm) (dorsal - ventral)	33.0 - 33.0	Fort et al. in press
Wing span (m)	0.39	Harding unpublished data
Wing area (cm^2)	180	Harding unpublished data
Physiological properties		
Body core temperature ($^{\circ}\text{C}$) (max-min)	40.1	Gabrielsen et al. 1988, 1991
Flesh thermal conductivity ($\text{W}/\text{m}^{\circ}\text{C}$)	0.5	Cheng and Plewes 2002
Oxygen extraction efficiency (%)	35	Hainsworth 1981, Arens and Cooper 2005
Digestive efficiency (%)	80	Wiens & Scott 1975, Harding unpublished data
Skin wet (%)	1	Meadows et al. unpublished data
Core temperature - Skin temperature ($^{\circ}\text{C}$)	0.1	Porter et al. unpublished data
Exhaled air Temperature - Local air Temperature ($^{\circ}\text{C}$)	2	Porter et al. 2000
Bird density (kg m^{-3})	932.9	Porter et al. 2006, Meadows et al. unpublished data
Flight metabolism (W)	10.57	Pennycook 1989, Fort et al. 2009, Harding unpublished data
Behavioural properties		
Ventral area contacting substrate (%)	25	Fort et al. in press
Flight speed (m s^{-1})	13.0	Nettleship and Birhead 1985
Dive depth (m)	3.3	This study
Flight altitude (m)	5	Gaston 2004
Proportion of time spent flying per day (%)	12	our estimate based on Fort et al. unpublished, Harding et al. 2009
Proportion of time spent diving per day (%)	17	This study
Diet		
% lipids	45%	Davis 1993
% proteins	45%	Davis 1993
% carbohydrates	1%	Davis 1993
Climate data		
Sea surface temperature ($^{\circ}\text{C}$)	1.33	*
Air temperature ($^{\circ}\text{C}$)	-10.3 - +1.5	*
Relative humidity (%)	63.6 - 93.2	*
Wind speed (m s^{-1})	2.0 - 17.5	*
Cloud cover (%)	0 - 100	*

* ICOADS data provided by NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, (<http://www.cdc.noaa.gov/>)

Table 3.A.2 (continued) Electronic Supplementary Material 1.

- Arens, J. R. & Cooper, S. J. 2005 Seasonal and diurnal variation in metabolism and ventilation in House Sparrows *Passer domesticus*. *Condor* **107**, 433-444
- Cheng, H. L. M. & Plewes, D. B. 2002 Tissue thermal conductivity by magnetic resonance thermometry and focused ultrasound heating. *J. Mag. Res. Imaging*. **16**, 598-609
- Davis, N. D. 1993 Caloric content of oceanic zooplankton and fishes for studies of salmonid food habits and their ecologically related species. (NPAFC Doc.) FRI-UW-9312. Fisheries Research Institute, University of Washington, Seattle. 10pp.
- Fort J, Porter W. P. & Grémillet D. 2009 Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *J. Exp. Biol.* 112: 2483-2490
- Gabrielsen, G. W., Mehlum, F. & Karlsen, H. E. 1988 Thermoregulation in 4 species of Arctic seabirds. *J. Comp. Physiol. B*. **157**, 703-708
- Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M. & Mehlum, F. 1991 Field and laboratory metabolism and thermoregulation in Dovekies (*Alle alle*). *Auk* **108**, 71-78
- Gaston, A. J. 2004 Seabirds - a natural history. Yale University Press, London
- Hainsworth, F. R. 1981 Energy regulation in hummingbirds. *Am. Scient.* **69**, 420-429
- Harding, A. M. A., Egevang, C., Walkusz, W. Merkel, F., Blanc, S. & Grémillet, D. 2009 Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biol.* (doi: 10.1007/s00300-009-0581-x)
- Nettleship, D. N. & Birkhead, T. R. 1985 The Atlantic Alcidae - The evolution, distribution and biology of the auks inhabiting the atlantic ocean and adjacent water areas. Academic Press, London
- Pennyquick, C. J. 1989 Bird flight performance: a practical calculation manual. Oxford University Press, Oxford
- Porter, W. P., Budaraju, S., Stewart, W. E. & Ramankutty, N. 2000 Calculating climate effects on birds and mammals: Impacts on biodiversity, conservation, population parameters, and global community structure. *Am. Zool.* **40**, 597-630
- Porter, W. P. & Mitchell, J. W. 2006 Method and system for calculating the spatial-temporal effects of climate and other environmental conditions on animals. <http://www.patentstorm.us/patents/7155377-fulltext.html> (ed. U.P Office). Wisconsin Alumni Research Foundation, USA
- Wiens, J. A. & Scott, J. M. 1975 Model estimation of energy flow in Oregon coastal seabird populations. *Condor* **77**, 439-452

Chapitre 4

Dépense énergétique hivernale : impacts des conditions abiotiques sur la survie



Introduction du chapitre

Les mécanismes sous-jacents à la mortalité hivernale et aux échouages massifs d'oiseaux marins sont aujourd'hui encore peu étudiés et donc peu connus. Ces échouages représentent pourtant plusieurs centaines, voir milliers d'oiseaux retrouvés morts chaque année (Gaston 2004, Camphuysen *pers. com.*), et on estime que ces oiseaux récupérés ne représentent qu'une toute petite fraction de l'ensemble des oiseaux échoués. Au cours de l'hiver, les conditions climatiques de l'Atlantique Nord sont très difficiles pour les oiseaux pélagiques, avec de fréquents épisodes extrêmes. On sait aujourd'hui que ces conditions affectent le comportement des oiseaux (Grémillet et al. 2005a, Daunt et al. 2006, 2007) et qu'elles pourraient donc agir directement sur leur balance énergétique. Ainsi, nous avons voulu tester au cours de cette partie l'hypothèse suivante :

« Les conditions hivernales très difficiles perturbent négativement la balance énergétique des oiseaux, affectant ainsi leur survie. »

Pour tester cette hypothèse, nous avons étudié l'évolution de la dépense énergétique des oiseaux tout au long de la période hivernale, ainsi que l'influence des facteurs climatiques sur celle-ci. Les oiseaux étant inaccessibles pour les mesures traditionnelles de dépense énergétique en hiver, nous avons utilisé une approche de modélisation permettant ce type d'étude lorsque peu de données de terrain sont disponibles et sans avoir à observer ou à manipuler l'oiseau. Cette partie est elle-même constituée de deux sous-parties.

Tout d'abord, un premier article s'attache à faire un état des lieux des différentes approches de modélisation disponibles qui permettent d'étudier la dépense énergétique chez les oiseaux marins. Il nous permet de comparer ces différentes approches, leur utilisation et leur niveau de précision, afin de mettre en évidence quelle est la plus adéquate dans notre situation.

Dans un deuxième temps, nous avons utilisé un nouveau modèle thermodynamique (Niche Mapper™, voir chapitre 2) afin d'estimer la dépense énergétique de deux espèces d'alcidés (le mergule nain et le guillemot de Brünnich) hivernant en Atlantique nord-ouest.

Energetic modelling: a comparison of the different approaches used in seabirds.

Jérôme Fort, Warren P. Porter & David Grémillet

Abstract

Studying energetics of marine top predators is essential to understand their role within food-webs and mechanisms associated with their survival and population dynamics. Several methods exist to estimate energy expenditure in captive and free-ranging animals. However, most of them are difficult to implement, restrained to specific periods, and are consequently inappropriate for seabirds. Supplementary and complementary approaches are therefore needed, and the use of modelling appears as an excellent option allowing energetic studies when field data collection is challenging. Currently three main energetics models are used, with various degrees of complexity and accuracy: allometric equations, time-energy-budget analyses and thermodynamic models. However, a comparison of their practicability and accuracy was still lacking. Here, we present an overview of these 3 model types, their characteristics, advantages and disadvantages, and areas of application in seabirds. We then investigate their accuracy by using them in parallel for the same dataset, and by comparing outputs with direct measurements (doubly-labelled water technique). We show that, when detailed data are available, time-energy-budget analysis is the best model to accurately predict seabird energy expenditures. Conversely, thermodynamic modelling allows reasonably accurate calculations when field data are scarce, and is therefore ideal to study energetics during the inter-breeding season.

Keywords: Allometric equations, Bioenergetics, Doubly-Labelled Water technique, Seabirds, Thermodynamics modelling, Time-budget analysis

B-1. Introduction

Bird energetics are studied to gain a better understanding of how they maintain their energy balance, survive and reproduce. More specifically, there are three good reasons to investigate avian energetics and those of other homeothermic animals. (1) From an ecophysiological perspective, energy expenditure and energy balance allow a rating of current morphological, physiological, and behavioural features, and how animals employ these features to optimise their energy budgets (Le Maho 2002). (2) From an evolutionary perspective, energetics can be used to rate the impact of phenotypic plasticity and microevolution on morphological, physiological, and behavioural traits, whereby natural selection tends to optimise energy balance to improve fitness (Rezende et al 2004). (3) Finally, from an ecological perspective, energetics allow calculation of food requirements, and an assessment of the role of birds within food webs (Brown et al 2004). This is essential as birds often operate at the apex of trophic networks, where they exert top-down control onto lower trophic levels and/or react to bottom-up forcing. They therefore potentially function as ecological indicators, and detailed knowledge of their energetics enables a functional approach to avian ecology, testing for relationships between environment constraints (e.g. climate change), food web characteristics (e.g. resilience), and bird responses affecting their energy balance (Einoder 2009).

Energetics are highly attractive in ecology because they employ one single currency (energy, expressed in Joules; J) to investigate and evaluate an infinity of processes, thereby providing a unifying approach and a powerful tool for comparative work and ecological synthesis (McNab 2002). This tool is equally valid to investigate the ecology of individuals, populations, species and communities at any spatio-temporal scale.

While interest in animal energetics dates as far back as Da Vinci and Lavoisier, it is the advent of thermodynamics in the 19th century (e.g. the work of James Joule) and technological developments of gas sensors, stable isotopes dosages, and electronics following the second world war that led the way to systematic investigations of energy expenditure in animals. Measurements were initially conducted under controlled conditions in the laboratory, but from the 1950s pioneers such as Knut Schmidt-Nielsen took physiology ‘into the field’ (Schmidt-Nielsen 1998). Miniaturisation of laboratory tools has been ongoing ever since, allowing measurement of an increasing number of parameters on an increasing number of (smaller) free-ranging species (Ropert-Coudert & Wilson 2005).

Technically, there are seven main approaches to assessing energy requirements in birds. We briefly mention these possibilities, most of them being subject to in-depth reviews in other

contributions to this special issue (Halsey 2010). (1) Automatic weighing of individuals at the nest before and after feeding allows quantifying food intake (e.g. Grémillet et al 1996). Subsequently, knowledge of the calorific value of the food and of the assimilation efficiency of the animal studied enables calculation of the energy equivalent (J) of the ingested food mass. (2) The doubly-labeled water (DLW) technique i.e. stable isotope injections and dosages also allow estimating energy expenditure (see Speakman 1997, Harding et al. 2009a). (3) Heart rate recordings of free-ranging animals can be used as an index of energy expenditure. Calibration curves of relationships between heart rate and oxygen consumption during different types of activities are then required to calculate the overall energy consumption of the animal during a given time period (Bevan et al 1994). (4) Similarly to the heart-rate method, overall dynamic body acceleration (OBDA, sensu Wilson et al 2006) can be used as a proxy for energy consumption in free-ranging animals. Converting OBDA to Joules also requires calibrating this variable versus a direct measurement such as oxygen consumption. (5) Time-energy budgets can be programmed to estimate energy requirements. They are typically compiled using measurements of the energetic costs of specific activities per unit time (for instance through respirometry studies of oxygen consumption), and of a detailed time budget stipulating the duration of each activity (Kendeigh et al 1977, Kooijman 2000). (6) Allometric equations serve the same purpose, while being based upon previous measurements of energy requirements in a large number of bird species relative to their body mass (Nagy 2005). (7) Finally, thermodynamic modelling uses the first principles of physics to perform theoretical calculations upon the energy requirements of birds of given shape, mass, and insulation within a specific abiotic environment (Fort et al 2009).

All techniques mentioned here have been applied to seabirds. Early studies performed in the 1950s and 1960s (Uspenski 1956 and Belopolskii 1961, quoted in Furness 1978) were based upon direct investigations of prey consumption. The 1970s saw the rise of the bioenergetics approach (sensu Kendeigh et al 1977), with an increasing number of publications addressing the energy requirements of seabirds using allometric equations and time-energy budgets. More technologically-refined investigations using the doubly-labelled water technique, respirometry and heart-rate measurements followed in the 1980s and the 1990s (e.g. Butler & Woakes 1984, Nagy et al 1984), and the adequacy of the OBDA is currently being evaluated (Halsey et al. 2009). The majority of energetics studies performed so far in seabirds were species-specific; only few considered processes occurring at the population and community level (e.g. Wiens & Scott 1975, Furness 1978, Grandgeorge et al. 2008).

Obviously these different techniques all have strengths and weaknesses. Direct measurements using automatic weighing, the DLW method, or respirometry are the most accurate, but they can only be performed under well-defined conditions (Grémillet et al. 2000a). For instance automatic weighing only works when birds are breeding, or at least affiliated to a specific perch. DLW investigations require catching and retrapping birds within a limited time period of a few hours to a few days, and costly analyses potentially limit sample sizes. In the case of respirometry, measurements can rarely be performed in free-living individuals (but see Brown & Adams 1984), and birds have to be investigated in captivity, which may introduce additional biases due to increased stress levels and lower flight muscle mass (McKechnie et al 2006). Therefore, whereas these measurements are routinely employed to determine the energy requirements of birds during specific activities and for specific time periods, general assessments of seabird energetics over the annual cycle, at the population and community level are rather conducted using the heart rate method (Green et al. 2009) and/or energetics modelling. Modelling exercises so far applied to seabirds were based upon time-energy budgets and/or the use of allometric equations. These calculations had varied levels of complexity/accuracy. The highest accuracy was reached when a complete time budget was available, and when the costs of virtually all activities had been determined via direct measurements as mentioned above (e.g. Grémillet et al 2003). However, such an approach is extremely time- and cost intensive, and a balance has to be found between model complexity and the accuracy of the final output (Burnham & Anderson 2002).

Moreover, many seabirds spend a large proportion (up to >90% of their time) offshore, where they are difficult, or even impossible to study directly. Hence the type of modelling approach might also be strongly conditioned by the amount of information available for a given species and time period. This is very much the case for pelagic seabirds during the winter phase. Indeed, their distribution zones, movements, and behavioural patterns are often totally unknown, and/or are currently being investigated using miniaturised electronic tags, stable isotopic and genetic analyses (e.g. Ramos et al 2009). This is unfortunate since the winter energetics of seabirds largely condition adult survival rates, which is the most important parameter shaping population dynamics (Lebreton et al 1992).

In this context thermodynamic modelling has been specifically designed to study the energetics of birds when very limited/no information is available beyond their morphological properties (Fort et al 2009). This method has so far been employed to predict the energy requirements of little auks (*Alle alle*) and Brünnichs guillemots (*Uria lomvia*) wintering in the

northwest Atlantic (Fort et al 2009). However, a comparative approach with some of the other approaches mentioned above was still lacking.

The objective of the paper is consequently to use thermodynamics modelling, conventional time-energy-budget analysis, allometric equations, and a direct measurement of energy expenditure (using the DLW method) to determine energy requirements of a wintering seabird, the great cormorant *Phalacrocorax carbo*, and to compare the practicability and the accuracy of these different methods.

B-2. Overview of the modelling approaches used to estimate energy expenditures in seabirds.

1) Allometric equations

This method being reviewed in-depth in another paper of this special issue, we will not investigate it in details (see White, this issue). Requiring very limited field data and general information on individuals and their environment, this modelling approach is the most frequently used to estimate energy expenditures in seabirds. Of convenient use, it allowed scientific investigations in a wide range of fields referring to seabird energetics and ecology, including comparative analyses (e.g. Wanless et al. 1998, Hunt et al. 2005, Grandgeorge et al. 2008).

Advantages of this method:

As stated above, allometric equations are based upon previous measurements of energy expenditure in relation to seabird body mass across many species (Ellis & Gabrielsen 2002, Nagy 2005). Now well-calibrated, these equations allow calculations of energy expenditure for any seabird species/individual, provided its body mass is known. This parameter being available for a majority of species, it allows calculations for any seabird, even when other field data are scarce or absent.

Disadvantages of this method:

General allometric equations specific to seabirds have been defined (Ellis & Gabrielsen 2002, Nagy 2005) as well as sub-equations for the different seabird orders (Charadriiformes, Pelecaniformes, Procellariiformes and Sphenisciformes; Ellis & Gabrielsen 2002). However, the relatively large sample size necessary to run these analyses, as well as the low intra-specific variations in individual body mass and energy expenditures, precluded the establishment of species-specific allometric equations. Therefore, the use of this method to estimate energy expenditure in a particular species which was not included in the overall sample may strongly affect the accuracy of the results (see below, Fig. 4.B.1). It is particularly true for species for which the relationship between body mass and energy expenditure is unusual. This is the case in seabirds with extremely high flight-associated costs compared to their body mass. For instance the alcids have a low wing area / body mass ratio compared to other seabirds (Pennycuick 1987), resulting in a continuous wing-flapping flight and thus in high flight costs. In the case of alcids, the use of allometric equations can therefore result in a significant under-estimation of overall energy expenditures.

Moreover, all allometric equations have been established for breeding birds. The relationship between seabird energetics and body mass is largely unknown during the inter-breeding period, as well as its potential intra-individual variability across seasons. Therefore, these allometric equations can only be accurately used in breeding birds, excluding any study during the inter-breeding season, a crucial period for seabird survival (Daunt et al. 2006, Rolland 2009).

Thirdly, it is now established that different environmental parameters such as wind speed (Daunt et al 2006), air temperatures (Fort et al. 2009), water temperatures and dive depths (Enstipp et al. 2006) strongly affect seabird energetics. By focusing on bird body mass, allometric equations do not integrate these environmental conditions, thereby weakening the accuracy of obtained results.

2) Time-energy-budget analysis

This modelling approach integrates two major components to reach its goal: the precise time-budget of the animal (i.e. the time devoted to different activities) as well as the energy expenditures associated with each activity. These two sets of parameters allow the calculation

of global energy expenditures, and therefore of the Field Metabolic Rate (FMR) of the animal for a defined period, following the general equation:

$$\sum_{k=1}^n \% \text{ time to activity } k \times \text{metabolism of } k$$

Beyond this simple equation some basic parameters affecting energy expenditures may also be integrated into the model. They will increase the accuracy of each activity-specific metabolism for a particular individual/context, and therefore improve the global accuracy of the model. In seabirds, such parameters may be individual body mass, bird status (breeding, non-breeding, incubating, chick-rearing) and brood size (e.g. Phillips et al. 1999). Climatic factors such as water temperature may also be considered since they can significantly modify avian energy expenditure, especially for polar versus temperate species (Grémillet et al. 2003). Standard input parameters used in time-energy-budgets are summarized in Table 4.B.1.

Seabirds can perform a wide variety of behaviours with high inter-individual and temporal variability, such as social, reproductive, parental care, or foraging behaviours. Knowledge of the complete and precise time-budget of any seabird is therefore nearly impossible due to this variety of existing activities. Nevertheless, and to simplify the models, 4 principal behavioural patterns are generally considered in time-energy-budget analyses: flying, diving, swimming and resting. Indeed, they make the bulk of a seabird's time-budget, and are assumed to be the only activities significantly affecting their energetics (e.g. Grémillet et al. 2000a, Tremblay et al. 2003). The energetic costs of most of these activities can be accurately measured via respirometry using captive and semi-captive individuals (Gabrielsen et al. 1988, Pennycuick et al. 1990, Enstipp et al. 2006). However, direct measurements of flight costs remains an extremely challenging task in large birds (Ward et al. 2002), and usually such costs are estimated using the Pennycuick Model (Pennycuick 1989).

This method was essentially used in seabirds to estimate their food requirements and their putative prey intake rates during different phases of the annual cycle (e.g., Grémillet et al. 1995, Grémillet et al. 2003, Votier et al. 2004) and therefore to understand their potential impact on prey stocks and their role within marine food webs. The ultimate objective of these

Table 4.B.1 Summary of the input parameters used by the 3 different models.

	Allometric equations	Time-energy-budget analysis	Thermodynamics modelling (Niche Mapper™)
Morphological parameters			
Body mass (kg) (max - min)	x	x	x
Plumage depth (mm) (dorsal - ventral)			x
Plumage reflectivity (%) (dorsal - ventral)			x
Feather length (mm) (dorsal - ventral)			x
Feather diameter (µm) (dorsal - ventral)			x
Wing span (m)			x
Wing area (cm ²)			x
Physiological parameters			
Body core temperature (°C) (max-min)			x
Flesh thermal conductivity (W/m°C)			x
Oxygen extraction efficiency (%)			x
Skin wet (%)			x
Exhaled air Temperature - Local air Temperature (°C)			x
Bird density (kg m ⁻³)			x
Dive metabolism (W)		x	
Resting metabolism (W)		x	
Flight metabolism (W)		x	x
Behavioural parameters			
Ventral area contacting substrate (%)			x
Flight speed (m s ⁻¹)			x
Swim speed (m s ⁻¹)		x	
Dive depth (m)		x	x
Flight altitude (m)			x
Time flying per day (% or min d ⁻¹)		x	x
Time diving per day (% or min d ⁻¹)		x	x
Time wing-spreading per day (% or min d ⁻¹)		x	
Time resting at night (% or min d ⁻¹)		x	x
Time resting in daytime (% or min d ⁻¹)		x	x
Total activities per day (min)		x	
Dive / pause ratio		x	
Bird status		x	
Brood size		x	
Climate parameters			
Sea surface temperature (°C)		x	x
Air temperature (°C)			x
Relative humidity (°C)			x
Wind speed (m s ⁻¹)			x
Cloud cover (%)			x
Latitude/Longitude			x

studies was also to foresee the consequences of the tri-interaction between fisheries, seabirds and prey stocks (Bunce 2001). Calculations of energy expenditures during the breeding season also permitted a better understanding of how parental foraging strategies and parental investment affect reproductive success (Gaston 1985; Houston et al. 1996).

To our knowledge, only one study used the time-energy-budget approach in a seabird outside of the breeding season (Grémillet et al. 2005a). It allowed first investigations of seabird energy expenditure throughout the winter period. These data, combined with behavioural and physiological information, permitted a better understanding of the potential adaptations of seabirds to winter conditions allowing adult survival.

Advantages of this method:

One of the greatest advantages of this method is that it does not need to take into account the specific environmental conditions to which birds are exposed to estimate its energy expenditure. This implies that researchers do not need to know where the bird is actually located. Another advantage is the great precision of this method which is nonetheless conditioned by the quality of behavioural and energetics input data (Kendeigh et al 1977).

Disadvantages of this method:

Exclusively based on known animal behavioural patterns, the principal disadvantage of this method is its limitation to periods during which the complete time-budget of the studied animal can be accurately determined. In seabirds, this period is mostly restricted to the breeding season during which they can be observed directly at the nest and/or fitted with data loggers due to record their time-budgets at sea (e.g. Tremblay et al. 2003). Conversely, it is extremely challenging to use time-energy-budgets to investigate seabird energetics during the inter-breeding season.

Nevertheless, it is important to note that the use of new technologies such as Time Depth Recorders (TDR) and heart rate recorders now bring accurate information about bird behaviour outside the breeding season and do allow this type of calculations in single, intensively-studied species (Grémillet et al. 2005a, Green et al. 2005, Green et al. 2009). These studies nonetheless remain scarce due to logistic constraints.

3) Thermodynamics modelling

Based on the first principles of thermodynamics, this approach allows an estimation of the metabolic rate necessary to an animal to maintain its homeothermic steady-state in a given environment. Recently, a new state-of-the-art model called NicheMapper™ has been developed (Porter & Mitchell 2006) and used with success in a variety of vertebrates for a large range of environmental contexts (Porter et al., 1994; Porter et al., 2000; Porter et al., 2006; Kearney and Porter, 2004; Kearney et al., 2008). Combining 2 sub-models (a climate and an animal model), NicheMapper™ integrates climate data as well as various morphological, physiological and behavioural animal parameters to solve a coupled system of mass and heat transfers between the organism and its environment. It thus allows calculation of metabolic energy and other animal-dependent requirements (such as water and food requirements) allowing it to maintain thermoneutrality, energy balance, and thereby self-maintenance and survival in a given environment.

The coupled heat and mass balance equations for the animal/environment exchanges, the digestive and respiratory systems are:

$$\text{Heat balance (W): } Q_{in} + Q_{gen} = Q_{out} + Q_{st}$$

$$\text{Mass balance (g/d): } m_{in} = m_{out} + m_{st}$$

Where Q_{in} is heat input (sum of absorbed incoming solar and infrared radiation reaching the skin), Q_{gen} is heat produced (by all body tissues), Q_{out} depicts heat loss (by air convection, respiration, infrared radiation emitted through the porous feathers, and conduction to the air and water) and Q_{st} is the stored heat (due to body temperature rising or falling). m_{in} depicts the mass input (food entering the gut or air entering the respiratory system), m_{out} is the mass lost (faeces or exhaled air), and m_{st} is the mass stored or absorbed (i.e. the food mass that must be absorbed by the gut, given the food type and properties, to meet daily energy demand).

This model is described in details in Porter & Mitchell (2006), Porter et al. (2006), and Fort et al. (2009). The different input parameters necessary for running NicheMapper™ are summarized in Table 4.B.1. Compared to the 2 previous modelling approaches, NicheMapper™ is sophisticated and therefore appears parameter-hungry. However, all of them can be easily obtained: any climate data is freely available from weather stations or from

the Internet (e.g. ICOADS data: <http://www.cdc.noaa.gov/>), while most required physiological and morphological data for any organism are readily accessible from the literature. Morphological properties and plumage characteristics assumed stable in each species can also be easily measured from a limited number of museum specimens. Behavioural data are often more difficult to obtain since animal time-budgets can be highly variable between individuals and through the different periods of their life cycle. However, the time-budget is not a central parameter of the thermodynamics model calculations and can therefore be estimated from the literature or from measurements conducted during the breeding season (Fort et al. 2009). Moreover, technologies such as time-depth recorders, accelerometers and/or on-board cameras allow these recordings (e.g. Wilson et al. 2006; Green et al. 2006; Watanuki et al. 2008) and seabird behaviour during the mysterious inter-breeding period is bound to be intensively studied during the next few years.

NicheMapper™ was recently validated in seabirds and is currently being used to investigate different research fields. For example, by calculating energy expenditures of animals under various climatic conditions, this model can be used to highlight how the environment can affect bird energy balance. Using these possibilities, Fort and colleagues (2009) identified an energetic bottleneck for North Atlantic seabirds toward the end of the year, which might explain recurrent events of winter mass mortality observed in some species. Moreover, by predicting energy demand, NicheMapper™ allows calculation of food consumption for a known diet (e.g. Göktepe et al. 2009). It can therefore be used to investigate the associated intake of contaminants and their potential effect on seabird reproductive success and survival (e.g. Meadows et al. 2009).

Advantages of this method:

Using a majority of parameters available from the literature or readily measurable in museums, the thermodynamic model NicheMapper™ can be used when available field data are scarce. This point is particularly important in seabirds for which fieldwork and data collection both at sea and land-based are logistically impossible, resulting in a lack of measured data for some species and some seasons.

Therefore, and contrary to other modelling approaches, Niche Mapper™ presents the great advantage to allow daily investigations of seabird energetics for the entire year (provided climatic data are available, see Meadows et al. 2009) and therefore permits studies during the

inter-breeding period. Today, biotelemetry is the only alternative technique available to study inter-breeding energetics of seabirds (cf. Green et al. and Shepard et al. this issue). Extremely promising, biotelemetry remains nonetheless logistically difficult to implement and can be used only on larger species, thereby excluding energetic studies of the large majority of smaller (<1kg) seabirds.

Furthermore, a thermodynamic modelling approach offers a vast range of research possibilities in seabirds. Indeed, by including climate data, NicheMapper™ can infer the potential range of environmental conditions that does not allow a specific animal to maintain a positive energy balance and to survive, therefore drawing limits of its fundamental niche and grounds for which it will not survive. Applied to this end in amphibians (Kearney et al. 2008), mosquitoes (Kearney et al. 2009a) reptiles (Kearney et al. 2009b), land birds (Porter et al. 2006) or mammals (Natori & Porter 2007), this aspect of the model has nonetheless not been used in seabirds. Undeniably, such investigations are particularly important in the current context of climate change and all new research questions associated. It could indeed be a first way to predict the capacity of any seabird species to adapt to future environmental conditions, especially altered temperature ranges and food availabilities (review in Kearney & Porter 2009).

Disadvantages of this method:

As mentioned before, the time-budget of an animal appears to hold an important place in the definition of its energy expenditure, since costs associated with each behaviour are highly variable (Ellis & Gabrielsen 2002). During the breeding season, time-budgets of most seabirds have been extensively studied and are now well defined, allowing the use of NicheMapper™ with high accuracy. During the inter-breeding season, NicheMapper™ uses behavioural assumptions based on the measured breeding behaviour or on data from the literature. As for the two other approaches, results are therefore not as accurate during such a period as during the breeding season. However, and contrary to time-energy-budgets (see above), NicheMapper™ integrates numerous other parameters (Table 4.B.1), all playing an important role in animal thermoregulation and energy balance. Thereby, it reduces the importance of behavioural parameters in the model, as well as output errors resulting from these estimations.

B-3. Comparison of the different modelling approaches: does an increase in model complexity improve output accuracy?

Using an increasing number of parameters, researchers often increase the complexity of their models in an attempt to fit complex natural conditions. The three approaches described above correspond to this trend. Indeed, the initial method (allometric equations) was based on a single morphological parameter (body mass). Later on, the use of respirometry to measure activity-specific metabolic rates (e.g. Brown & Adams 1984, Culik et al. 1991) as well as the possibility to accurately investigate animal behaviour (Krebs & Davies 1981) allowed time-energy-budget modelling. Finally, the recent emergence of new technologies and the possibility to determine environmental conditions associated with bird geolocation lead to the emergence of the thermodynamic approach, integrating further physiological and morphological parameters, as well as climatic data (Table 4.B.1). These 3 methods are now commonly used to investigate seabird energetics and their implications for various aspects of their ecology (see above). Nevertheless, their respective accuracies have so far not been compared and the assumption that ‘an increase of the model complexity leads to an increase of the model accuracy’ still tends to rule.

To address this issue we tested each of these 3 approaches against the same empirical dataset. In 1994 and 1995, Keller and Visser (1999) measured the daily energy expenditure of wintering, free-ranging great cormorants (*Phalacrocorax carbo*) using DLW, as well as numerous morphological, physiological, behavioural and climate parameters. Here, we used these data measured in cormorants (Keller & Visser, 1999, complemented with unpublished data provided by T. Keller), and physiological data for great cormorants (Porter & Grémillet unpublished) to estimate their daily energy expenditure using the 3 modelling approaches detailed in the previous sections. We then compared results obtained from each method with ‘direct’ investigations using DLW, a method allowing accurate empirical results (Bevan et al. 1995, Sparling et al. 2008). Results from Keller & Visser (1999) were used since it was the only study in which all parameters necessary to run the 3 models were available, and where energy expenditure was also measured directly, therefore allowing interpretations.

Models derived from the allometric, time-energy-budget and thermodynamics approaches are numerous. Here, we used for each method the commonest model described in the literature:

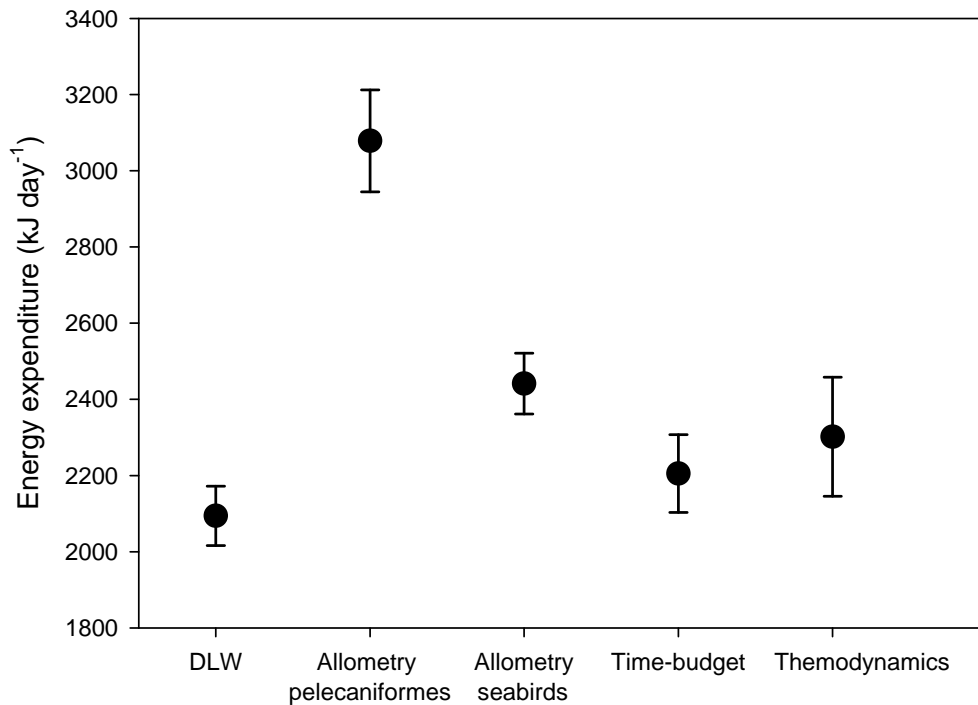


Fig. 4.B.1 Mean energy expenditures measured and predicted using DLW, allometric equations, time-budget analysis, and thermodynamic modelling. Standard deviations correspond to inter-individual variability ($n=5$).

Table 4.B.2 Empirical energy expenditures measured in 5 free-ranging great cormorants with the DLW method (Keller & Visser 1999) as well as theoretical values estimated using 3 modelling methods.

	DLW (Keller & Visser, 1999)	Allometric equation 'pelecaniformes'	Allometric equation 'seabirds'	Time-energy budget analysis	Thermodynamic modelling (Niche Mapper™)
Bird 1	2307	3273	2558	2353	2558
Bird 2	1927	3433	2651	2477	2737
Bird 3	2052	3135	2477	2247	2272
Bird 4	2244	2715	2224	1928	2060
Bird 5	1941	2837	2298	2020	1886
Mean	2094	3079	2441	2205	2302

- (1) For the allometric approach, the model generally used for seabirds is from Ellis & Gabrielsen (2002): $16.69 \times \text{mass}^{0.651}$. Here, we also used the equation established for pelecaniformes ($3.90 \times \text{mass}^{0.871}$) to test whether it can be used to accurately predict energy expenditure in a species excluded from the calibration analyses (Ellis & Gabrielsen 2002).
- (2) For the time-energy-budget analysis, we used a model presented and detailed in Grémillet et al. (2003). This algorithm can be downloaded from the website (<http://www.cefe.cnrs.fr/esp/DGremillet.htm>).
- (3) For the thermodynamics modelling, we used the new model Niche Mapper™, described in detail in Fort et al. (2009).

Energy expenditures estimated using each modelling approach are presented and compared with empirical results in Figure 4.B.1 and Table 4.B.2.

Overall, each modelling approach tends to overestimate seabird daily energy expenditures compared to DLW results (Table 4.B.2). Nevertheless, and for each general method, theoretical outputs are not significantly different from empirical results from the DLW study (DLW vs. Allometric equations: Mann-Whitney test, $U = 3.0$, $p = 0.06$; DLW vs. time-budget analysis: $U = 8.0$, $p = 0.42$; DLW vs. NicheMapper™: $U = 8.0$, $p = 0.42$). The specific allometric equation for pelecaniformes is the only method which significantly overestimate predicted expenditure ($U = 0.00$, $p = 0.008$). In that example, output values given by the time-energy-budget model are closer to the DLW results, with an average overestimation of 5.3%, followed by thermodynamic modelling with 9.9% overestimation, while allometric equations for seabirds and for pelecaniformes overestimated cormorant energy expenditures by 16.6% and 47.0%, respectively.

B-4. Conclusions

Interestingly, by comparing results obtained using the different approaches, we showed that, when sufficient data are available, time-energy-budgets provide the best prediction of energy expenditure in wintering great cormorants. These results are relative to one particular species within a specific context, and should therefore be considered with the required caution. Nonetheless, they demonstrate that a model does not necessarily become more accurate with an increase in the number of input variables.

Table 4.B.3 Summary of the advantages and disadvantages linked to each modelling approach for seabird energetic studies.

	Advantages	Disadvantages
Allometric equations	<ul style="list-style-type: none"> • Remains tractable when body mass is the only information available 	<ul style="list-style-type: none"> • Lack of accuracy when the studied species was not a part of the allometric analysis • Results have to be carefully interpreted when used outside of the breeding season
Time-energy-budgets	<ul style="list-style-type: none"> • Gives the more accurate results obtained from a modelling approach when accurate information is available for time-budgets and activity-specific metabolism 	<ul style="list-style-type: none"> • Often precludes an accurate analysis during the inter-breeding season even if new technologies recently developed might enhance future possibilities
Thermodynamic modelling (Niche Mapper™)	<ul style="list-style-type: none"> • Allows accurate energetic calculations when field data are scarce • Permits energetic studies at individual, population or community level, as well as at large temporal and spatial scales throughout the complete annual cycle including the crucial inter-breeding season 	<ul style="list-style-type: none"> • Requires numerous physiological, morphological and behavioural parameters as well as climate data which can nonetheless be obtained from the literature or measured in museum specimens

A majority of mathematical models applied to ecology tend to take into account as many parameters affecting output variables as possible, thereby seeking the closest-possible match with a natural situation. However, such an increase in the number of considered variables simultaneously accumulates the uncertainty associated to each one of them, and might thereby strongly increase the overall, cumulative variance of the model output. Our results indicate that future studies should probably rather define ‘intermediate’ models, balancing the number of key parameters with the level of additive noise.

A further modelling approach based on a dynamic system has been developed to study flows of matter and energy at an individual scale: the Dynamic Energy Budget (DEB) model (Kooijman 2000). Situated at the interface between allometry, time-energy-budgets and thermodynamic models, this approach investigates energy acquisition and its allocation to different life-history traits depending on the states of the organism and of its environment (Nisbet et al. 2000, Kooijman et al. 2008, Sousa et al. 2008). Based on estimated parameters,

it can therefore be used to estimate the global energy expenditures of an organism (Kooijman 2000). However, this detailed approach for which the quantification of thermodynamic parameters is demanding (Kooijman et al. 2008) has rarely been applied to vertebrates (van der Veer et al. 2001, 2003) and never to any endothermic animal. This approach has nonetheless to be developed in our context and compared to those already existing within the framework of future studies.

