Feeding ecology of Northern Gannets (Morus bassanus) in the North Atlantic Ocean at various spatio-temporal scales

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UNIVERSITE MONTPELLIER II - SCIENCES ET TECHNIQUES DU LANGUEDOC

THESE

Pour obtenir le grade de

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Discipline : Biologie des Populations et Ecologie

Formation : Evolution, Ecologie, Ressources Génétiques, Paléontologie

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Par

Emeline PETTEX

Ecologie alimentaire du fou de Bassan *Morus bassanus* en Atlantique Nord à des échelles spatio-temporelles multiples.

Soutenue publiquement le 17 mai 2011

Membres du jury :

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La mer est sans routes, la mer est sans explications.

Alessandro Baricco

L’embêtant avec les oiseaux, c’est les becs.

Albert Dupontel

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Liste des publications scientifiques et communications

Publications présentées dans la thèse

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Fort J.[*], **Pettex E.*,** Tremblay Y., Lorentsen S.H., Votier S., Garthe S., Montevecchi W., Pons JB., and Grémillet D. The Shetland – Senegal flyway: meta-population evidence of oriented migration in European northern gannets. In prep

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Pettex, E., Lorentsen, S.H., Barrett, R.T. & Grémillet, D. 2009. The foraging ecology of Norwegian gannets. *SEAPOP Short report* 6-2009.

Pettex, E., Lorentsen, S.H., Barrett, R.T. & Grémillet, D. 2008. The foraging ecology of Norwegian gannets. In Anker□Nilssen, T. (ed.). SEAPOP studies in the Barents and Norwegian Seas in 2007. NINA Report 363, pp. 26-31

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- Fort J., Steen H., Strøm H., Tremblay Y., Pettex E., Gabrielsen G.W., Le Maho Y., Porter W.P., Grønningsæter E., Grémillet D. Poster : *Contrasted migratory strategies in a sympatric high-Arctic seabird duet*

Mars 2009 10th Seabird Group meeting, Bruges (Belgium).

Pettex E., Lorentsen S.H., Barrett R.T., Grémillet D. Communication orale: *Are Norwegian gannets constrained by their foraging environment?*

Juin 2009 46th Animal Behavior Meeting, Pirenópolis (Brazil)

Nesterova A., Mardon J., Couchoux M., Pettex E., Bonadonna F. Communication orale: *King penguin chicks orientation and the importance of visual landmarks*

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Chapitre 1. Introduction générale

Tous les organismes, indépendamment de leur place dans la classification du vivant, sont soumis à une contrainte commune et incontournable, celle de pouvoir acquérir des ressources qu'ils transforment en énergie ou en éléments constitutifs pour assurer leurs fonctions vitales. Les êtres vivants qu'ils soient mobiles ou non, ont ainsi évolué en fonction du milieu qu'ils occupent, développant un ensemble de caractères physiologiques, morphologiques, comportementaux et démographiques définis par les contraintes de leur environnement et destinés à assurer leur survie et leur reproduction (Roff 1992). Ces caractères forment un ensemble que l'on désigne par le terme de traits d'histoire de vie. Par ailleurs, pour que les populations soient viables, les individus doivent pouvoir répondre rapidement aux variations de leur milieu afin de subvenir à leurs besoins énergétiques. La modification des comportements d'alimentation est la réponse la plus immédiate aux changements de distribution des ressources (Menge 1972; Holmes & Schultz 1988). Dans ce travail de thèse, nous nous sommes intéressés aux stratégies comportementales de recherche alimentaire d'un prédateur marin en réponse à la stochasticité environnementale à différentes échelles, stochasticité aujourd'hui aggravée par les activités humaines. De la capacité d'adaptation à des changements rapides opérant dans les écosystèmes marins fragiles et complexes, dépend la survie des espèces marines. Il y a là un enjeu majeur pour le maintien de la biodiversité et pour les populations humaines qui tirent leurs ressources des océans.