In conclusion, we showed that time-budget analyses may be given priority in seabird energetics studies. Nevertheless, in our example, all modelling approaches resulted in coherent values of predicted daily energy expenditures. Two approaches were within 10% of the direct measurements using the DLW method with the allometric equation specific to pelecaniformes having the greatest deviation from DLW data. Hence, no model should be systematically excluded. On the contrary, we have seen that each method is essential, and highly practicable in particular situations (see Table 4.B.3).

Acknowledgements

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Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic

Jérôme Fort, Warren P. Porter & David Grémillet

Abstract

Studying the energetics of marine top predators such as seabirds is essential to understand processes underlying adult winter survival and its impact on population dynamics. Winter survival is believed to be the single most important life-history trait in long-lived species but its determinants are largely unknown. Seabirds are inaccessible during this season, so conventional metabolic studies are extremely challenging and new approaches are needed. This paper describes and uses a state-of-the-art mechanistic model, Niche MapperTM, to predict energy expenditure and food requirements of the two main seabird species wintering in the northwest Atlantic. We found that energy demand increased throughout the winter phase in both species. Across this period, mean estimated daily energy requirements were 1306 kJ day⁻¹ for Brünnich's guillemots (*Uria lomvia*) and 430 kJ day⁻¹ for little auks (*Alle alle*) wintering off Greenland and Newfoundland. Mean estimated daily food requirements were 547 g wet food day⁻¹ for Brünnich's guillemots, and 289 g wet food day⁻¹ for little auks. For both species and both wintering sites, our model predicts a sharp increase in energy expenditure between November and December, primarily driven by climatic factors such as air temperature and wind speed. These findings strongly suggest the existence of an energetic bottleneck for North Atlantic seabirds towards the end of the year, a challenging energetic phase which might explain recurrent events of winter mass-mortality, so called 'seabird winter wrecks'. Our study therefore emphasizes the relevance of thermodynamics/biophysical modelling for investigating the energy balance of wintering marine top predators and its interplay with survival and population dynamics in the context of global change.

Keywords: alcids, bioenergetics, daily energy requirement, Niche MapperTM, winter wrecks

C-1. Introduction

The strong link between animal energetics and individual survival has been put forward in a variety of studies (Schmidt-Hempel and Wolf, 1988; Speakman and Racey, 1989; Hobbs, 1989; Golet et al., 1998; Golet et al., 2000). During reproduction, parental care such as offspring provisioning forces adults to spend energy at a high rate, potentially threatening their own survival (Dijkstra et al., 1990; Golet et al., 2000). In temperate and polar species, the winter phase can be equally challenging. Here post-breeding individuals face extreme weather conditions with high wind speeds, elevated relative humidity, low air and water temperatures, as well as shorter days (Møller et al., 2006; Rey et al., 2007). Such environmental conditions have a profound effect on winter survival, indirectly affect future reproductive performance and ultimately shape population dynamics (Mysterud et al., 2001; Stenseth et al., 2002; Barbraud and Weimerskirch, 2003; Grosbois and Thompson, 2005; Daunt et al., 2006).

Seabirds occupy a pivotal role as top predators within marine ecosystems, but the interplay of winter environmental conditions, seabird energetics and winter survival remains largely unknown. Several techniques are available to study energy requirements and prey intake rates in free-ranging seabirds. They essentially consist of (1) daily food intake measurements using stomach content or pellet analysis (Duffy and Jackson, 1986), (2) time–energy budget analysis (Furness, 1978; Furness, 1990; Grémillet et al., 2003), (3) assessment of food intake rates *via* stomach temperature measurements (Wilson et al., 1995a), (4) automatic weighing (Grémillet et al., 1996), and (5) biotelemetry studies using miniaturized recorders such as heart rate data loggers or accelerometers to measure energy expenditure (Wilson et al., 2006; Green et al., 2009). However, most of these techniques are inappropriate for estimating the energy needs of wintering seabirds, as birds spend this period offshore, where they are virtually inaccessible. Others are logistically extremely difficult to set up. For example, biotelemetry studies require surgery and recapture of the equipped birds and are currently only possible in large seabird species. Overall, very few studies have investigated seabird winter energy requirements (Wiens and Scott, 1975; Grémillet et al., 2003; Green et al., 2009).

To solve this problem and to be able to investigate wintering energetics of marine top predators such as seabirds, a complementary and alternative method is required. We propose the use of a new spatially and temporally explicit model, Niche MapperTM (for details, see Porter and Mitchell, 2006; Kearney et al., 2009). This model allows energy balance calculations using the characteristics of the animals and their environment and is particularly

suitable for situations where field data are scarce. Niche MapperTM is based on the first principles of thermodynamics and on the physiological and behavioural responses of individual organisms to their environment. This refined model has been successfully employed to estimate the energy requirements of representative amphibians, reptiles, birds and mammals living in a variety of ecological contexts (e.g. Kearney et al., 2008; Mitchell et al., 2008; Porter et al., 2006; Natori and Porter, 2007). To date, however, it has not been deployed within marine ecosystems.

We applied Niche MapperTM to the study of little auks (*Alle alle* L.) and Brünnich's guillemots (*Uria lomvia* L.), which are the smallest and the largest extant alcid species living in the North Atlantic, respectively. These diving seabirds from Arctic waters are components of simple food webs. They are particularly sensitive to changes occurring at low trophic levels (Nettleship and Birkhead, 1985; Gaston and Jones, 1998) and are outstanding candidates as ecological sentinels of global change (Gjerdrum et al., 2003). They are among the most abundant seabird species in the northern hemisphere and on a worldwide scale [little auk and Brünnich's guillemot population size is estimated to be >80 million and 20 million breeding individuals, respectively (Gaston and Jones, 1998; Kampp et al., 2000; Isaksen and Gavrilo, 2000; Egevang et al., 2003). Hence, they play an important role within arctic marine ecological processes, notably in terms of energy transfer. Indeed, the Brünnich's guillemot population is the third largest seabird prey consumer worldwide (Brooke, 2004) whilst the North Water Polynya little auk population is responsible for 92–96% of the carbon flux to seabirds in that region (Karnovsky and Hunt, 2002). However, these two species are confronted with a high winter mortality, especially during events called ‘winter wrecks’, in which large numbers of seabirds cast ashore and/or are found dead inland (Gaston, 2004). The factors responsible for these wrecks are unknown and we considered it important to have a better understanding of the potential underlying mechanisms for this winter mortality.

Therefore, the aims of this study were (1) to highlight a new modelling approach for studying the energy balance of wintering aquatic top predators, and (2) to study the energy balance of two key species and investigate how energetic requirements potentially impact on winter survival. We hypothesize that winter conditions critically challenge the energy balance of alcids wintering in the northwest Atlantic, therefore negatively affecting their survival. To accomplish these goals we calculated little auks' and Brünnich's guillemots' energy

requirements and food needs during the winter off southwest Greenland and Newfoundland using Niche Mapper™.

C-2. Materials and Methods

Study sites and period

Energy requirements and food needs were estimated for birds wintering in two areas (Fig. 4.C.1) with different environmental conditions, therefore potentially affecting their energy balance. These two areas are part of the most important wintering sites for little auks and Brünnich's guillemots (Brown, 1985; Boertmann et al., 2004). The first is situated off southwest Greenland (63–65°N, 53–55°W), while the second stretches along the northeast coast of Newfoundland (50–52°N, 52–54°W).

We defined ‘winter’ as the inter-breeding period extending from September 1st to March 1st [the latter date corresponding to the start of the spring migration towards the breeding areas (Nettleship and Birkhead, 1985)]. During this period, adults of both species are assumed to require energy only for their own maintenance. We used climate data for the winter of 2004/2005, and all modelling was consequently performed for the time period between September 1st 2004 and March 1st 2005.

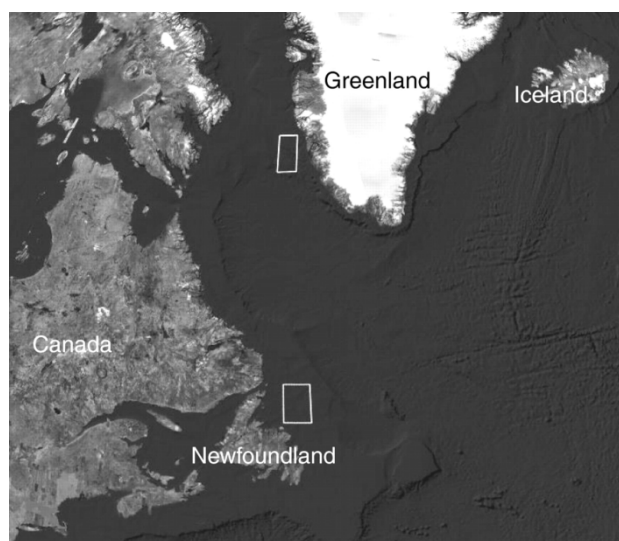


Fig. 4.C.1 Map of the two study sites off Greenland and off Newfoundland.

Niche MapperTM model

Niche MapperTM (US Patent 7,155,377B2; wporter@wisc.edu) integrates two different sub-models to investigate individual energy balance: a microclimate model and an endotherm model (see below).

Climate model and climate input data

We used the latest version of the microclimate model (Micro2006c) described by Porter and colleagues (Porter et al., 2000; Porter et al., 2006; Kearney and Porter, 2004). The microclimate model uses calculated maximum and minimum shade and sunlight conditions for each location to subsequently compute the locally available coolest and hottest microhabitats for each hour of the day. Instead of using solid substrates, this climate model was modified to calculate local microclimates from 2 m above to 2 m below the water surface using a turbulent velocity profile above the surface and the temperature-dependent and solar and infrared radiation properties of salt water. Despite turbulent mixing of oceanic surface waters, birds might encounter different water temperatures when diving through the water column (e.g. Takahashi et al., 2008). However, as a sensitivity analysis (see below; Table 4.C.4) showed that the range of water temperatures naturally encountered by the birds does not radically affect their energy expenditure, we considered water temperature to be constant across the birds' diving range (Table 4.C.2).

All climatic and environmental input values used in this model were ICOADS data provided by NOAA/OAR/ESRL PSD (Boulder, CO, USA; <http://www.cdc.noaa.gov/>) (Table 4.C.1).

Endotherm model and input data

We used an updated version (Endo2007d) of the endotherm model originally developed by Porter and Gates (Porter and Gates, 1969), upgraded and modified substantially by Porter and Mitchell (Porter and Mitchell, 2006) and described in Porter et al. (Porter et al., 2006). This endotherm model uses local environmental parameters generated by the microclimate model (see above), as well as morphological, physiological and behavioural characteristics of the animal. The model solves the coupled heat and mass balance equations for the animal–environment exchanges, and the digestive and respiratory system:

Table 4.C.1 Climate data used for modelling daily energy requirements of Brünnich's guillemots and little auks off Greenland and Newfoundland between September 2004 and March 2005.

	Year	Month	Air temperature (°C)		SST (°C)		Relative humidity (%)		Scalar wind speed (ms ⁻¹)		Cloud cover (%)	
			Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Newfoundland	2004	September	11.3	6.6	12.1	8.0	88.0	66.6	12.4	5.3	100	0
	2004	October	11.5	2.0	9.5	4.4	100.0	76.7	20.6	0.0	100	0
	2004	November	10.0	-1.5	5.9	1.6	100.0	83.4	18.4	3.6	100	0
	2004	December	5.3	-10.5	5.0	0.1	99.7	70.4	17.3	4.1	100	0
	2005	January	4.9	-7.0	0.3	-1.3	98.8	88.4	19.9	8.0	100	0
Greenland	2005	February	0.9	-9.0	-0.1	-1.5	98.6	66.4	13.9	5.9	100	0
	2005	March	0.4	-5.9	-1.6	-1.6	96.0	71.1	15.3	7.3	100	0
	2004	September	6.4	4.0	6.3	4.3	83.8	75.5	14.2	4.8	100	0
	2004	October	5.5	0.0	4.3	1.9	97.2	68.6	16.0	4.0	100	0
	2004	November	3.5	-0.3	4.5	1.7	89.8	74.2	12.1	2.4	100	0
	2004	December	-5.7	-9.9	2.3	-1.2	64.8	64.4	8.6	6.4	100	0
	2005	January	1.5	-10.3	4.0	-1.3	93.2	63.6	17.5	2.0	100	0
	2005	February	-0.6	-10.7	0.9	-1.3	95.3	55.0	14.0	6.0	100	0
	2005	March	3.2	-4.6	0.1	-1.3	69.1	69.1	12.7	8.0	100	0

For each parameter [air temperature, sea surface temperature (SST), relative humidity, scalar wind speed and cloud cover], maximum and minimum monthly values are taken into account by Niche Mapper™ (ICOADS data provided by NOAA/OAR/ESRL PSD, Boulder, CO, USA; <http://www.cdc.noaa.gov/>).

Table 4.C.2 Parameters used in the energetic model for both alcid species.

	Brünnich's guillemot	Little auk	References
Morphological properties			
Body mass (max.–min.) (kg)	0.75–1.00	0.14–0.17	Schreiber and Burger, 2002
Plumage depth (dorsal–ventral) (mm)	5.6–16.0	7.4–12.8	This study
Plumage reflectivity (dorsal–ventral) (%)	38.0–74.4	40.4–65.0	This study
Feather length (dorsal–ventral) (mm)	32.4–25.0	20.0–19.2	This study
Feather diameter (dorsal–ventral) (µm)	33.0–33.0	33.0–33.0	This study
Wing span (m)	0.72	0.39	Croll et al., 1991; Elliot and Gaston, 2005, A. M. A. Harding, unpublished
Wing area (cm ²)	550	180	Croll et al., 1991; Elliot and Gaston, 2005, A. M. A. Harding, unpublished
Physiological properties			
Body core temperature (max.–min.) (°C)	39.6–40.3	40.1	Gabrielsen et al., 1988; Gabrielsen et al., 1991
Flesh thermal conductivity (W m ⁻¹ °C ⁻¹)	0.5	0.5	Cheng and Plewes, 1992
Oxygen extraction efficiency (%)	35	35	Hainsworth, 1981; Arens and Cooper, 2005
Digestive efficiency (%)	70	80	Wiens and Scott, 1975; Harding et al., 2009
Core temperature–skin temperature (°C)	0.1	0.1	W.P.P., unpublished
Exhaled air temperature–local air temperature (°C)	2	2	Porter et al., 2000
Bird density (kg m ⁻³)	932.9	932.9	Porter et al., 2006
Flight metabolism (W)	88.00	10.57	Pennycuik, 1989; A. M. A. Harding, unpublished; this study
Behavioural properties			
Ventral area contacting substrate (%)	25	25	This study
Flight speed (ms ⁻¹)	18.1	13.0	Nettleship and Birhead, 1985
Dive depth (m)	48.0	27.3	Falk et al., 2000; Mori et al., 2002
Flight altitude (m)	5	5	Gaston, 2004, see methods
Proportion of time spent flying per day (%)	7	7	Our estimate based on Falk et al., 2000; Falk et al., 2002; J.F., unpublished
Proportion of time spent diving per day (%)	17	17	Our estimate based on Falk et al., 2000; Falk et al., 2002; J.F., unpublished

$$\text{Heat balance (W): } Q_{in} + Q_{gen} = Q_{out} + Q_{st}$$

$$\text{Mass balance (g/d): } m_{in} = m_{out} + m_{st}$$

where Q_{in} is heat input (sum of absorbed incoming solar and infrared radiation reaching the skin), Q_{gen} is heat produced (by all body tissues), Q_{out} depicts heat loss (by air convection, respiration, infrared radiation emitted through the porous feathers, and conduction to the water) and Q_{st} is the stored heat (due to body temperature rising or falling); m_{in} is the mass input (food entering the gut or air entering the respiratory system), m_{out} is the mass lost (faeces or exhaled air) and m_{st} is the mass stored or absorbed (i.e. the food mass that must be absorbed by the gut, given the food type and properties, to meet the daily energy demand).

This endotherm model ultimately estimates daily energy and food requirements for an adult individual for the Julian day at the centre of each month throughout the winter period. However, the current version can accommodate daily simulations for the entire year, if sufficient climate data are available. Because Brünnich's guillemots and little auks are monomorphic and because males and females presumably seek the same wintering areas (Gaston and Jones, 1998) (J.F., unpublished), they face similar environmental conditions. We therefore assumed that energy requirements were the same for males and females in both species. Moreover, egg laying for both species usually occurs in the second half of June (Stempniewicz, 2001). We consequently assumed that the energy requirements and energy budget of females in March are still not affected by reproductive preparations.

Morphological properties

An ellipsoid body shape was assumed following Porter et al. (Porter et al., 2000). Plumage properties were measured on bird carcasses for five little auks and five Brünnich's guillemots from the Field Museum of Natural History in Chicago. All birds were from the northwest Atlantic waters and in winter plumage. Plumage depth, feather length, diameter and reflectivity were measured mid-dorsally and mid-ventrally for each species. The reflectivity was measured using a portable ASD spectrometer (Analytical Spectral Devices FieldSpec Pro ASD, Boulder, CO, USA) with grating-based optics, using a contact probe with a 10 nm resolution for all wavelengths between 350 and 2500 nm. This range covers approximately 97% of the solar spectrum that reaches the earth's surface. All morphological properties measured and used for this study are presented in Table 4.C.2.

Physiological properties

Physiological properties for both species are presented in Table 4.C.2. The effective flesh thermal conductivity was based on *in vivo* measurements of muscle tissue (Cheng and Plewes, 2002).

Resting metabolic rates were estimated using heat production required to maintain a body core temperature of 40.1°C for little auks (Gabrielsen et al., 1991) and between 39.6 and 40.3°C for Brünnich's guillemots (Gabrielsen et al., 1988) according to their morphological properties, the physical environment available to them, and their behavioural choices.

Water loss rates from the respiratory system were based on the calculated air volume passing through the lungs on a daily basis to meet metabolic demands. We assumed that the air was saturated with water vapour in the lungs at the average body temperature integrated radially from the core to the skin. Exhaled air was assumed to be 2°C warmer than local air temperature at each hour (Porter et al., 2000; Welch, 1980). The minimum core–skin temperature difference under which the bird could not dissipate the heat efficiently enough to maintain homeostasis was set at 0.1°C (Porter et al., 2000).

Flight costs were estimated for each species using Pennycuick's model and software Flight 1.18 (Pennycuick, 1989). We used default model parameters and different literature values (Table 4.C.2) for body mass, wingspan and wing area (Croll et al., 1991; Elliott and Gaston, 2005) (A. M. A. Harding, personal communication). For a body mass of 0.15 kg, little auk flight costs were estimated to be 10.57 W, whereas flight costs for a 1 kg Brünnich's guillemot were estimated to be 88 W. Variability of these flight costs linked to body mass variations of the birds during the winter period (Pennycuick, 1989; Croll et al., 1991) were taken into account by Niche MapperTM (see Porter and Mitchell, 2006).

Behavioural properties

Conduction, convection, evaporation, and solar and infrared radiation all affect heat loss, heat gain and energy expenditure. These processes are affected by the physical characteristics of the media surrounding the bird's body during its different activities (flying in air, diving under water or resting at the water surface). We therefore incorporated bird behavioural parameters (flying, diving and resting) into Niche MapperTM, as well as air and water temperatures, flight altitude, dive depth and flight speed. Winter time budgets (i.e. proportions of time spent

flying, diving and resting) were estimated using published data concerning breeding Brünnich's guillemots (Falk et al., 2000; Falk et al., 2002). According to this information, Brünnich's guillemots were assumed to spend 7% of the time flying, 17% of the time diving (submerged under water), and the rest of the time resting on the water surface. In the absence of any comparable behavioural information for little auks, we assumed that the proportion of time spent diving and flying was the same for the two species during the winter period (J.F., unpublished). The model takes into account the fact that the bird cannot dive and fly at the same time, and that birds resting at the water surface are one-quarter submerged. Most seabirds at sea remain less than 100 m above the sea surface in flight (Gaston, 2004). However, this altitude varies with weather and wind conditions. For wing flapping seabirds such as alcids, flying close to the sea surface is advantageous when wind speed is high. However, this is probably not the case during periods of little wind. As these variations are extremely difficult to consider in our model, we assumed that both species studied fly at an altitude of 5 m above the sea throughout the winter. In any case, pressure and temperature variations between 0 and 100 m are very low (pressure: 196 Pa difference at 0°C air and salt water temperature; vertical temperature: less than 2°C difference because of cloudy conditions, high winds, a turbulent velocity profile and sea surface evaporation (Tracy et al., 1980; Niche MapperTM)). Thus, we considered that neither variable significantly affected the birds' energetics. Both little auks and Brünnich's guillemots were assumed to be diurnal and crepuscular during winter, and also to stay inactive at the water surface during darkness (Birkhead and Nettleship, 1981; Gaston and Jones, 1998) (J.F., unpublished).

Diet

The relative proportions of different prey items within the diet of Brünnich's guillemot was estimated across the wintering season using published data (Elliot et al., 1990; Falk and Durinck, 1993; Rowe et al., 2000). This diet was composed of fish (capelin *Mallotus villosus* and cod *Gadus* spp.), squid, euphausiids and amphipods, in variable proportions.

There is little information about the winter diet of little auks, but Karnovsky and Hunt (Karnovsky and Hunt, 2002) found that post-breeding adults consume approximately 50% fish (juvenile Arctic cod *Boreogadus saida*) and 50% amphipods. This trend was confirmed by opportunistic winter observations (Stempniewicz, 2001). We consequently assumed that wintering little auks fed half on fish (Arctic cods) and half on amphipods. Nonetheless,

additional simulations using different ratios of cod/amphipods showed that energy density values for cod and amphipods are not different enough to significantly affect our results.

Protein, lipid and carbohydrate content, as well as dry matter proportions, were estimated for each month after Lawson, Magalhaes and Miller (Lawson et al., 1998) and Percy and Fife (Percy and Fife, 1981) (Table 4.C.3). Protein, lipid and carbohydrate content were estimated as a percentage of dry matter.

Sensitivity analysis

A sensitivity analysis was performed to examine the robustness of the model and to identify key input parameters affecting the birds' daily energy requirements. To this end, we used selected microclimate and endotherm parameters, focusing on parameters that could vary substantially between individuals and/or across the winter period. These input values were modified according to minimum and maximum recorded values, or they were set to a standard variability of 10% of the average, when minimum and maximum values were not available (Grémillet et al., 2003).

Table 4.C.3 Protein, lipid and carbohydrate content, and dry matter proportion for each prey consumed by little auks and Brünnich's guillemots during the winter.

	Protein (% dry matter)	Lipid (% dry matter)	Carbohydrate (% dry matter)	Dry matter proportion
Euphausiids ^a	43.9	52.4	0.7	26.1
Amphipods ^a	47.5	26.4	1.2	22.4
Fish				
Capelin ^b	50.6	43.1	0.0	31.8
Arctic cod ^b	71.1	17.5	0.0	21.1
Squid				
Gonatus sp. ^b	51.7	41.1	0.0	26.5

^aPercy and Fife, 1981. ^bLawson et al., 1998.

C-3. Results

Little auks

Niche MapperTM predicts little auk daily energy requirements to increase throughout the winter period (September–March), from 353 to 470 kJ day⁻¹ off Newfoundland and from 385 to 484 kJ day⁻¹ off southwest Greenland. At both sites, this increase is not constant through the winter; birds face a strong and sudden rise in daily energy requirements between November and December (+16.4% off Newfoundland and +19.5% off Greenland) (Fig. 4.C.2). Before and after this rise, energy requirements are on average 397±6.4 and 468±9.7 kJ day⁻¹ (means±s.e.m.), respectively, off Greenland and 377±12.5 and 457±5.3 kJ day⁻¹, respectively, off Newfoundland.

Little auk daily energy requirements before this sudden rise (from September to November) are similar at the two wintering sites, with values slowly increasing from 385 to 405 kJ day⁻¹ off Greenland, and from 353 to 396 kJ day⁻¹ off Newfoundland. During this period, the overall increase in daily energy demand is nonetheless stronger off Newfoundland (+5.9±1.1%), than off Greenland (+2.6±2.1%).

Predicted energy expenditure between December and March remains high, yet constant, with a mean variation of -2.9±3.3% off Greenland (min. 442, max. 481 kJ day⁻¹) and of +0.1±2.8% off Newfoundland (min. 444, max. 470 kJ day⁻¹).

Predicted individual daily food requirements follow similar trends, with values between 258 and 322 g wet food day⁻¹ off Greenland (mean 297±8.6 g), and between 256 and 313 g wet food day⁻¹ off Newfoundland (mean 280±8.1 g). Off Greenland, the beginning of the winter period is marked by a slight diminution in daily food requirements until November, followed by a general increase throughout the rest of the season. Off Newfoundland, despite minor variations, food requirements generally increase throughout the season (Fig. 4.C.2).

Brünnich's guillemots

Predicted daily energy requirements during winter for Brünnich's guillemots show an overall increase from 1156 to 1473 kJ day⁻¹ off southwest Greenland and from 1061 to 1417 kJ day⁻¹ off Newfoundland (Fig. 4.C.2). As for little auks, this increase is not constant throughout the wintering period but is characterized by a sharp rise between November and

December(+19.5% and +16.5% off Greenland and Newfoundland, respectively). Before and after this rise, energy requirements are on average 1202 ± 23.8 and 1440 ± 12.6 kJ day^{-1} , respectively, off Greenland and 1127 ± 40.4 and 1381 ± 16.1 kJ day^{-1} , respectively, off Newfoundland.

Before this phase (i.e. from September to November), predicted energy requirements are similar at the two sites (between 1156 and 1233 kJ day^{-1} off Greenland, and between 1061 and 1201 kJ day^{-1} off Newfoundland). However, while energy requirements are relatively constant until November off Greenland ($+3.3 \pm 2.2\%$), they increase off Newfoundland ($+6.4 \pm 0.9\%$).

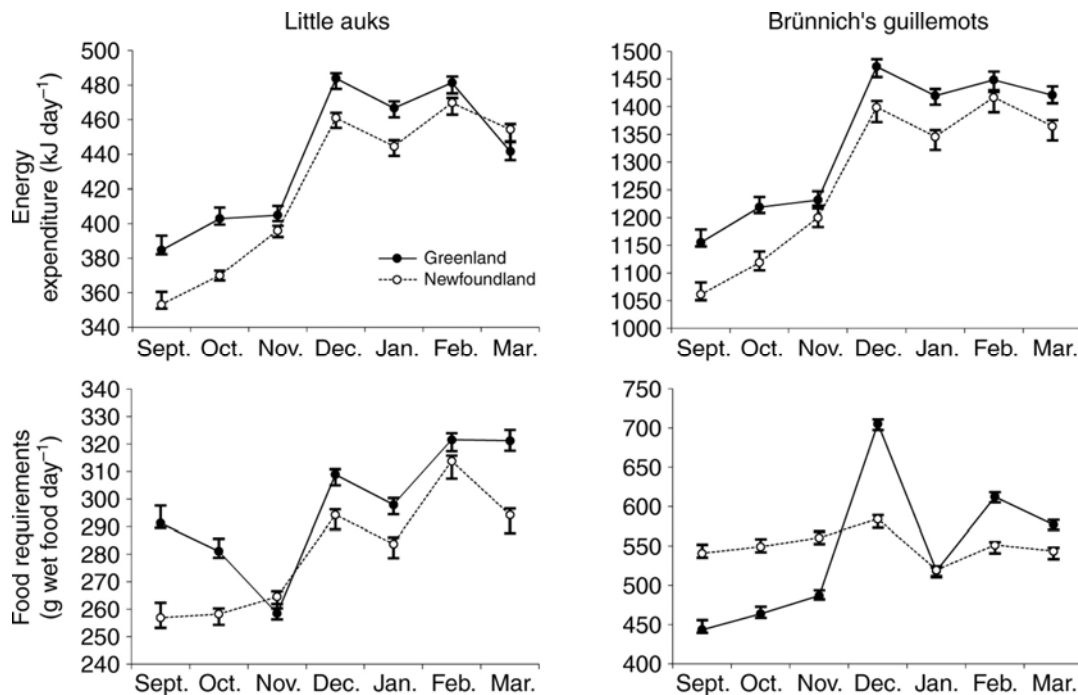


Fig. 4.C.2 Energy and food requirements predicted by the model Niche MapperTM for little auks and Brünnich's guillemots wintering off southwest Greenland and Newfoundland. Error bars were calculated using average maximum ranges for all parameters as estimated in the sensitivity analysis (Table 4.C.4).

After December, energy requirements stay high and relatively constant at both sites with a mean monthly variation of $-1.2 \pm 1.7\%$ off Greenland (min. 1420, max. 1449 kJ day⁻¹) and -0.7 ± 3.0 off Newfoundland (min. 1346, max. 1417 kJ day⁻¹).

Predicted daily food requirements of Brünnich's guillemots wintering off Newfoundland remain constant throughout the study period, with an average of 550 ± 7.5 g wet food day⁻¹ (min. 540.7, max. 584.2 g). Off Greenland, food requirements are more variable and increase throughout the winter period (from 443 g wet food day⁻¹ in September to 577 g wet food day⁻¹ in March), with a sharp increase between November and December (from 487 to 705 g wet food day⁻¹). After this sharp increase food requirements decrease between December and January (from 705 to 518 g wet food day⁻¹) (Fig. 4.C.2). Note that differences between energy and food requirements at the different locations are due to differences in the calorific value of the preferred diet (Table 4.C.3). For instance, guillemots off Newfoundland progressively shift from a fish to a crustacean diet across the winter (Elliot et al., 1990; Rowe et al., 2000), which explains why food requirements remain more or less constant over this period. Off Greenland, a similar shift occurs for guillemots (Falk and Durinck, 1993). However, in December and February, birds primarily consume Arctic cod, whereas they mostly eat capelin during other months (Falk and Durinck, 1993). Cod are energetically less profitable than capelin (essentially because of a lower lipid content; see Table 4.C.3), which results in an increase in food requirements for these 2 months.

Sensitivity analysis

For the sake of simplicity, the results of the sensitivity analysis are only presented for little auks and Brünnich's guillemots wintering off southwest Greenland (Table 4.C.4). The results and the most important factors influencing the individual daily energy demand are nonetheless identical at the two sites (Greenland and Newfoundland). Taking into account the variability of single input parameters, the sensitivity analysis shows that air temperature is a key factor influencing daily energy requirements. Plumage depth and wind speed also substantially affect energy requirements (Table 4.C.4).

Table 4.C.4 Sensitivity analysis for the daily energy requirements of little auks and Brünnich's guillemots wintering off southwest Greenland.

Parameters	Brünnich's guillemots				Little auks			
	Min. value	Max. value	Range	Variation of seasonal energy requirements (%)	Min. value	Max. value	Range	Variation of seasonal energy requirements (%)
Endotherm								
Plumage depth: dorsal, ventral (mm)	5.0, 14.4	6.2, 17.6	±10%	±7.16	6.7, 11.5	8.1, 14.1	±10%	±5.34
Plumage reflectivity: dorsal, ventral (%)	0.34, 0.67	0.42, 0.82	±10%	±0.01	0.36, 0.58	0.44, 0.71	±10%	±0.02
Feather length: dorsal, ventral (mm)	29.2, 22.5	35.6, 27.5	±10%	±0.21	18.0, 17.3	22.0, 21.1	±10%	±1.45
Feather diameter (µm)	29.7	36.3	±10%	±2.18	29.7	36.3	±10%	±0.48
Plumage density (1 cm ⁻²)	4114.8	5029.2	±10%	±0.66	4114.8	5029.2	±10%	±0.89
Body core temperature (°C)	39.6	40.3	Min.–max.	±1.83	36.1	40.1	±10%	±2.02
Digestive efficiency (%)	0.63	0.77	±10%	±0.01	0.72	0.88	±10%	±0
Exhaled air temperature–local air temperature (°C)	1.8	2.2	±10%	0.01	1.8	2.2	±10%	0.01
Flight metabolism (W)	79.2	96.8	±10%	±0.84	9.513	11.627	±10%	±0.31
Ventral area contacting substrate (%)	0.225	0.275	±10%	±0.06	0.225	0.275	±10%	±0.17
Flight speed (m s ⁻¹)	16.25	19.87	±10%	±0.23	11.7	14.3	±10%	±0.28
Dive depth (m)	43.3	52.8	±10%	±0.01	24.57	30.03	±10%	±0.01
Flight altitude (m)	4.5	5.5	±10%	±0.01	4.5	5.5	±10%	±0.01
Climate								
Air temperature (°C)	-7.80	5.17	Min.–max.	±8.52	-7.80	5.17	Min.–max.	±8.87
Sea surface temperature (°C)	-0.60	5.27	Min.–max.	±0.04	-0.60	5.27	Min.–max.	±0.03
Relative humidity (%)	55.0	97.2	Min.–max.	±1.20	55.0	97.2	Min.–max.	±1.44
Wind speed (m s ⁻¹)	2.0	17.5	Min.–max.	±2.57	2.0	17.5	Min.–max.	±2.70
Cloud cover (%)	0	100	Min.–max.	±0.01	0	100	Min.–max.	±0.01

Minimum and maximum input values from Micro2006c and Endo2007d are the minimum and maximum values recorded for each parameter or ±10% of the average. As body mass is highly correlated with field metabolic rate (FMR) in most animals (Ellis and Gabrielsen, 2002), a strong variation in energy requirements is expected when body mass varies, independently of the model. Therefore, this parameter does not appear in the sensitivity analysis. The maximum variation of calculated energy requirements is marked in bold. It highlights the fact that air temperature is the critical parameter affecting the energy balance of wintering alcids. However, it is also important to note that plumage depth is the second most important parameter.

C-4. Discussion

We used Niche Mapper™ to estimate the daily energy expenditure and food requirements of little auks and Brünnich's guillemots wintering in northwest Atlantic waters. As in all bioenergetics studies, even the most elaborate model is incapable of fully grasping nature's complexity. We ran the most refined and extensively field-tested energetic model currently available, and also took great care in compiling accurate input values. Nonetheless, we wish to stress that all results presented here are theoretical in nature, and that the values provided are therefore estimates.

Beyond these limitations, Niche Mapper™ is currently the only tool available to accurately study heat exchange mechanisms associated with porous media (fur and feathers), climatic conditions, and their impact on the energy balance of seabirds wintering offshore, where direct metabolic studies are impossible. It therefore appears to be a good complementary method to biotelemetry, especially for small-sized species, which cannot be easily caught and fitted with

internal data loggers recording heart rate. Furthermore, our sensitivity analysis supports the robustness of Niche MapperTM, with few parameters critically affecting the predicted energy requirements (Table 4.C.4). These are mainly environmental parameters, such as air temperature or wind speed, which can be measured *in situ* or *via* remote sensing. Other important factors are morphological parameters, such as plumage depth, a parameter particular to each species.

The most important outcome of our study is the sharp increase in energy expenditure between November and December, which occurs for both species at both study sites. Similar patterns have been found for great cormorants (*Phalacrocorax carbo*) wintering in Greenland (Grémillet et al., 2005a). The end of the year therefore appears to be a particularly challenging phase of the annual cycle for North Atlantic seabirds, with decreasing air temperatures being the main driving force (Table 4.C.4).

In most situations, species confronted with fluctuating environmental conditions maintain an energetic steady state and ensure their survival *via* physiological and/or behavioural plasticity (Komers, 1997; Dawson and O'Connor, 1996). Alcids wintering in the North Atlantic carry very limited body reserves and cannot survive longer than 3–4 days without foraging, even at the best of their body condition (Gaston et al., 1983; Gaston and Jones, 1998). They are therefore bound to increase their energy intake rates substantially in November and December, if they are to survive (as observed in other wintering seabird species) (e.g. Grémillet et al., 2005a).

On the other hand, this critical period is characterized by harsh storms (Arctic Climate Impact Assessment, 2004), which are known to have a negative impact on seabird flying and diving performance (Finney et al., 1999). Storms also increase wind-driven water turbidity and affect prey behaviour and distribution (Schreiber, 2001), thus decreasing the birds' predatory efficiency. November and December storms therefore affect seabird foraging performance and their ability to acquire energy at a time of peak energy demand. This critically challenges their energy balance and creates an energetic bottleneck. Our results, which strongly suggest such a bottleneck, might explain the timing of seabird winter wrecks, during which large numbers of seabirds cast ashore and/or are found dead inland (Gaston, 2004). During the past 50 years, major wrecks of little auks and Brünnich's guillemots have more or less always occurred in late November and December in the North Atlantic (Gaston and Jones, 1998; Gaston, 2004). Gaston (Gaston, 2004) explained this timing by the abundance of inexperienced and

vulnerable juvenile birds, which is higher in November and December than in late winter. This might well be the case, but we argue that the energetic bottleneck identified in this study is most probably the major determinant of the magnitude and of the timing of winter mortality in adult and juvenile seabirds wintering in the North Atlantic.

The end of the winter (December to March) may also play a crucial role for seabird energetics, with a 4 month plateau of maximum energy expenditure. This plateau stands at an average of 463 kJ day⁻¹ for little auks and 1411 kJ day⁻¹ for Brünnich's guillemots. During the breeding season, when provisioning chicks, different studies have shown that these two species cope with energy expenditures as high as 696 and 1860 kJ day⁻¹, respectively (Ellis and Gabrielsen, 2002). These values are noticeably higher than those predicted by Niche MapperTM for the winter period. However, breeding energy expenditures occur in a favourable energetic context, with mostly good weather conditions and maximum prey abundance (e.g. Arnkværn et al. for copepods (Arnkværn et al., 2005)), and they occur for a limited time period only (the nestling period lasts for 28.3 days on average in Greenland (Evans, 1981)). In contrast, the winter energy requirements predicted in our study occur in a demanding and unpredictable environment, when storms make prey capture challenging for seabirds (Finney et al., 1999). This phase lasts for a third of the annual cycle, causing an enormous total energy demand compared with that of the short breeding period.

Current climate models predict drastic changes in the north Atlantic, with rising air and water temperatures, as well as more frequent winter storms (Arctic Climate Impact Assessment, 2004; Corell, 2006). From this study, we could expect that higher temperatures will have a positive effect upon the energy budget of seabirds wintering in this region, as it would potentially widen the November/December energetic bottleneck. However, indirect effects of global warming on prey availability and distribution might counterbalance the positive effect of higher temperatures on seabird energetics. More frequent winter storms might also critically perturb seabird foraging conditions, and changing water temperatures are already causing major ecosystem shifts in the North Atlantic (Beaugrand et al., 2002b ; Sandvik et al., 2005). Therefore, additional energetic studies, combining multi-year climate data and climate change scenarios, as well as data on energetics, behaviour and the distribution of birds and prey stocks are now necessary on larger temporal and spatial scales. From these it might be possible to predict fundamental niches of species in the future and to investigate and foresee

the impact of climate change on seabird energetics and distribution during their wintering season (see Kearney et al., 2008) (for a review, see Kearney and Porter, 2009).

Outlook

Our study highlights the relationship that exists between harsh environmental conditions and the energy balance of alcids wintering in the northwest Atlantic. Predicting the existence of an energetic bottleneck in December, it provides important insights into the determinants of winter mass-mortality in these marine top predators.

Furthermore, our work presents and emphasizes the importance of a generic thermodynamic/biophysical/behavioural model to understand energy limitations in wintering marine animals. This algorithm, here applied at the individual level, also appears to be a powerful tool to define energetic constraints on population dynamics, and is of considerable applied interest. Indeed, with the ability to calculate daily energetics and food requirements from simple biotic and abiotic information, Niche MapperTM can be used to estimate the food requirements of warm-blooded marine predators at the population and community level, to predict their impact on economically valuable fish stocks, and to evaluate their capacity to adapt to global change (e.g. overfishing and climate change).

Acknowledgments

Niche MapperTM can be obtained and used for free in collaboration with Warren Porter (<http://www.zoology.wisc.edu/faculty/por/por.html>) or purchased in its present form by contacting Warren Porter (wpporter@wisc.edu). We are grateful to the Field Museum of Natural History in Chicago and to Paula Holahan from the University of Wisconsin Zoological Museum for their help in examining bird carcasses. This manuscript also greatly benefited from the critical comments made by A. Harding, H. Sandvik and M. Enstipp. We also thank Y. Cherel, J. M. Fromentin, I. Chuine and T. Boulinier for useful discussions and comments. J.F. is supported by a grant from the University Louis Pasteur (Strasbourg, France).

Chapitre 5

**Acquisition énergétique hivernale :
écologie alimentaire et réponses aux
conditions biotiques de
l'environnement**



Introduction du chapitre

Dans le chapitre précédent, nous avons vu comment les conditions climatiques rencontrées par les oiseaux au cours de l'hiver pouvaient, en affectant directement leur dépense énergétique, avoir un effet négatif sur leur survie hivernale. Face à ces conditions, une alternative permettant aux oiseaux de faire face à cette forte augmentation de la dépense énergétique au cours de l'hiver, de maintenir une balance énergétique à l'équilibre et donc d'assurer au mieux leur survie réside dans leur acquisition d'énergie, c'est à dire dans leur écologie alimentaire et leur comportement de prédation.

La plupart des proies des oiseaux marins changent de comportement et de mode de vie pour, elles aussi, faire face aux conditions climatiques extrêmes au cours de l'hiver. Par exemple, les copépodes calanoides (principales proies des mergules nains) effectuent à l'automne une migration verticale pour entrer en diapause plusieurs mois à des profondeurs importantes (> 400 m), diapause au cours de laquelle ils ne sont donc plus accessibles à leurs prédateurs. De même, certaines espèces de poissons qui possèdent des préférences thermiques restreintes, changent elles-aussi de distribution. Certaines migrent ainsi vers des eaux plus au sud et donc plus chaudes (e.g. Hobson et al. 2009), alors que d'autres se retrouvent dans des masses d'eaux plus profondes (e.g. Godø & Michalsen 2000, Johansen 2002, Neat et al. 2006). Pendant cette période, les oiseaux marins qui doivent continuer de s'alimenter (voire même accroître cette alimentation pour faire face à la hausse de leur dépense énergétique) doivent donc s'adapter à ces changements.

L'objectif de cette partie a donc été de tester l'hypothèse que **« les oiseaux marins répondent aux changements de disponibilité des proies en hiver soit en modulant leur comportement alimentaire et en suivant leur proies lorsque cela est possible, soit en changeant leur alimentation et en consommant de nouvelles proies »**.

Pour cela, ce chapitre est décomposé en deux parties. En utilisant les analyses en isotopes stables, un premier article étudie le niveau trophique et le régime alimentaire des mergules nains tout au long de leur cycle annuel afin de déterminer comment celui-ci évolue au cours des différentes saisons, notamment entre l'été et l'hiver. Par la suite, un second article étudie le comportement ainsi que l'énergétique de deux espèces de guillemots tout au long de l'hiver avec pour but de mieux comprendre comment les oiseaux répondent aux variations de leur environnement en termes de comportement alimentaire.

Geographic and seasonal variability in the isotopic niche of little auks

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Abstract

The inter-breeding season of seabirds is extremely challenging to study, because it is often spent offshore under harsh environmental conditions. We used stable isotope analysis to investigate little auk (*Alle alle*) feeding ecology throughout the annual cycle. The geographic distribution of little auks in the Arctic covers a wide range of oceanographic conditions. We sampled birds from five different colonies located in the most important breeding areas (Greenland and Spitsbergen) to examine how individuals breeding in contrasting marine environments differ in their diet throughout the year. We found differences in summer $\delta^{15}\text{N}$ values amongst the colonies suggesting different target species despite overall low $\delta^{15}\text{N}$ values in blood which indicates a diet primarily composed by calanoid copepods. A rise of $\delta^{15}\text{N}$ values between summer and autumn indicated that adults changed their diet to feed at a higher trophic level, probably on primary carnivores such as amphipods and fish. During autumn, a large overlap in feathers $\delta^{13}\text{C}$ values between colonies suggests a common moulting area off North-East Greenland. During winter, the isotopic signatures show that diet of Greenland and Spitsbergen-birds differed, with birds from Greenland feeding at low trophic levels, probably mostly on copepods, while birds from Spitsbergen maintained a higher trophic level. These findings highlight contrasted seasonal and regional diet in little auk populations, and reveal possible population exchanges during their autumn moult. We found substantial trophic variability in little auks, which may indicate unsuspected capabilities to adapt to current, drastic environmental change in the North Atlantic.

Keywords: Alcid, Annual cycle, Climate change, Copepod, Diet, North Atlantic, Pelagic ecosystem, Seabird

D-1. Introduction

In polar and temperate regions, the inter-breeding season has a profound impact on seabird ecology. During this period, they have to cope with harsh and highly variable environmental conditions, which can directly affect their body condition, energy balance and survival (Grosbois & Thompson 2005, Rolland et al. 2009) and ultimately shape their population dynamics (Barbraud & Weimerskirch 2003, Daunt et al. 2006). However, the underlying mechanisms and the different factors involved often remain a ‘black box’ and further studies are therefore needed to explore seabird ecology throughout the inter-breeding period. Between breeding seasons, seabirds are typically far offshore and are consequently inaccessible for conventional scientific studies (Gaston 2004). In recent years, technical developments have started to alleviate this problem. For example, miniaturized electronic tracking tags allow investigations of winter movements and migration routes (e.g. Grémillet et al. 2000b), fatty acids analyses can provide information on specific dietary components (e.g. Williams et al. 2008), and modelling has improved our knowledge of seabird winter energetics (e.g. Fort et al. in press). Studies focused on seabird inter-breeding ecology are nonetheless still scarce and often restricted temporally or spatially, thereby ignoring potential environmental variability which may affect individual strategies. Stable isotope analysis is a powerful technique in the study of animal feeding ecology under variable conditions (West et al. 2006). It is based on the fact that the ratios of the stable isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) in predator proteins reflect those in prey species in a predictable manner. Consumer tissues are enriched in ^{15}N relative to their food and consequently $\delta^{15}\text{N}$ measurements serve as indicators of a consumer trophic position (Kelly 2000). In contrast, $\delta^{13}\text{C}$ values vary little along the food chain and are mainly used to determine primary production sources in a trophic network (Kelly 2000). In the marine environment, $\delta^{13}\text{C}$ values indicate consumer foraging areas (Hobson et al. 1994). This approach therefore permits the identification of animal isotopic niches and definition of their ecological niches (Newsome et al. 2007, Cherel 2008). In seabirds, stable isotope analysis has been used to track both migration and diet (e.g. Hobson 1999, Cherel et al. 2007). Different body tissues incorporate the isotopic signatures of resources at different rates and can therefore integrate information over different time periods (a few days for plasma, a few weeks for whole blood, or several months/years for bone collagen; Hobson & Clark 1992, Evans-Ogden et al. 2004). Moreover, and because they are metabolically inert, feathers provide isotopic information for the specific time period of feather growth during moult

(Bearhop et al. 2002). Hence, the analysis of different tissues can allow us to track changes in feeding ecology over different time periods and at different time scales (Hobson 1993, Cherel et al. 2008).

The little auk (*Alle alle*) is a small diving seabird that feeds almost exclusively on zooplankton in Arctic and North Atlantic waters, with a breeding distribution covering a wide range of ocean current regimes and contrasted water masses (Gaston & Jones 1998, Stempniewicz 2001). With recent estimations of more than 80 million individuals (Gaston & Jones 1998, Kampp et al. 2000, Isaksen & Gavriilo 2000, Egevang et al. 2003), this species is the most abundant seabird of the North Atlantic and one of the most abundant seabird species in the world (Stempniewicz 2001). It therefore plays a crucial role within Arctic ecosystems, notably in terms of energy and organic matter transfer. For example, the North Water Polynya breeding little auks are responsible for 92-96% of the carbon flux to seabirds, and consume up to 24% of the copepod standing stock in this region (Karnovsky & Hunt 2002). Thus, it is considered as a keystone species to functioning Arctic ecosystems (Stempniewicz 2006). During the inter-breeding season, knowledge of their spatial distribution and diet are more elusive. Vertical migration of their main prey (*Calanus* spp.) during winter, which tend to descend to depths unreachable to little auks (>100m; Falk-Petersen et al. 2009), suggests a strong seasonal shift in little auk diet. Only one study (Karnovsky et al. 2008) has investigated the inter-breeding diet of little auks, and concludes that these birds show dietary shifts during the different seasons, especially during autumn. However, this study was limited to one particular site, the North Water Polynya off North-West Greenland, where random birds were sampled during different seasons. This procedure does not allow the comparative analysis of little auk diet across the annual cycle for birds of known origin. Such investigations are essential in the context of rapid and drastic environmental change in the North Atlantic. Indeed, this region is seriously affected by climate change, with significant warming of surface waters (ACIA 2004). Higher temperatures are predicted to trigger large-scale modifications in zooplankton communities (Beaugrand & Reid 2003). Given that little auks are highly specialised copepod consumers, global warming may negatively impact their populations (Stempniewicz et al. 2007, Harding et al. 2009a, Karnovsky *in press*). To test this hypothesis it is critically important to assess dietary flexibility in little auk populations across a large portion of their breeding range in the North Atlantic. This flexibility may indicate their capacity to buffer the impact of climate change by exploiting alternative prey.

Table 5.D.1 Stable isotopic signatures of samples collected from little auks. All data presented are raw (uncorrected).

Status	Site	Colony	Symbol	Tissue	Time period	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)			
Breeding adults	East Greenland	Kap Hoegh (70°43'N, 21°38'W)	EG	Whole Blood	Summer	20	-21.7 ± 0.1	11.4 ± 0.1			
				Body Feathers	Autumn	19	-20.5 ± 0.7	13.1 ± 0.7			
				Head Feathers	Spring	19	-19.6 ± 0.8	11.4 ± 1.0			
	Spitsbergen	-	-	-	mean Whole Blood	Summer	73	-20.1 ± 0.2	10.7 ± 0.4		
					mean Body Feathers	Autumn	80	-20.3 ± 0.6	13.4 ± 0.6		
					mean Head Feathers	Spring	80	-19.4 ± 0.5	13.2 ± 0.8		
					Magdalenefjorden (79°35'N, 11°05'E)	S1	Whole Blood	Summer	14	-20.1 ± 0.1	10.5 ± 0.2
							Body Feathers	Autumn	20	-20.6 ± 0.6	13.5 ± 0.6
							Head Feathers	Spring	20	-19.4 ± 0.5	12.9 ± 0.9
					Kongfjorden (79°01'N, 12°25'E)	S2	Whole Blood	Summer	20	-20.2 ± 0.2	10.4 ± 0.2
							Body Feathers	Autumn	20	-20.3 ± 0.5	13.2 ± 0.7
							Head Feathers	Spring	20	-19.8 ± 0.4	13.3 ± 0.8
	Longearbyen (78°13'N, 15°19'E)	S3	Whole Blood	Summer	20	-20.0 ± 0.3	11.0 ± 0.4				
			Body Feathers	Autumn	20	-19.6 ± 0.5	13.2 ± 0.5				
			Head Feathers	Spring	20	-18.9 ± 0.4	13.3 ± 0.6				
	Hornsund (77°00'N, 15°22'E)	S4	Whole Blood	Summer	19	-20.3 ± 0.2	11.1 ± 0.3				
Body Feathers			Autumn	20	-20.6 ± 0.4	13.8 ± 0.3					
Head Feathers			Spring	20	-19.5 ± 0.4	13.4 ± 0.8					
Wintering adults	Nuuk	(64°00'N, 55°00'W)	SWG	Whole Blood	Late winter	21	-19.5 ± 0.4	11.7 ± 0.4			
Chicks	East Greenland	Kap Hoegh	EG	Body Feathers	Autumn	20	-20.3 ± 0.4	13.2 ± 0.5			
				Whole Blood	Summer	20	-22.3 ± 0.1	11.8 ± 1.2			
				Body Feathers	Summer	19	-21.6 ± 0.4	11.6 ± 0.3			
	Spitsbergen	Hornsund	S4	Chick food	-	16	-22.3 ± 0.5	8.4 ± 0.5			
				Chick food	-	12	-21.8 ± 0.3	8.3 ± 0.4			

Values are mean ± SD

Therefore, using isotopic signatures of different body tissues from birds breeding at different geographical sites, the present study had two objectives: (1) to assess trophic level variability in little auks throughout the annual cycle, and (2) to compare the isotopic niches across little auk populations at different spatial scales.

D-3. Materials and Methods

Sample collection. This study was conducted during the 2007 breeding season at four colonies on Spitsbergen and one colony at East Greenland. A total of 291 breeding adults and 20 chicks of little auks were sampled, and 28 chick meals collected (Table 5.D.1, Fig. 5.D.1). Hereafter, these five colonies are referred to as EG for the East Greenland colony, and as S1 to S4 following a north-south gradient for the Spitsbergen colonies (Fig. 5.D.1).

Blood samples (~0.2 ml) were collected from the brachial vein. Seventy percent ethanol was then added to the whole blood, which was kept frozen at -20°C until isotopic analysis. To check if results were not sex-biased, an additional small amount of blood was taken at EG, S2 and S4 for subsequent molecular sexing as detailed in Fridolfsson and Ellegren (1999).

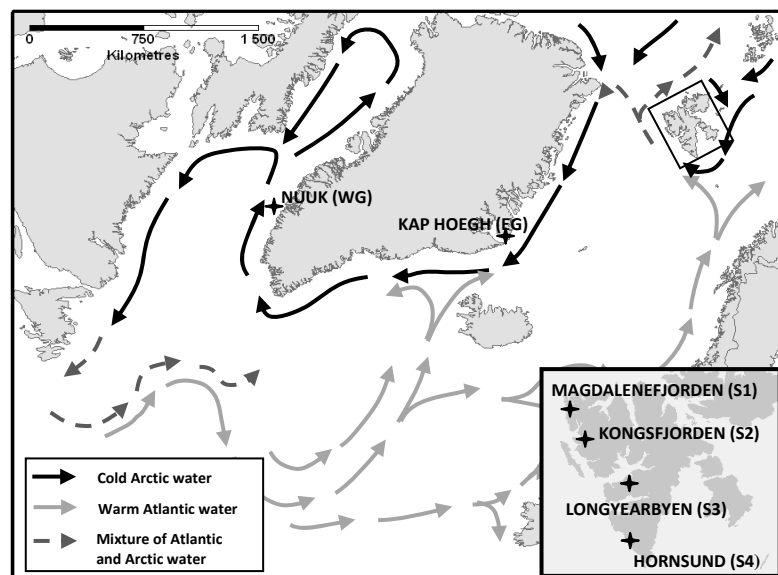


Fig. 5.D.1 Map of the studied little auk breeding colonies which are labelled as follows in the text: S1 to S4 for Spitsbergen (from north to south), EG for the East Greenland and WG for West Greenland wintering birds. After AMAP (1998).

Little auks have two distinct moults per year: one complete moult in autumn (September-October) that involves the replacement of the complete body plumage, and a partial moult in winter (March) when only feathers from the neck and head are replaced (Gaston & Jones 1998, Stempniewicz 2001). Therefore, two batches of cover feathers were plucked on each breeding adult in summer: one from their body (back or belly, reflecting the autumn period), and one from the head (cheek, neck or throat, reflecting the winter period). These 2 batches are hereafter called ‘body feathers’ and ‘head feathers’. All feathers were randomly plucked to avoid a bias due to an eventual patchy moult pattern. For chicks, only newly-grown cover feathers were plucked during the late chick-rearing period, when down had totally disappeared. All collected feathers were kept at ambient temperature in sealed plastic bags until analysis.

Chick meals were collected from adult birds, which transport food to the nest in a sublingual (gular) pouch (Stempniewicz 2001). Adult birds were caught in the colony using mist nets or noose carpets. Each food load was gently scooped out of the gular pouch, and immediately preserved in 70% ethanol. Caught adults were released unharmed after 5-10 min of handling. In the laboratory, a random sample of each chick meal was taken for dietary analyses. Each diet sample was divided into broad classes (copepods, amphipods and others). Prey items were then numbered and identified after Keast & Lawrence (1990), Kwasniewski et al. (2003), and Walkusz (*personal communication*). To estimate the composition by mass of the chick meals, we dried items of each taxon and calculated individual dry mass. We then reconstituted the proportion by dry mass of each taxon in the different chick meal samples.

Twenty additional birds legally shot at sea by Greenlandic hunters for commercial sale were bought. Birds were shot off Nuuk (64°10'N 51°45'W; South-West Greenland, hereafter symbolized as WG) in winter (January 2007) and immediately kept frozen until dissected in the laboratory. Blood samples were collected from the cardiac clot, ‘body feathers’ randomly plucked from belly, back or throat, and birds were visually sexed from gonads. Blood and body feathers were stored as for breeding birds. No head feathers were sampled from these birds because both body and head feathers in winter plumage originate from the same moult (autumn moult). Stomach contents were also removed, but the advanced digestion stage of the prey precluded identifying them.

Sample preparation and isotopic analysis. Prior to isotopic analysis, blood samples were dried for 48h at 60°C and homogenized. Feathers were rinsed in a 2:1

chloroform:methanol solution, rinsed 2x in a methanol solution, dried for 48h at 60°C and homogenized with scissors. Food samples were dried for 48h at 60°C and ground to powder. Lipids and carbonates were then removed from food samples using cyclohexane and 1N HCl, respectively. All isotopic analyses were performed by Mylnefield Research Services Stable Isotope Laboratory (SCRI, Dundee, Scotland). Analyses were performed on 1 mg subsamples of dried and homogenized materials loading into tin cups and combusting at 1000°C in a ANCA-GSL elemental analyzer (Sercon, Crewe, UK). Resultant CO₂ and N₂ gases were then analyzed for carbon-13 and nitrogen-15 isotope abundance in continuous-flow mode using a SerCon 20:20 isotope ratio mass spectrometer (SerCon, Crewe, UK). Measured data were scale-calibrated using two international reference materials (IAEA-600 and IAEA-CH6) as well as one in-house standard (leucine). Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$, where X is ¹³C or ¹⁵N and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N. The R_{standard} values were based on the Vienna-PeeDee Belemnite (VPDB) for ¹³C and atmospheric N₂ (AIR) for ¹⁵N.

Data analysis. Following little auk moulting sequences (see above), the tissue-specific isotopic assimilation rates and temporal integrations (Hobson & Clark 1992, Bearhop et al. 2002), blood collected from breeding birds reflects summer isotopic signature (July), body feathers the autumn signature (September-October), and head feathers the winter signature (March). Blood collected on hunted birds also reflects the winter isotopic niche (January) of little auks.

In order to compare blood and feather results and consequently to investigate the bird isotopic niche at different periods of their annual cycle, we needed to take into account the tissue-dependent metabolic routing and enrichment factors for little auks (Quillfeldt et al. 2008a, Podlesak & McWilliams 2006). We thus compared stable isotope ratios obtained from growing feathers and blood samples simultaneously collected on chicks, and calculated correction factors to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from these two tissues in adult birds. We found differences between chick feathers and blood of -0.25‰ for nitrogen and 0.65‰ for carbon, and used these values as correction factors. Therefore, we corrected adult body and head feathers isotopic data by subtracting the correction factors before comparing them with blood and zooplankton (uncorrected) isotopic results.

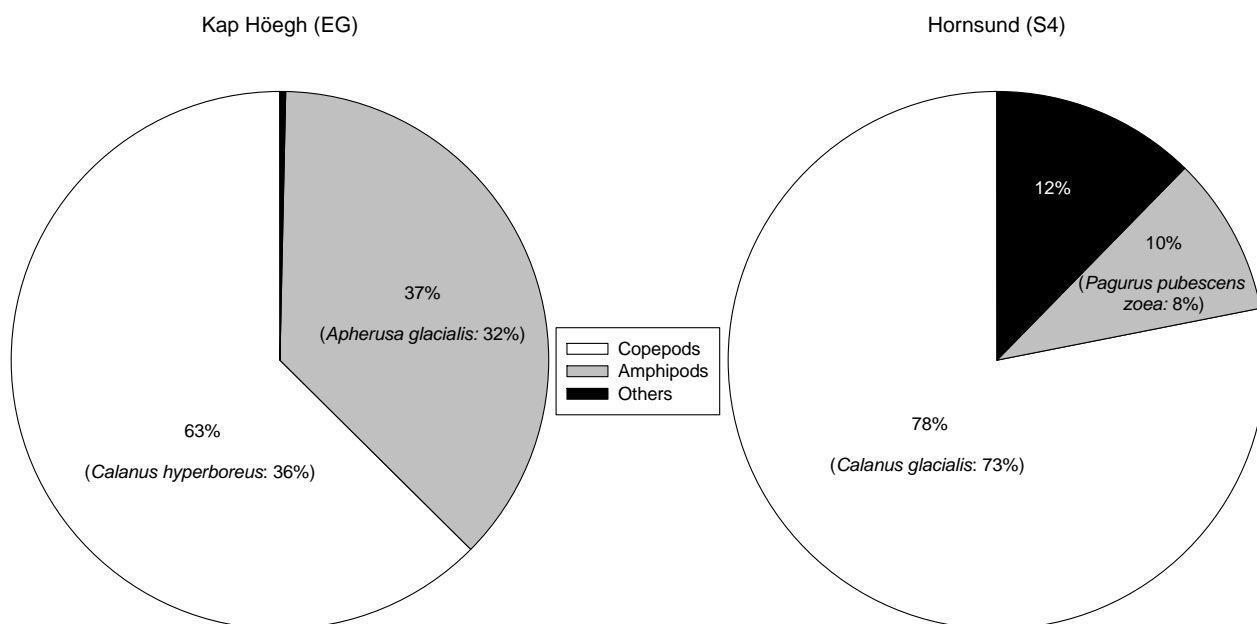


Fig. 5.D.2 Composition of little auk chick meals (expressed in % dry mass) collected from adults at Kap Höegh (East Greenland, EG; n=16) and Hornsund (Spitsbergen, S4; n=12).

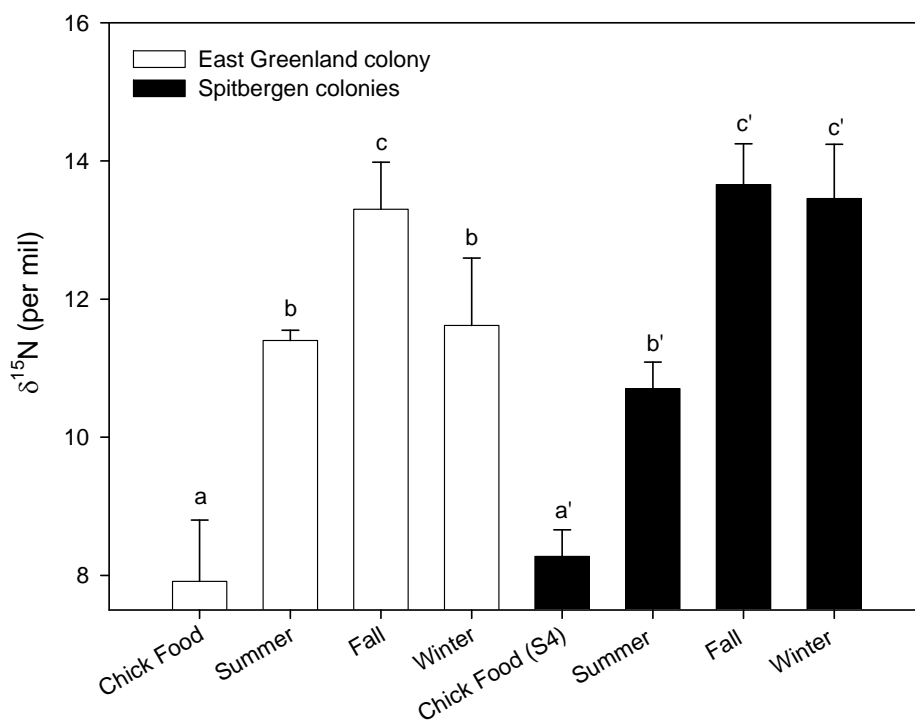


Fig. 5.D.3 Stable nitrogen isotope values of little auks samples from East Greenland and Spitsbergen during the different seasons, and of chick meals collected at two colonies (EG and S4). Values (uncorrected) are means \pm SD. At each site, values not sharing the same superscript letter are significantly different (see results).

Statistics were computed using Statistica 6.0. We used multivariate analysis of variance (MANOVA) with Wilk's lambda statistics to compare simultaneously $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between colonies, as well as analysis of variance (ANOVA) followed by *post-hoc* range tests (Tukey multiple comparison test for unequal sample sizes) to compare independently $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sexes, seasons and colonies. Presented values are means \pm SD, and statistical significance was assumed at $p < 0.05$.

D-4. Results

For all colonies on which birds were sexed and for all tissues, no difference between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of adult males and females were observed (ANOVA, $\delta^{15}\text{N}$: $F_{5,162} = 1.27$, $p = 0.28$; $\delta^{13}\text{C}$: $F_{5,162} = 0.52$, $p = 0.76$). Therefore, results for the two sexes were pooled in the following analyses.

Chick meals and adult $\delta^{15}\text{N}$ values

Chick meals collected at S4 and EG were mostly (78% and 63%) composed of copepods (almost exclusively *Calanus glacialis* and *C. hyperboreus*, respectively; Fig. 5.D.2). However, chick meals from EG also included the eponitic (associated with sea ice) amphipod *Apherusa glacialis* (32%). The mean $\delta^{15}\text{N}$ value measured on chick meals was similar for both colonies (Mann-Whitney test, $U = 72.0$, $p = 0.28$, $n = 12$ and $n = 16$ for S4 and EG, respectively) (Table 5.D.1, Fig. 5.D.3). Moreover, chicks and adults from EG had similar $\delta^{15}\text{N}$ values measured in blood samples (t-test, $t = 1.56$, $df = 38$, $p = 0.13$) (Table 5.D.1).

Adult breeding birds at EG showed significant variation in their $\delta^{15}\text{N}$ isotopic ratio during the different seasons (ANOVA, $F_{2,55} = 43.99$, $p < 0.001$). *Post hoc* Tukey multiple comparison tests indicated an increase of this ratio between summer and autumn ($p < 0.001$), followed by a decrease between autumn and winter ($p < 0.001$). $\delta^{15}\text{N}$ isotopic values were similar between summer and winter ($p = 0.59$) (Fig. 5.D.3). Birds breeding in Spitsbergen also present a significant variation in $\delta^{15}\text{N}$ values between seasons ($F_{2,230} = 541.97$, $p < 0.001$). Like the Greenland birds, this ratio increased between summer and autumn ($p < 0.001$). However, it remained high in winter with a similar mean value to that in autumn ($p = 0.100$). This winter ratio was significantly higher than in summer ($p < 0.001$) (Fig. 5.D.3).

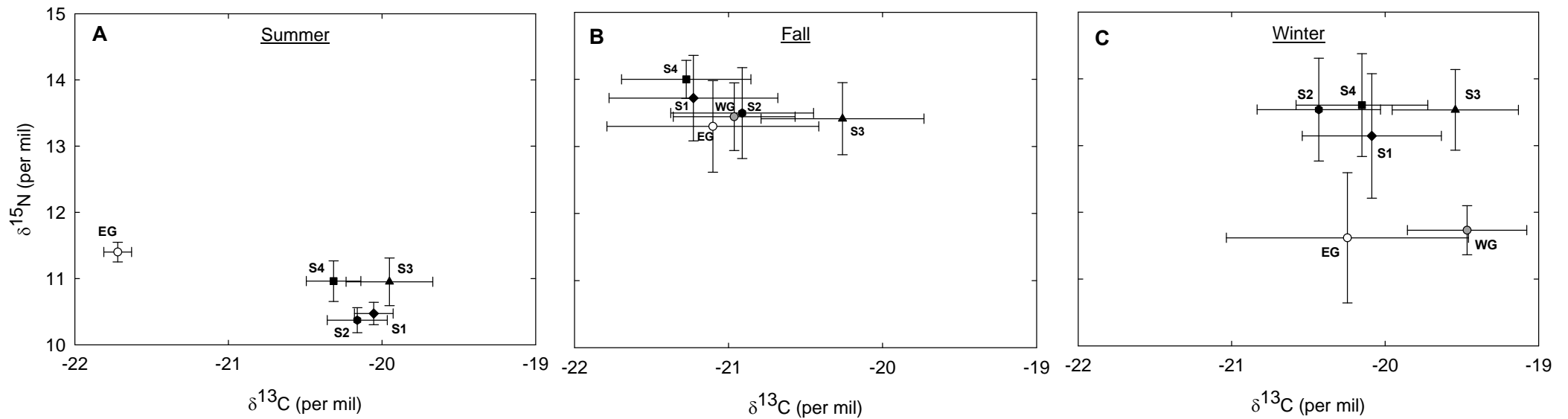


Fig. 5.D.4 Stable carbon and nitrogen isotope values of adult little auk samples from each colony and during the different seasons. Values are means \pm SD. Summer values (from blood) are uncorrected values while autumn and winter values (from feathers) are corrected values. Open symbols are values measured on birds from the East Greenland colony, black-filled symbols are values from the Spitsbergen colonies, and grey-filled symbol are values for the West-Greenland winter-shot birds.

Seasonal and colony variations

During summer, the different colonies were segregated by their overall isotopic signatures (MANOVA, Wilk's lambda, $F_{8,174} = 95.50$, $p < 0.001$) and in an univariate analysis, by their $\delta^{13}\text{C}$ (ANOVA, $F_{4,88} = 282.20$, $p < 0.001$) and $\delta^{15}\text{N}$ values ($F_{4,88} = 51.15$, $p < 0.001$) measured for blood samples (Fig. 5.D.4A). *Post hoc* Tukey multiple comparison tests indicated that among Spitsbergen birds, the 2 southern colonies (S3 and S4) had higher $\delta^{15}\text{N}$ values than the 2 northern colonies (S1 and S2). Also S3 had higher $\delta^{13}\text{C}$ values than S2 and S4, whereas S4 had lower $\delta^{13}\text{C}$ values than S1. Moreover, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured in EG were higher than in all Spitsbergen colonies (all $p < 0.001$)

During autumn, birds from the different colonies were also segregated by their overall isotopic signatures ($F_{10,224} = 7.31$, $p < 0.001$), as well as by their $\delta^{13}\text{C}$ ($F_{5,113} = 10.30$, $p < 0.001$) and $\delta^{15}\text{N}$ values ($F_{5,113} = 4.00$, $p = 0.002$). However, multiple comparison tests indicated that only birds from S3 differed from birds from the other sites, because of higher $\delta^{13}\text{C}$ values (all $p < 0.01$). Furthermore, only birds from S4 had significantly higher $\delta^{15}\text{N}$ values than those from S3, EG and WG ($p = 0.02$, $p = 0.003$ and $p = 0.03$, respectively) (Fig. 5.D.4B).

During winter, birds from all colonies were again segregated by their overall isotopic signatures ($F_{10,226} = 20.10$, $p < 0.001$) and in an univariate analysis by their $\delta^{13}\text{C}$ ($F_{5,114} = 12.75$, $p < 0.001$) and their $\delta^{15}\text{N}$ values ($F_{5,114} = 30.14$, $p < 0.001$). However, multiple comparison tests indicated that $\delta^{13}\text{C}$ values measured on birds from S3 and WG were similar ($p = 1.00$) but differed from all other colonies (all $p < 0.01$), whereas $\delta^{15}\text{N}$ values of EG and WG were similar ($p = 1.00$) but differed from all Spitsbergen colonies (all $p < 0.001$) (Fig. 5.D.4C).

D-5. Discussion

Detailed knowledge of seabirds feeding ecology through the inter-breeding season is essential as a first step towards understanding the determinants of winter mortality, and how individuals adapt to ongoing environmental change, notably in terms of prey availability. Karnovsky et al. (2008) studied little auk diet and found large seasonal changes through the year. However, their study was restricted to one site (the North Water Polynya off North-West

Greenland) and did not take into account individual and spatial variation. Additional investigations were therefore needed to define the trophic niche of this essential component of Arctic marine food webs across the North Atlantic.

Our study shows that little auks from all colonies (East Greenland and Spitsbergen) occupy variable isotopic niches through the different seasons of their annual cycle, with some important variations between bird populations at different spatial scales. Moreover, we observe strong inter-seasonal variation in individuals from particular colonies. As central place foragers during the breeding season, foraging distance is constrained by the need to frequently feed their chick at the colony (Welcker et al. 2009b). This constraint is reflected by a low variance of their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic values in summer (Fig. 5.D.4A).

However, stable isotopic results and standard deviations show that during the inter-breeding season, the isotopic niche occupied by little auks from the same colony is wider, as found for other species (Cherel et al. 2007, 2008), strongly suggesting that little auks disperse across contrasted water masses of the North Atlantic and feed on a larger range of prey.

Spatial variability in the isotopic niche of little auks

The coasts of Spitsbergen and Greenland, on both sides of the Greenland Sea, are characterized by water masses from two highly contrasted sources (Buch 2000; Fig. 5.D.1). The West coast of Spitsbergen is dominated by the northward flowing Norwegian Atlantic current which is an extension of the relatively warm North Atlantic current. In contrast, the East Greenland coast is characterized by cooler, less saline water of the East Greenland current flowing southward from the central Arctic basin (Buch 2000). The two distinct summer isotopic habitats ($\delta^{13}\text{C}$ values) of the East Greenland and Spitsbergen birds reflect these two different oceanographic environments (Fig. 5.D.1). However, it is important to note that the $\delta^{15}\text{N}$ signatures measured on zooplankton (chick meals) from East Greenland and Spitsbergen were similar, and identical to the diet $\delta^{15}\text{N}$ value in Hornsund (S4) in a previous year (Harding et al. 2008). This suggests little spatio-temporal changes in $\delta^{15}\text{N}$ values at the base of the food web in the Greenland Sea and allows comparing little auk nitrogen signatures as reflecting their relative trophic position, with no detrimental effect linked to different $\delta^{15}\text{N}$ baseline levels.

The summer diet of little auks has been described in detail in previous studies (e.g. Karnovsky et al. 2003 and 2008, Harding et al. 2008). Here, only chick meals were collected, but the similar $\delta^{15}\text{N}$ isotopic values measured both in chick and adult blood samples strongly suggest that adult and chick little auks feed on similar prey. Therefore, results obtained in this study (isotopes and prey identification) confirm that birds from the different colonies and populations mostly feed on *Calanus* copepods in summer. However, several differences are apparent amongst colonies at large and smaller spatial scales (Fig. 5.D.2). For example, the main copepod species consumed by East Greenland (EG; *C. hyperboreus*) and Spitsbergen (S4; *C. glacialis*) birds differ, a result that mirrors prey availability at both sites (Karnovsky et al. 2003, Falk-Petersen et al. 2009). Moreover, the presence of sea-ice near the East Greenland colony allowed breeding birds to feed on the eponitic amphipod *Apherusa glacialis*. In Spitsbergen, the two northern colonies are also segregated from the two southern colonies by their $\delta^{15}\text{N}$ values (Fig. 5.D.4A). During summer, and according to the hypothesis of a bimodal foraging strategy (Welcker et al. 2009b), birds from S1 and S2 can reach distant feeding grounds where multi-year ice prevail during their long foraging trips of several hours. There, little auks can feed on *Apherusa glacialis*, an ice-associated amphipod (Søreide et al. 2008), which is known to have a low nitrogen isotopic signature (Tamelander et al. 2006). Consequently, it is likely that adults from the two northern colonies feed on a higher proportion of *Apherusa glacialis* than those from the two southern colonies for which these northern cooler waters are unreachable.

Temporal variability in the isotopic niche of little auks

Between summer and autumn, little auks from all studied colonies showed a drastic change in their diet (reflected by $\delta^{15}\text{N}$ isotopic ratio), with similar values for males and females. A previous investigation also found no sexual differences in the isotopic niche of little auks during the summer breeding season (Harding et al. 2008). The present investigation however extends these findings to the autumn and winter. Like the guillemots (*Uria* spp.), little auks perform transition from biparental to uni-paternal care prior to chick fledging (Harding et al. 2004). Females usually leave their colony earlier, while males accompany the chicks during fledging and the first period at sea (Stempniewicz 2001). Given these behavioural differences we expected that the autumn moulting grounds and migration routes may be different for the two sexes. Contrary to this expectation, our results indicate that both sexes have an identical isotopic niche and are therefore more likely to moult in the same

zones. The increase in little auks $\delta^{15}\text{N}$ values and thus of their feeding trophic level between summer and autumn is consistent with results obtained by Karnovsky et al. (2008) on little auks from the North Water Polynya, and with the ecology of copepods (Falk-Petersen et al. 2009). Indeed, soon after summer, *Calanus* spp. species are known to perform a vertical migration to depths of several hundred meters, where they become inaccessible to little auks, which can only dive to 40 meters (Harding et al. 2009a). During this period, little auks are expected to feed on alternate prey. Moreover, larger amphipods with a higher calorific value relative to copepods become more available in early autumn (Stempniewicz 2001), potentially also explaining this shift. Birds in North-West Greenland had high $\delta^{15}\text{N}$ ratios measured during autumn, during which they shifted their diets to feed on *Themisto* spp. and Arctic cod larvae (*Boreogadus saida*) (Karnovsky et al. 2008, Karnovsky & Hunt 2002). In a similar way, birds from East Greenland and Spitsbergen had high $\delta^{15}\text{N}$ ratios in autumn (similar to those measured by Karnovsky et al. 2008) and likely make a similar shift to feed on *Themisto* spp. and Arctic cod larvae that are present throughout North Atlantic surface layers during that period. During autumn, birds from all colonies displayed similar $\delta^{13}\text{C}$ values (except birds from S3; Fig. 5.D.4B). Existing information about Spitsbergen populations suggest that birds move quickly after the breeding season to ice-filled areas of the West Greenland Sea and start to moult there (Stempniewicz 2001). Information about movements or wintering of East Greenland populations is scarce and moulting places unknown. However, our results indicate that in autumn, breeding birds from East Greenland and Spitsbergen moult in a similar isotopic habitat/water mass, possibly in the West Greenland Sea.