1. La variabilité de l'environnement marin

1.1 L'environnement marin : une forte hétérogénéité spatiale

Pour l'œil humain qui ne peut voir sous la surface, les océans peuvent sembler absolument monotones. Il est vrai que les eaux pélagiques sont moins riches en éléments nutritifs et moins productives que les eaux côtières, qui bénéficient d'apports importants grâce aux fleuves (Mann & Lazier 2006). En réalité, il convient de considérer les océans comme d'immenses déserts abritant des oasis de vie. Ils se caractérisent par une hétérogénéité physique exceptionnelle (Haury, McGowan, & Wiebe 1978; Hunt & Schneider 1987) qui favorise la production biologique et conditionne la distribution des ressources disponibles pour les prédateurs (Bakun 1996). Certains paramètres physiques tels que la bathymétrie et les mouvements de masses d'eau (courants, marées..) génèrent des mouvements de convection entrainant la remontée de masses d'eau profondes et chargées en nutriments (azote, phosphore…) vers la surface (système *d'upwelling*). En surface, l'intensité lumineuse permet la photosynthèse et ainsi le développement des algues planctoniques (production primaire). Ce phytoplancton constitue la base des réseaux trophiques marins (Belgrano et al. 2005) sur laquelle vont se nourrir les espèces phytophages (zooplancton, poissons), qui vont elles-mêmes être des proies disponibles pour les prédateurs (poissons, oiseaux marins, mammifères marins). En résumé, la combinaison de processus physiques et biologiques génère des zones de forte productivité primaire (Wolanski & Hamner 1988), dont dépendent la distribution et l'abondance des autres organismes marins (Hunt et al. 1999). La prévisibilité de ces points chauds de productivité dépend de l'échelle spatiale considérée. A large échelle (plus de 1000 km), les courants marins (Figure 1.1) vont permettre la rencontre de masses d'eau de température et de salinité contrastées le long de zones de convergence appelés « fronts océaniques », relativement stables dans le temps et l'espace (Park, Charriaud, & Fieux 1998). A méso-échelle (entre 100 et 1000km), des tourbillons océaniques appelés « *eddies* » peuvent se former et générer des mouvements *d'upwelling* (ou de *downwelling*) et favoriser localement une augmentation de la productivité primaire (ou au contraire la diminuer). Issus de l'instabilité de courants marins, ils sont de taille variable (jusqu'à 100-200km) et présentent une durée de vie de quelques mois en moyenne (Pond & Pickard 1983; Mellor 1996).