The pattern of changes of bird trophic levels between autumn and winter is different for the East Greenland and Spitsbergen colonies. Birds breeding in East Greenland fed in winter at a lower trophic level than during autumn but similar to that in summer. This second dietary shift may reflect the end of herbivorous copepods diapause that return to food-rich surface waters and consequently become again available to diving little auks. Indeed, the ascent of copepods is mostly synchronized with the phytoplankton spring bloom which occurs from the end-February/early-March at different places of the winter range of little auks throughout the North Atlantic (Henson et al. 2009). In contrast, birds from all Spitsbergen colonies adopt a different feeding strategy during winter. $\delta^{15}\text{N}$ values show that little auks maintain a high trophic level during the winter that is similar to that in the autumn and most likely reflects a diet based on *Themisto* and Arctic cod larvae (Karnovsky et al. 2008). During the winter moult, Greenland and Spitsbergen populations share similar habitat/water mass

(similar $\delta^{13}\text{C}$ isotopic ratios), but are probably in distinct areas where prey availability is different at a smaller spatial scale. Interestingly, during all the inter-breeding season, birds from S3 clearly adopted a different strategy and moult in different water masses than birds from all other colonies (Fig. 5.D.4). Mechanisms underlying such a difference remain unknown and merit further investigation.

The isotopic niche of birds wintering off South-West Greenland

During the autumn, birds shot off South-West Greenland (WG) had identical isotopic niches as those from other colonies (with the exception of S3). This suggests that birds were moulting in similar water masses, feeding on the same prey, and therefore probably sharing similar ice-filled areas of the West Greenland Sea with other seabirds. These results also suggest that WG birds originate either from East Greenland or from Spitsbergen. However, during winter, they occupy a different isotopic niche than birds from Spitsbergen and occupy a different water mass (different $\delta^{13}\text{C}$ values) than EG birds, even if consuming similar food (similar $\delta^{15}\text{N}$ values). Therefore, it seems that wintering birds caught off Nuuk (WG) represent a different population than those sampled during summer. However, it is important to note that the analysis performed on winter bird blood samples reflects isotopic signatures from January, a period during which birds are still on their wintering grounds. In contrast, analyses performed on breeding bird head feather samples reflect isotopic signatures from the March moult, during which birds already start their spring migration (Stempniewicz 2001). Consequently, and even if both tissues represent the winter dietary and isotopic niche, they are separated by a period of about 1-2 months during which birds probably moved, potentially affecting their $\delta^{13}\text{C}$ isotopic ratios. Therefore, these isotopic results are not totally comparable and have to be interpreted carefully, supporting the fact that further studies are necessary to confirm bird location during the different seasons.

Conclusions

Consideration of temporal and spatial variation in seabirds feeding ecology is essential to a better understanding of how they adapt to environmental stochasticity, and of how varying constraints affect their survival. Few studies have investigated seabird diet across seasons using stable isotopes on different tissues (e.g. Cherel et al. 2008; Quillfeldt et al.

2008b), while others have compared different populations during a specific period (e.g. Cherel et al. 2006). However, hardly any study considered both variables simultaneously in a seabird species. Presenting two distinct moults per year, both occurring during a short time window, and with a geographic distribution covering a wide range of current regimes and water characteristics (Stempniewicz 2001), little auks are excellent candidates to study spatio-temporal variation in feeding ecology by way of stable isotopic analyses. Using these particularities, our study is therefore one of the first to track trophic niche variation in a seabird across the annual cycle while comparing strategies adopted by birds from distant colonies.

We showed that during their inter-breeding season, individual little auks display an important seasonal change in diet, and highlighted significant variations between colonies and populations at both small and large spatial scales. Our study also provides the first description of the winter feeding ecology of little auks and gives important insights into their moulting and wintering grounds. Sharing similar isotopic niches in the autumn, birds breeding in East Greenland and Spitsbergen as well as those wintering off South-West Greenland seem to moult in the same area, potentially allowing exchanges between populations.

Little auks originated from all the North Atlantic are capable of exploiting a wide range of prey, ranging from calanoid copepods to fish larvae (this study, Karnovsky et al. 2008). Such information is essential since it indicates that spatio-temporal dietary flexibility might enable little auks to feed on zooplankton species which currently do not occur in the North Atlantic. Such species are bound to invade oceanic areas subject to global warming (Beaugrand & Reid 2003). The capacity of little auks to survive upon these new resources will condition the fate of their populations in a warming Arctic.

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Contrasted ‘cultural’ migratory strategies in a sympatric high-Arctic seabird duet

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Abstract

At the onset of winter warm-blooded animals inhabiting seasonal environments either remain resident and face degraded living conditions, or migrate towards more suitable habitats. While the origins and evolution of migratory choices have been extensively studied, their consequences on avian energy balance and winter survival are poorly understood, especially in cryptic species such as seabirds.

Using miniaturized data loggers and a thermodynamic model (Niche Mapper™) we investigated the activity levels and the energy expenditure of the closely-related, sympatrically breeding Brünnich’s guillemots (*Uria lomvia*) and common guillemots (*U. aalge*) from Svalbard. In winter the former population migrates to south Greenland, while the latter remains resident to the Barents and the Norwegian Seas. Overall, we show that Brünnich’s guillemots have lower flying activity, equal diving activity, and 18% lower total energy expenditure than common guillemots during the inter-breeding period. Brünnich’s guillemots therefore apparently face better wintering conditions. However, their population is declining in Svalbard, whereas the common guillemot population is currently increasing by 6% per annum. We propose that this difference is due to substantial anthropogenic pressure such as hunting on Brünnich’s guillemots wintering off Greenland. Further, we speculate that differential wintering strategies of these closely-related, sympatric species may be due to self-organised asymmetries resulting in ‘cultural’ differences.

Keywords: common guillemots, Brünnich’s guillemots, data loggers, dispersal, energetics, winter survival

E-1. Introduction

Climate seasonality affects most of the planet and is particularly marked across temperate, boreal and polar regions. Fluctuating environmental conditions associated with this phenomenon, such as changes in light levels, temperature, rainfall, and resulting food availability significantly affect endothermic animals (Stenseth 2002, Scantlebury et al. 2005, Vasey 2005) by challenging their energy balance (McNamara et al. 2008). Winter-time, for instance, is primarily marked by colder conditions and a decrease in day length, which both increase thermoregulatory costs while diminishing food availability (Broggi et al. 2003). Winter therefore features an energetic bottleneck which potentially affects the survival of organisms in seasonal environments, and ultimately shapes their population dynamics (e.g. in marine mammals: Ochoa-Acuña et al. 2009, terrestrial mammals: Schmidt et al. 2008 or in birds: Maldonado et al. 2009).

Among the many morphological, physiological and behavioural responses allowing an animal to face winter energy constraints, such as hibernation (e.g. Tanaka 2006), daily torpor (e.g. Turbill 2009), nocturnal hypothermia (e.g. Nieminen 2005) or huddling (e.g. Gilbert et al. 2007), migration appears as an attractive strategy. Indeed, this behaviour results in the avoidance of difficult winter conditions via movement towards energetically less challenging areas (Berthold et al. 2003). Birds, with their ability to fly distances of up to several thousand kilometres (e.g. Guilford et al. 2009), are obvious candidates for migration, but not all of them choose this strategy. In the autumn, birds from temperate to polar regions may: 1) stay and overwinter at the same place (residency), or 2) move towards lower latitudes (migration). Residency entails increased living costs due to degraded environmental conditions which migrants avoid. However, migration also affects avian energetics, notably through an increase in flight activity which requires elaborate energy management *en route* (Klaassen 1996, Shmueli et al. 2000, McWilliams et al. 2004). Migration timing, behaviours and associated costs have also a clear impact on bird fitness and survival (Møller 1994, Weber et al. 1998, Klassen 2003).

Interestingly, different species or sub-populations occupying sympatric breeding grounds can adopt different migration strategies, notably by using different flyways and therefore by wintering in different areas (Helbig 1991). Studying sympatric groups thus appears as a powerful way to assess the specific impact of inter-breeding conditions since birds share a

common environment during the breeding season. Such studies are nonetheless seldom done (Bearhop et al. 2005, Rolshausen et al. 2009).

While passerines and waders are the primary targets of migration studies, seabirds have been largely neglected, essentially because of technical difficulties. Indeed, most seabirds are offshore during the entire inter-breeding period, where they are difficult or even impossible to observe directly. This results in a lack of winter-time information about their movements, distribution, behaviour, and energetics. Such knowledge is nonetheless particularly important since this period is equally crucial for seabirds as it is to land birds, notably by conditioning adult winter survival, the most important life-history trait in these long-lived species (Lebreton et al. 1992). Today, the use of new biotelemetry tools finally opens new avenues in the study of the ecophysiology of wintering seabirds (e.g. Grémillet et al. 2005a, Rey et al. 2007, Green et al. 2009, Guilford et al. 2009).

The winter in Arctic and North Atlantic waters is a particularly drastic time-period during which seabirds have to cope with high wind speeds and frequent storm events, elevated relative humidity, extremely low air and water temperatures as well as short daylight periods and diminished food availability (Fort et al. 2009). Moreover, these ecosystems are critically challenged by ongoing climate change (Grémillet & Le Maho 2003, Stendel et al. 2008) which may severely affect seabird winter energetics, behaviour and survival (Oedekoven et al. 2001, Grosbois & Thompson 2005, Fort et al. 2009). It is therefore essential to investigate seabird winter migration strategies in these particular ecosystems.

Brünnich's guillemots (*Uria lomvia*) and common guillemots (*U. aalge*) are among the most abundant seabird species of the North Atlantic marine ecosystem (Gaston & Jones 1998). They are also respectively the 1st and the 4th prey biomass consumers in the North Atlantic (the 3rd and the 7th worldwide) (Brooke 2004). Both of them therefore play a crucial role in the energy flow through Arctic marine food webs. Both species of these diving seabirds are known to feed essentially on fish species, capelin (*Mallotus villosus*), Polar cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*) being the favourite prey of Brünnich's guillemots while herring (*Clupea harengus*), sprat (*Sprattus sprattus*), sandlance (*Ammodytes spp.*) and capelin are consumed by common guillemots (Barrett et al. 1997, Rowe et al. 2000, Wilson et al. 2004). Brünnich's guillemots also feed in a smaller extent on various crustaceans and squids (Falk & Durinck 1993, Barrett et al. 1997, Gaston & Jones 1998). Importantly, these two species also have a very close morphology and appearance (Brown 1985, Gaston & Jones

1998). Body mass measured in common and Brünnich's guillemots is 1093 ± 26 g and 1040 ± 26 g, respectively (this study). Despite their obvious ecological importance in Arctic and North Atlantic ecosystems, and the regular occurrence of events of winter mass-mortality (Gaston & Jones 1998, Gaston 2004), little is known about the inter-breeding biology of these two species and how they cope with challenging winter conditions. However, new information about their winter movements indicates that these two sympatric species, breeding in common areas of the High-Arctic, adopt two different migration strategies, thereby facing highly contrasted winter environments. Indeed, Brünnich's guillemots breeding in Svalbard perform a long southward migration to winter off south Greenland coasts (Bakken & Mehlum 2005, Steen et al. *unpublished*). Conversely, common guillemots from the same region stay close to their breeding site during winter, in the Barents and Norwegian Seas, above the polar circle, without any pattern of large movements (Gaston & Jones 1998, Anker-Nilssen et al 2000, Steen et al. *unpublished*). These two closely-related, sympatric breeding species consequently reply very differently to seasonal constraints via different strategies which may result in equally different survival rates and population dynamics.

In this study, we compared the behaviour and the energetics of common and Brünnich's guillemots over the entire inter-breeding season using biotelemetry tools to understand how they cope with the different environmental conditions encountered during their winter movements, and how these two distinct migratory responses affect their energy balance and potentially their population trends. Specifically, we tested the hypothesis that the migration strategy displayed by Brünnich's guillemots was more profitable than the residency strategy typical of common guillemots, both at the individual and the populational level.

E-2. Materials and Methods

Study sites, species and data-loggers.

During the 2007 breeding season, 45 geolocation archival tags (LTD 2400; Lotek Wireless, St. Johns, NF, Canada; mass in air = 5.5g; diameter = 11mm; length = 35mm) were deployed on common and Brünnich's guillemots nesting at Bjørnøya (Bear Island; 74°21'N, 19°05'E; n=10 and n=15, respectively) and on Brünnich's guillemots nesting at Ossian Sarsfjellet (Spitsbergen; 87°56'N, 12°27'E, n=15). Attached to conventional leg rings used for individual identification, these tags were programmed to record time, pressure, external

temperature and light every eight minutes through the 2007-2008 inter-breeding period, defined as extending from September 1st 2007 to May 31th 2008 (Gaston & Jones 1998, Steen et al. *unpublished*).

In July 2008, all resighted equipped birds from Ossian Sarsfjellet and Bjørnøya were recaptured at their colony. In total, 12 of the 30 loggers deployed on Brünnich's guillemots were recovered (seven from Ossian Sarsfjellet and five from Bjørnøya). Ten of these 12 loggers succeed in recording depth, light and temperature while two only recorded depth and temperature. Seven loggers ran for the whole inter-breeding season, while the five others recorded data for 1, 5, 5, 5 and 7 months. All ten loggers deployed in common guillemots in 2007 were retrieved in 2008. Five of them recorded all three parameters for the entire period, while one recorded depth only and the last four failed.

All birds recaptured were sexed according to the protocol described by Fridolfsson and Ellegren (1999) to identify a potential sex effect on seabird behaviour, time-budget and energy balance.

Time-budget analysis:

Weekly time-budgets consisting of time per week allocated to flying, diving and resting were compiled with Viewer 2000 (version 2.5.8; Lotek Wireless, St. Johns, NF, Canada) for the entire inter-breeding period using recorded depth and temperature data.

Diving behaviour.

Diving behaviour was analyzed from pressure data using MultiTrace-Dive (Jensen Software Systems, Laboe, Germany). Due to limited tag memory and the extended recording period the sampling frequency was set to 8 min. This sampling rate precludes detailed analysis of diving behaviour in these species for which dives usually last 90 sec in Brünnich's guillemots (Takahashi 2008) and 40 sec in common guillemots (Tremblay et al. 2003). Therefore only dives to depths >3m were analyzed (Elliott et al. 2008a; 2008b) and it was not possible to distinguish individual dives. However, following Gentry and Kooyman (1986), we defined diving phases as periods of successive recorded dives interrupted by surface time greater than 2220 seconds for Brünnich's guillemots and greater than 3000 seconds for common

guillemots (such inter-diving phases were spent either resting or flying). We also collected information on weekly maximum dive depth.

Flying behaviour.

Time spent flying by birds was estimated from external temperature. Indeed, when flying, guillemots tend to keep their legs into their plumage, thereby warming the tag towards body temperature (about 39°; Gabrielsen 1988, Croll & McLaren 1993). On the contrary, during other behavioural phases (diving or resting at the water surface) legs are not in the plumage and the tag is therefore in contact with cold water. Within our entire study area water temperature is lower than 10°C year-round, and we therefore considered that birds were in a flying phase when the recorded external temperature was higher than 10°C. As for the dive analysis, and following Gentry & Kooyman (1986), we considered two different flying phases when two flying events were separated by an inter-flight phase (spent resting or diving) greater than 1380 seconds for Brünnich's guillemots and greater than 1225 seconds for common guillemots.

Geolocation analysis:

The intensity of visible light was also recorded by loggers from June 2007 to June 2008 in ten Brünnich's guillemots and five common guillemots (Steen et al. *unpublished*). From these light level data, the daily latitudinal and longitudinal positions of birds were estimated throughout the inter-breeding season using Viewer2000 software (version 2.5.8; Lotek Wireless, St. Johns, NF, Canada). Given the inaccuracy of latitude estimation from light recordings during equinoxes (Hill 1994), all clearly affected estimated locations were excluded from the analysis (one week before and one week after the vernal and the autumnal equinoxes). Geolocation data were then corrected using an iterative forward/backward-averaging filter (McConnell et al. 1992) to remove any location that required unrealistic flight speed and any location situated on land.

From these geolocation data, we calculated the average weekly location of each bird throughout the inter-breeding period as well as the climate conditions associated with these locations and therefore encountered by seabirds. These climate parameters were water and air temperatures, wind speed and relative humidity (ICOADS monthly data provided by NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, (<http://www.cdc.noaa.gov/>)). All climate

data associated with bird locations were then entered into the bioenergetic model (see below). Common guillemots spent all the inter-breeding season at high latitude, close to their breeding site (Gaston & Jones 1998, Steen et al. *unpublished*) therefore exposed to a continuous darkness period. During the winter, the precision of the geolocators at such high latitudes is affected and it was only possible to determine a range of possible locations for these birds. Therefore, we considered that all common guillemots spent the entire inter-breeding season in an area between 68-78°N and 2-37°E (Steen et al. *unpublished*).

Bio-energetic analysis:

Seabird daily energy requirements were estimated throughout the inter-breeding period using Niche Mapper™. This thermodynamic model, designed to investigate energy balance and energy transfer in a variety of animals, has been previously validated to accurately estimate the energy demand of wintering seabirds, in particular guillemots in the North Atlantic (Fort et al. 2009). This model is composed by two different sub-models: (1) a climate model (micro2006c) compiled to calculate local microclimate. This sub-model uses calculated maximum and minimum shade and sunlight conditions for each location to subsequently compute local coolest and hottest available microhabitats for each hour of the day. (2) An endotherm model (endo2007d) which ultimately calculates the bird's energy requirements. This sub-model uses local environmental parameters generated by the microclimate sub-model (see above), as well as morphological, physiological and behavioural characteristics of the animal to solve the coupled heat and mass balance equations for the animal-environment exchanges, the gut and respiratory systems:

$$\text{Heat balance (W): } Q_{in} + Q_{gen} = Q_{out} + Q_{st}$$

$$\text{Mass balance (g/d): } m_{in} = m_{out} + m_{st}$$

Where Q_{in} is heat input (sum of absorbed incoming solar and infrared radiation reaching the skin), Q_{gen} is heat produced (by all body tissues), Q_{out} heat loss (by air convection, respiration, infrared radiation emitted through the porous feathers and conduction to the air and water) and Q_{st} stored heat (due to body temperature rising or falling). m_{in} is the mass input (food entering the gut or air entering the respiratory system), m_{out} is the mass lost (faeces or exhaled

air) and m_{st} the mass stored or absorbed (i.e. the food mass that must be absorbed by the gut given the food type and properties to meet daily energy demand).

Niche Mapper™ is described in detail in Porter and Mitchell (2006) and in Fort et al. (2009).

In this study, Niche Mapper™ was used to estimate energy requirements for a single adult for the Julian day at the centre of each week throughout the inter-breeding season. Birds' morphological and physiological properties used as input data are those described for Brünnich's guillemots in Fort et al. (2009). These two guillemot species being morphologically very similar (Gaston & Jones 1998), we assumed identical values for both species.

Behavioural properties.

Conduction, convection, evaporation and infrared radiation affect heat loss, heat gain, and energy expenditure. These processes are affected by the physical characteristics of the media surrounding the bird's body during its different activities (flying in air, diving under water, or resting at the water surface). We therefore incorporated bird behavioural parameters (flying, diving, and resting as defined above) into Niche Mapper™, as well as air and water temperatures, flight altitude, dive depth and flight speed. Average time budget (i.e. proportions of time spent flying, diving, and resting) for each week was estimated using recorded diving and flying behaviours (see above).

Statistical analysis:

Statistics for behavioural and energetic results were computed using the GenStat® statistical package (Genstat 2003). The effects of the time of the inter-breeding period, as well as those of sex and breeding site, on all recorded variables were analysed using residual maximum likelihood for repeated measures analyses (REML, Patterson and Thompson, 1971). In these analyses, week, sex and breeding site were entered as a fixed factors, and bird as a random factor. This method accounted for the fact that we were dealing with time series. In all REMLs, the effects of week, sex and breeding site were determined by comparing Wald statistic (expressed as χ^2 throughout the results) with F distributions (with a 5% significance threshold). All data are presented as mean \pm S.E.

E.3. Results

There was no effect of the breeding site on Brünnich's guillemots foraging behaviour, time budget and energetics along the inter-breeding season (all $P > 0.05$). Therefore, results for the two sampled sites were pooled in the following analyses. In the same way, (except when indicated in the following results), there was no effect of sex in both species and results for males and females were also pooled.

Brünnich's guillemot

Foraging behaviour.

The foraging behaviour of Brünnich's guillemots varied markedly along the inter-breeding season.

Average weekly maximum dive depth showed significant variability throughout this period ($\chi^2=468.37$; d.f=38; $P < 0.001$). Indeed, it increased progressively from September to January (from 57 ± 4 m to 145 ± 8 m; Fig. 5.E.1A). After that peak, it generally decreased until the end of the inter-breeding season to reach 51 ± 4 m at the end of May (Fig. 5.E.1A). Despite similar trends over this period, there was a significant difference between males and females ($\chi^2=4.68$; d.f=1; $P < 0.031$), with females diving shallower than males across the winter period (December to March).

The number of diving phases per week also varied significantly across the inter-breeding season ($\chi^2=241.87$; d.f=38; $P < 0.001$; Fig. 5.E.1B). After a slight increase until November (min= 21.2 ± 1.7 , max= 27.3 ± 1.3), it decreased to reach a minimum in early December at 15.1 ± 1.5 foraging phases per week. This variable remained relatively constant during the winter period and increased again from the end of February to late May (from 20 ± 2.7 to 27.3 ± 3.4 ; Fig. 5.E.1B). Spring values were similar to those observed in autumn.

However, the mean duration of these foraging phases followed a reverse, significant trend ($\chi^2=304.59$; d.f=38; $P < 0.001$; Fig. 5.E.1C). Indeed, the mean foraging phase duration was low and constant during the first few weeks (from September to mid-October: mean = 60.9 ± 3.3 min; Fig. 5.E.1C). At the end of October, and until mid-December, this value increased sharply, to reach a maximum duration of 181.1 ± 20.2 min. The foraging phase duration was

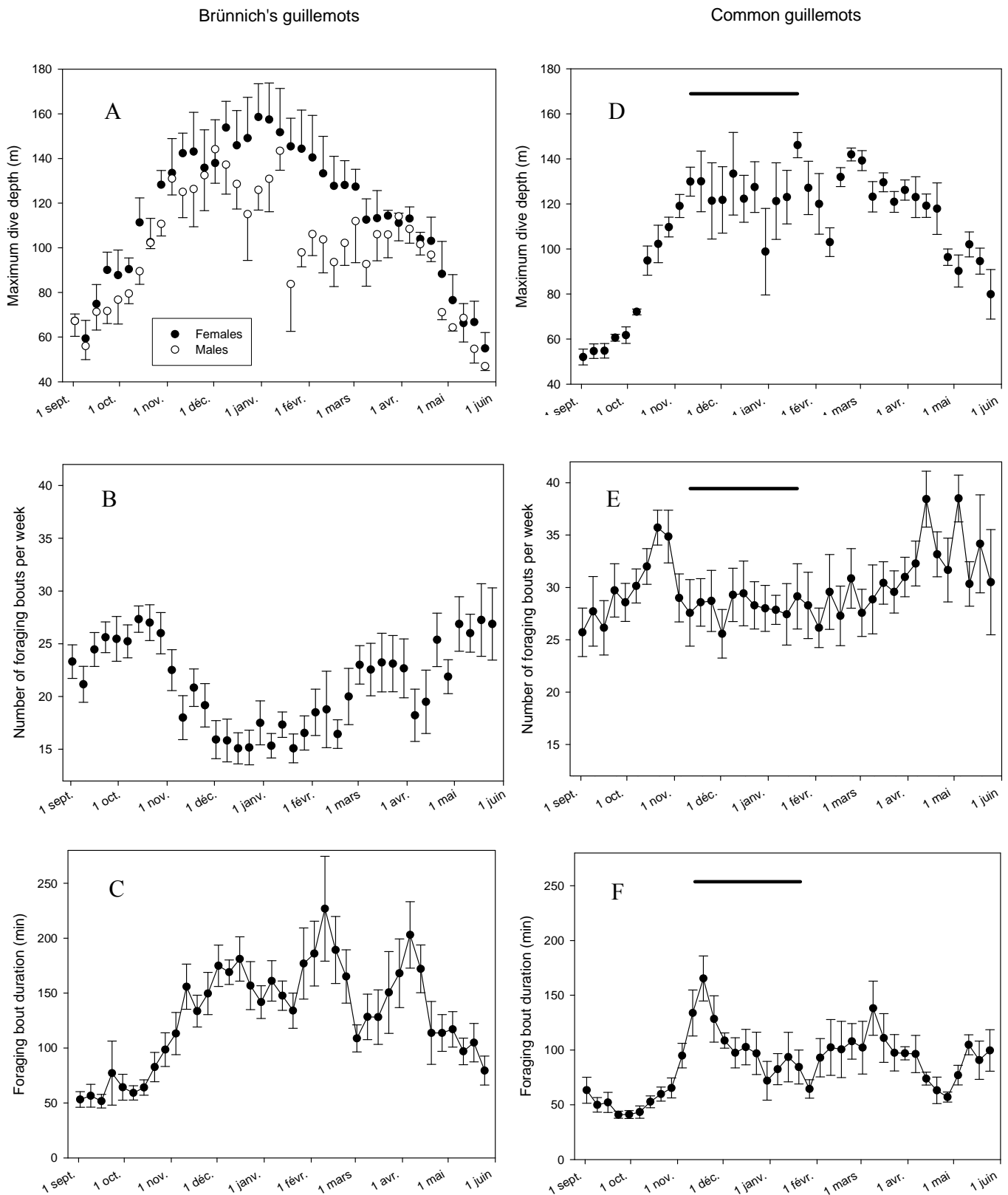


Fig. 5.E.1 Weekly foraging behaviours of Brünnich's and common guillemots throughout the inter-breeding season. Values are \pm SE ($n=5-12$). When significant differences existed between males and females, both sexes were represented separately. The straight line indicates the period during which common guillemots are exposed to polar night.

then much more variable with 2 peaks in mid-February and mid-April, respectively, before decreasing again towards the end of the inter-breeding season (Fig. 5.E.1C).

Time-budget.

The proportion of time spent diving per week followed a similar pattern as diving phase duration, with a significant effect of time ($\chi^2=225.36$; d.f.=38; $P<0.001$; Fig. 5.E.2A). Indeed, it progressively increased until the end of November from $11.8\pm 1.4\%$ to $25.4\pm 2.0\%$. From

December to the end of the inter-breeding period, this time spent diving was then relatively constant (mean = $25.4\pm 0.6\%$).

The proportion of time spent flying was highly variable throughout the season ($\chi^2=260.70$; d.f.=38; $P<0.001$; Fig. 5.E.2A) with two peaks during the migration periods (September-October and March). After the autumn migration it strongly and linearly decreased from September ($42.0\pm 4.2\%$) to January ($11.6\pm 2.6\%$). Flight time increased again slowly towards the end of winter, to reach a peak in late March (max = $23.7\pm 4.6\%$) and decrease again until the end of the inter-breeding period (Fig 5.E.2A).

On average, Brünnich's guillemots spent a total of 1407 hours diving and 1320 hours flying throughout the inter-breeding season.

Daily energy expenditure

Despite missing geolocation data around the equinoxes precluding energetic calculations for these specific periods, the predicted daily energy expenditure of Brünnich's guillemots presented significant variability across the inter-breeding season ($\chi^2=50.19$; d.f.=30; $P=0.012$; Fig. 5.E.3A). After a strong decrease in September and October, it slowly but continuously increased from November to May (from 1147 ± 76 kJ d⁻¹ early November to 1473 ± 71 kJ d⁻¹ late April; +12% in 27 weeks). In May, the energy expenditure strongly decreased to 1076 ± 175 kJ d⁻¹. However, during this last month, the low sample size for which location was known and thus energy expenditure estimated should be noted (n=3).

The total energy expenditure predicted for Brünnich's guillemots across the inter-breeding season was in average 2.8×10^5 kJ per bird (over 31 weeks). It represents in average 1290 kJ d⁻¹ per bird.

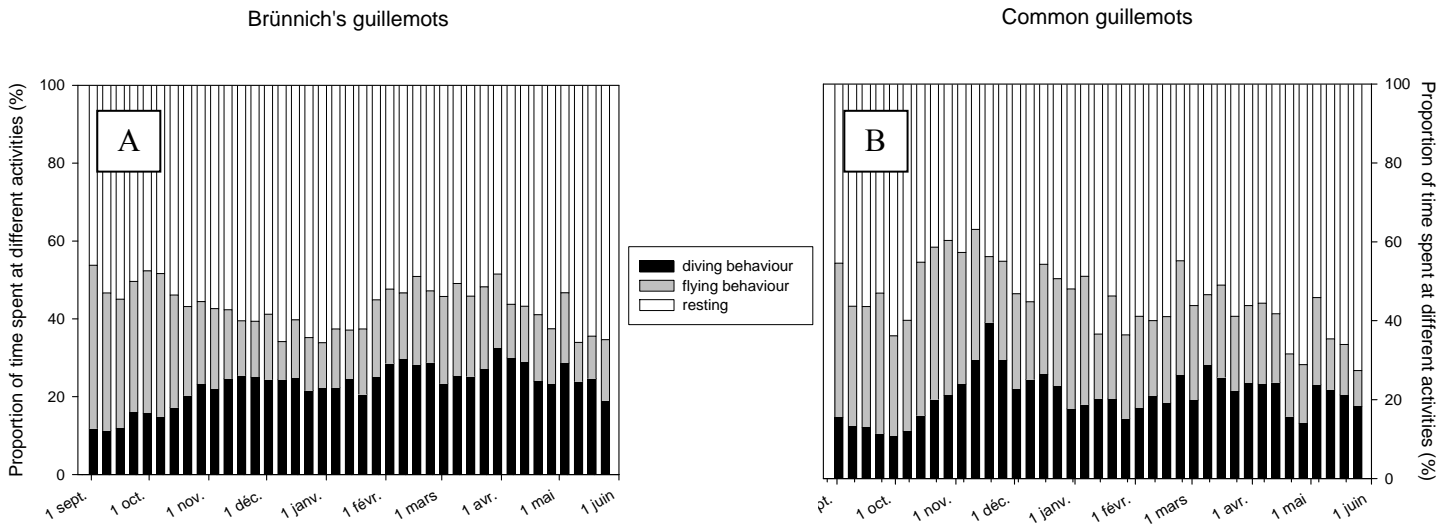


Fig. 5.E.2 Weekly time-budget (proportion of time devoted to different activities) of Brünnich's and common guillemots throughout the inter-breeding season.

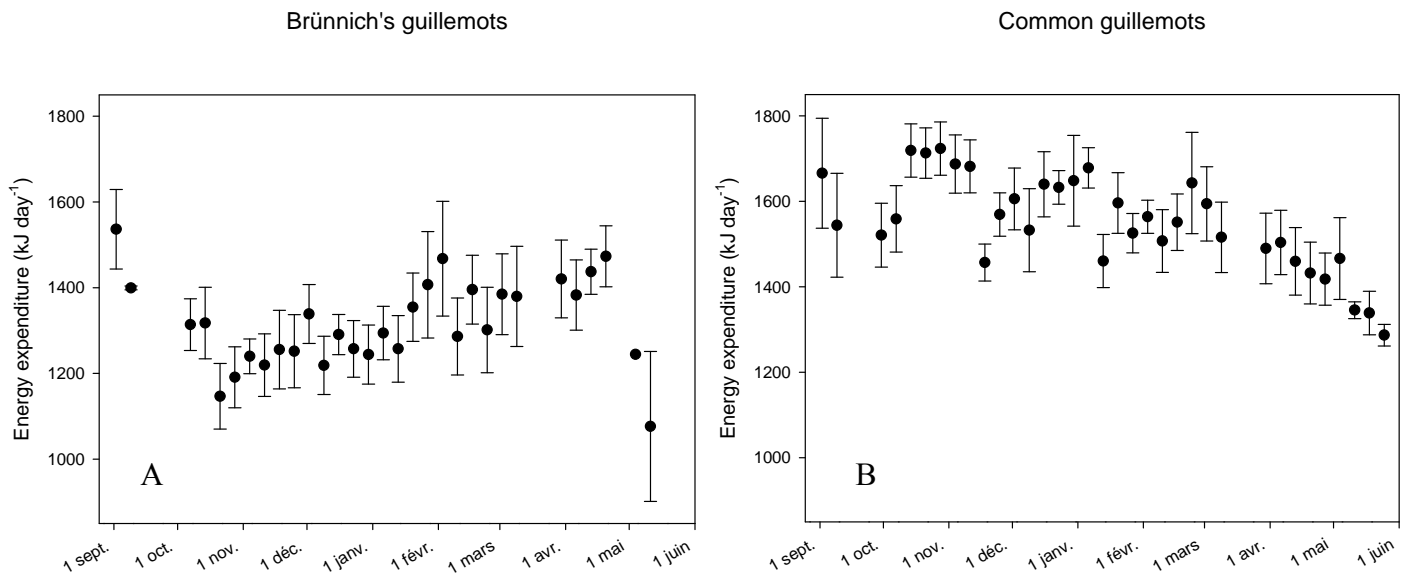


Fig. 5.E.3 Predicted daily energy expenditure of Brünnich's and common guillemots throughout the inter-breeding season. Values are \pm SE ($n=1-9$). Each data point represents the estimated expenditure for the Julian day at the center of each week.

Common guillemot

Foraging behaviour.

The average, weekly maximum dive depth recorded for common guillemots followed a similar pattern to that of Brünnich's guillemots, with a significant effect of the considered time-period ($\chi^2=323.01$; d.f.=38; $P<0.001$; Fig. 5.E.1D). Indeed, maximum dive depth sharply increased after the breeding season and until mid-November (min = 52 ± 3 m, max = 130 ± 6 m). It then remained constant, yet with a high inter-individual variability, throughout winter. After this period and until the end of the inter-breeding, maximum dive depth slowly and progressively decreased from 142 ± 3 to 90 ± 7 meters (Fig. 5.E.1D).

The mean number of diving phases per week also presented significant variability through time ($\chi^2=64.54$; d.f.=38; $P=0.004$; Fig. 5.E.1E). However, after a peak between September and November (min= 25.7 ± 2.3 , max= 35.7 ± 1.7), it remained constant over a long period until early-April (mean= 28.7 ± 0.3). It then increased at the end of the inter-breeding season, yet with high inter-individual variability (Fig. 5.E.1E).

The duration of these diving phases was also affected by the temporal phase ($\chi^2=140.82$; d.f.=38; $P<0.001$; Fig. 5.E.1F). It decreased slightly over the first 4 weeks. Then, it strongly increased during 8 weeks, to reach a peak of 165.3 ± 20.5 minutes (Fig. 5.E.1F). The average foraging phase duration then remained constant at ~ 90 minutes per phase, until the end of the inter-breeding phase.

Time-budget.

The proportion of time spent diving per week in Common guillemots followed a very similar trend to that of other parameters (number and duration of diving phases) with a significant effect of time ($\chi^2=133.72$; d.f.=18; $P<0.001$; Fig. 5.E.2B). However, both sexes responded differently ($\chi^2=6.94$; d.f.=1; $P=0.008$). From October to December, both sexes presented a strong increase in their foraging effort. Subsequently, the proportion of time spent diving decreased continuously in males, until the end of the inter-breeding period. In females, this proportion was divided by four in December, before increasing again from late-February, following similar values to those recorded for males (Fig. 5.E.2B).

The proportion of time spent flying in this species generally decreased throughout the inter-breeding season, yet with substantial inter-individual variability (max=39±10%, min=9±3%; $\chi^2=131.03$; d.f.=38; $P<0.001$; Fig. 5.E.2B).

On average, common guillemots individually spent a total of 1344 hours diving and 1615 hours flying throughout the inter-breeding season.

Daily energy expenditure

Predicted daily energy expenditures were generally higher in common guillemots than in Brünnich's guillemots, yet it decreased through the inter-breeding season from 1723±62 kJ day⁻¹ to 1286±25 kJ day⁻¹ ($\chi^2=118.33$; d.f.=34; $P<0.001$; Fig. 5.E.3B). Across the inter-breeding period, common guillemots had a total energy expenditure of 3.8×10^5 kJ per bird on average (over 35 weeks). It represents an average of 1551 kJ d⁻¹ per bird.

Species comparison

The weekly foraging effort was on average similar between the two species throughout the inter-breeding season ($t=0.45$, $P=0.65$). However, average weekly flying effort displayed by common guillemots was 22% higher than the one measured in Brünnich's guillemots ($t=2.48$, $P=0.02$). Finally, throughout the study period, Niche Mapper™ predicted higher daily energy expenditures in common than in Brünnich's guillemots ($t=8.90$, $P<0.001$).

E-4. Discussion

In the autumn, from temperate to polar regions, endotherms such as seabirds choose between two strategies: either face degraded environmental conditions on site, or migrate towards milder climates. The mechanisms behind this decision-taking, and its consequences for avian energetics and survival are well documented in a large variety of terrestrial birds and waders (Weber et al. 1998, Kvist et al. 2001, Gordo 2007). However, there is a lack of studies focused on seabirds, despite the fact that winter conditions also play a central role in modulating their survival, future breeding success and, ultimately, their population dynamics (Barbraud & Weimerskirch 2003, Rolland et al. 2009).

By focusing on two closely-related species of similar body size breeding sympatrically but adopting resident versus migrating strategies during the Arctic winter, we evaluated the implications of each strategy for their energy balance, and for their population trends.

Migrating Brünnich's guillemots

The migratory strategy adopted by Brünnich's guillemots allowed them to spend the winter off south Greenland (Bakken & Mehlum 2005, Steen et al. *unpublished*) where winter feeding conditions are good (Mehlum 1999, Boertmann et al. 2004) and climatic conditions (including the photoperiod) are less drastic than further north. Under these conditions, birds displayed significant behavioural plasticity, with important differences between the winter period and the rest of the inter-breeding season (Fig. 5.E.1A-C). Previous studies showed that Brünnich's guillemots usually forage at depths of 20-50m when breeding, with maximum dive depths >100m (Falk et al. 2002, Tremblay et al. 2003, Takahashi et al. 2008). Our results confirm these observations, with an average maximum dive depth of 50-60m at the end of the breeding season (Fig. 5.E.1A). Soon after, maximum dive depth increased sharply and remained high during the entire winter period before decreasing in the spring (Fig. 5.E.1A). Brünnich's guillemots probably modified their behaviour in response to a variation in winter prey availability, either by following prey vertical migration (Godø & Michalsen 2000, Rowe et al. 2000, Johansen 2002, Neat et al. 2006), and/or by feeding on a different prey type (Falk & Durinck 1993, Rowe et al. 2000). Further studies investigating guillemot diet along with diving behaviour are necessary to test these hypotheses. However, observed behavioural changes are unlikely due to variations in climatic conditions encountered during the inter-breeding season. Indeed, maximum dive depth is the only measured parameter which varies similarly in common and Brünnich's guillemots. Since these two species experienced very different climatic conditions, day length or light intensity, this similar trend is more likely to be linked to changes in prey vertical availability.

As a result of migration, Brünnich's guillemots also show high flexibility in their flying behaviour (Fig. 5.E.2A). They flew 35% and >20% per week during autumn and spring migrations, three and two times more than in the middle of the winter spent off south Greenland, respectively (Fig. 5.E.2A). This result indicates that feeding conditions and prey availability are good enough and/or that prey items are distributed continuously at a relatively small spatial scale, so that birds can meet their food requirements without having to move

long distances to find profitable prey patches. This might result from a larger part of crustaceans in Brünnich's guillemots diet (Elliot et al. 1990, Rowe et al. 2000), a food more stable and predictable than shoaling fish. Foraging effort nonetheless remained high from November to May compared to the breeding season (Fig. 5.E.2A; Falk et al. 2002, Tremblay et al. 2003). This pattern is similar to those observed in other high-latitude seabirds such as Great cormorants (Grémillet et al. 2005a) or European shags (Daunt et al. 2006, 2007). It therefore confirms that seabirds generally increase their foraging effort as day length decreases because the altered photoperiod affects both prey availability and the seabirds ability to detect them (Daunt et al. 2006, White et al. 2009).

Overall, the migration strategy adopted by Brünnich's guillemots allowed them to achieve significantly lower average and overall energy expenditures than common guillemots across the inter-breeding season (Fig. 5.E.3A). Moreover, during the winter-time, these expenditures were low compared to those predicted or measured during their breeding season (Barrett et al. 2002, Benvenuti et al. 2002). This strategy therefore also permits to Brünnich's guillemots to have decreased energetic costs during the season presenting the most challenging environmental conditions.

Resident common guillemots.

Common guillemots are not strictly resident wintering birds. However, they do not perform long migrations as the sympatric, closely-related Brünnich's guillemot, and remain 250-1000 km south of their colony during the entire inter-breeding season (Gaston & Jones 1998, Anker-Nilssen et al 2000, Steen et al. *unpublished*). In these areas of the Norwegian and the Barents Seas, they face climatic conditions substantially more challenging than those encountered by Brünnich's guillemots off south Greenland, with several weeks of continuous darkness.

Both guillemot species reached highest levels of maximum dive depth in the middle of winter, probably as an adaptation to altered vertical prey availability (see above; Fig. 5.E.1D). Beyond this pattern, the winter foraging behaviour of common guillemots appeared far more stable than that of Brünnich's guillemots (Fig. 5.E.1D-F), except for an activity peak in October/November, which corresponds to the beginning of the polar night. We speculate that birds may then take advantage of temporally and spatially higher prey abundance to fatten up

rapidly (e.g. in cods: Huse et al. 2004). Such a behaviour has already been observed in Arctic great cormorants which increase their foraging activity in the spring when stocks of spawning capelins become abundant (Grémillet et al. 2005a).

Crucially, and contrary to Brünnich's guillemots, common guillemots sustained high levels of flight activity across the winter period (Fig. 5.E.2B). Indeed, the proportion of time spent flying was high (>20% of their time-budget) during most of the inter-breeding season, although birds did not engage in a significant southward migration. Guillemots are critically dependent upon high-density prey patches for profitable foraging (Mehlum 1999) and actively track these feeding patches at different spatial scales (Fauchald et al. 2000). In contrast to southwest Greenland where wintering Brünnich's guillemots seemed to prey upon spatially continuous prey resources and therefore flew little, common guillemots wintering in the Barents and the Norwegian Seas may have exploited highly labile prey patches and therefore flew significantly more to track these resources. These results are in agreement with previous investigations of the (unstable) spatial overlap between guillemots and capelin patches in the Barents Sea (Fauchald et al. 2000), as well as with the notion that high densities of seabirds foraging on fish shoals of limited size might critically break-up the shoal structure via predation and disturbance, thereby making this local resource unprofitable for the birds (Lewis et al. 2001).

Overall, common guillemots wintering in the Barents and the Norwegian seas faced the double constraint of harsh climatic conditions and of labile prey resources, which induced putative energy expenditures far in excess of those predicted for Brünnich's guillemots wintering off Southwest Greenland (Fig. 5.E.3). Indeed, while the diving effort was relatively similar between both species (only 5% different), common guillemots spent in average 22% more time flying weekly than their congeners. This flying effort combined with higher thermoregulatory costs therefore compelled common guillemots to higher daily energy expenditures. Interestingly, during the first half of the inter-breeding season, these expenditures are as high as those predicted for breeding birds evolving in a relatively good environment (Barrett et al. 2002). It means that the residency strategy adopted by studied common guillemots did not allow them to decrease their energy demand during the harsh winter-time, making this period even more challenging.

Conclusions

Due to the elevated specific heat capacity of water the world oceans function as a giant buffer and seasonality is generally less marked in the sea than on land. As many marine organisms, seabirds therefore live in an environment which is less prone to seasonal contrasts than land birds, with resulting lowered migration pressure. Moreover, seabirds have often been thought to disperse at sea during the non-breeding period, with little evidence for distinct, directional migration patterns across different climate zones. Contrary to these assumptions, recent biotelemetry studies showed that seabirds do display spectacular migration patterns which dwarf the performances of their terrestrial relatives (Shaffer et al. 2006, Gonzalez-Solis et al. 2007, Guilford et al. 2009). These studies posit that many seabirds may actually live in an endless summer by constantly commuting between the northern and southern hemispheres (Shaffer et al. 2006). This may well apply to procellariiformes which have the capacity to glide over thousands of km, but it does not apply to seabirds relying on energy-demanding flapping-flight such as the alcids investigated in this study.

The decision to fly south in winter is therefore energetically not trivial for high-arctic guillemots. However, our comparative study of wintering common and Brünnich's guillemots from Svalbard strongly suggests that southward migration is a better option than high-arctic winter residency. Indeed, non-migrating common guillemots have an overall energy expenditure which is 18% higher than that calculated for migrating Brünnich's guillemots. This difference is even more striking during the winter period (27% between the two species in November-December). Surprisingly, this is not only due to harsher weather conditions further north, but also to the fact that common guillemots wintering in the Barents and Norwegian Seas flew significantly more in the middle of winter, probably to track labile prey patches.

Interestingly, inter-species differences found in the winter energy expenditure of the two species do not translate arithmetically at the population level. Indeed, while the population of common guillemots from the Bjørnøya has been rising by 6% per year since 1987 (Strøm et al. *unpublished*), the neighbouring population of Brünnich's guillemot is actually slowly declining (by about 3% per year for the last 10 years; Strøm et al. *unpublished*). This might be due to the fact that, despite better climatic and energetic conditions, Brünnich's guillemot overwintering in the northwest Atlantic are exposed to other factors of mortality such as high

hunting pressure (Elliot 1991, Falk & Durinck 1992) not undergone by common guillemots in the Barents and Norwegian Seas.

Beyond these climatic and anthropogenic constraints, we may wonder why common guillemots do not migrate south as the closely-related, sympatric Brünnich's guillemot? As extensively studied in land birds, migratory patterns have a genotypic and a phenotypic component (Berthold et al. 2003, Helbig 1991). Guillemots are therefore tributary to their evolutionary past, as well as to short-term adaptation. Current North Atlantic climatic conditions are changing rapidly, but their general 'normal' trends have been set since the end of the last glaciation some 15 000 years ago. It is therefore surprising that common guillemots persist in an apparently sub-optimal wintering strategy. We speculate that this intriguing pattern might be due to local 'cultural' patterns which may affect both the phenotypic and the genotypic component bird migratory behaviour. Under this principle, sympatric species, or even sub-populations of the same species might engage in contrasted strategies leading to spatial segregation. This has been observed in Cape gannets from neighbouring colonies which nonetheless used mutually exclusive foraging areas at sea (Grémillet et al. 2004). Different patterns of self-organisation within each seabird group have been proposed as the potential driver of these puzzling 'cultural' differences (Grémillet et al. 2004). Here we propose that the contrasted wintering strategies observed in North Atlantic guillemots also result from self-organisation within each group, which then becomes a heritable 'cultural' trait within each population. Such cultural traits can then be considered as the population-level occurrence of animal personality traits and behavioural syndromes (Biro & Stamps 2009). We posit that forthcoming studies of migration strategies will confirm the existence of such (potentially sub-optimal) 'cultural' patterns in a wide range of species.

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Chapitre 6

**Environnement estival :
une autre source de mortalité hivernale**



Introduction du chapitre

Les précédents chapitres nous ont permis de mettre en évidence comment l'environnement hivernal en Atlantique Nord, que ce soit par ses facteurs abiotiques ou biotiques, était susceptible de profondément marquer la balance énergétique et la survie des oiseaux marins qui y évoluent. Cela sera d'ailleurs discuté dans le dernier chapitre de cette thèse (Chapitre 7). Avant de refermer notre étude, nous avons également souhaité nous intéresser au lien potentiel pouvant exister entre l'environnement des oiseaux au cours de leur saison de reproduction (c'est-à-dire l'été) et leur survie hivernale. En effet, plusieurs études ont montré que cette période de reproduction était énergétiquement très difficile pour les oiseaux, notamment à cause de l'ampleur des soins parentaux (e.g. Golet et al. 1998, 2000). Ainsi, les conditions environnementales (notamment la disponibilité des proies) modulent également l'aptitude des oiseaux à maintenir une balance énergétique à l'équilibre au cours de l'été, déterminant de ce fait leur condition corporelle. Les oiseaux finissant leur saison de reproduction avec des conditions corporelles diminuées pourraient alors avoir du mal, après une migration elle aussi difficile, à survivre aux conditions hivernales très rudes.

L'objectif de cette dernière partie a donc été de tester l'hypothèse que « **les conditions environnementales rencontrées durant la saison de reproduction, en affectant l'énergétique et la condition corporelle des oiseaux avant l'hiver, vont moduler leur survie hivernale** ».

Pour cela, deux colonies de mergules nains situées au Groenland Est et au Svalbard ont été étudiées durant plusieurs années au cours desquelles des mesures de masse corporelle et de survie ont été effectuées et analysées en relation avec les conditions océanographiques locales.

Reproductive costs of a high Arctic seabird increase under adverse foraging conditions

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Abstract

Trade-offs between current reproduction and future survival are widely recognized but may occur only when food is limited: when foraging conditions are good, parents may be able to raise their offspring without compromising their own survival. We investigated these tradeoffs in the little auk (*Alle alle*), a small seabird with a single-egg clutch. First, we examined the body masses of breeding little auks under contrasting foraging conditions at two colonies, using baseline levels of corticosterone in breeding adults as a physiological indicator of foraging conditions in each colony-year, and found that end of season body mass was lower when conditions were poor. Second, we examined whether there was a fitness cost associated with low body mass, and whether this cost increased when food was limited. When foraging conditions were poor, breeding birds had lower overwinter survival rates but there was no effect of body mass on survival. In contrast, there was a positive relationship between mass and survival when conditions were good; the majority of birds had high survival and only light birds incurred a survival cost. This study suggests that higher body mass provides an important buffer against adverse winter conditions, and reproductive costs of little auks increase when conditions are poor. These results have important demographic implications because even a small change in adult survival may have a large effect on populations of long-lived species.

Keywords: *Alle alle*, body mass, dovekie, investment, life history tradeoff, little auk, prey availability, winter survival

F-1. Introduction

The cost of reproduction is a central concept in life history theory, whereby an increase in investment in the current reproductive period is predicted to result in a decrease in future reproduction, either through elevated mortality or a reduction in fecundity (Roff 1992, Stearns 1997). All species that breed more than once face a tradeoff between current and future reproductive success, and long-lived species are predicted to restrict their current reproductive investment because a small reduction in survival will have a large negative impact on lifetime reproductive output (Charlesworth 1980). Support for this prediction is, however, mixed. Although some studies have found that parents will abandon a breeding attempt or reduce their investment in offspring rather than compromise their survival (Wernham and Bryant 1998), other studies have shown that long-lived species do incur such reproductive costs (Reid 1987, Hanssen et al. 2005). Some of these differences may be explained by confounding factors such as food availability (Bryant 1988). When foraging conditions are good, parents may be able to raise their offspring without compromising their own survival; i.e., the tradeoff between current reproduction and survival may occur only when food is limited (Erikstad et al. 1998, Oro and Furness 2002). In other cases, these differences may be explained by low sample sizes in experimental manipulations, the direction of manipulation (an increase or decrease in reproductive effort; summarized in Velando and Alonso-Alvarez 2003), and species-specific differences in life-history traits such as clutch size and life expectancy (e.g., Erikstad et al. 1998). Further studies on species with contrasting life history traits and on wild populations across a wide range of breeding conditions (e.g. Weimerskirch et al. 2001) are therefore essential to understand the selective forces shaping reproductive investment strategies in long-lived species.

Measuring long-term reproductive costs in wild populations is complicated and usually requires the use of a short-term parameter that accurately signals a longer-term fitness cost (e.g. Reid 1987, Bryant 1988, Jacobsen et al. 1995). Changes in body mass are often presumed to be a good proxy for reproductive costs because of a presumed link to survival (Bryant 1979). However, whilst there is good evidence that body mass can decrease with increased parental effort (Golet and Irons 1998, Holt et al. 2002, Moe et al. 2002), and that low survival is associated with low body mass (Reid 1987, Golet et al. 1998), interpreting mass loss as a direct correlate of reproductive cost is complicated (Holt et al. 2002, Rands et al. 2006). It has been suggested that mass loss is an adaptive mechanism to reduce flight costs and thereby increase the efficiency of food delivery to offspring (Slagsvold and Johansen

1998). Thus, the most conclusive evidence that reproductive costs are expressed through a drop in body mass comes from the few studies that simultaneously measure parental body mass and either survival, fecundity or both (Golet et al. 1998, Golet and Irons 1999, Weimerskirch et al. 2001).

In this study we examined whether there are long-term costs associated with reproduction in the little auk (*Alle alle*), and whether or not these costs increase when food is limited (e.g. Erikstad et al. 1998, Oro and Furness 2002). The little auk is a small planktivorous diving seabird that lays a single-egg clutch annually (Stempniewicz 2001). There is experimental evidence for a decrease in the body mass of breeding little auks under conditions of increased parental effort (Harding et al. 2009b), but the relationship between body mass and long-term costs is unknown and very little is understood about how individuals optimize their lifetime reproductive success in a stochastic environment. Here, we use a two-pronged study approach. First, we examine how body mass varies with local foraging conditions. We predicted that little auk parents will have lower body reserves at the end of the season in years when foraging conditions are poor (Kitaysky et al. 1999, Golet and Irons 1999). Second, we examine whether there is a fitness cost associated with low body mass, and whether these costs increase when food is limited.

To examine these questions we measured adult body mass, overwinter survival rates and the fledging success of little auks over two breeding seasons at two colonies located in highly contrasting oceanographic conditions in the Greenland Sea (Welcker et al. 2009b). Differences in oceanographic conditions are likely to have a strong impact on food availability for little auks because of the restriction of different zooplankton species to different water masses (Scott et al. 2000, Beaugrand et al. 2002a). Large-scale patterns of zooplankton community distribution are fairly well established (e.g., Beaugrand et al. 2002a, 2002b), although quantifying the availability of prey to breeding little auks is more difficult because of a complex interplay between variables such as the patchiness, density, predictability and depth of the prey species, and the distance of prey from the colony. Because of these difficulties, indirect behavioral, physiological or diet-based indices are often used to characterize seabird foraging conditions (e.g., Piatt et al. 2007). In this study we use chick diet as an indication of prey species, and baseline levels of the steroid hormone corticosterone (CORT) in breeding adults as a physiological indicator of foraging conditions in each colony-year. CORT plays an important role in an individual's adaptive response to environmental stress (Wingfield et al. 1998, Romero et al. 2000, Pravosudov et al. 2001), and observational

and experimental studies of seabirds have shown that the secretion of CORT is largely driven by changes in food availability (Kitaysky et al. 1999, Kitaysky et al. 2007, Doody et al. 2008), with high levels of baseline CORT associated with poor foraging conditions. A negative relation between the abundance of zooplankton prey and baseline CORT has also been shown for the little auk (Karnovsky et al., unpublished data). Thus, in this study we use CORT as a proxy for differences in food availability between colonies and years.

F-2. Materials and Methods

Study system

Little auks breed in the Arctic and feed almost exclusively on zooplankton, with calanoid copepods (*Calanus* species) accounting for 84-96% of the energetic content of chick meals across their range (e.g., Pedersen and Falk 2001). Prey items are carried back to the chick at the colony in a gular pouch (a pocket of skin under their tongue; Stempniewicz 2001). Little auks are not sexually size dimorphic (there is a high degree of overlap between the sexes, with males 0-5% larger than females; Jakubas and Wojczulanis 2007). Both parents share incubation and chick-feeding duties, although there is evidence that the male does the majority of provisioning towards the end of the chick-rearing period, before escorting the fledgling to sea (Harding et al. 2004). Chicks are usually fed more than 5 meals per day (Stempniewicz 2001), and leave the colony when they reach, on average, 25 days old (Harding et al. 2004).

We studied two colonies located in contrasting oceanographic conditions in the Greenland Sea (Welcker et al. 2009b). Kap Höegh is located on the east coast of Greenland (Greenland; 70°43'N, 21°38'W), and Kongsfjorden is located on the north-west coast of Spitsbergen (Spitsbergen: 79°01'N, 12°25'E). Field work was conducted in Greenland in 2005 (11 June-20 Aug) and 2007 (23 June-9 Aug), and in Spitsbergen in 2006 (25 June-4 Aug) and 2007 (16 June-1 Aug). Median hatch dates in Greenland were 15 Jul in 2005 (min = 12 Jul; max = 29 July; range = 17d, $n = 42$ nests), and 18 Jul in 2007 (min = 12 July; max = 28 July; range = 16d, $n = 62$ nests). Median hatch dates at Spitsbergen were 30 June in 2006 (min = 27 June; max = 3 July, $n = 45$ nests) and 7 July in 2007 (min = 2 July; max = 11 July, $n = 42$ nests). Resights (see survival methods, below) were also conducted at Greenland in 2006 and 2008, and at Spitsbergen in 2008 to generate a more complete data-set of adult survival. We only resighted birds at the two study colonies, and so were unable to distinguish between

winter survival and dispersal. However, although our measure of survival only represents local winter survival rates, emigration (e.g. Brown et al. 2008) or a skipped breeding opportunity also result in reduced reproductive output.

The east coast of Greenland is characterized by cold Arctic water which is carried southward by the East Greenland Current (Bourke et al. 1987, Buch 2000), whereas the northwest coast of Spitsbergen is largely influenced by warmer Atlantic water that is brought to the area by an extension of the North Atlantic current (Aagaard et al. 1987, Buch 2000, Saloranta and Svendsen 2001). Differences in oceanographic conditions between the two sites are illustrated by mean sea-surface temperatures (SST, °C) during July, calculated from satellite data for an area of 4000 km² adjacent to each colony (see Welcker et al. 2009b for method details). During the four years of this study, the mean July sea surface temperature in Greenland was on average ca 5 °C colder than at Spitsbergen (mean SST: Greenland 2005 = 0.85 °C, 2007 = 0.06 °C; Spitsbergen 2006 = 5.85 °C, 2007 = 5.62 °C). The distribution and composition of little auk prey is closely linked to oceanographic conditions, with different zooplankton species adapted to different water characteristics (Scott et al. 2000, Beaugrand et al. 2002a). Arctic zooplankton communities are generally dominated by large, cold water species that store more lipids and are more energy rich than their smaller counterparts in warmer Atlantic waters (Scott et al. 2000).

Adult body mass

Breeding birds were captured at each colony using noose carpets (Pedersen and Falk 2001) and mist nets. Active breeding status was determined by the presence of a brood patch or full gular pouch (Stempniewicz 2001). Birds were captured during the late chick-rearing period in order to determine body mass near the end of the breeding season (mean capture time = 19d post median hatch date, min = 12d, max = 28d). Total number of birds caught in each colony year: Greenland 2005 $n = 71$, 2007 $n = 57$; Spitsbergen 2006 $n = 57$, 2007 $n = 78$.

The following two body dimensions were measured on all birds sampled: total head plus bill length (headbill) using Vernier calipers with precision of ± 0.1 mm, defined as the greatest distance from the back of the head to the tip of the upper mandible, and flattened wing length using a stopped ruler. All birds carrying meals for chicks were weighed and measured after the food had been collected. Blood was taken from the brachial vein for each bird for CORT

analysis and genetic sexing. Birds were banded with an individual identification band before release at the colony, and no bird was caught more than once.

Adult survival

A survival plot, measuring 9x12m in Greenland and approx. 50x50m in Spitsbergen, was marked with permanent stakes. Populations of individually marked breeding birds within the survival plot were established in Greenland during the incubation period in 2005 ($n = 147$) and in Spitsbergen during chick-rearing in 2006 ($n = 299$). A further 147 birds were banded in Spitsbergen in 2007 during both incubation ($n = 117$) and chick-rearing ($n = 100$). Morphometrics were taken for all ringed individuals, and a small blood sample (25 μ l) was taken for later sex identification.

A blind was set up in subsequent years in order to watch the birds without disturbing them, and birds were observed on the plot for 7 hours/day. Resighting effort was standardized between colonies, with each team aiming to resight at least 50% of birds observed the previous year during each primary resighting session. Resighting at Greenland was conducted during four primary sessions: one in 2006 and 2008 (2006 = 1-14 July; 2008 = 10-15 July), and two in 2007 (4-5 July and 5-10 August). Resighting in Spitsbergen was conducted during five primary sessions: three in 2007 (12-15 June; 3-6 July; 26-28 July), and two in 2008 (3-6 June; 8-12 July).

Corticosterone (CORT)

Baseline levels of CORT reflect short-term (days) variation in foraging conditions (Kitaysky et al. 2007). We therefore measured circulating levels of baseline CORT from breeding adults at 7-14d intervals across the breeding season in order to obtain an index of foraging conditions in each colony-year (Greenland 2005 $n = 171$, 2007 $n = 153$; Spitsbergen 2006 $n = 84$, 2007 $n = 210$). All birds were sampled according to a standardized technique (Kitaysky et al. 1999), with a blood sample (< 100 μ l) collected within three minutes of capture. It takes at least three minutes for levels of CORT to begin to rise in the blood in response to a stressor (Romero and Reed 2005), so this sample provided a baseline measure of circulating CORT and should not reflect the stress induced by capture. After blood collection, all samples were centrifuged, and plasma was preserved for later analysis. Spun red blood cells were stored for subsequent molecular sexing of individuals (Griffiths et al. 1998), using methods outlined in Handel et al. (2006).

Fledging success

Active nest-sites were marked in late incubation and visited every 2-3 days until hatching. Where an adult blocked the sight of an egg or chick, the adult's brooding posture and the presence of eggshell fragments were used as evidence of hatching. Nests at both colonies were visited at least every five days during the chick-rearing period; with nest checks increasing to every 2-3 days during the fledging period to accurately determine fledging success. Chicks that disappeared from the nest after 20 days old were considered fledged (Harding et al. 2004). Fledging success (defined as the number of chicks fledged or reaching 20d/ number hatched) was calculated for both the Greenland (2005 = 43 nests, 2007 = 61 nests) and Spitsbergen (2006 = 45 nests, 2007 = 42 nests) colony.

Chick diet

Prey that parent little auks brought back to their chicks (chick diet) was quantified in each colony-year (Kap Höegh, 2005 $n = 28$ meals, 2007 $n = 38$; Spitsbergen, 2006 $n = 46$, 2007 $n = 54$). Meals were removed from the gular pouch by gently opening the bill, and stroking the zooplankton out of the mouth; birds were then released in the colony (within five minutes of capture). Chick diet samples were preserved in 5% formalin.

Laboratory Analysis

Corticosterone: Plasma collected in 2006 at Spitsbergen was frozen prior to analysis, whereas plasma samples collected in Greenland 2005, 2007, and Spitsbergen 2007 were preserved in 70% ethanol. A trial conducted to allow the direct comparison of samples preserved by both methods showed there was a significant positive relationship between frozen CORT levels and ethanol preserved CORT levels (Harding et al. 2009b).

Total CORT was measured using a radioimmunoassay (Wingfield et al. 1992). Each sample was equilibrated with 2000 cpm of tritiated CORT prior to extraction with 4.5 ml distilled dichloromethane. Samples were reconstituted in PBSG-buffer and combined with antibody and radiolabel in a radioimmunoassay. Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. Inter- and intra-assay variations were less than 8% and 2%, respectively.

Data analysis

Body Mass and CORT: We used headbill and wing length to correct body mass for structural size by including them both as covariates in our analysis. We tested for a relationship between mass and measurements of structural size (Green 2001). Both wing ($r = 0.45$, $P < 0.001$), and headbill ($r = 0.56$, $P < 0.001$) increased with body mass, and transformations (loge or log10) did not improve the strength of the relationship. We therefore did not transform either measurement before analysis.

We used ANCOVA to examine annual and colony differences in body mass. Separate analyses were done for each study site, and colonies were compared for 2007 only. ANCOVAs were also used to assess interannual differences in baseline CORT within and between colonies in 2007. CORT values for Spitsbergen in 2006 were corrected for different storage methods used across years (frozen versus ethanol; Harding et al. 2009b) using the equation $Y = 1.1329X + 0.0297$, where Y = frozen samples and X = ethanol stored samples. All CORT data were then log-transformed to meet of the assumption of normality. We included sex as an additional predictor variable to assess potential differences between genders. Models containing all predictor variables and interaction terms were simplified by likelihood ratio tests.

Adult survival: To estimate survival rates we used Cormack-Jolly-Seber (CJS; Seber 1982, Pollock et al. 1990, Lebreton et al. 1992) models implemented in MARK (White and Burnham 1999). All individuals seen during each primary session were registered and given a 1 if seen during any given day and a 0 if not seen at all. All possible models allowing for time and sex varying survival were examined, and model selection was conducted following Lebreton et al. (1992) using AICc (Anderson and Burnham 1999). As a measure of over-dispersion we used \hat{c} that was calculated by dividing the deviance from the global model with the mean of the bootstrapped deviances (MARK: White and Burnham 1999). We adjusted for over-dispersion before model selection, using QAICc if the data were over-dispersed, and AICc if data were not over-dispersed (MARK: White and Burnham 1999). The data from the Greenland site only allowed us to model yearly survival. In contrast, we had three primary sessions during summer 2007 and two in 2008 for the Spitsbergen dataset. In the global CJS model, where survival varies both in time and between the sexes, the last survival and resighting probability are confounded. To enable full time and sex dependent

models for the two winter survival rates at Spitsbergen we chose to model monthly survival. For comparison purposes we also report winter survival estimates calculated following:

$\hat{\phi}_g = (\hat{\phi}_g)^m$ (**Equation 1:** where ϕ denotes monthly survival rate, g denotes sex and m is the number of winter months).

The variance for overall survival rate estimate is:

$\text{var}(\hat{\phi}_g) = \left[m * (\hat{\phi}_g)^{m-1} \right]^2 \text{var}(\hat{\phi}_g)$ (**Equation 2:** W. Kendall, personal communication),

We were interested in examining whether breeding body mass affected the following winter survival. Residual mass was calculated as the residuals from a multiple regression of body mass on headbill and wing length, and entered as a covariate in the analysis. The model structure as implemented in MARK does not allow missing covariate values. Therefore, because not all individuals were recaptured at all recapture occasions at Spitsbergen, we modeled the effect of residual body mass on winter survival separately for 06-07 and 07-08 at this colony. Similarly, the effect of residual body mass was estimated only for winter survival 05-06 at Greenland as we did not recapture and obtain body mass data during subsequent years. To allow for direct comparison of the effect of residual body mass on survival between years at Spitsbergen we only include birds caught during the chick-rearing period in this analysis.

F-3. Results

Body mass

The two size variables (headbill and wing length) explained a significant part of the variance in body mass in all analyses ($P < 0.05$ in all cases). When differences in size were accounted for, overall body mass at Greenland was on average 4% higher in 2007 than in 2005 ($F_{1,122} = 14.63$, $P < 0.001$), and this difference was larger in females than in males (sex*year interaction: $F_{1,122} = 5.70$, $P = 0.001$). Body mass also differed between years in Spitsbergen, with birds heavier in 2007 than 2006 ($F_{1,147} = 11.25$, $P = 0.02$; Fig. 6.F.1), but there was no difference between the sexes ($F_{1,146} < 0.01$, $P = 0.97$). When corrected for size, there was no difference in body mass between colonies in 2007 ($F_{1,130} = 0.09$, $P = 0.77$).

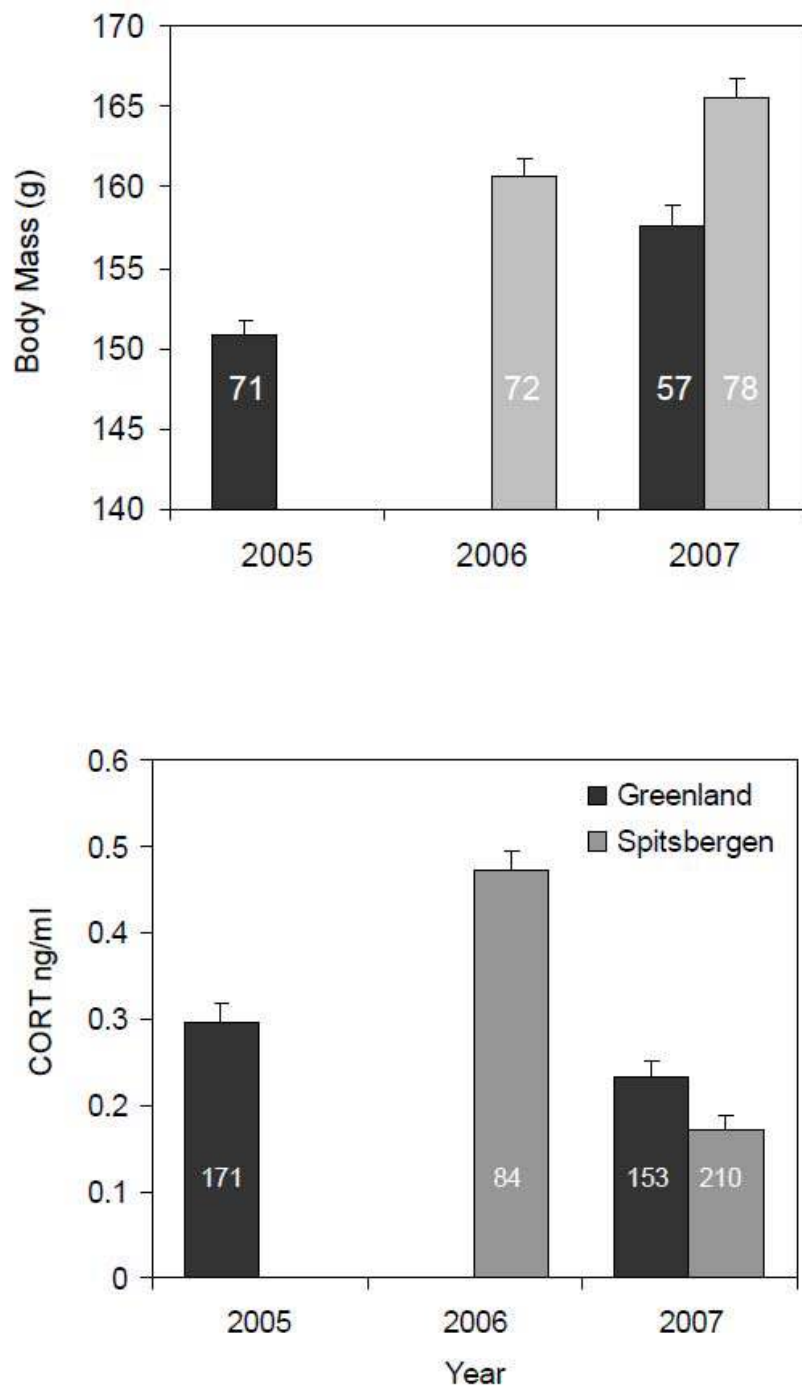


Fig. 6.F.1 Mean \pm 1SE body mass (g) and mean \pm 1SE LOG baseline CORT (ng/ml) of breeding little auks at the Greenland and Spitsbergen study sites. Numbers of birds sampled in each year are shown.

CORT

Baseline CORT in Greenland differed between years ($F_{1,322} = 4.87, P = 0.03$), with higher CORT in 2005 than in 2007 (Fig. 6.F.1). Baseline CORT also differed between years in Spitsbergen ($F_{1,292} = 94.31, P < 0.001$), with CORT higher in 2006 than 2007. CORT levels of birds in 2007 differed between colonies ($F_{1,361} = 6.06, P = 0.01$), with higher levels in Greenland. There was no difference in CORT between sexes at either Greenland ($F_{1,321} = 1.40, P = 0.2$) or Spitsbergen ($F_{1,291} = 0.63, P = 0.4$).

Adult survival

The best model describing survival indicated time-dependent survival at the Greenland colony and in Spitsbergen 2007. The Spitsbergen 2006 dataset indicated constant survival (Table 6.F.1). The effect of body condition, expressed as residual mass, on survival the following winter was variable. The model incorporating residual mass as a covariate for winter survival of birds caught in Greenland 2005 was not supported; the QAICc value was 1.94 larger than the best model (Table 6.F.1, Fig. 6.F.2). The best model for Spitsbergen birds caught in 2006 indicated that there was no effect of residual mass on subsequent winter survival (Table 6.F.1, Fig. 6.F.2). There was, however, a strong positive effect of residual body mass on winter survival in Spitsbergen birds caught in 2007 (Table 6.F.1, Fig. 6.F.2).

The distribution of residual mass of Spitsbergen birds caught in 2006 follows a normal distribution with fairly low variance, whereas the distribution of birds caught in 2007 had a significantly higher mean ($F_{1,383} = 44.9, P < 0.001$) and an almost four times larger variance around the mean (Fig. 6.F.3).

Fledging success

There was no difference in fledging success between years in Greenland (2005 = 92.3%; 2007 = 93.4%, Fisher's Exact: $P = 1.00$). In contrast, fledging success at Spitsbergen was significantly higher in 2007 (97.6%) than in 2006 (80.0%, Fisher's Exact test: $P = 0.015$).

Chick diet

Calanus copepods dominated the diet of little auk chicks at both colonies, comprising over 75% of the diet in each colony year (Fig. 6.F.4). *Calanus hyperboreus* was the most common prey species in Greenland, whereas *C. glacialis* was the most common in Spitsbergen and there were relatively few *C. hyperboreus* in the diet of chicks at Spitsbergen.

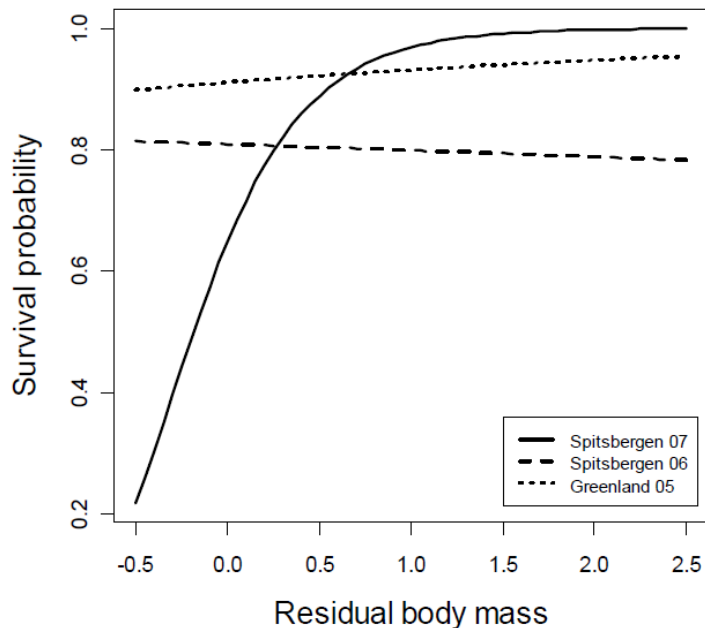


Fig. 6.F.2 The relationship between body mass (residual body mass) and the winter survival of little auks caught in 2006 and 2007 at the Spitsbergen colony and in 2005 at the Greenland colony using data estimates from the best model incorporating the residual body mass variable (see Table 6.F.1).

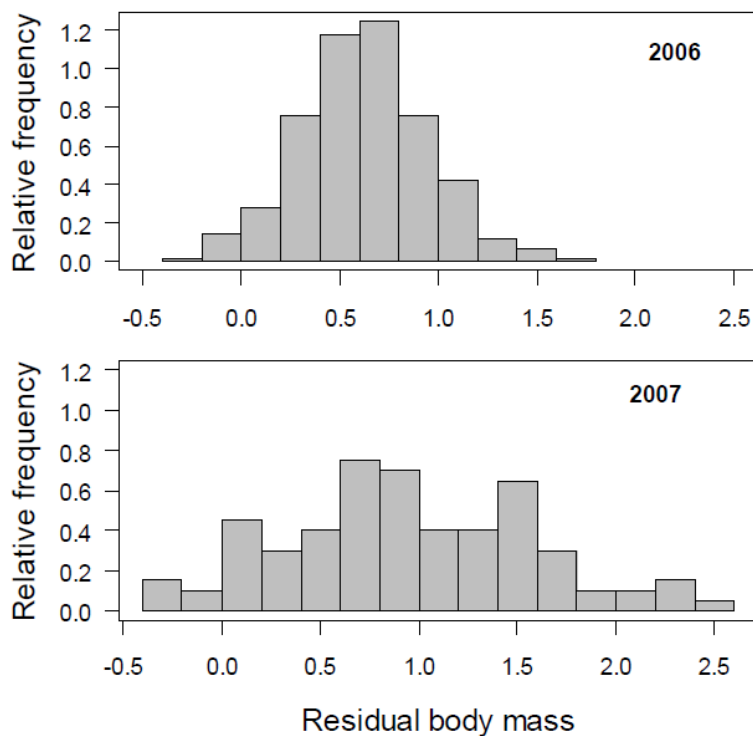


Fig. 6.F.3 Histogram showing the distribution (probability density) of residual body mass of birds caught in the survival plot in Spitsbergen during the chick-rearing period in 2006 ($n = 285$) and 2007 ($n = 101$).

F-4. Discussion

Foraging conditions and body mass

Differences in the oceanographic conditions surrounding each colony are clearly reflected in the species composition of chick meals. As expected, there was a much higher proportion of *Calanus hyperboreus*, a large energy-rich copepod associated with cold Arctic waters, in the diet of little auk chicks in Greenland. Despite the higher proportion of *C. hyperboreus* in Greenland, measurements of adult CORT suggest that foraging conditions in 2007 (the one year when CORT was measured at both colonies) were generally better in Spitsbergen. This result is presumably explained by a combination of factors such as prey density, weather and sea ice conditions that reduced the foraging efficiency of birds in Greenland. Interestingly, the higher number of *Calanus glacialis* than *C. finmarchicus* in the diet of Spitsbergen birds suggests they may have been preferentially feeding on this lipid-rich zooplankton.