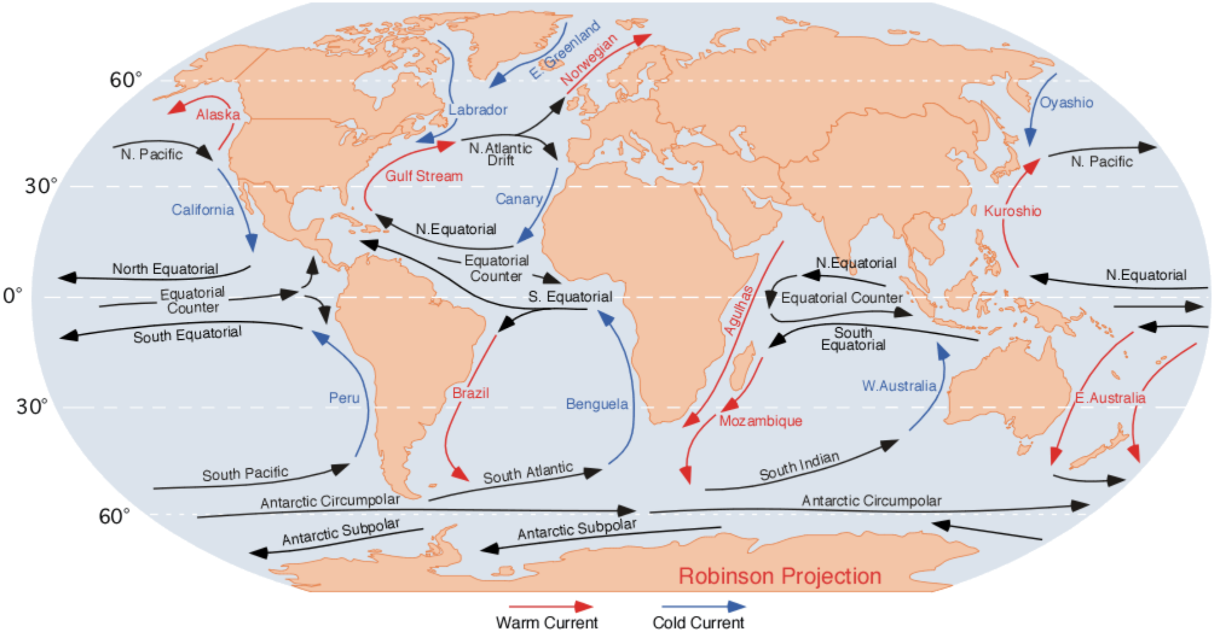

Figure 1.1 Principaux courants océaniques. Les flèches rouges indiquent des courants chauds, les flèches bleues indiquent des courants froids (selon Pidwirny 2006).

A une échelle spatiale inférieure (de 1 à 100km), les zones de forte productivité, où les proies sont abondantes, sont nettement moins prévisibles dans le domaine pélagique (Hunt & Schneider 1987). A contrario, à proximité des côtes, la disponibilité des nutriments dans les eaux de surface est plus élevée. Les plateaux continentaux et les *upwellings* côtiers sont des zones où la production primaire est forte et globalement prévisible (Weimerskirch 2007). Les courants tidaux[1] augmentent la disponibilité des proies, soit en les faisant remonter en surface (courants forts), soit en les empêchant de descendre (courants faibles). Ces agrégations de proies sont vulnérables aux prédateurs marins (Vermeer, Szabo, & Greisman 1987; Irons 1998). L'ensemble de ces processus physiques intervenant à des échelles variables et emboitées les unes dans les autres engendrent une distribution des ressources non uniforme définie par une structuration spatiale variable et hiérarchisée (Kotliar & Wiens 1990). On parle alors d'agrégation des ressources en patches (Fauchald 1999). Cette hétérogénéité spatiale de la production primaire ainsi que la concentration en phytoplancton nettement plus élevée en milieu côtier sont clairement visibles sur les images satellites (Figure 1.2).

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[1] Courants liés aux marées