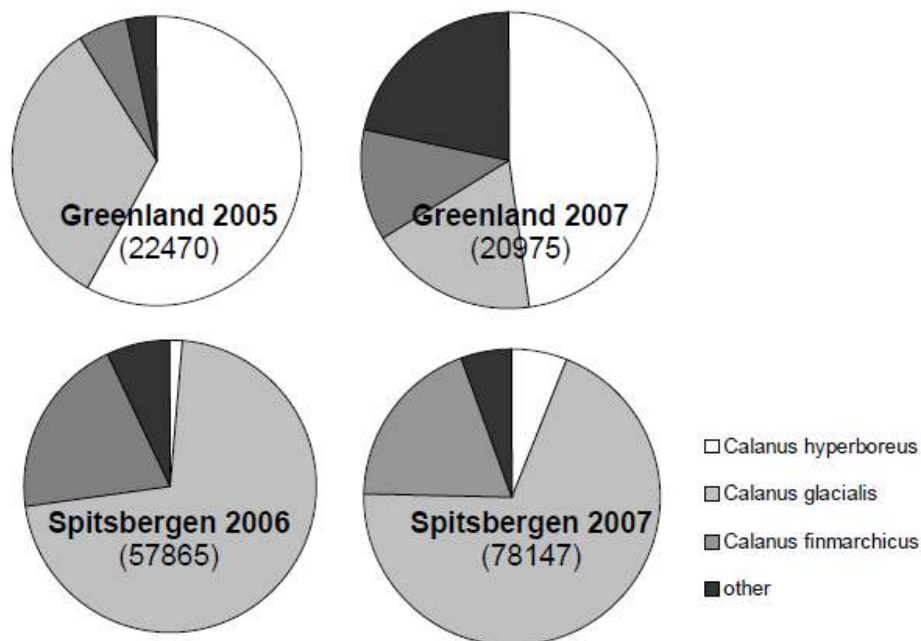


Fig. 6.F.4 Chick diet of little auks breeding at Greenland and Spitsbergen study colonies. Total number of individual prey items analyzed in each year is presented in each chart in parenthesis. Chick meals were collected using noose carpets at each colony (Greenland 2005 $n = 28$ meals, 2007 $n = 38$; Spitsbergen 2006 $n = 46$, 2007 $n = 54$).

Measurements of CORT also suggest that interannual differences in foraging conditions at each colony were more pronounced than spatial differences. Conditions in Spitsbergen were relatively good in 2007 and poor in 2006, and conditions in Greenland were relatively good in 2007 and poorer in 2005. The less pronounced interannual differences in Greenland most likely reflect the more stable oceanographic conditions along the west coast of the Greenland Sea (Buch 2000). However, although baseline CORT levels varied between colonies and years, the high fledging success in each study year suggests that foraging conditions encountered in this study were relatively favourable and all results should therefore be viewed within this context.

Low body condition is often associated with poor foraging conditions (Golet et al. 1998, Kitaysky et al. 1999, Weimerskirch et al. 2001, Pinaud et al. 2002), and is usually interpreted as the reallocation of limited reserves towards reproductive effort at the expense of body maintenance. In our study, end of season body mass at each colony was lower when foraging conditions were poor, results that support the prediction that parents will have lower end-of-breeding season energy reserves when foraging conditions are poor.

Body mass and survival

Spitsbergen

The relationship between residual body mass and survival differed between the two study years at Spitsbergen. There was a strong positive relationship between body mass and survival in 2007, the year with apparently better foraging conditions. The majority of birds had high survival and only light birds incurred a survival cost. Reduced winter survival has been associated with low body mass or condition at the end of the breeding season in a number of species (e.g. Haramis et al. 1986, Golet et al. 1998, Oro and Furness 2002). Mass-dependent winter mortality is most likely explained by a direct relationship between body mass and nutritional reserves, but may also reflect indirect mechanisms such as lower foraging efficiency of individuals in poor condition.

In contrast, survival rates were lower in 2006 than in 2007 (Fig. 6.F.2) but there was no relationship between residual body mass and survival in 2006. The actual difference in survival between years may have been even more pronounced because the apparent survival for Spitsbergen birds released in 2007 might be negatively biased because any individual that skipped breeding in the following year will be considered dead if it did not return to the

colony. The lack of a relationship between residual mass and survival in 2006 may be partially explained by the distribution of body mass. There was a more even distribution in the body mass of breeding birds caught in 2007, whereas there were relatively few heavy or light birds in 2006 (see Fig. 6.F.3). This pattern suggests that the quality of breeding individuals differed between years; only high quality birds bred when foraging conditions were challenging, whereas both low and high quality individuals bred when foraging conditions were good. The poor foraging conditions in 2006 are most likely responsible for the absence of heavy birds (e.g., Pinaud et al. 2002), and light birds may have either skipped breeding or abandoned the breeding attempt that year (e.g., Chastel et al. 1995, Anker-Nilssen 1992). A threshold in body condition has been proposed as a mechanism to ensure adult survival at the expense of current reproductive success in long-lived species (Chaurand and Weimerskirch 1994, Olsson 1997, Tveraa et al. 1998), and our data are consistent with the suggestion by Erikstad et al. (1998) that individuals should skip breeding when conditions are poor and show a steep increase in reproductive effort above a certain threshold of environmental conditions. The survival of birds breeding in 2006 was lower due to poor foraging conditions, whereas only poor quality individuals died after reproduction in 2007 when conditions were good.

Our results show that reproductive costs increase with parental effort under poor conditions, but are lower when conditions are good. The lower fledging success in 2006 suggests however that these parents were unable to fully buffer their chick from poor foraging conditions, even at an expense to their own body condition and survival. In contrast, the higher fledging success and generally higher survival of birds in 2007 suggest that parents were able to both increase parental effort and maintain their body condition when conditions were good. A recent study supports these results, showing that little auk parents had higher rates of daily expenditure with no apparent increase in mortality when foraging conditions were good (Welcker et al. 2009a). Weimerskirch et al. (2001) also found that yellow-nosed albatross (*Diomedea chlororhynchos*) parents were able to increase the allocation of resources to both body reserves and parental effort in good years to produce high quality offspring at no apparent cost.

Higher body mass may provide an important buffer against adverse winter conditions in little auks, with a buffer of reserves allowing parents to successfully rear their chick without a survival cost when conditions are good. Although reproductive costs in long-lived species have been shown to increase when conditions are poor (Oro and Furness 2002, this

study), yellow-nosed albatross parents did not compromise their survival when conditions were poor (Weimerskirch et al. 2001). Species-specific differences in life history traits such as adult longevity and the plasticity or clutch size (e.g. Erikstad et al. 1998) may explain why parents of some species safeguard their survival when conditions are poor whereas other species accept a reproductive cost. Albatross have a longer life expectancy than little auks, and may therefore be predicted to be more conservative in reproductive investment.

Greenland

We can make fewer conclusions about the effect of body mass on the survival of birds from Greenland because we have only one year of data, and these birds were caught during the incubation period (see methods). Body mass during chick-rearing is likely to be more reflective of parental investment over the whole reproductive event, or, birds caught earlier in the season may have subsequently abandoned breeding. Additional years are therefore required to determine whether there is a relationship between end of chick-rearing body mass and survival at the Greenland colony, and compare this relationship to Spitsbergen.

Conclusion

In conclusion, our results suggest that body mass provides an important buffer against adverse winter conditions and that reproductive costs are higher when conditions are poor. We found a difference in the relationship between body mass and survival between two years of study at one colony; additional research is now required to determine whether this pattern holds, and to fully understand how food availability affects the reproductive strategy of little auks. Further work should also employ state-dependent dynamic models to examine how changes in body reserves determine changes in parental care decisions at an individual level (e.g. Webb et al. 2002), and whether reproduction affects individual fecundity (Hanssen et al. 2005) in addition to survival.

Life history theory predicts that long-lived species should be conservative in their current reproductive investment, because a small reduction in survival will have a large negative impact on lifetime reproductive output (Charlesworth 1980). Contrary to this expectation, a number of studies have shown that survival rates can be affected directly by food availability (e.g., Oro and Furness 2002, Olsson and van der Jeugd 2002), and indirectly by climate change through changes in the food chain (e.g., Harris et al. 2005, Sandvik et al. 2005). Our study has shown that breeding little auks do sometimes pay a survival cost, and

these costs are higher when conditions are poor. Little auks feed on zooplankton, and the distribution and composition of zooplankton communities is linked to oceanographic conditions, with different copepod species adapted to different water characteristics (Scott et al. 2000, Beaugrand et al. 2002b). The restructuring of zooplankton communities associated with changes in the North Atlantic current system (Hurrell 2000) and predicted changes in water temperature may therefore directly affect little auk food availability, and this could have an effect on adult survival. Even a small change in adult survival will have a large effect on the population size of long-lived species (Doherty et al. 2004) and high variability in survival rates are also expected to decrease long-term population growth rates (Schmutz 2009).

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Table 6.F.2 The parameter estimates from the three best models are given. Model description follows those of table 1. Winter survival is denoted by the two years and monthly summer survival is subscribed as either MS incubation (*inc*) or MS chick rearing (*ch*). Winter survival and SE for both Spitsbergen releases are estimated following equations 1 and 2 (see text for details).

Greenland	Model	Period	Survival	SE	Resighting probability	SE		
	Phi(t) p(.)	6-May	0.907	0.06	0.879	0.052		
		7-Jun	0.596	0.084	0.879	0.052		
		8-Jul	0.736	0.118	0.879	0.052		
Spitsbergen	Model	Period	Survival	SE	♀ resighting probability	SE	♂ resighting probability	SE
Released 06	Phi(.) p(g+t)	7-Jun	0.825	0.005	0.81	0.05	0.878	0.035
		MS- inc	0.983	0.003	0.542	0.064	0.667	0.056
		MS - ch	0.983	0.003	0.516	0.064	0.643	0.058
		8-Jul	0.836	0.006	0.701	0.064	0.798	0.05
		MS-inc	0.983	0.003	0.835	0.058	0.896	0.04
Released 07	Phi(t) p(g+t)	8-Jul	0.968	0.021	0.614	0.073	0.916	0.045
		MS-inc	0.886	0.035	1.000	0	1.000	0

Table 6.F.1 The best 10 models for adult survival at the Spitsbergen and Greenland colonies. We follow standard labeling where Φ denotes survival, p denotes resighting probability and whether the Residual Body mass (RM) was included or not. Both Φ and p can vary with time (t) sex (g) or be constant. In models denoted t^*g the parameter varies independently between the sexes and in those denoted $(t+g)$ it varies in time but the two groups show the same trajectory over time. The data was over-dispersed for the Greenland dataset ($\hat{c} = 3.14$) and the Spitsbergen birds released in 2006 ($\hat{c} = 2.57$), hence for those two datasets we use QAICc as measure of fit while for the Spitsbergen 2007 dataset we use AICc.

Greenland	Φ	p	Covariate	QAICc	Delta QAICc	Num. Par	QDeviance
	t	const		156.49	0	4	148.37
	t	const	RM	158.43	1.94	5	148.24
	g+t	const		158.47	1.97	5	148.28
	t	g		158.55	2.06	5	148.36
	t	g		158.55	2.06	5	148.36
	t	t		158.55	2.06	5	148.37
	t	t		158.55	2.06	5	148.37
	g+t	t		160.52	4.03	6	148.26
	g+t	g		160.54	4.05	6	148.28
	t	g+t		160.58	4.08	6	148.31

Spitsbergen 06	Φ	p	Covariate	QAICc	Delta QAICc	Num. Par	QDeviance
	const	g+t		641.2	0	7	627.08
	g	g+t		642.45	1.24	8	626.28
	const	t		643.69	2.48	6	631.59
	t	g+t		644.11	2.9	10	623.86
	const	g*t		644.52	3.31	11	622.22
	g	t		645.26	4.06	7	631.14
	g+t	g+t		645.4	4.2	11	623.1
	g	g*t		645.87	4.66	12	621.51
	t	g+t	RM	646.15	4.95	11	623.85
	g+t	g+t	RM	647.45	6.25	12	623.1

Spitsbergen 07	Φ	p	Covariate	AICc	Delta AICc	Num. Par	Deviance
	t	g+t	RM	200.31	0	5	189.95
	t	g*t	RM	202.28	1.96	6	189.76
	g+t	g+t	RM	203.51	3.2	7	188.82
	g*t	g+t	RM	203.51	3.2	7	188.82
	g*t	g*t	RM	203.51	3.2	7	188.82
	t	g+t		210.42	10.11	4	202.18
	g	g*t		211.39	11.07	6	198.87
	g+t	g+t		211.39	11.07	6	198.87
	g*t	g+t		211.39	11.07	6	198.87
	g*t	g*t		211.39	11.07	6	198.87

Chapitre 7

Synthèse & Perspectives.



I) Synthèse des résultats

Grâce à une approche multidisciplinaire couplant écophysiologie, écologie alimentaire et comportement, ce travail de thèse s'est attaché à répondre au mieux à la problématique posée. Il s'agit ainsi de la première étude à allier ces différentes approches et à combiner diverses méthodes théoriques et empiriques afin de produire une étude synthétique de l'écologie hivernale chez les oiseaux marins. Centrée sur des espèces clés de l'écosystème arctique et nord atlantique, son objectif était de comprendre les réponses de ces oiseaux marins face aux conditions environnementales et aux événements climatiques extrêmes rencontrés en hiver, mais aussi de mettre en évidence les conséquences possibles de ces réponses sur leur survie. Nous nous sommes pour cela focalisés sur un paramètre central commun à tous les endothermes : la balance énergétique (Blem 2000, voir Brown et al. 2004). Nous avons ainsi décomposé cette balance pour étudier tour à tour 1) les conséquences des conditions climatiques rencontrées sur leur dépense énergétique et 2) l'impact d'un changement de disponibilité des proies sur leur écologie alimentaire et donc sur leur acquisition d'énergie. Par des études réalisées à une échelle individuelle mais aussi populationnelle, nous avons pu appréhender les réponses adoptées par les oiseaux leur permettant de maintenir leur balance énergétique à l'équilibre et d'assurer leur survie.

I-1 Conditions climatiques et dépense énergétique : impacts directs sur la survie

Déterminer la dépense énergétique d'un oiseau marin par des mesures directes pendant sa période de non-reproduction s'avère extrêmement difficile. Ainsi, les études théoriques et la mise en place de modèles de bioénergétique apparaissent comme la meilleure alternative. Parmi les différents modèles permettant d'étudier l'énergétique de vertébrés endothermes, nous avons montré que l'approche basée sur la thermodynamique est celle qui permet d'estimer de manière la plus précise les dépenses énergétiques des oiseaux au cours de l'hiver, lorsque les données de terrain sont rares. Nous avons donc mis en place et utilisé un nouveau modèle de thermodynamique basé sur les échanges de chaleur entre un organisme et son environnement et permettant de calculer la dépense énergétique de vertébrés aquatiques plongeurs (Niche Mapper™).

Grâce à l'utilisation de ce modèle, modifié et adapté aux oiseaux marins, nous avons mis en évidence le rôle de l'environnement hivernal sur la balance énergétique et donc indirectement

sur la survie des mergules nains et des guillemots de Brünnich. Tout comme chez d'autres espèces d'oiseaux marins des milieux polaires (e.g. Grémillet et al. 2005a), les conditions climatiques difficiles rencontrées entre novembre et décembre, et notamment les températures de l'air et la vitesse des vents, augmentent de façon très importante la dépense énergétique quotidienne des oiseaux hivernant en Atlantique nord-ouest. Ces conditions créent ainsi un goulot d'étranglement énergétique chez des espèces faisant face simultanément à une forte augmentation de leur dépense énergétique et à une diminution de leur efficacité prédatrice et de leur capacité à acquérir de l'énergie. Ce goulot d'étranglement pourrait ainsi être une des principales raisons de la mortalité hivernale et des échouages massifs observés chez certaines espèces d'oiseaux marins sur les côtes canadiennes, américaines et nord-européennes.

I-2 Changements de la disponibilité alimentaire : réponses comportementales et acquisition d'énergie

Les organismes répondent de manières variées à la saisonnalité des conditions climatiques et notamment à l'arrivée de l'hiver. Parmi ces organismes se trouvent des proies elles-mêmes consommées par des prédateurs, lesquels doivent à leur tour s'adapter à cette saisonnalité et aux réponses de leurs proies. La période hivernale se traduit chez de nombreux animaux marins par des migrations verticales et/ou horizontales. C'est le cas de certains copépodes qui migrent à de fortes profondeurs pour y entrer en diapause (Falk-Petersen et al. 2009), de certaines espèces de poissons qui, elles aussi, peuvent migrer verticalement pour se retrouver dans des eaux plus profondes (e.g. Neat et al. 2006) ou horizontalement vers des zones plus au sud (e.g. Hobson et al. 2009). Ces déplacements et changements de distribution de proies potentielles entraînent une diminution de la disponibilité alimentaire qui pourrait affecter des prédateurs incapables de s'y adapter. Afin de faire face à ces mouvements et s'assurer une acquisition d'énergie suffisante à leur survie, ces prédateurs ont donc la possibilité d'adopter différentes stratégies en fonction du comportement de leurs proies préférentielles et de leurs propres limites physiologiques. Ils peuvent ainsi 1) suivre les proies dans leur déplacement vertical, 2) modifier leur propre distribution horizontale à la recherche de zones plus riches, ou 3) changer de proies et de régime alimentaire.

I-2-1 Changements de la distribution verticale (comportement de plongée)

Par le biais d'une étude comportementale, nous avons montré que lorsque les proies consommées pendant la saison de reproduction changent de distribution à l'arrivée de l'hiver mais restent disponibles aux oiseaux (i.e. à des profondeurs qu'ils peuvent atteindre), ceux-ci font preuve de plasticité comportementale. Elle leur permet de suivre les déplacements verticaux de leurs proies préférentielles. Multipliant leur profondeur de plongée maximale par trois, ils peuvent ainsi continuer de s'alimenter sur ces mêmes proies, ce qui leur permettrait de préserver leurs gains d'énergie. C'est ce que nous avons montré chez les deux espèces de guillemots étudiées. D'autre part, nous avons vu que les guillemots de Brünnich étaient également capables de modifier leur effort de recherche alimentaire, en augmentant notamment leur temps passé en plongée. Ceci pourrait leur permettre de maintenir une ingestion de proies suffisante, et de faire face à des conditions d'alimentation plus difficiles (avec entre autres une période d'ensoleillement réduite voire inexistante ; Daunt et al. 2006, 2007) entraînant une efficacité prédatrice plus faible (Finney et al. 1999). Une telle plasticité comportementale a également été mise en évidence chez diverses autres espèces d'oiseaux marins telles que les grands cormorans (*Phalacrocorax carbo*), les gorfous macaroni (*Eudyptes chrysolophus*) et 5 autres espèces de manchots (Wilson et al. 1993, Green et al. 2005, Grémillet et al. 2005a).

I-2-2 Changements de la distribution horizontale (migration)

La capacité de vol des oiseaux leur permet de parcourir rapidement de longues distances (Berthold et al. 2003). Les oiseaux marins ont donc la possibilité de fuir une diminution de la disponibilité alimentaire, de même que les conditions climatiques âpres et extrêmes de l'hiver, par de longues migrations géographiques. C'est ainsi qu'à l'arrivée de la saison hivernale, la plupart des espèces quittent leur site de reproduction et migrent à la recherche d'un environnement plus riche et moins contraignant où passer cette période (Shaffer et al. 2006, Guilford et al. 2009). Cependant, chez les alcidés caractérisés par un ratio surface alaire / masse corporelle très faible et un vol ardu (Pennycuick 1987), un tel comportement migratoire est coûteux d'un point de vue énergétique. Ainsi, alors que la plupart des espèces d'alcidés optent pour un déplacement horizontal de plusieurs milliers de kilomètres, d'autres telles que les guillemots de Troil privilégient la stratégie contraire, restant à proximité de leur site de reproduction (< 400 km), malgré les changements environnementaux. Un tel comportement sédentaire existe également chez d'autres espèces d'oiseaux marins (Ainley et al. 1998). La stratégie adoptée (migrer ou rester) risque donc d'avoir des conséquences importantes sur

l'écologie et la survie des oiseaux selon qu'ils engagent ou non des efforts énergétiques dans une migration, mais également selon l'environnement hivernal (alimentaire et climatique) rencontré sous chacune de ces deux stratégies. Nous avons donc confirmé chez deux populations d'espèces sympatriques¹³ de guillemots que ces stratégies différentes ont des conséquences sur le comportement et la balance énergétique des oiseaux. Des populations d'espèces migratrices telles que les guillemots de Brünnich se retrouvent au cours de l'hiver dans un environnement plus favorable en termes de disponibilité alimentaire et de conditions climatiques (Boertmann et al. 2004, Steen et al. *unpublished*). De par cette disponibilité, ils peuvent à la fois diminuer leur activité de vol et leur dépense énergétique quotidienne, mais aussi maintenir une acquisition d'énergie nécessaire pour faire face à cette dépense. En revanche, pour les populations d'espèces « résidentes » des milieux polaires telles que les guillemots de Troïl du Spitzberg, cette période apparaît comme plus difficile énergétiquement, malgré une absence de coûts migratoires. En effet, au cours de l'hiver, ces oiseaux doivent maintenir une activité soutenue (de vol et de plongée) qui, combinée à des conditions climatiques rudes, entraîne une forte dépense énergétique hivernale. Par conséquent, et de par les dépenses énergétiques associées, le choix de la stratégie adoptée pourraient avoir des répercussions sur la survie hivernale de ces deux espèces. Cependant, nous n'avons pas mis en évidence de lien entre ces dépenses énergétiques contrastées et la dynamique des deux populations étudiées puisque les guillemots de Troïl qui ont des besoins énergétiques supérieurs présentent une population croissante, au contraire de ce que l'on observe chez les guillemots de Brünnich. Cette tendance pourrait être le résultat d'autres facteurs agissant sur la mortalité hivernale des guillemots, et ce de manière plus importante chez les guillemots de Brünnich. Parmi ces facteurs possibles, la chasse semble jouer un rôle important. On sait en effet que les guillemots de Brünnich hivernants au large du Groenland font face à une pression de chasse considérable (Falk & Durinck 1992), pression à laquelle les guillemots de Troïl résidents de la mer de Barents ne sont pas soumis.

I-2-3 Changement de régime alimentaire

Certaines proies peuvent effectuer des migrations si importantes au cours de l'hiver qu'elles ne sont plus du tout disponibles à certains de leurs prédateurs, même par des déplacements verticaux ou horizontaux. C'est par exemple le cas des trois principales espèces de copépodes

¹³ On définit ici comme sympatriques deux espèces qui occupent les mêmes zones géographiques pendant une période donnée, mais qui ne peuvent pas se reproduire entre elles de façon viable.

de l'Atlantique Nord qui effectuent à l'automne, dans leur grande majorité, une migration verticale importante pour entrée en diapause à plusieurs centaines de mètres de profondeur (Falk-Petersen et al. 2009). Ils deviennent ainsi indisponibles aux oiseaux marins qui les consomment. Dans une telle situation de réduction extrême de la disponibilité alimentaire, la seule alternative viable semble être un changement d'alimentation pendant cette période. Cependant, certaines espèces sont spécialistes, inféodées à un type de proie particulier, et pourraient ne pas être en mesure d'effectuer un tel changement, subissant ainsi de fortes contraintes énergétiques.

Par une étude de l'alimentation combinant des approches directe et indirecte, nous avons montré qu'en réponse à la diminution de la disponibilité alimentaire pendant la migration verticale des copépodes, les mergules nains changent de régime alimentaire et se nourrissent de proies disponibles situées à des niveaux trophiques supérieurs (amphipodes et larves de poisson). Cette plasticité écophysologique, elle aussi déjà observée chez d'autres espèces (e.g. Elliot 1990, Litzow et al. 2002, Karnovsky et al. 2008) est particulièrement intéressante chez les mergules nains. En effet, cette espèce est considérée comme spécialiste, se nourrissant presque exclusivement de zooplancton et essentiellement de copépodes (Stempniewicz 2001, Harding et al. 2009a). Or on sait que face aux changements climatiques, les oiseaux marins n'auront comme choix s'ils ne veulent pas disparaître que de 1) modifier leur statut trophique et donc leur écologie alimentaire, et/ou 2) modifier leurs aires de distribution (Grémillet & Boulinier 2009). Ainsi, les espèces spécialistes sont souvent considérées comme extrêmement sensibles aux futurs changements climatiques car moins aptes que des espèces plus généralistes à s'adapter à des modifications de la disponibilité et de la distribution de leur ressource (Furness & Tasker 2000). Dans le cas du mergule nain, le changement de régime alimentaire mis en évidence montre donc une flexibilité possible chez cette espèce, flexibilité qui pourrait jouer un rôle important pour sa survie face à des changements environnementaux qui ont déjà un impact marqué sur la distribution des copépodes en Atlantique Nord (Beaugrand et al. 2002b, Beaugrand 2003).

Ces différentes études confirment donc que les oiseaux marins des milieux tempérés et subpolaires sont capables pendant l'hiver, pour s'adapter à la variabilité et à l'appauvrissement de la disponibilité alimentaire, de mettre en place différentes stratégies comportementales et écophysologiques. Elles leur assurent une balance énergétique à l'équilibre et donc leur survie.

Nos travaux ont cependant mis en évidence qu'il est nécessaire d'être prudent quant à la notion de disponibilité alimentaire et aux interprétations qui en découlent. En effet, même si l'Atlantique Nord est intensivement étudié depuis de nombreuses années, il est impossible de déterminer et de quantifier cette disponibilité pour l'ensemble de cette zone, ni au cours des différentes saisons. Pourtant, les oiseaux sont capables de fréquenter ce territoire dans sa quasi-totalité, s'alimentant dans des zones pour lesquelles nos connaissances du milieu et donc de la ressource sont nulles. Ainsi, sans remettre en cause les études sur la diapause hivernale des copépodes, ni même leurs résultats restreints à certaines zones géographiques particulières, nous avons montré qu'ils n'étaient cependant pas toujours généralisables. En effet, il apparaît que les mergules hivernants au large des côtes du Groenland ouest se nourrissent principalement de copépodes. Cela signifie donc qu'une quantité importante de ces organismes se retrouve dans les eaux de surface de l'Atlantique nord-ouest en hiver, ainsi disponible à leurs prédateurs (estimée entre 3900 et 7800 tonnes consommées par jour par les mergules nains).

I-2-4 Réponses aux contraintes environnementales : variations inter-populationnelles

Nous avons mis en évidence que les différentes populations d'une même espèce répondent de manière similaire aux mêmes variabilités et contraintes hivernales de leur environnement. C'est par exemple ce que nous avons observé chez les mergules nains où toutes les populations étudiées répondent de façon identique à un changement de la disponibilité alimentaire à l'automne (cette étude, Karnovsky et al. 2008). De même, les deux populations de guillemots de Brünnich étudiées ne présentent pas de différence dans leur réponse comportementale face aux conditions climatiques et alimentaires de leur site d'hivernage.

Cette similarité inter-populationnelle est un résultat important pour les futures études cherchant à comprendre l'impact des changements climatiques sur ces espèces. En effet, certaines populations d'oiseaux marins sont déjà en proie à des conditions environnementales changeantes. C'est par exemple le cas des populations du Spitzberg qui se trouvent dans un environnement relativement chaud et instable influencé par le courant Nord Atlantique (Buch 2000), à l'inverse des populations groenlandaises, canadiennes ou russes qui vivent quant à elles dans des environnements plus froids et plus stables.

L'étude et la comparaison de ces différentes populations et de leurs réponses aux conditions environnementales actuelles pourrait permettre, chez les alcidés et chez d'autres espèces de

prédateurs marins supérieurs, de mieux comprendre comment les populations réagiront face aux futurs changements de leur environnement. Ce type d'étude comparative est aujourd'hui l'objet d'un large programme international s'intéressant aux mergules nains, nichant de part et d'autre de la mer du Groenland, au cours de leur saison de reproduction (Welcker et al. 2009b, Karnovsky et al. *in press*). Il doit maintenant être étendu à un éventail d'espèces plus large et s'appliquer à la période hivernale

I-3 Reproduction et survie hivernale

La saison de reproduction peut, elle aussi, être une période énergétiquement difficile pour les oiseaux marins, notamment à cause d'un investissement parental coûteux (e.g. Golet et al. 2000). Au cours de cette période, les oiseaux peuvent faire face à des conditions environnementales contrastées, notamment en termes de composition, de distribution et d'abondance des proies, qui pourraient comme en hiver affecter leur survie hivernale au travers de leur balance énergétique. Afin d'élargir notre étude de l'impact des conditions environnementales sur la survie hivernale des oiseaux marins de l'Atlantique Nord et des réponses leur permettant de maximiser cette dernière, il nous a donc paru important de consacrer une partie de notre projet à la période de reproduction.

Grâce à une étude comparative effectuée sur différentes colonies de mergules nains, nous avons mis en évidence que l'environnement et les conditions alimentaires rencontrées pendant l'été ont un impact sur la survie hivernale des individus. Ainsi, les populations qui s'alimentent dans des conditions défavorables ont une survie hivernale plus faible, par des coûts de reproduction plus élevés qu'ils ne sont pas en mesure de contrebalancer. Ce résultat est important pour la dynamique des populations de mergules nains. En effet, le changement de distribution des communautés de zooplancton sous l'effet d'un réchauffement climatique (Beaugrand et al. 2002b) risque d'accroître le nombre de populations exposées à des conditions d'alimentation difficiles, ainsi qu'à la dégradation de ces conditions. Il pourrait alors profondément affecter cette espèce philopatric¹⁴ si celle-ci ne met pas en place, comme en hiver, de réponse spécifique à ces contraintes pendant la saison de reproduction (modification du statut trophique et/ou des zones de reproduction ; voir Grémillet & Boulinier 2009).

¹⁴ Une espèce philopatric est composée d'individus se reproduisant chaque année sur le même site, celui sur lequel ils sont nés.

II) Limites des méthodes utilisées, recommandations et perspectives

Les différentes méthodes utilisées au cours de ce travail de thèse nous ont donc permis d'étudier des facettes variées de l'écologie hivernale des alcidés. Cependant, prise indépendamment, chacune de ces méthodes présente certaines limites, notamment dans l'interprétation des résultats, et différents ajustements doivent être mis en place pour les futures études de ce type.

II-1 Méthode des isotopes stables.

Cette méthode apporte des renseignements précis et cruciaux sur le statut trophique d'un animal. Cependant, les interprétations en termes d'alimentation et de proies consommées sont souvent difficiles puisqu'il n'est pas possible de discriminer des proies ayant des signatures isotopiques similaires. C'est le cas des différentes espèces de copépodes retrouvées dans le milieu marin nord-atlantique qui constituent une importante source alimentaire chez les oiseaux marins. Afin de faire face à ces difficultés, de nombreuses études couplent cette méthode indirecte à une méthode directe d'étude du régime alimentaire. Chez les oiseaux marins, l'utilisation en parallèle de ces deux méthodes est possible au cours de la saison de reproduction (c'est par exemple ce que nous avons fait chez les mergules nains), mais apparaît beaucoup plus compliqué pendant l'hiver. Nous avons ainsi essayé au cours de cette thèse d'obtenir des contenus stomacaux d'oiseaux pendant la saison hivernale afin de déterminer de manière directe le régime alimentaire associé à une signature isotopique particulière. Cependant, le zooplancton et notamment les copépodes sont des proies très rapidement digérées. De ce fait, les contenus stomacaux récupérés sont dans leur très grande majorité impossible à identifier, empêchant l'étude précise du régime alimentaire de l'oiseau considéré.

Ainsi, un des objectifs à court terme serait d'échantillonner l'Atlantique Nord en hiver afin de récupérer, le long de transects, les différentes proies potentielles des oiseaux marins au cours de cette saison et dans diverses zones géographiques. Nous pourrions ainsi déterminer de manière précise les signatures isotopiques en azote ($\delta^{15}\text{N}$) de chacune des proies (par zone) pendant cette période. L'utilisation de nouveaux modèles associant signatures isotopiques du prédateur et celles de ses différentes proies (e.g. Harper 2007, Dang et al. 2009) permettrait alors de déterminer de manière plus fine le régime alimentaire des oiseaux hors reproduction et d'interpréter au mieux les résultats obtenus.

Une autre difficulté d'interprétation rencontrée lors de l'utilisation des isotopes stables dans l'hémisphère nord concerne les zones d'alimentation des oiseaux, renseignées par le ratio $\delta^{13}\text{C}$ (voir introduction et Fig. 2.3). Dans notre étude, nous avons seulement pu interpréter ces ratios en termes de masses d'eau et d'habitats occupés (similaires ou différents), mais pas en termes de localisation géographique plus précise tel qu'il est possible de le faire en hémisphère sud avec un gradient latitudinal de ce ratio. De ce fait, dans notre étude sur les mergules nains, nous avons mis en évidence qu'après la période de reproduction (pendant laquelle les oiseaux sont contraints de s'alimenter dans des zones similaires ; contrainte de « central place foragers », Orians & Pearson 1979), ils se dispersent pour occuper des aires d'hivernage différentes. Cette dispersion se traduit par une augmentation de la variabilité du ratio $\delta^{13}\text{C}$. Elle est également accompagnée d'une augmentation de la variabilité du ratio $\delta^{15}\text{N}$ qui reflète quant à elle des différences interindividuelles accrues du régime alimentaire. Cependant, cette méthode ne permet ni de déterminer où se trouvent ces différentes zones d'hivernage, ni de tester l'hypothèse que les zones d'hivernage occupées par les oiseaux et les conditions environnementales associées déterminent leur régime alimentaire et pourraient ainsi jouer un rôle indirect sur leur condition corporelle et leur survie. Deux objectifs de travail sont alors envisageables à court terme.

Le premier est de coupler les deux méthodes d'analyses isotopiques et d'utilisation d'appareils de géo-localisation tels que les GLS¹⁵. Cette combinaison permettrait ainsi de définir la localisation des oiseaux par les enregistreurs ainsi que leur niveau trophique associé, par les isotopes stables. Une telle association des deux méthodes a été utilisée avec succès très récemment chez quelques espèces d'oiseaux marins des milieux polaires et tempérés (Furness et al 2007, Phillips et al. 2007, 2009, Bost et al. 2009). Elle est actuellement en cours chez les mergules nains, et dirigée par des collègues norvégiens chez les guillemots de Troil et de Brünnich.

Le deuxième objectif est d'utiliser les proies échantillonnées le long de transects en Atlantique Nord pendant l'hiver (mentionnées plus haut) afin d'en déterminer cette fois les ratios $\delta^{13}\text{C}$. Cela permettrait de déterminer les ratios en carbone associés aux différentes zones géographiques, et donc de constituer une carte isotopique du zooplancton et des principales espèces de poisson en hiver dans ces régions. On pourrait ainsi, par comparaison avec les signatures isotopiques mesurées chez les oiseaux ($\delta^{13}\text{C}$), déterminer de manière plus précise

¹⁵ Se reporter à la définition en page 27

les zones géographiques occupées. L'avantage de cette perspective par rapport à l'utilisation d'appareils de géo-localisation est que, même si elle est plus lourde à mettre en place logistiquement, cette carte pourrait ensuite servir à d'autres études visant à déterminer les zones d'alimentation d'espèces de prédateurs marins de l'Atlantique Nord et de l'arctique, depuis les poissons carnivores jusqu'aux mammifères marins, en passant par les oiseaux marins.

Enfin, dans le cas précis de notre étude sur les mergules nains, l'utilisation d'enregistreurs combinée à des analyses isotopiques permettrait de confirmer que les différentes populations du Spitzberg et du Groenland Est muent à l'automne dans des zones communes situées dans la Mer du Groenland. Une telle information est très importante car elle permettrait de mettre en évidence des échanges génétiques possibles entre les différentes populations, soit par la formation de nouveaux couples sur ces sites entre individus ayant atteint l'âge de la première reproduction, soit par le recrutement de juvéniles à la recherche d'un site de reproduction.

II-2 Enregistrement du comportement de plongée.

Au cours de cette thèse, l'utilisation d'appareils miniaturisés enregistreurs de pression pour l'étude des comportements de plongée des alcidés, aura été la méthode la plus délicate à mettre en œuvre d'un point de vue logistique. En effet, malgré des progrès considérables réalisés depuis les dernières années, une limite s'impose toujours lors de leur utilisation : celle de la mémoire et du nombre d'enregistrements possibles. Ainsi, il est important de connaître cette limite et de l'utiliser en fonction de la question scientifique posée.

Lors de l'étude du comportement alimentaire des mergules nains, nous avons utilisé une fréquence d'enregistrement élevée (un point toutes les 2 secondes). Ce choix de fréquence était basé sur le temps de plongée observé chez cette espèce au cours de sa saison de reproduction (Harding et al. 2009a) et sur une étude de Wilson et collègues (1995b) ayant déterminé que seul un intervalle d'enregistrement $< 10\%$ de la durée moyenne d'une plongée permet une étude précise de ce comportement. Nous avons ainsi réalisé la première étude du comportement de plongée hivernal chez une espèce d'oiseau marin de petite taille. Nous avons pu déterminer avec précision la profondeur des plongées de ces oiseaux, les périodes consacrées à cette activité, leur budget-temps ou encore leur dépense énergétique. Cependant, une telle précision a pour conséquence un nombre d'enregistrements plus fréquent et donc une utilisation de la mémoire plus rapide. Cette contrainte ne nous a permis d'estimer ces paramètres que sur quelques courtes périodes de 24h réparties le long de l'hiver. Le risque qui

apparaît alors, mais qu'on ne peut éviter, est que certaines de ces périodes ne reflètent pas de manière exacte le comportement quotidien de l'oiseau hors-reproduction (à cause d'un épisode ponctuel de tempête par exemple). Par conséquent, il serait à présent intéressant de réitérer ces enregistrements en changeant cette fois le protocole de manière à n'enregistrer qu'une seule période de plusieurs jours consécutifs. Cependant, ce type d'étude devra soit se focaliser sur une période précise, soit utiliser ces appareils sur de nombreux oiseaux avec des phases d'enregistrement séparées et/ou chevauchantes afin de couvrir l'ensemble de l'hiver. On peut également penser que de nouveaux appareils avec une mémoire supérieure et permettant des enregistrements plus longs seront disponibles d'ici quelques années.

A l'inverse, lors de l'étude du comportement alimentaire des guillemots de Brünnich et des guillemots de Troil, nous avons décidé d'augmenter l'intervalle d'enregistrement (un point toutes les 8 minutes) afin de pouvoir maintenir l'étude sur l'ensemble de l'année. Cependant, une telle décision excluait une étude précise du comportement de plongée hivernal et nous a uniquement permis de nous focaliser sur une étude du budget temps et des profondeurs maximales de plongée.

II-3 Autres perspectives

II-3-1 Conservation des communautés d'oiseaux marins confrontés aux conséquences de la pêche industrielle.