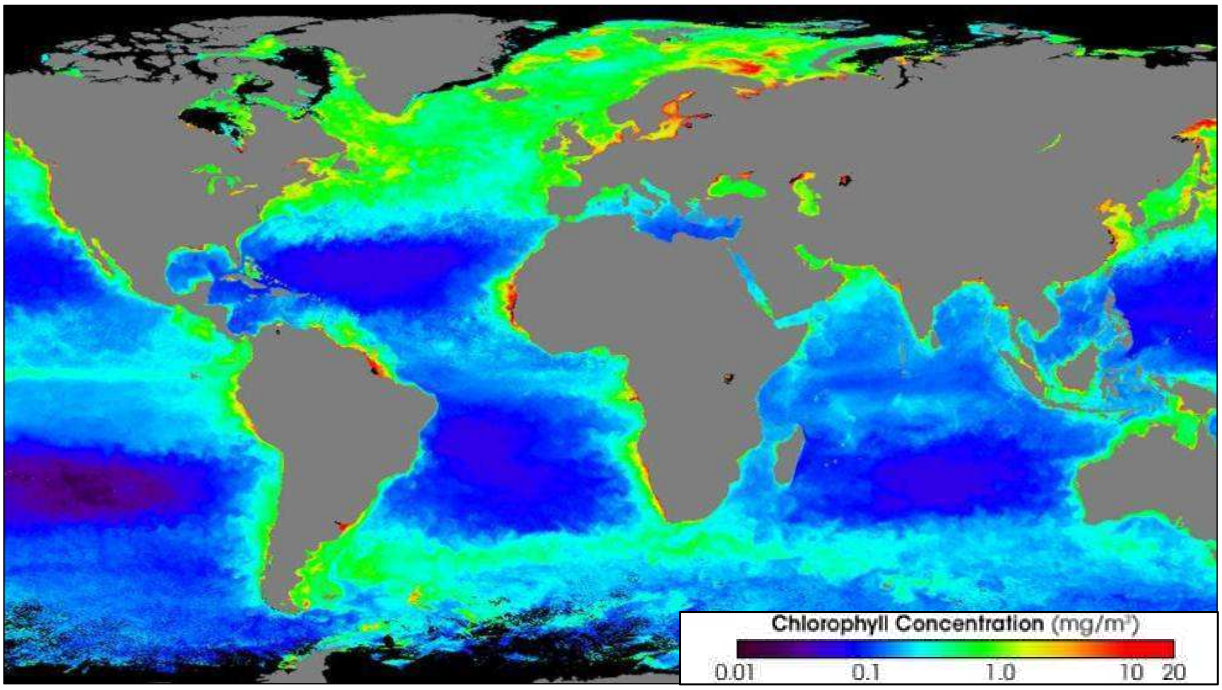

Figure 1.2 Image du satellite SEAWiFS représentant la concentration en chlorophylle A en mg/m3 dans les océans entre le 20 mars et le 21 juin 2006 (d'après le site Internet de la NASA http://earthobservatory.nasa.gov).

1.2 L'environnement marin : une forte hétérogénéité temporelle

La variation des facteurs physiques et chimiques (températures, vents, courants…) influence le développement des organismes phytoplanctoniques au cours du temps et induit donc également une variabilité temporelle des écosystèmes marins.

a) La saisonnalité de la production primaire

Dans les milieux tempérés et polaires, les conditions climatiques sont marquées en hiver entre autres par une diminution importante de la température de l'eau et une augmentation des vents. Les vents hivernaux favorisent le mélange entre les eaux profondes, plus denses et riches en nutriments et les eaux de surface. Au printemps, l'augmentation des rayonnements solaires permet au phytoplancton présent dans la zone euphotique d'utiliser les nutriments et de réaliser la photosynthèse. La biomasse phytoplanctonique connait alors une croissance exponentielle identifiée sous le nom de *bloom de printemps* (Figure 1.3). En été, la productivité primaire diminue car en l'absence de mélange des couches d'eau, les apports en nutriment cessent. Les algues croissent et consomment les nutriments disponibles jusqu'à épuisement.

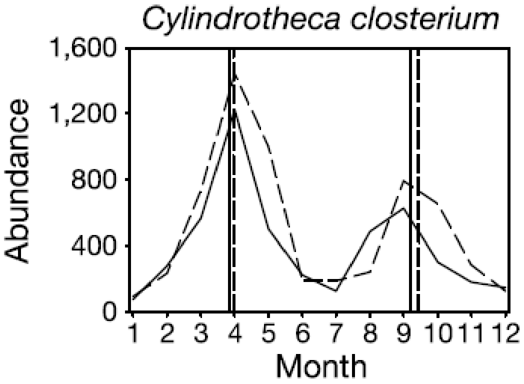

Figure 1.3 Exemple de la variation saisonnière d'une algue diatomée Cylindrotheca closterium en mer du Nord (selon Edwards & Richardson 2004).

b) Les variations interannuelles et les oscillations climatiques

A l'échelle des hémisphères nord et sud ou des grands bassins océaniques, les phénomènes météorologiques appelés *oscillations* entrainent des modifications importantes des conditions climatiques par effet de circulation de masses d'air (Hurrell 1995). Ces oscillations correspondent à des variations de la différence de pression atmosphérique au niveau de la mer entre des zones de haute pression et des zones de basse pression au sein du bassin océanique. Dans l'Atlantique Nord, l'Oscillation Nord Atlantique (NAO en anglais) correspond à des variations de pression entre les masses d'air situées aux Açores (38°N) et autour de l'Islande (65°N). Cette oscillation est positive lorsque les pressions arctiques sont inférieures à la normale et que les pressions subtropicales sont supérieures à la normale, et elle est négative lorsque ces tendances s'inversent (Hurrell & Dickson 2005). Une NAO positive provoque des étés frais et des hivers doux et pluvieux alors qu'une NAO négative entraine des étés caniculaires et des hivers froids en Europe. La NAO a des effets sur les courants de surface (Hurrell & Dickson 2005) et des conséquences dans les écosystèmes marins : modification de la distribution spatiale, des abondances spécifiques, des relations proies-prédateurs et des dates de reproduction (Ottersen et al. 2001).

1.3 La variation d'origine anthropique

Dans une étude de 2008, Halpern et ses collaborateurs ont proposé une carte globale des impacts humains sur les écosystèmes marins (Halpern et al. 2008). Cette étude dresse un bilan sombre : sur plus d'un tiers de la surface des océans (41%), l'impact direct et indirect des activités humaines est qualifié de « moyen-haut » à « très élevé » (Figure 1.4). Les impacts les plus forts sont relevés au niveau des pentes et des plateaux continentaux proches des pays les plus industrialisés. En Europe, les zones les plus touchées sont la mer du Nord, la mer de Norvège et la mer Méditerranée. Dans ces régions, ce sont à la fois les activités terrestres (agriculture intensive, industrie, rejets urbains…) et marines (exploitations minières, pêche, aquaculture…) qui entrainent une détérioration des écosystèmes (Halpern et al. 2008).

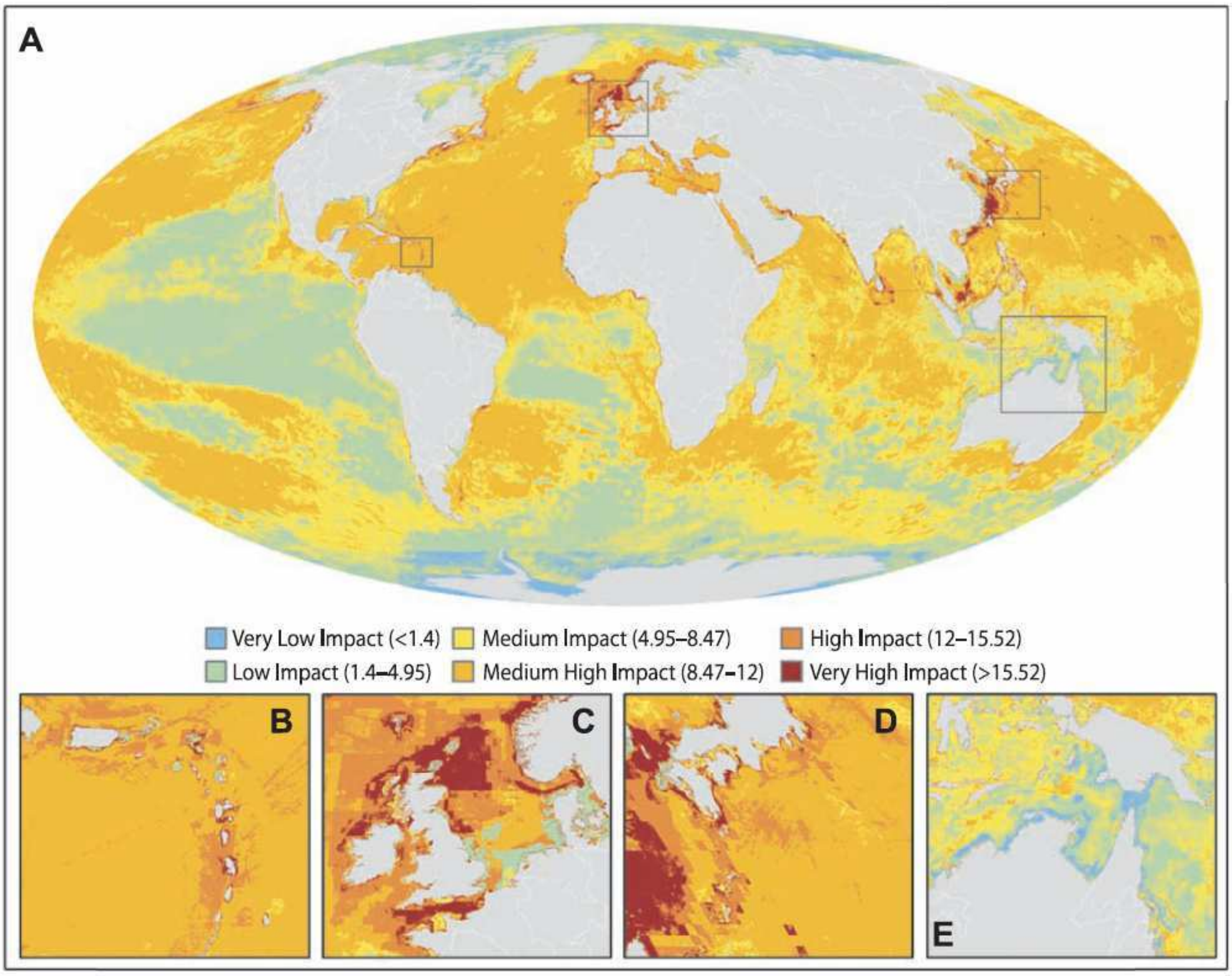

Figure 1.4 Impacts globaux des activités humaines sur l'environnement marin (tiré de Halpern et al. 2008).

a) La surpêche

Lorsque les premières explorations européennes atteignirent les côtes nord-américaines à la fin du XVème siècle, elles furent frappées par les immenses populations de morues *Gadus* *morhua* (Cury & Miserey 2008). La mer semble alors si féconde que le mythe de ressources marines inépuisables se développe. Dans *L'Histoire naturelle des animaux* (Salerne & Nobleville 1756), on peut lire que « quelque grand que soit le nombre des morues consommées par les hommes chaque année, ou dévorées en mer par d'autres poissons, ce qui en reste est toujours plus que suffisant pour nous en redonner un pareil nombre en un an ou deux ans ». Pourtant, cinq siècles d'exploitation intensive ont suffi pour que les habitats soient détruits et que les morues de Terre-Neuve disparaissent (Kurlansky 1998; Cury & Miserey 2008). Le développement des navires usines, des chaluts, l'utilisation de sonars pour détecter les bancs de poissons et le subventionnement à grande échelle des pêcheries