Au cours de cette thèse, nous avons adapté un modèle de bioénergétique (Niche Mapper™, Porter & Mitchell 2006) afin de l'utiliser sur des organismes aquatiques et plongeurs tels que les oiseaux marins. Ce modèle apparaît aujourd'hui comme une très bonne alternative pour étudier de façon précise la balance énergétique et les besoins alimentaires de ces animaux tout au long de leur cycle annuel. Cette estimation des besoins en proies au niveau individuel est d'une grande valeur chez les oiseaux marins. En effet, à partir de ces résultats individuels, Niche Mapper™ permet l'étude de ces besoins à l'échelle des populations et des communautés et apporte donc une meilleure compréhension du rôle des oiseaux marins dans leur écosystème (e.g. Grandgeorge et al. 2008). Il sera ainsi possible, en premier lieu, de déterminer si les proies des oiseaux sont présentes en quantité suffisante pour leur permettre de se maintenir (effet de bottom-up control ; Frederiksen et al. 2006, Frank et al. 2007). A l'inverse, il sera possible d'étudier les conséquences de cette alimentation et de ces prélèvements sur les populations de proies concernées (effet de top-down control ; Frank et al.

2007). De plus, on sait que les changements climatiques ont et auront des impacts forts sur les populations de zooplancton et de poisson (e.g. Beaugrand et al. 2002b, Beaugrand 2003, Sandvik et al. 2005). Connaître les besoins alimentaires des oiseaux à l'échelle des populations et des communautés permettrait alors de déterminer quels pourraient être les impacts indirects de ces changements environnementaux sur les oiseaux marins, via leur ressource alimentaire. Enfin, on sait aujourd'hui que dans certaines zones océaniques et maritimes, les pêcheries humaines et les oiseaux sont en compétition pour les mêmes proies (Okes et al. 2009, Pichegru et al. 2009). Quand la ressource est peu disponible, cette compétition devient forte et les oiseaux sont souvent menacés par les pêcheries (Arcos et al. 2008). Connaître les besoins en proies des oiseaux à une large échelle et sur des zones ciblées permettrait d'estimer l'intensité de cette compétition ainsi que les risques pour les oiseaux, pour leur survie et les conséquences possibles sur la dynamique de leurs populations. Basées sur ces résultats, des mesures environnementales pourraient alors être mises en place afin de diminuer cette compétition et assurer le maintien des populations et des communautés d'oiseaux marins menacés. De telles études sont déjà réalisées depuis quelques années (Grangeorge et al 2008, Okes et al. 2009) et ont notamment permis la mise en place d'aires marines protégées sur lesquelles les pêcheries sont partiellement ou totalement interdites (e.g. Louzao et al. 2006, Arcos et al. 2009). Cependant, ces études sont quasiment toutes restreintes à la période de reproduction des oiseaux (excepté Wiens & Scott 1975, Furness 1978). L'utilisation de Niche Mapper™ permettra alors de les élargir à la période de non-reproduction pendant laquelle la pêche continue, et qui représente également une période critique pour la balance énergétique des oiseaux.

II-3-2 Impacts des changements climatiques sur les populations hivernantes d'oiseaux marins en Atlantique Nord.

L'objectif à long terme du projet dans lequel s'est inscrit cette thèse est d'étudier comment les futurs changements de l'environnement, associés au réchauffement climatique, vont directement ou indirectement affecter l'écologie et la distribution hivernale des oiseaux marins de l'Atlantique Nord et plus particulièrement des populations de mergules nains. Mais avant de pouvoir comprendre ce qu'il se passera dans le futur, il est primordial de connaître le présent. Or, comme nous l'avons déjà mentionné à plusieurs reprises, l'écologie hivernale de ces oiseaux était jusque là quasi inconnue. Ce travail de thèse a donc permis de décrire

quelques-uns des paramètres de base de la biologie et de l'écologie de ces espèces au cours de l'hiver. L'ensemble de ces résultats pourront être utilisés afin de modéliser la distribution future des oiseaux marins dépendamment des conditions rencontrées. En effet, grâce à l'utilisation combinée d'un modèle de bioénergétique (NicheMapper™), de l'ensemble des résultats obtenus pendant cette thèse, de données sur la distribution des proies (zooplanctons et poissons) et leurs réponses aux changements environnementaux (e.g. Beaugrand et al. 2002b, Sandvik et al. 2005), et de scénarios des futurs changements climatiques (incluant les tempêtes), il sera possible de :

- 1) Localiser les niches énergétiques favorables aux oiseaux au cours des dernières années, leurs évolution récentes et comment les oiseaux ont modifié leur distribution en conséquence.
- 2) Estimer l'état et l'emplacement de ces niches énergétiques dans le futur sous la contrainte des changements climatiques afin de prédire comment la niche fondamentale des différentes espèces sera affectée et comment les oiseaux devraient répondre à cette contrainte par un changement de leur distribution (Kearney & Porter 2009, Kearney et al. 2009a).

Ce type d'étude a déjà été utilisé sur des organismes ectothermes tels que les lézards ou les crapauds (Buckley 2008, Kearney et al. 2008) ainsi que sur une espèce endotherme (Porter et al. 2006), mais jamais encore sur des vertébrés longévifs ou des organismes aquatiques.

Références

- Aagaard, K., Foldvik, A. & Hillman, S.R. (1987) The West Spitsbergen Current-disposition and water mass transformation. *Journal of Geophysical Research* **92** (C4): 3778-3784.
- ACIA (2004) Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.
- Ainley, D.G., Ribic, C.A. & Fraser, W.R. (1994) Ecological Structure among Migrant and Resident Seabirds of the Scotia-Weddell Confluence Region. *Journal of Animal Ecology* **63**: 347-364.
- AMAP (1998) Assessment Report: Arctic Pollution Issues. Arctic Monitoring and Assessment Programme (AMAP), Oslo.
- Anderson, D.R. & Burnham, K.P. (1999) Understanding information criteria for selection among capture–recapture or ring recovery models. *Bird Study* **46 suppl.**: 261–270.
- Anker-Nilssen, T. (1992) Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*. Dissertation. University of Trondheim, Trondheim. Norway.
- Anker-Nilssen, T., Bakken, V., Strøm, H., Golovkin, A.N., Bianki, V.V. & Tatarinkova, I.P. (2000) The status of marine birds breeding in the Barents Sea region. Rapport nr. 113 Norsk Polarintitutt, Tromsø.
- Arcos, J.M., Louzao, M., Oro, D. (2008) Fisheries ecosystem impacts and management in the Mediterranean: Seabirds point of view. In: *Reconciling Fisheries with Conservation, Vol I & II*. (eds. Nielsen, J., Dodson, J.J., Friedland, K., Hamon, T.R., Musick, J. & Verspoor, E.), **49**: 1471-1479, American Fisheries Society and Symposium.
- Arcos, J.M., Bécarea, J., Rodríguez, B., Ruiz, A. (2009) Important areas for the conservation of seabirds in Spain. LIFE04NAT/ES/000049-SEO/BirdLife, Madrid.
- Arens, J.R. & Cooper, S.J. (2005) Seasonal and diurnal variation in metabolism and ventilation in House Sparrows *Passer domesticus*. *The Condor* **107**: 433-444.
- Arnkvaern, G., Daase, M. & Eiane, K. (2005) Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. *Polar Biology* **28**: 528-538.
- Bakken, V. & Mehlum, F. (2005) Wintering areas and recovery rates of Brünnich's guillemots *Uria lomvia* ringed in the Svalbard archipelago. *Arctic* **58**: 268-275.
- Barber, D., Marsden, R., Minnett, P., Ingram, G. & Fortier, L. (2001) Processus physiques dans la polynie des eaux du nord. *Atmosphere-Ocean* **39**: 167-171.
- Barbraud, C. & Weimerskirch, H. (2003) Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society B* **270**: 2111-2116.
- Barrett, R.T., Bakken, V. & Krasnov, J.V. (1997) The diets of common and Brunnich's guillemots *Uria aalge* and *U-lomvia* in the Barents Sea region. *Polar Research* **16**: 73-84.

- Barrett, R. T., Anker-Nilssen, T., Gabrielsen, G. W., & Chapdelaine, G. (2002) Food consumption by seabirds in Norwegian waters. *ICES Journal of Marine Science* **59**: 43-57.
- Barrett, R.B., Chapdelaine, G., Anker-Nilssen, T., Mosbech, A., Montevecchi, W.A., Reid, J.B. & Veit, R.R. (2006) Seabird numbers and prey consumption in the North Atlantic. *ICES Journal of Marine Science* **63**: 1145-1158.
- Battley, P.F., Dekinga, A., Dietz, M.W., Piersma, T., Tang, S., & Hulsman, K. (2001) Basal metabolic rate declines during long-distance migratory flight in Great Knots. *The Condor* **103**: 838-845.
- Bearhop, S., Waldron, S., Voltier, S.C. & Furness, R.W. (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* **75**: 451-458.
- Bearhop, S., Fiedler, W., Furness, R.W., Voltier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P. & Farnsworth, K. (2005) Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**: 502-504.
- Beaugrand, G. (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries Oceanography* **12**: 270-283.
- Beaugrand, G., Ibañez, F., Lindley, J.A. & Reid, P.C. (2002a) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Marine Ecology Progress Series* **232**: 179-195.
- Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A. & Edwards, M. (2002b) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**: 1692-1694.
- Beaugrand, G. & Reid, P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* **9**: 801-817.
- Belopolskii, L.O. (1961) Ecology of the Sea Colony Birds of the Barents Sea. Trans. Israel Programme for Scientific Translations, Jerusalem.
- Berge, J., Cottier, F., Last, K.S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygård, H. et al. 2009 Diel vertical migration of Arctic zooplankton during the polar night. *Biology Letters* **5**: 69-72.
- Berthold, P., Gwinner, E. & Sonnenschein, E. (2003) Avian Migration. Springer-Verlag, Berlin.
- Bevan, R.M., Woakes, A.J., Butler P.J. & Boyd I.L. (1994) The use of heart-rate to estimate oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys*. *The Journal of Experimental Biology* **193**: 119-137.
- Bevan, R.M., Speakman, J.R. & Butler, P.J. (1995) Daily energy expenditure of tufted ducks: a comparison between indirect calorimetry, doubly labelled water and heart rate. *Functional Ecology* **9**: 40-47.

- Biebach, H. (1996) Energetics of winter and migratory fattening. In *Avian energetics and nutritional ecology* (ed. C. Carey) pp280-323. Chapman & Hall, NY.
- Birkhead, T.R. & Nettleship, D.N. (1981) Reproductive-biology of Thick-billed murre (*Uria lomvia*) – an inter-colony comparison. *The Auk*. **98**: 258-269.
- Biro, P.A. & Stamps, J.A. (2009) Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution* **23**: 361-368.
- Birt-Friensen, V.L., Montevecchi, W.A., Cairns, D.K. & Macko, S.A. (1989) Activity-specific metabolic rate of free-living Northern Gannets and other seabirds. *Ecology* **70**: 357-367
- Bjerknes, J. (1964) Atlantic air-sea interaction. *Advances in Geophysics* **10**: 1-82.
- Blem, C. R. (2000) Energy balance. In: *Sturkie's avian physiology*. (ed. Whittow, G. C.), pp. 327-341, Academic press.
- Boertmann, D., Lyngs, P., Merkel, F.R. & Mosbech, A. (2004) The significance of Southwest Greenland as winter quarters for seabirds. *Bird Conservation International* **14**: 87-112.
- Bost, C.A., Thiebot, J.B., Pinaud, D., Cherel, Y., Trathan, P.N. (2009) Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni penguin. *Biology Letters* **5**: 473-476.
- Bourke, R.H., Newton, J.L., Paquette, R.G. & Tunnicliffe, M.D. (1987) Circulation and water masses of the East-Greenland shelf. *Journal of Geophysical Research* **92**: 6729-6740.
- Broggi, J., Koivula, K., Lahti, K. & Orell, M. (2003) Seasonality in daily body mass variation in a hoarding boreal passerine. *Oecologia* **137**: 627-633.
- Brooke, M. de L. (2004) The food consumption of the world's seabirds. *Proceedings of the Royal Society B* **271**: S246-S248.
- Brown, R.G.B. (1985) The atlantic alcidae at sea. In *The Atlantic Alcidae - The evolution, distribution and biology of the auks inhabiting the atlantic ocean and adjacent water areas* (ed. D. N. Nettleship and T. R. Birkhead), pp 384-426, Academic Press, London.
- Brown, R.G.B. (1991) Marine birds and climatic warming in the north-west Atlantic. In: *Studies of high-latitude Seabirds. I. behavioural, energetics, and oceanographic aspects of seabird feeding ecology*. (eds. Montevecchi, W.A. & Gaston, A.J.) pp. 49-54, Canadian Wildlife Service – Occasional Paper No 68.
- Brown, C.R. & Adams, N.J. (1984) Basal metabolic-rate and energy expenditure during incubation in the wandering albatross (*Diomedea exulans*). *The Condor* **86**: 182-186.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Towards a metabolic theory of ecology. *Ecology* **85**: 1771-1789.
- Brown, C.R., Brown, M.B. & Brazeal, K.H. 2008. Familiarity with breeding habitat improves daily survival in colonial cliff swallows. *Animal Behaviour* **76**: 1201-1210.

- Bryant, D.M. (1979) Reproductive costs in the house martin *Delichon urbica*. *Journal of Animal Ecology* **48**: 655-675.
- Bryant, D.M. (1988) Energy expenditure and body mass changes as measures of reproductive costs in birds. *Functional Ecology* **21**: 23-34.
- Buch, E. (2000) A monograph on the physical oceanography of the Greenland waters. A Danish Meteorological Institute scientific report No. 00-12.
- Buckley, L.B. (2008) Linking Traits to Energetics and Population Dynamics to Predict Lizard Ranges in Changing Environments. *The American Naturalist* **171**: E1-E19.
- Bunce, A. (2001) Prey consumption of Australian gannets (*Morus serrator*) breeding in Port Phillip Bay, southeast Australia, and potential overlap with commercial fisheries. *ICES Journal of Marine Science* **58**: 904-915.
- Burger, A.E. (1991) Maximum diving depths and underwater foraging in alcids and penguins. In *Studies of high-latitude seabirds. 1. Behavioural, energetic and oceanographic aspects of seabird feeding ecology* (eds W. A. Montevecchi & A. J. Gaston), pp. 9-15, Can. Wildl. Serv. Occ. Pap. No 68.
- Burger, J. & Gochfeld, M. (1990) The Black skimmer: social dynamics of a colonial species. Columbia University Press, New York
- Burnham KP & Anderson DR (2002) Model selection and multimodel inference – A practical Information-Theoretic Approach.
- Butler, P.J. & Woakes, A.J. (1984) Heart-rate and aerobic metabolism in Humboldt penguins, *Spheniscus humboldti*, during voluntary dives. *Journal of Experimental Biology* **108**: 419-428.
- Charlesworth, B. (1980) The evolution of age-structured populations. Cambridge University Press. Cambridge.
- Chastel, O., Weimerskirch, H. & Jouventin, P. (1995) Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. *The Auk* **112**: 964-972.
- Chaurand, T. & Weimerskirch, H. (1994) The regular alternation of short and long-foraging trips in the Blue Petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* **63**: 275-282.
- Cheng, H.L.M. & Plewes, D.B. (2002) Tissue thermal conductivity by magnetic resonance thermometry and focused ultrasound heating. *Journal of Magnetic Resonance Imaging* **16**: 598-609.
- Cherel, Y. (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. *Marine Biology* **154**: 813-821.
- Cherel, Y. & Hobson, K.A. (2005) Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *Proceeding of the Royal Society B* **272**: 1601-1607.

- Cherel, Y., Phillips, R.A., Hobson, K.A. & McGill, R. (2006) Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters* **2**: 301-303.
- Cherel, Y., Hobson, K.A. Guinet, C. & Vanpe, C. (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *Journal of Animal Ecology* **76**: 826-836.
- Cherel, Y., Le Corre, M., Jaquemet, S., Ménard, F., Richard, P. & Weimerskirch, H. (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology Progress Series* **366**: 281-291.
- Ciannelli, L., Hjermann, D.Ø., Lehodey, P., Ottersen, G., Duffy-Anderson, J.T. & Stenseth, N.C. (2005) Climate forcing, food web structure, and community dynamics in pelagic marine ecosystems. In: *Aquatic food webs – an ecosystem approach*. (eds. Belgrano, A., Scharler, U.M., Dunne, J. & Ulanowicz, R.E.), pp. 143-169, Oxford University Press, Oxford.
- Corell, R.W. (2006) Challenges of climate change: An Arctic perspective. *Ambio* **35**: 148-152.
- Croll, D.A., Gaston, A.J. & Noble, D.G. (1991) Adaptive loss of mass in Thick-billed murres. *The Condor* **93**: 496-502.
- Croll, D.A., Gaston, A.J., Burger, A.E. & Konnoff, D. (1992) Foraging behavior and physiological adaptation for diving in thick-billed murres. *Ecology* **73**: 344-356.
- Croll, D.A. & McLaren, E. (1993) Diving metabolism and thermoregulation in common and thick-billed murres. *Journal of Comparative Physiology B* **163**: 160-166.
- Culik, B.M., Wilson, R.P., Dannfeld, R., Adelung, D., Spairani, H.J. & Coria, N.R.C. (1991) Pycoscelid penguins in a swim canal. *Polar Biology* **11**: 277-282.
- Cuthill, I.C. & Houston, A.I. (1997) Managing time and energy. In: *Behavioural Ecology. An Evolutionary Approach*. 4th edn (ed. Krebs, J.R. & Davies, N.B.), pp. 97-120, Blackwell Scientific, Oxford.
- Dang, C., Sauriau, P.G., Savoye, N., Caill-Milly, N., Martinez, P., Millaret, C., Haure, J. & de Montaudouin, X. (2009) Determination of diet in Manila clams by spatial analysis of stable isotopes. *Marine Ecology Progress Series* **387**: 167-177.
- Daunt, F., Afanasyev, V., Silk, J.R.D. & Wanless, S. (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology* **59**: 381-388.
- Daunt, F., Afanasyev, V., Adam A., Croxall, J.P. & Wanless, S. (2007) From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters* **3**: 371-374.
- Dawson, W.R. & O'Connor, T.P. (1996) Energetic features of avian thermoregulatory responses. In *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp 85-123, 1st edn. Chapman & Hall, New York.

- Dickson, R.R., Osborn, T.J., Hurrell, J.W., Meincke, J., Blindheim, J., Aadlandsvik, B., Vinje, T., Alekseev, G. & Maslowski, W. (2000) The Arctic Ocean response to the North Atlantic Oscillation. *Journal of Climate* **13**: 2671-2696.
- Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. (1990) Brood size manipulations in the kestrel (*Falco Tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology* **59**: 269-285.
- Doherty, P.F.Jr., Schreiber, E.A., Nichols, J.D., Hines, J.E., Link, W.A., Schenk, G.A. & Schreiber, R.W. (2004) Testing life history prediction in a long-lived seabird: a population matrix approach with improved parameter estimation. *Oikos* **105**: 606-618.
- Donaldson, G.M., Gaston, A.J., Chardine, J.W., Kampp, K., Nettleship, D.N. & Elliot, R.D. (1997) Winter distributions of thick-billed murres from the eastern Canadian Arctic and western Greenland in relation to age and time of year. *Canadian Wildlife Service - Occasional Paper No 96*.
- Doody, L.M., Wilhelm, S.I., McKay, D.W., Walsh, C.J. & Storey, A.E. (2008) The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. *Hormones and Behavior* **53**: 140-148.
- Duffy, D.C. & Jackson, S. (1986) Diet studies of seabirds: a review of methods. *Waterbirds* **9**: 1-17.
- Egevang, C., Boertmann, D., Mosbech, A. & Tamstorf, M.P. (2003) Estimating colony area and population size of little auks *Alle alle* at Northumberland Island using aerial images. *Polar Biology* **26**: 8-13.
- Elliot, R.D., Ryan, P.C. & Lidster, W.W. (1990) The winter diet of thick-billed murres in coastal Newfoundland waters. *Studies in Avian Biology* **14**: 125-138.
- Elliott, K.H. & Gaston, A.J. (2005) Flight speeds of two seabirds: a test of Norberg's hypothesis. *Ibis* **147**: 783-789.
- Elliott, K.H., Davorren, G.K. & Gaston, A.J. (2008a) Increasing energy expenditure for a deep-diving bird alters time allocation during the dive cycle. *Animal Behaviour* **75**: 1311-1317.
- Elliott, K.H., Davorren, G.K. & Gaston, A.J. (2008b) Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal behaviour* **75**: 1301-1310.
- Ellis, H.I. & Gabrielsen, G.W. (2002) Energetics in free-ranging seabirds. In *Biology of marine birds* (ed. E. A. Schreiber & J. Burger), pp 359-407, Boca Raton: CRC Press.
- Einoder, L.D. (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* **95**: 6-13.
- Enstipp, M.R., Grémillet, D., Jones, D.R. (2006) The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). *Journal of Experimental Biology* **209**: 845-859.

- Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. (1998) On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**: 1781-1788.
- Evans, P.G.H. (1981) Ecology and behaviour of the Little Auk *Alle alle* in west Greenland. *Ibis* **123**: 1-18.
- Evans-Ogden, L.J., Hobson, K.A. & Lank, D.B. (2004) Blood isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) turnover and diet-tissue fractionation factors in captive Dunlin. *The Auk* **121**: 170-177.
- Falk, K. & Durinck, J. (1993) The winter diet of thick-billed murres, *Uria lomvia*, in western Greenland, 1988-1989. *Canadian Journal of Zoology* **71**: 264-272.
- Falk, K., Benvenuti, S., Dall'Antonia, L., Kampp, K. & Ribolini, A. (2000) Time allocation and foraging behaviour of chick-rearing Brünnich's Guillemots *Uria lomvia* in high-arctic Greenland. *Ibis* **142**: 82-92.
- Falk, K., Benvenuti, S., Dall'Antonia, L., Gilchrist, G. & Kampp, K. (2002) Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison. *Marine Ecology Progress Series* **231**: 293-302.
- Falk-Petersen, S., Mayzaud, P., Kattner, G. & Sargent, J.R. (2009) Lipids and life strategy of Arctic *Calanus*. *Marine Biology Research* **5**: 18-39.
- Fauchald, P., Erikstad, K.E. & Skarsfjord, H. (2000) Scale-dependant predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* **91**: 773-783.
- Finney, S.K., Wanless, S. & Harris, M.P. (1999) The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. *Journal of Avian Biology* **30**: 23-30.
- Fort, J., Porter, W.P. & Grémillet, D. (2009) Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *Journal of Experimental Biology* **212**: 2483-2490.
- Fortier, M., Fortier, L., Hattori, H., Saito, H. & Legendre, L. (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. *Journal of Plankton Research* **23**: 1263-1278.
- Frank, K.T., Petrie, B. & Shackell, N.L. (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution* **22**: 236-242.
- Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C. & Wanless, S. (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* **75**: 1259-1268.
- Frederiksen, M., Daunt, F., Harris, M.P. & Wanless, S. (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology* **77**: 1020-1029.
- Fridolfsson, A.K. & Ellegren, H. (1999) A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**: 116-121.

- Froese, R. & Pauly, D. (2009) FishBase, Editors. World Wide Web electronic publication. www.fishbase.org, version (09/2009).
- Furness, R.W. (1978) Energy-requirements of seabird communities – bioenergetics model. *Journal of Animal Ecology* **47**: 39-53.
- Furness, R.W. (1990) A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. *Ibis*. **132**: 205-217.
- Furness, R.W. & Camphuysen, K. (1997) Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* **54**: 726-737.
- Furness, R.W. & Tasker, M.L. (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* **202**: 253-264.
- Furness, R.B., Crane, J.E., Bearhop, S., Garthe, S., Käckelä, A., Käckelä, R., Kelly, A., Kubetzki, U., Votier, S.C. & Waldron, S. (2007) Techniques to link individual migration patterns of seabirds with diet specialization, condition and breeding performance. *Ardea* **94**: 631-638.
- Gabrielsen, G.W., Mehlum, F. & Karlsen, H.E. (1988) Thermoregulation in 4 species of Arctic seabirds. *Journal of Comparative Physiology B* **157**: 703-708.
- Gabrielsen, G.W., Taylor, J.R.E., Konarzewski, M. & Mehlum, F. (1991) Field and laboratory metabolism and thermoregulation in Dovekies (*Alle alle*). *The Auk* **108**: 71-78.
- Gaston, A.J. (1985) Energy invested in reproduction by thick-billed murres (*Uria lomvia*). *The auk* **102**: 447-458.
- Gaston, A.J. (2004) Seabirds - a natural history. Yale University Press, London.
- Gaston, A.J. & Jones, I.L. (1998) Bird families of the world: the auks. Oxford University press, Oxford.
- Gaston, A.J., Goudie, R.I., Noble, D.G. & MacFarlane, A. (1983) Observations on turr hunting in Newfoundland: age, body composition and diet of Thick-billed Murres (*Uria lomvia*) and proportions of other birds killed off Newfoundland in winter. *Canadian Journal of Zoology* **61**: 2465-2475.
- Genstat (2003) Genstat for Windows. (Lawes Agricultural Trust Rothamsted Experimental Station).
- Gentry, R.L. & Kooyman, G.L. (1986) Methods of dive analysis. In: *Fur seals – Maternal strategies on land and at sea* (eds. Gentry, R.L. & Kooyman, G.L.), pp 28-40, Princeton University Press, New Jersey.
- Gilbert, C., Le Maho, Y., Perret, M. & Ancel, A. (2007) Body temperature changes induced by huddling in breeding male emperor penguins. *American Journal of Physiology, Regulatory, Integrative and Comparative Physiology* **292**: R176–R185.

- Gjerdrum, C., Vallee, A.M.J., St Clair, C.C., Bertram, D.F., Ryder, J.L. & Blackburn, G.S. (2003) Tufted puffin reproduction reveals ocean climate variability. *The Proceedings of the National Academy of Sciences USA* **100**: 9377-9382.
- Godø, O.R. & Michalsen, K. (2000) Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. *Fisheries Research* **48**: 127-140.
- Göktepe, Ö., Hundt, P., Porter W.P. & Pereira, D. (2009) Comparing bioenergetics models of double-crested cormorant (*Phalacrocorax auritus*) fish consumption. *Waterbirds in press*.
- Golet, G.H., Irons, D.B. & Estes, J.A. (1998) Survival costs of chick rearing in black-legged kittiwakes. *Journal of Animal Ecology* **67**: 827-841.
- Golet, G.H. & Irons, D.B. (1999) Raising young reduced body condition and fat scores in black-legged kittiwakes. *Oecologia* **120**: 530-538.
- Golet, G.H., Irons, D.B. & Costa, D.P. (2000) Energy costs of chick rearing in Black-legged Kittiwakes (*Rissa tridactyla*). *Canadian Journal of Zoology* **78**: 982-991.
- Gordo, O. (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* **35**: 37-58.
- Grandgeorge, M., Wanless, S., Dunn, T., Maumy, M., Beaugrand, G. & Grémillet, D. (2008) Resilience of the British and Irish seabird community in the 20th century. *Aquatic Biology* **4**: 187-199.
- Green, A.J. (2001) Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology* **82**: 1473-1483.
- Green, J., Boyd, I.L., Woakes, A.J., Green, C.J. & Butler, P.J. (2005) Do seasonal changes in metabolic rate facilitate changes in diving behaviour? *Journal of Experimental Biology* **208**: 2581-2593.
- Green, J., Boyd, I.L., Woakes, A.J. & Butler, P.J. (2006) Flexibility in the behavior, physiology and ecology of diving in Macaroni Penguins. *Journal of Ornithology* **147** (S1): 64-64.
- Green, J.A., Boyd, I.L., Woakes, A.J., Warren, N.L. & Butler, P.J. (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *Journal of Avian Biology* **40**: 529-538.
- Grémillet, D., Schmid, D. & Culik, B. (1995) Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. *Marine Ecology Progress Series* **121**: 1-9.
- Grémillet, D., Dey, R., Wanless, S., Harris, M.P. & Regel, J. (1996) Determining food intake by great Cormorants and European shags with electronic balances. *Journal of Field Ornithology* **67**: 637-648.

- Grémillet, D., Storch, S. & Peters, G. (2000a) Determining food requirements in marine top-predators: a comparison of three independent methods in Great Cormorants *Phalacrocorax carbo*. *Canadian Journal of Zoology* **78**:1567-1579.
- Grémillet, D., Wilson, R.P., Wanless, S. & Chater, T. (2000b) Black-browed albatrosses, international fisheries and the Patagonian shelf. *Marine Ecology Progress Series* **195**: 269-280.
- Grémillet, D. & Le Maho, Y. (2003) Arctic and Antarctic ecosystems: poles apart? In *Antarctic biology in a global context* (eds. Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM & Wolff WJ), pp. 169-175, Backhuys Publishers, Leiden.
- Grémillet, D., Wright, G.A., Lauder A., Carss, D.N. & Wanless, S. (2003) Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. *Journal of Applied Ecology* **40**: 266-277.
- Grémillet, D., Kuntz, G., Woakes, A.J., Gilbert, C., Robin, J.P., Le Maho, Y. & Butler, P. (2005a) Year-round recording of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. *Journal of Experimental Biology* **208**: 4231-4241.
- Grémillet, D., Kuntz, G., Gilbert, K., Woakes, A.J., Butler, P.J. & le Maho, Y. (2005b) Cormorants dive through the Polar night. *Biology Letters* **1**: 469-471.
- Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A.G., Wilkinson, S., Crawford, R.J.M., Ryan, P.G. (2008) A junk-food hypothesis for gannets feeding on fishery waste. *Proceeding of the Royal Society B* **275**: 1149-1166.
- Grémillet, D. & Boulinier, T. (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series* **391**: 121-137.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology* **7**: 1071-1075.
- Grosbois, V. & Thompson, P.M. (2005) North Atlantic climate variation influences survival in adult fulmars. *Oikos* **109**: 273-290.
- Guilford, T., Meade, J., Willis, J., Phillips, R.A., Boyle, D., Roberts, S., Collett, M., Freeman, R. & Perrins, C.M. (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B* **276**: 1215-1223.
- Gwinner E & Helm B. (2003) Circannual and circadian contributions to the timing of avian migration. In *Avian migration* (eds Berthold P, Gwinner E & Sonnenschein E), pp 81-95, Springer.
- Hainsworth, F.R. (1981) Energy regulation in hummingbirds. *American Scientist* **69**, 420-429.
- Halsey, L.G., Green, J.A., Wilson, R.P., Frappell, P.B. (2009) Accelerometry to estimate energy expenditure during activity: best practice with data loggers. *Physiological and Biochemical Zoology* **82**: 396-404.

- Handel, C.M., Pajot, L.M., Talbot, S.L. & Sage, G.K. (2006) Use of buccal swabs for sampling DNA from nestling and adult birds. *Wildlife Society Bulletin* **34**: 1094-1100.
- Hanssen, S.A., Hasselquist, D., Folstad, I. & Erikstad, K.E. (2005) Cost of reproduction in long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B* **272**: 1039-1046.
- Haramis, G. M., Nichols, J.D., Pollock, K.H. & Hines, J.E. (1986) The relationship between body mass and survival of wintering Canvasbacks. *The Auk* **103**: 506-514.
- Harding, A.M.A., Van Pelt, T.I., Lifjeld, J.T. & Mehlum, F. (2004) Sex differences in Little Auk *Alle alle* parental care: transition from biparental to paternal-only care. *Ibis* **146**: 642-651.
- Harding, A.M.A., Hobson, K.A., Walkusz, W., Dmoch, K., Karnovsky, N.J., Van Pelt, T.I. & Lifjeld, J.T. (2008) Can stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) measurements of little auks (*Alle alle*) adults and chicks be used to track changes in high-Arctic marine foodwebs? *Polar Biology* **31**:725-733.
- Harding, A.M.A., Egevang, C., Walkusz, W., Merkel, F., Blanc, S. & Grémillet, D. (2009a) Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biology* **32**: 785-796.
- Harding, A.M.A., Kitaysky, A.S., Hall, M.E., Welcker, J., Karnovsky, N.J., Talbot, S.L., Hamer, K.C. & Grémillet, D. (2009b) Flexibility in the parental effort of an Arctic-breeding seabird. *Functional Ecology* **23**: 348-358.
- Hamer, K.C., Humphreys, E.M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips, R.A., Harris, M.P. & Wanless, S. (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series* **338**: 295-305
- Harper, G.A. (2007) Detecting predation of a burrow-nesting seabird by two introduced predators, using stable isotopes, dietary analysis and experimental removals. *Wildlife Research* **34**: 443-453.
- Harris, M.P., Anker-Nilssen, T., McCleery, R.H., Erikstad, K.E., Shaw, D.N., & Grosbois, V. (2005) Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula actica* in the eastern Atlantic. *Marine Ecology Progress Series* **297**: 283-296.
- Helbig, A.J. (1991) SE- and SW-migrating Blackcap (*Sylvia atricapilla*) populations in Central Europe: Orientation of birds in the contact zone. *Journal of Evolutionary Biology* **4**: 657-670.
- Hensen, V. (1892) Ergebnisse der (in den Atlantischen Ozean von Mitte Juli bis Anfang November 1889) Plankton Expedition der Humboldt Stiftung. Kiel und Leipzig: Lipsius & Tischer Verlag.
- Henson, S.A., Dunne, J.P. & Sarmiento, J.L. (2009) Decadal variability in North Atlantic phytoplankton blooms. *Journal of Geophysical Research* **114**: C04013.

- Hill, R.D. (1994) Theory of geolocation by light levels. In: *Elephant seals: population ecology, behavior, and physiology*. (eds. Le Boeuf, B.J. & Laws, R.M.), pp 227-236, University of California Press, Berkeley.
- Hobbs, N.T. (1989) Linking energy balance to survival in mule deer: Development and test of a simulation model. *Wildlife Monograph* **101**: 1-39.
- Hobson, K.A. (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Marine Ecology Progress Series* **95**: 7-18.
- Hobson, K.A. (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**: 314-326.
- Hobson, K.A. & Clark, R.G. (1992) Assessing avian diets using stable isotopes I: Turnover of ¹³C in tissues. *The Condor* **94**: 181-188.
- Hobson, K.A., Piatt, J.F. & Pitocchelli, J. (1994) Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* **63**: 786-798.
- Hobson, V.J., Righton, D., Metcalfe, J.D. & Hays, G.C. (2009) Link between vertical and horizontal movement patterns of cod in the North Sea. *Aquatic Biology* **5**: 133-142.
- Holberton, R.L. & Able, K.P. (2000) Differential migration and an endocrine response to stress in wintering dark-eyed juncos (*Junco hyemalis*). *Proceedings of the Royal Society B* **267**: 1889-1896.
- Holt, S. Whitfield, D.P., Duncan, K., Rae, S. & Smith, R.D. (2002) Mass loss in incubating Eurasian dotterel: adaptation or constraint? *Journal of Avian Biology* **33**: 219-224.
- Horner, R.A., Syvertsen, E.E., Thomas, D.P. & Lange, C. (1988) Proposed Terminology and Reporting Units for Sea Ice Algal Assemblages. *Polar Biology* **8**: 249-253.
- Horner, R., Ackley, S.F., Dieckmann, G.S., Guiliksen, B., Hoshiai, T., Legendre, L., Melnikov, I.A., Reeburgh, W.S., Spindler, M. & Sullivan, C.W. (1992) Ecology of sea ice biota – 1. Habitat, terminology, and methodology. *Polar Biology* **12**: 417-427
- Houston, A.I., Thompson, W.A. & Gaston, A.J. (1996) The use of a time and energy budget model of a parent bird to investigate limits to fledging mass in the thick-billed murre. *Functional Ecology* **10**: 432-439.
- del Hoyo, J., Elliott, A. & Sargatal, J. (1992) *Handbook of the Birds of the World. Volume 1. Ostrich to Ducks*. Lynx Edicions, Barcelona.
- del Hoyo, J., Elliott, A. & Sargatal, J. (1996) *Handbook of the Birds of the World. Volume 3. Hoatzin to Auks*. Lynx Edicions, Barcelona.
- Hunt, G.L.Jr., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B. & Becker, P.H. (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: *Proceedings of the 22nd International Ornithological Congress*. (eds. Adams, N.J. & Slotow, R.), pp. 2040-2056, BirdLife South Africa, Johannesburg.

- Hunt, G.L.Jr., Drew, G.S., Jahncke, J. & Piatt, J.F. (2005) Prey consumption and energy transfer by marine birds in the Gulf of Alaska. *Deep Sea Research II* **52**: 781-797.
- Hurrell, J.W. (2000) Climate: Northern Atlantic and Arctic Oscillation (NAO/AO). In: *Encyclopedia or Atmospheric Sciences*. (eds. Holton, J., Pyle, J. & Curry, J.), New York Academic Press, New York.
- Hurrell, J.W. & Dickson, R.R. (2004) Climate variability over the North Atlantic. In: *Marine ecosystems and climate variations*. (eds. Stenseth, N.C., Ottersen, G., Hurrell, J.W. & Belgrano, A.), pp. 15-32, Oxford University Press, Oxford.
- Huse, G., Johansen, G.O., Bogstad, B., & Gjøsæter, H. (2004) Studying spatial and trophic interactions between capelin and cod using individual-based modelling. *ICES Journal of Marine Science*, **61**: 1201-1213.
- Isaksen, K. & Gavrilov, M. (2000) Little auk *Alle alle*. In *The status of marine birds breeding in the Barents Sea region* (ed. T. Anker-Nilssen, V. Bakken, H. Strøm, A. N. Golovkin, V. V. Bianki and I. P. Tatarinkova), pp 131-136. Rapport No 113. Oslo: Norsk Polarinstitutt.
- Isachsen, P.E., LaCasce, J.H., Mauritzen, C. & Häkkinen, S. (2003) Wind-driven variability of the large-scale recirculating flow in the Nordic Seas and Arctic Ocean. *Journal of Physical Oceanography* **33**: 2534-2550.
- IPCC, Core Writing Team (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change (eds. Pachauri, R.K. & Reisinger, A.), 104 pp., IPCC, Geneva, Switzerland.
- Jacobsen, K.O., Erikstad, K.E. & Sæther, B.-E. (1995) An experimental study of the costs of reproduction in the Kittiwake (*Rissa tridactyla*). *Ecology* **76**: 1636-1642.
- Jakubas, D. & Wojczulanis, K. (2007) Predicting the Sex of Dovekies by Discriminant Analysis. *Waterbirds* **30**: 92-96.
- Jenni, L. & Kéry, M. (2001) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceeding of the Royal Society B* **270**: 1467-1471.
- Johansen, G.O. (2002) Temporal and spatial variation in predation on juvenile herring (*Clupea harengus* L.) by Northeast Arctic cod (*Gadus morhua* L.) in the Barents Sea in 1984–1997. *ICES Journal of Marine Science* **59**: 270-292.
- Jones, I.L., Rowe, S., Carr, S.M., Fraser, G. & Taylor, P. (2002) Different patterns of parental effort during chick-rearing by female and male thick-billed murres (*Uria lomvia*) at a low-Arctic colony. *The Auk* **119**: 1064-1074.
- Jónsson, S. (1991) Seasonal and interannual variability of wind stress curl over the Nordic Seas. *Journal of Geophysical Research* **96**: 2649-2659.
- Kampp, K., Falk, K. & Pedersen, C. E. (2000) Breeding density and population of little auks (*Alle alle*) in a Northwest Greenland colony. *Polar Biology* **23**: 517-521.