par les états industriels ont abouti à une surexploitation mondialisée des stocks de poissons (Pauly et al. 2002; Pauly 2009). Une récente étude à partir de données de pêche recueillies par la FAO[2] depuis les années 50 a montré qu'une pêcherie sur quatre avait surexploité l'espèce pêchée jusqu'à son effondrement (Mullon, Freon, & Cury 2005). Les populations de poissons prédateurs ne représentent plus que 10% de la biomasse à l'ère pré-industrielle et 15 années ont suffi pour que les pêcheries industrielles réduisent de 80% la biomasse des communautés marines (Myers & Worm 2003). Les scientifiques sont d'autant plus inquiets que la dynamique des populations de poissons est encore mal comprise et que seul un tiers des effondrements de stock fait suite à une décroissance constante des captures, rendant prévisible la disparition des poissons ciblés (Mullon et al. 2005). Cette surexploitation massive, associée à la détérioration des habitats marins par le passage des chaluts engendre une diminution des ressources disponibles pour les prédateurs marins et la déstructuration des réseaux trophiques (Pauly & Maclean 2002). Les écosystèmes perdent leur capacité de résilience et les stocks ne se reconstituant pas, les pêcheries exploitent des niveaux trophiques de plus en plus bas dans la chaine alimentaire (« *fishing down marine food webs* » Figure 1.5, Pauly et al. 1998). Il en résulte une diminution des tailles moyennes de capture, une disparition des classes d'âges les plus âgées et une diminution des densités d'animaux qui peut entraîner des difficultés de reproduction à cause d'un faible taux de rencontre entre individus sexuellement matures (Pauly & Maclean 2002). La diminution des poissons prédateurs favorise également la

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[2] Food and Agriculture Organisation (Nations Unies)

prolifération d'espèces telles que les méduses (Lynam et al. 2006), et pourrait entrainer des inversions de niveaux trophiques[3] (Fauchald 2010).