- Karnovsky, N.J. & Hunt, G.L. (2002) Estimation of carbon flux to dovekies (*Alle alle*) in the North Water. *Deep Sea Research II* **49**: 5117-5130.
- Karnovsky, N.J., Kwaśniewski, S., Węśławski, J.M., Walkusz, W. & Beszczyńska-Möller, A. (2003) Foraging behavior of little auks in a heterogeneous environment. *Marine Ecology Progress Series* **253**: 289-303.
- Karnovsky, N.J., Hobson, K.A., Iverson, S. & Hunt Jr., G.L. (2008) Seasonal changes in diets of seabirds in the North Water Polynya: a multiple-indicator approach. *Marine Ecology Progress Series* **357**: 291-299.
- Karnovsky, N.J., Harding, A.M.A., Walkusz, W., Kwaśniewski, S., Goszczko, I., Wiktor Jr, J., Routti, H., Bailey, A., McFadden, L., Brown, Z., Beaugrand, G. & Grémillet, D. Foraging distributions of little auks (*Alle alle*) across the Greenland Sea: Implications of present and future Arctic climate change. *Marine Ecology Progress Series in press*.
- Kearney, M. & Porter, W.P. (2004) Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85**: 3119-3131.
- Kearney, M., Phillips, B.L., Tracy, C.R., Christian, K.A., Betts, G. & Porter, W.P. (2008) Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography* **31**: 423-434.
- Kearney, M. & Porter, W. P. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**: 334-350.
- Kearney, M., Porter, W.P., Williams, C., Ritchie, S. & Hoffmann, A.A. (2009a) Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Functional Ecology* **23**: 528-538.
- Kearney, M., Shine, R. & Porter W.P. (2009b) The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proceedings of the National Academy of Science USA* **10**: 3835-3840.
- Keast, M.A., Lawrence, M.J. (1990) A collection of amphipoda from the Southern Beaufort Sea. Canadian Data Report of Fisheries and Aquatic Sciences No. 799.
- Keller, T. M. and Visser, G. H. (1999) Daily energy expenditure of Great Cormorants *Phalacrocorax carbo sinensis* wintering at lake Chiemsee, southern Germany. *Ardea* **87**: 61-69.
- Kelly, J.F. (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* **78**: 1-27.
- Kendeigh, S.C., Dol'nik, V.R. & Gavnlov, V.M. (1977) Avian energetics. In: *Granivorous birds in ecosystems*. (eds Pinowski, J. & Kendeigh, S.C.), pp 127-204, Cambridge University Press, Cambridge.
- Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (1999) Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology* **13**: 577-584.

- Kitaysky, A.S., Piatt, J.F. & Wingfield, J.C. (2007) Stress hormones link food availability and population processes in seabirds. *Marine Ecology Progress Series* **352**: 245-258.
- Klaassen M. (1996) Metabolic constraints on long-distance migration in birds. *Journal of Experimental Biology* **199**: 57-64.
- Klaassen, M. (2003) Relationships between migration and breeding strategies in arctic breeding birds. In: *Avian migration*. (eds Berthold, P., Gwinner, E. & Sonnenschein, E.), pp. 237-249, Springer-Verlag, Berlin.
- Komers, P.E. (1997) Behavioural plasticity in variable environments. *Canadian Journal of Zoology* **75**: 161-169.
- Konarzewski, M., Taylor, J.R.E. & Gabrielsen, G.W. (1993) Chick energy requirements and adult energy expenditures of Dovekies (*Alle alle*). *The Auk* **110**: 343-353.
- Kooijman, S.A.L.M. (2000) Dynamic energy and mass budgets in biological systems. Cambridge University Press, Cambridge.
- Kooijman, S.A.L.M., Sousa, T., Pecquerie, L., van der Meer, J. & Jager, T. (2008) From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. *Biological Reviews* **83**: 533-552.
- Kooyman, G.L., Drabek, C.M., Elsner, R. & Campbe, W.B. (1971) Diving behavior of the emperor penguin, *Aptenodytes forsteri*. *The Auk* **88**: 775-795.
- Kooyman, G.L., Davis, R.W., Croxall, J.P., Costa, D.P. (1982) Diving Depths and Energy Requirements of King Penguins. *Science* **20**: 726-7.
- Krebs, J.R. & Davies, N.B. (1981) An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford.
- Kvist, A., Lindström, A., Green, M., Piersma, T. & Visser, G.H. (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* **413**: 730-732.
- Kwasniewski, S., Hop, H., Falk-Petersen, S. & Pedersen, G. (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *Journal of Plankton Research* **25**: 1-20.
- Lavigne, D.M. (1991) Ecological interactions between marine mammals, commercial fisheries, and their prey: unraveling the tangled web. In: *Studies of high-latitude seabirds. – 4. Trophic relationships and energetics of endotherms in cold ocean systems*. (ed. Montevecchi), pp. 59-71, Canadian Wildlife Service – Occasional Paper No 91.
- Lawson, J.W., Magalhaes, A.M. & Miller, E.H. (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Marine Ecology Progress Series* **164**: 13-20.
- Le Maho, Y. (2002) Ecophysiology: Nature and function. *Nature* **416**: 21.

- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs* **62**: 67-118.
- Lewis, S., Sherratt, T.N., Hamer, K.C. & Wanless, S. (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* **412**: 816-819.
- Lilliendahl, K. (2009) Winter diets of auks in Icelandic coastal waters. *Marine Biology Research* **5**: 143-154.
- Litzow MA, Piatt JF, Prichard AK, Roby DD (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* **132**: 286-295.
- Loeng, H., Brander, K., Carmack, E., Denisenko, S., Drinkwater, K., Hansen, B., Kovacs, K., Livingston, P., et al. (2005) Marine ecosystems. In: *Arctic Climate Impact Assessment*. chap. 9, pp. 454–522, Cambridge University Press, Cambridge.
- Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abello, P., De Sola, L.G. & Oro, D. (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: Implications for marine protected areas. *Ecological Applications* **16**: 1683-1695.
- MacNab, B.K. (2002) *The physiological Ecology of Vertebrates – A View from Energetics*. Cornell University Press.
- Maldonado, K.E., Cavieres, G., Veloso, C., Canals, M. & Sabat, P. (2009) Physiological responses in rufous-collared sparrows to thermal acclimation and seasonal acclimatization. *Journal of Comparative Physiology B* **179**: 335-343.
- McConnell, B.J., Chambers, R.C. & Fedak, M.A. (1992) Foraging ecology of Southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* **4**: 393-398.
- McKechnie, A.E., Freckleton, R.P. & Jetz, W. (2006) Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proceedings of the Royal Society B* **273**: 931-937.
- McNamara, J.M., Barta, Z., Wikelski, M. & Houston, A.I. (2008) A theoretical investigation of the effect of latitude on avian life histories. *The American Naturalist* **172**: 331-345.
- McWilliams, S.R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* **35**: 377-393.
- Meadows, S., Porter, W.P. & Craven, S.R. (2009) Modeling the organochlorine contaminant intake of cormorants. *Waterbirds in press*.
- Mehlum, F. (2001) Crustaceans in the diet of adult Common and Brünnich's Guillemots *Uria aalge* and *U. lomvia* in the Barents Sea during the breeding period. *Marine Ornithology* **29**: 19-22.
- Mehlum, F., Hunt Jr, G.L., Klusek, Z. & Decker, M.B. (1999) Scale-dependent correlations between the abundance of Brünnich's guillemots and their prey. *Journal of Animal Ecology* **68**: 60-72.

- Mehlum, F., Watanuki, Y. & Takahashi, A. (2001) Diving behaviour and foraging habitats of Brunnich's guillemots (*Uria lomvia*) breeding in the High-Arctic. *Journal of Zoology* **255**: 413-423.
- Michener, R. & Kaufman, L. (2007) Stable isotope ratios as tracers in marine food webs: an update. In: *Stable isotopes in ecology and environmental science*. (eds. Michener, R. & Lajtha, K.), pp. 238-282, Blackwell Publishing.
- Michener, R. & Lajtha, K. (2007) *Stable isotopes in ecology and environmental science*. Blackwell Publishing.
- Mitchell, N.J., Kearney, M.R., Nelson N.J. & Porter W.P. (2008) Predicting the fate of a living fossil: how will global warming affect embryonic development, sex determination and hatching phenology in tuatara? *Proceedings of the Royal Society B* **275**: 2185-2193.
- Moe, B., Langseth, I., Fyhn, M., Gabrielsen, G.W., & Bech, C. (2002) Changes in body condition in breeding kittiwakes. *Rissa tridactyla*. *Journal of Avian Biology* **33**: 225-234.
- Møller, A.P. (1994) Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* **35**: 115-122.
- Møller, A.P., Flensted-Jensen, E. & Mardal, W. (2006) Dispersal and climate change: a case study of the Arctic tern *Sterna paradisaea*. *Global Change Biology* **12**: 2005-2013.
- Mori, Y., Takahashi, A., Mehlum, F. & Watanuki, Y. (2002) An application of optimal diving models to diving behaviour of Brunnich's guillemots. *Animal Behaviour* **64**: 739-745.
- Murray, J.L. (1998) Ecological characteristics of the Arctic. In: *AMAP Assessment Report: Arctic Pollution Issues*. pp. 117-140, Arctic Monitoring and Assessment Programme, Oslo.
- Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R. & Steinheim, G. (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* **410**: 1096-1099.
- Nagy, K.A. (2005) Field metabolic rate and body size. *Journal of Experimental Biology* **208**: 1621-1625.
- Nagy, K.A., Siegfried, W.R. & Wilson, R.P. (1984) Energy-utilisation by free-ranging jackass penguins, *Spheniscus demersus*. *Ecology* **65**: 1648-1655.
- Nakamura, H. (1996) Year-to-year and interdecadal variability in the activity of intraseasonal fluctuations in the Northern Hemisphere wintertime circulation. *Theoretical and Applied Climatology* **55**: 19-32.
- Natori, Y. & Porter, W.P. (2007) Model of Japanese serow (*Capricornis crispus*) energetics predicts distribution on Honshu, Japan. *Ecological Applications* **17**: 1441-1459.

- Neat, F.C., Wright, P.J., Zuur, A.F., Gibb, I.M., Gibb, F.M., Tulett, D., Righton, D.A. & Turner, R.J. (2006) Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). *Marine Biology* **148**: 643-654.
- Nettleship, D.N. & Birkhead, T.R. (1985) The Atlantic Alcidae - The evolution, distribution and biology of the auks inhabiting the atlantic ocean and adjacent water areas. Academic Press, London.
- Newsome, S.D., del Rio, C.M., Bearhop, S. & Phillips, D.L. (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment* **5**: 429-436.
- Nieminen, P., Hohtola, E., Pyykonen, T., Paakkonen, T., Aho, J., Cittova-Kontu, M., Asikainen, J., Mononen, J. & Mustonen, A.M. (2005) Thermoregulatory adaptations of the overwintering captive raccoon dog (*Nyctereutes procyonoides*) in boreal climate. *Journal of Experimental Zoology A* **303**: 776-784.
- Niizuma, Y., Gabrielsen, G.W., Sato, K., Watanuki, Y. & Naito, Y. (2007) Brunnich's guillemots (*Uria lomvia*) maintain high temperature in the body core during dives. *Comparative Biochemistry and Physiology A* **147**: 438-444.
- Nisbet, R.M., Muller, E.B., Lika, K. & Kooijman, S.A.L.M. (2000) From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology* **69**: 913-926.
- Ochoa-Acuña, H.G., McNab, B.K. & Miller, E.H. (2009) Seasonal energetics of northern phocid seals. *Comparative Biochemistry and Physiology A* **152**: 341-350.
- Oedekoven, C.S., Ainley, D.G. & Spear, L.B. (2001) Variable responses of seabirds to change in marine climate: California Current, 1985-1994. *Marine Ecology Progress Series* **212**: 265-281.
- Okes, N.C., Hockey, P.A.R., Pichegru, L., van der Lingen, C., Crawford, R.J.M. & Grémillet, D. (2009) Competition for shifting resources in the southern Benguela upwelling: seabirds versus purse-seine fisheries. *Biological Conservation* **142**: 2361-2368.
- Olsson, O. (1997) Clutch abandonment: a state-dependent decision in king penguins. *Journal of Avian Biology* **28**: 264-267.
- Olsson, O. & van der Jeugd, H.P. (2002) Survival in king penguins *Aptenodytes patagonicus*: temporal and sex-specific effects on environmental variability. *Oecologia* **132**: 509-516.
- Orians, G.H. & Pearson, N.E. (1979) On the theory of the central place foraging. In: *Analysis of ecological systems*. (eds. Horn, D.J., Mitchell, R.D. & Stairs, G.R.) pp. 154-177, Ohio State University Press, Columbus.
- Oro, D. & Furness, R.W. (2002) Influences of food availability and predation on survival of kittiwakes. *Ecology* **83**: 2516-2528.
- Ottersen, G., Alreit, J, Drinkwater, K., Friedland, K., Hagen, E. & Stenseth, NC. (2004) The responses of fish populations to ocean climate fluctuations. In: *Marine ecosystems and*

- climate variations*. (eds. Stenseth, N.C., Ottersen, G., Hurrell, J.W. & Belgrano, A.), pp. 73-94, Oxford University Press, Oxford.
- Ottersen, G., Stenseth, N.C. & Hurrell, J.W. (2004b) Climatic fluctuations and marine systems: a general introduction to the ecological effects. In: *Marine ecosystems and climate variations*. (eds. Stenseth, N.C., Ottersen, G., Hurrell, J.W. & Belgrano, A.), pp. 3-14, Oxford University Press, Oxford.
- Patterson, H.D. & Thompson, R. (1971) Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**: 545-554.
- Pedersen, C.E. & Falk, K. (2001) Chick diet of dovekies *Alle alle* in Northwest Greenland. *Polar Biology* **24**: 53-58.
- Pennycuik, C.J. (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. *Journal of Experimental Biology* **128**: 335-357.
- Pennycuik, C.J. (1989) Bird flight performance: a practical calculation manual. Oxford University Press, Oxford.
- Pennycuik, C.J., Schaffner, F.C., Fuller, M.R., Obrecht, H.H. & Sternberg, L. (1990) Foraging flights of the white-tailed tropicbird (*Phaethon lepturus*) – radiotracking and doubly-labeled water. *Colonial Waterbirds* **13**: 96-102.
- Percy, J.A. & Fife, F. J. (1981) The biochemical-composition and energy content of Arctic marine macrozooplankton. *Arctic* **34**: 307-313.
- Phillips, R.A., Thompson, D.R. & Hamer, K.C. (1999) The impact of great skua predation on seabird populations at St Kilda: a bioenergetics model. *Journal of Applied Ecology* **36**: 218-232.
- Phillips, R.A., Catry, P., Silk, J.R.D., Bearhop, S., McGill, R., Afanasyev, V. & Strange, I.J. (2007) Movements, winter distribution and activity patterns of Falkland and brown skuas: insights from loggers and isotopes. *Marine Ecology Progress Series* **345** : 281-291.
- Phillips, R.A., Bearhop, S., McGill, R.A.R. & Dawson, D.A. (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* **160**: 795-806.
- Piatt, J.F. & Nettleship, D.N. (1985) Diving depths of four alcids. *Auk* **102**: 293-297.
- Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., van Pelt, T.I., Drew, G.S. & Kettle, A.B. (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* **352**: 221-234.
- Pichegru, L., Ryan, P.G., Le Bohec, C., van der Lingen, C.D., Navarro, R., Petersen, S., Lewis, S., van der Westhuizen, J. & Grémillet D. (2009) Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecology Progress Series* **391**: 199-208.

- Pinaud, D. & Weimerskirch, H. (2002) Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* **99**: 141-150.
- Podlesak, D.W. & McWilliams, S.R. (2006) Metabolic routing of dietary nutrients in birds: effect of diet quality and macronutrient composition revealed using stable isotopes. *Physiological and Biochemical Zoology* **79**: 534-549.
- Pollock, K.H. Nichols, J.D., Brownie, C. & Hines, J.E. (1990) *Statistical Inference for Capture-Recapture Experiments*. *Wildlife Monographs* **107**: 1-97.
- Porter, W.P. & Gates, D.M. (1969) Thermodynamic equilibria of animals with environment. *Ecological Monographs* **39**: 227-244.
- Porter, W.P., Munger, J.C., Stewart, W.E., Budaraju, S. & Jaeger, J. (1994) Endotherm energetics – from a scalable individual-based model to ecological applications. *Australian Journal of Zoology* **42**: 125-162.
- Porter, W.P., Budaraju, S., Stewart, W.E. & Ramankutty, N. (2000) Calculating climate effects on birds and mammals: Impacts on biodiversity, conservation, population parameters, and global community structure. *American Zoologist* **40**: 597-630.
- Porter, W.P. & Mitchell, J.W. (2006) Method and system for calculating the spatial-temporal effects of climate and other environmental conditions on animals. <http://www.patentstorm.us/patents/7155377-fulltext.html> (ed. U.P Office). Wisconsin Alumni Research Foundation, USA.
- Porter, W.P., Vakharia, N., Klousie, W.D. & Duffy, D. (2006) Po'ouli landscape bioinformatics models predict energetics, behavior, diets, and distribution on Maui. *Integrative and Comparative Biology* **46**: 1143-1158.
- Pravosudov, V.V., Kitaysky, A.S., Wingfield, J.C. & Clayton, N.S. (2001) Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). *General and Comparative Endocrinology* **123**: 324-331.
- Prinsenberg, S.J., Peterson, I.K., Narayanan, S. & Umoh, J.U. (1997) Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962-1992. *Canadian Journal of Aquatic Science* **54**: 30-39.
- Quillfeldt, P., Bugoni, L., McGill, R.A.R., Masello, J.F. & Furness, R.W. (2008a) Differences in stable isotopes in blood and feathers of seabirds are consistent across species, age and latitude: implications for food web studies. *Marine Biology* **155**: 593-598.
- Quillfeldt, P., McGill, R.A.R., Masello, J.F., Weiss, F., Strange, I.J., Brickle, P., Furness, R.W. (2008b) Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of thin-billed prions. *Marine Ecology Progress Series* **373**: 137-148.
- Ramos, R., Gonzalez-Solis, J. & Ruiz, X. (2009) Linking isotopic and migratory patterns in a pelagic seabird. *Oecologia* **160**: 97-105.
- Rands, S.A. Cuthill, I.C., & Houston, A.I. (2006) Explaining individual variation in patterns of mass loss in breeding birds. *Theoretical biology and medical modeling* **3**: 20.

- Rau, G.H., Sweeney, R.E. & Kaplan, I.R. (1982) Plankton 13C:12C ratio changes with latitude: differences between northern and southern oceans. *Deep Sea Research II* **29**: 1035-1039.
- Reid, W.V. (1987) The cost of reproduction in the Glaucous-winged Gull. *Oecologia* **74**: 458-467.
- Rey, A. R., Trathan, P., Putz, K. and Schiavini, A. (2007) Effect of oceanographic conditions on the winter movements of rockhopper penguins *Eudyptes chrysocome* from Staten Island, Argentina. *Marine Ecology Progress Series* **330**: 285-295.
- Rezende, E.L., Bozinovic, F. & Garland, T. (2004) Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution* **58**: 1361-1374.
- Richardson, A.J. & Schoeman, D.S. (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* **305**: 1609-1612.
- Rodway, M.S., Chardine, J.W. & Montevecchi, W.A. (1998) Intra-colony variation in breeding performance of Atlantic puffins. *Colonial Waterbirds* **21**: 171-184.
- Roff, D.A. (1992) The evolution of life histories. Chapman and Hall. New York, New York.
- Rogers, J.C. (1990) Patterns of low-frequency monthly sea level pressure variability (1899-1986) and associated wave cyclone frequencies. *Journal of Climate* **3**: 1364-1379.
- Rolff, C. (2000) Seasonal variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of size-fractionated plankton at a coastal station in the northern Baltic proper. *Marine Ecology Progress Series* **203**: 47-65.
- Rolland, V., Barbraud, C., Weimerskirch, H. (2009) Combined effects of fisheries and climate on a migratory long-lived marine predator. *Journal of Applied Ecology* **45**: 4-13.
- Rolshausen, G., Hobson, K.A. & Schaefer, H.M. (2009) Spring arrival along a migratory divide of sympatric blackcaps (*Sylvia atricapilla*). *Oecologia* (doi: 10.1007/s00442-009-1445-3).
- Romero, L.M., Reed, M.J. & Wingfield, J.C. (2000) Effects of weather on corticosterone responses in wild free-living passerine birds. *General and Comparative Endocrinology* **118**: 113-122.
- Romero, L.M. & Reed, J.M. (2005) Collecting baseline corticosterone samples in the field: is under 3 minutes good enough? *Comparative Biochemistry and Physiology A* **140**: 73-79.
- Ropert-Coudert, Y. & Wilson, R.P. (2005) Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**: 437-444.
- Rowe, L., Ludwig, D. & Schluter, D. (1994) Time, condition and the seasonal decline of avian clutch size. *The American Naturalist* **143**: 698-722.
- Rowe, S., Jones, I.L., Chardine, J.W., Elliot, R.D. & Veitch, B.G. (2000) Recent changes in the winter diet of murre (*Uria spp.*) in coastal Newfoundland waters. *Canadian Journal of Zoology* **78**: 495-500.

- Saloranta, T.M. & Svendsen, H. (2001) Across the Arctic front west of Spitsbergen: high-resolution CTD sections from 1998-2000. *Polar Research* **20**: 177-184.
- Sandvik, H.A.N.N., Erikstad, K.E., Barrett, R.T. & Yoccoz, N.G. (2005). The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology* **74**: 817-831.
- Sato, M., Sasaki, H. & Fukuchi, M. (2002) Stable isotopic compositions of overwintering copepods in the arctic and subarctic waters and implications to the feeding history. *Journal of Marine Systems* **38**: 165-174.
- Scantlebury, M., Oosthuizen, M.K., Speakman, J.R., Jackson, C.R. & Bennett, N.C. (2005) Seasonal energetics of the Hottentot golden mole at 1500m altitude. *Physiology and Behavior* **84**: 739-745.
- Schmid-Hempel, P. & Wolf, T. (1988) Foraging effort and life span of workers in a social insect. *Journal of Animal Ecology* **57**: 509-522.
- Schmidt, N.M., Berg, T.B., Forchhammer, M.C., Hendrichsen, D.K., Kyhn, L.A., Møller, H., Høye, T.T. (2008) Vertebrate predator-prey interactions in a seasonal environment. *Advances in Ecological Research* **40**: 345-370.
- Schmidt-Nielsen (1998) *The Camel's Nose: Memoirs of a curious scientist*. Washington Editions.
- Schmutz, J.A. (2009) Stochastic variation in avian survival rates: life-history predictions, population consequences, and potential responses to human perturbations and climate change. In: *Modeling Demographic Processes in Marked Populations*. (eds. Thomson, D.L., Cooch, E.G. & Conroy, M.J.), pp. 441-461, Springer, U.S.
- Schreiber, E.A. (2001) Climate and weather effects on seabirds. In *Biology of Marine Birds*. (ed. Schreiber, E.A. & Burger, J.), pp 179-207, Boca Raton: CRC Press.
- Schreiber, E. A. and Burger, J. (2002). *Biology of marine birds*. Boca Raton: CRC Press.
- Scott, C.L., Kwasniewski, S., Falk-Petersen, S. & Sargent, J.R. (2000) Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biology* **23**: 510-516.
- Seber, G.A.F. (1982) *The estimation of animal abundance and related parameters*. Charles Griffin, London.
- Serreze, M.C., Carse, F., Barry, R.G. & Rogers, J.C. (1997) Icelandic low activity: climatological features, linkages with the NAO, and relationships with recent changes in the Northern Hemisphere circulation. *Journal of Climate* **10**: 453-464.
- Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R. & Sagar, P.M., Møller, H., Taylor, G.A., Foley, D.G., Block, B.A. & Costa, D.P. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *The Proceedings of the National Academy of Sciences USA* **103**: 12799-12802.

- Shmueli, M., Izhaki, I., Arieli, A., Arad, Z. (2000) Energy requirements of migrating Great White Pelicans *Pelecanus onocrotalus*. *Ibis* **142**: 208-216.
- Slagsvold, T. & Johansen, M.A. (1998) Mass loss in female Pied Flycatchers *Ficedula hypoleuca* during late incubation: supplementation fails to support the reproductive stress hypothesis. *Ardea* **86**: 203-211.
- Søreide, J.E., Falk-Petersen, S., Hegseth, E.N., Hop, H., Carroll, M.L., Hobson, K.A. & Blachowiak-Samolyk, K. (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep Sea Research II* **55**: 2225-2244.
- Sousa, T., Domingos, T. & Kooijman, S.A.L.M. (2008) From empirical patterns to theory: a formal metabolic theory of life. *Philosophical Transactions of the Royal Society B* **363**: 2453-2464.
- Sparling, C.E., Thompson, D., Fedak, M.A., Gallon, S.L. & Speakman, J.R. (2008) Estimating field metabolic rates of pinnipeds: doubly labelled water gets the seal of approval. *Functional Ecology* **22**: 245-254.
- Speakman, J.R. (1997) *Doubly-Labelled Water – Theory and Practice*. Chapman and Hall.
- Speakman, J. R. & Racey, P. A. (1989) Hivernal ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. *Journal of Animal Ecology* **58**: 797-813.
- Stearns, S.C. (1992) *The evolution of life histories*. Oxford University Press, Oxford.
- Stempniewicz, L. (2001) *Alle alle* Little Auk. *The Journal of the Birds of the western Palearctic*. BWP Update, vol. 3: 175-201, Oxford University Press, Oxford.
- Stempniewicz, L. (2006) Keystone species and ecosystem functioning. Seabirds in polar ecosystems. *Ecological Questions* **6**: 129-134.
- Stempniewicz, L., Błachowiak-Samołyk, K. & Węśławski, J.M. (2007) Impact of climate change on zooplankton communities, seabird populations and Arctic terrestrial ecosystem - a scenario. *Deep Sea Research II* **54**: 2934-2945.
- Stendel, M., Christensen, J.H. & Petersen, D (2008) Arctic climate and climate change with focus on Greenland. *Advances in Ecological Research* **40**: 13-43.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K-S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*. **297**: 1292-1296.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W. & Belgrano, A. (2004) *Marine ecosystems and climate variations*. Oxford University Press, Oxford.
- Stephenson, R., Butler, P.J. & Woakes, A.J. (1986) Diving behaviour and heart rate in tufted ducks (*Aythya fuligula*). *Journal of Experimental Biology* **126**: 341-35.
- Sukhanova, I.N., Semina, H.J. & Venttsel, M.V. (1999) Spatial distribution and temporal variability of phytoplankton in the Bering Sea. In: *Dynamics of the Bering Sea*. (eds. Loughlin, T.R. & Ohtani, K.), pp. 453-483, University of Alaska Fairbanks.

- Takahashi, A., Matsumoto, K., Hunt, G.L., Shultz, M. T., Kitaysky, A. S., Sato, K., Iida, K. & Watanuki, Y. (2008) Thick-billed murres use different diving behaviors in mixed and stratified waters. *Deep Sea Research II* **55**: 1837-1845.
- Tameler, T., Renaud, P.E., Hop, H., Carroll, M.L., Ambrose, W.G. & Hobson, K.A. (2006) Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. *Marine Ecology Progress Series* **310**: 33-46.
- Tameler, T., Reigstad, M., Hop, H., Carroll, M.L. & Wassmann, P. (2008) Pelagic and sympagic contribution of organic matter to zooplankton and vertical export in the Barents Sea marginal ice zone. *Deep Sea Research II* **55**: 2330-2339.
- Tanaka H. (2006) Winter hibernation and body temperature fluctuation in the Japanese badger, *Meles meles anakuma*. *Zoological Science* **23**: 991-997.
- Thompson, P. & Ollason, J. (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature* **413**: 417-420.
- Tracy, C.R., Welch, W.R. and Porter, W.P. (1973) Properties of Air. Tech. Rept. #1, Biophysical Ecology Lab., 18pp.
- Tremblay, Y., Cherel, Y., Oremus, M., Tveraa, T. & Chastel, O. (2003) Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour in seabirds. *Journal Experimental Biology* **206**: 1929-1940.
- Turbill, C. (2009) Temperature effects on metabolic rate and torpor in southern forest bats (*Vespadelus regulus*). *Australian Journal of Zoology* **57**: 125-127.
- Tveraa, T., Sæther, B.E., Aanes, R. & Erikstad, K.E. 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental condition and chick body mass. *Journal of Animal Ecology* **67**: 699-704.
- Uspenski, S.M. (1956) The Bird Bazaars of Novaya Zemlya. Transactions of the Canadian Wildlife Service, Trans. Russian Game Reports N°4, Ottawa.
- Vasey, N. (2005) Activity budgets and activity rhythms in red ruffed lemurs (*Varecia rubra*) on the Masoala Peninsula, Madagascar: Seasonality and reproductive energetics. *American Journal of Primatology* **66**: 23-44.
- van der Veer, H.W., Kooijman, S.A.L.M. & van der Meer, J. (2001) Intra- and interspecific comparison of energy flow in north atlantic flatfish species by means of dynamic energy budgets. *Journal of Sea Research* **45**: 303-320.
- van der Veer, H.W., Kooijman, S.A.L.M., Leggett, W.C. & van der Meer, J. (2003) Body size scaling relationships in flatfish as predicted by dynamic energy budgets (deb theory): implications for recruitment. *Journal of Sea Research* **50**: 255-270.
- Velando, A. & Alonso-Alvarez, C. (2003) Differential body condition regulation by males and females in response to experimental manipulation of brood size and parental effort in the blue-footed booby. *Journal of Animal Ecology* **72**: 846-856.

- Votier, S.C., Bearhop, S., Ratcliffe N., Phillips, R.A. & Furness, R.W. (2004) Predation by great skua at a large Shetland seabird colony. *Journal of Applied Ecology* **41**: 1117-1128.
- Walker, G.T. & Bliss, E.W. (1932) World weather V. *Mem. Royal Meteorological Society* **4**: 53-84.
- Wanless, S., Harris, M.P. & Greenstreet, P.R. (1998) Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland. *ICES Journal of Marine Science* **55**: 1141-1151.
- Wanless, S., Finney, S.K., Harris, M.P. & McCafferty, D.J. (1999) Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag *Phalacrocorax atriceps* and the European shag *P-aristotelis*. *Marine Ecology Progress Series* **188**: 219-224.
- Ward, S., Bishop, C.M., Woakes, A.J., Butler, P.J. (2002) Heart rate and the rate of oxygen consumption of flying and walking barnacle geese (*Branta leucopsis*) and bar-headed geese (*Anser indicus*). *Journal of Experimental Biology* **205**: 3347-3356.
- Watanuki, Y., Daunt, F., Takahashi, A., Newei, M., Wanless, S., Sat, K. & Miyazaki, N. (2008) Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. *Marine Ecology Progress Series* **356**: 283-293.
- Webb, J.N., Székely, T., Houston, A.I., & McNamara, J.M. (2002) A theoretical analysis of the energetic costs and consequences of parental care decisions. *Philosophical Transactions of the Royal Society B* **357**: 331-340.
- Weber, T.P., Ens, B.J. & Houston, A.I. (1998) Optimal avian migration: A dynamic model of fuel stores and site use. *Evolutionary Ecology* **12**: 377-401.
- Weimerskirch, H., Zimmermann, L., & Prince, P.A. (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology* **12**: 22-30.
- Welch, W.R. (1980) Evaporative water loss from endotherms in thermally and hygrially complex environments: an empirical approach for interspecific comparisons. *Journal of Comparative Physiology B* **139**: 135-143.
- Welcker, J., Harding, A.M.A., Kitaysky, A.S., Speakman, J.R & Gabrielsen GW. (2009a) Daily energy expenditure increases in response to low nutritional stress in an Arctic-breeding seabird with no effects on mortality. *Functional Ecology* doi: 10.1111/j.1365-2435.2009.01585.x.
- Welcker, J., Harding, A.M.A., Karnovsky, N.J., Steen, H., Strøm, H. & Gabrielsen, G.W. (2009b) Flexibility in the bimodal foraging strategy of a high Arctic alcid, the Little Auk *Alle alle*. *Journal of Avian Biology* **40**: 388-399.
- Wernham, C.V. & Bryant, D.M. (1998) An experimental study of reduced parental effort and future reproductive success in the puffin *Fratercula arctica*. *Journal of Animal Ecology* **67**: 25-40.

- West, J.B., Bowen, G.J., Cerling, T.E. & Ehleringer, J.R. (2006) Stable isotopes as one of nature's ecological recorders. *Trends in Ecology and Evolution* **21**: 408-414.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**: 120-139.
- White, C.R., Butler, P.J., Grémillet, D. & Martin, G.R. (2008) Behavioural strategies of cormorants (Phalacrocoracidae) foraging under challenging light conditions. *Ibis* **150**: 231-239.
- Wienecke, B., Robertson, G., Kirkwood, R. & Lawton, K. (2007) Extreme dives by free-ranging emperor penguins. *Polar Biology* **30**: 133-142.
- Wiens, J.A. & Scott, J.M. (1975) Model estimation of energy flow in Oregon coastal seabird populations. *The Condor* **77**: 439-452.
- Williams, C.T., Iverson, S.J. & Buck, C.L. (2008) Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. *Marine Ecology Progress Series* **363**: 287-298.
- Wilson, R.P. & Bain, C.A.R. (1984) An inexpensive depth gauge for penguins. *Journal of Wildlife Management* **48**: 1077-1084.
- Wilson, R.P., Culik, B.M., Adelung, D., Spairani, H.J. & Coria, N.R. (1991) Depth utilisation by breeding Adélie penguins, *Pygoscelis adeliae*, at Esperanza Bay, Antarctica. *Marine Biology* **109**: 181-189.
- Wilson, R.P., Puetz, K., Bost, C.-A., Culik, B.M., Bannasch, R., Reins, T. & Adelung, D. (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series* **94**: 101-104.
- Wilson, R.P., Putz, K., Grémillet, D., Culik, B.M., Kierspel, M., Regel, J., Bost, C.-A., Lage, J. & Cooper, J. (1995a) Reliability of stomach temperature-changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology* **198**: 1115-1135.
- Wilson, R.P., Pütz, K., Charrassin, J.B. & Lage, J. (1995b) Artifacts arising from sampling interval in dive depth studies of marine endotherms. *Polar Biology* **15**: 575-581.
- Wilson, L.J., Daunt, F., & Wanless, S. (2004) Self-feeding and chick provisioning diet differ in the Common Guillemot *Uria aalge*. *Ardea* **92**: 197-207.
- Wilson, R.P., White C.R., Quintana, F., Halsey, L.G., Liebsch, N., Martin, G.R. & Butler P.J. (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**: 1081-1090.
- Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M., & Richardson, R.D. (1998) Ecological Basis of Hormone-Behavior Interactions: The "Emergency Life History Stage". *American Zoologist* **38**: 191-206.

Wingfield, J.C., Vleck, C.M. & Moore, M.C. (1992) Seasonal changes in the adrenocortical response to stress in birds of the Sonoran Desert. *Journal of Experimental Zoology* **264**: 419-428.

Réponses des oiseaux marins de l'Arctique aux contraintes environnementales hivernales dans le contexte des changements climatiques

L'Atlantique Nord en hiver est un environnement rude soumis à des événements climatiques extrêmes ; il fait partie des milieux les plus défavorables aux endothermes. Parmi eux, les oiseaux marins jouent un rôle majeur en temps que prédateurs supérieurs et bioindicateurs des écosystèmes pélagiques. Dans le contexte actuel de changements globaux très marqués en Atlantique nord, il est essentiel de comprendre comment ces organismes répondent aux contraintes environnementales qui conditionnent leur survie hivernale et façonnent leur populations.

Par une approche multidisciplinaire (alliant microélectronique, analyses isotopiques, modélisation énergétique et démographie) centrée sur la balance énergétique des individus, nous nous sommes attachés à étudier la plasticité écophysiological des 3 espèces d'alcidés les plus communes de l'Atlantique nord.

Nous avons montré que les tempêtes hivernales provoquent un goulot d'étranglement énergétique qui pourrait être une des principales causes de la mortalité observée. Face à cette dépense énergétique accrue, les oiseaux mettent en place différentes stratégies leur permettant d'augmenter leurs gains en énergie. Ils ajustent leurs déplacements verticaux (modes de plongée) et horizontaux (migration hivernale), ainsi que leur régime alimentaire en fonction de la disponibilité spatio-temporelle de leurs proies.

L'ensemble de ces résultats constitue une des toutes premières études de l'écologie hivernale des oiseaux marins. Ils sont essentiels à une meilleure compréhension des dynamiques de leurs populations et forment une base solide aux futures investigations de l'effet des changements climatiques sur les prédateurs marins supérieurs.

Mots-clés : Bioénergétique • Ecologie alimentaire • Ecosystème Nord Atlantique • Oiseaux marins • Plasticité écophysiological • Survie hivernale

Responses of Arctic marine birds to winter environmental constraints in the context of climate change

Harsh environmental conditions encountered in North Atlantic during wintertime, characterized by frequent extreme weather events, are among the most challenging constraints for endothermic animals. Seabirds, which experience this environment for many months per year, play a central role in North Atlantic food webs, notably as top predators and indicators of marine ecosystems. In the current context of climate change, pronounced in North Atlantic waters, it is therefore a major objective to understand how seabirds respond and adapt to these environmental constraints shaping their survival and their population dynamics.

We used a multidisciplinary approach (combining microelectronics, stable isotopic analyses, bioenergetics modelling and demography) focused on individual energy balance, to study the ecophysiological plasticity of the 3 main alcid species of the North Atlantic.

We found that harsh winter conditions induce an energetic bottleneck for seabirds which might explain recurrent events of winter mass mortality, so called 'seabird winter wrecks'. In response to increased energy expenditure, we showed that seabirds can adopt different strategies allowing higher energy intake. They can modulate their vertical (diving behaviour) and/or horizontal (migration) movements, as well as their trophic status, depending on the spatial and temporal availability of their prey.

All together, these results constitute one of the first comprehensive studies of seabird winter ecology. These insights are essential to a better understanding of their population dynamics and constitute a firm foundation to future investigations of the impact of climate change on marine top predators.

Key-words: Bioenergetics • Ecophysiological plasticity • Feeding ecology • North Atlantic ecosystem • Seabirds • Winter survival