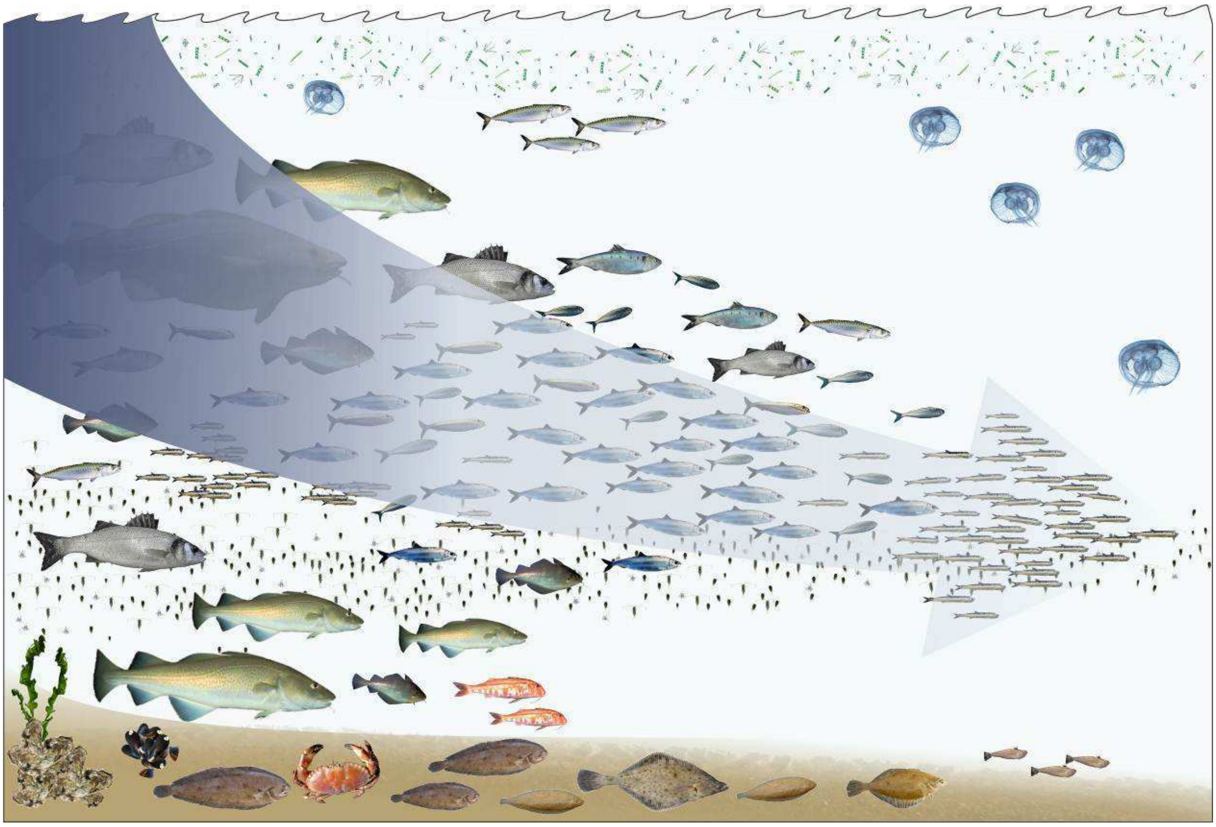

Figure 1.5 "Fishing down the marine food webs" (tiré de Pauly et al. 1998)

Une autre conséquence des pêcheries industrielles est l'augmentation des captures accidentelles responsables de l'augmentation de la mortalité des prédateurs supérieurs (dauphins, tortues marines, oiseaux marins) mais également d'invertébrés et d'espèces non commercialisables qui se transforment en déchets de pêche (Jennings & Kaiser 1998; Hall, Alverson, & Metuzals 2000). Ces déchets représentent un apport substantiel de proies pour les prédateurs (Arcos & Oro 2002; Votier et al. 2004) mais leur apport énergétique moins élevé n'est pas sans conséquences, notamment pour le succès reproducteur des oiseaux marins (Furness 2007a; Pichegru et al. 2007; Grémillet et al. 2008).

b) Les changements climatiques

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[3] Les proies devenant prédateurs des œufs ou des larves du niveau trophique supérieur.

Les activités humaines entrainent le relâchement dans l'atmosphère de nombreux polluants et de grandes quantités de gaz à effet de serre, liés à la consommation d'énergie fossile (IPCC 2007). Les rapports des experts du GIEC ne laissent aucun doute sur la réalité de changements climatiques complexes qui s'opèrent, avec notamment une augmentation globale des températures atmosphériques (IPCC 2007). A une échelle locale, les variations de température sont très hétérogènes et marquées (Walther et al. 2002). Les conditions environnementales changent et l'impact sur les organismes peut être fort : modification de la phénologie, des aires de distribution (extension, réduction voire extinctions locales), asynchronies trophiques, variations de l'abondance et des dynamiques de population (Parmesan 2006)… Les communautés peuvent s'en trouver altérées, certaines espèces étant favorisées par ces variations, d'autres atteignant leurs limites physiologiques (Stachowicz et al. 2002; Perry et al. 2005). Dans le milieu marin, de nombreux organismes sont ectothermes[4] et présentent des préférendums thermiques (Edwards & Richardson 2004). Ainsi chez certaines espèces de poissons, les routes migratoires, les périodes de reproduction, le taux de fécondité et le taux de survie des larves seront modifiés par l'augmentation ou la diminution des températures de l'eau (Loeng et al. 2005).

Les changements climatiques vont également affecter les processus physiques abordés précédemment : la variation des températures et des précipitations modifie la vitesse des vents qui influencent la circulation des courants (Jónsson 1991). La fonte des glaces des milieux polaires modifie la composition chimique des eaux et intensifie la stratification de la colonne d'eau (IPCC 2007). Il est aisé de comprendre que ces changements en chaine affectent la localisation des zones de forte productivité et altèrent la production primaire (Loeng et al. 2005) donc l'abondance et la distribution des planctonivores et celles des prédateurs supérieurs en bout de chaine trophique (Walther et al. 2002).

Aux variations environnementales naturelles s'ajoutent donc des variations d'origine anthropique dont les effets ou la combinaison des effets sont peu prévisibles, particulièrement à une échelle locale, c'est-à-dire celle d'un prédateur marin dont la mobilité est limitée. La distribution et l'abondance des ressources sont donc variables dans le temps et l'espace et les

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[4] Dont la température corporelle varie en fonction de la température du milieu

consommateurs de ces poissons doivent adopter des stratégies adaptées à chacune de ces variations.

2. La réponse évolutive des oiseaux marins à la variabilité environnementale

2.1 Un mode de vie adapté à l'environnement marin

Les oiseaux marins évoluent dans trois milieux différents dont les contraintes diffèrent : marin, aérien et terrestre. Cette caractéristique a entrainé de nombreuses adaptations physiologiques et morphologiques, comportementales et démographiques. Cet ensemble de traits d'histoire de vie a été défini sous le nom de *seabird syndrome* (Gaston 2004). Entre autres particularités, les oiseaux marins ont une espérance de vie remarquablement longue (entre 20 et 60 ans), une maturité sexuelle retardée, des tailles de ponte réduites (souvent limitées à un œuf unique), une durée d'élevage des jeunes allongée (souvent jusqu'à 6 mois) et un mode de vie colonial. Les oiseaux marins se caractérisent également par une taille généralement plus grande que les oiseaux terrestres, un plumage moins coloré et peu de dimorphisme sexuel (Schreiber & Burger 2001).

Comme beaucoup d'espèces terrestres, les oiseaux marins migrent après leur saison de reproduction. Une ségrégation spatiale s'opère au cours du cycle annuel, elle s'accompagne de la disparition du mode de vie terrestre en dehors de la saison de reproduction. Les oiseaux rejoignent des zones d'hivernage et vivent alors exclusivement en mer. Ces zones d'hivernage sont encore mal connues et si les oiseaux sont observés en mer, leur origine géographique ne peut pas être déterminée. La difficulté d'accès aux oiseaux pendant la période hivernale a concentré les études sur la période de reproduction. Depuis quelques années, le développement d'appareils GLS[5] miniatures (Wilson et al. 1992), a permis une évolution rapide des connaissances de l'écologie hivernale des oiseaux marins (González-Solís et al. 2007; Kubetzki et al. 2009; Guilford et al. 2009; Quillfeldt, Voigt, & Masello 2010).

En été, les oiseaux marins se reproduisent à terre. Ils établissent leurs colonies dans des sites relativement isolés et peu accessibles, à l'abri des prédateurs terrestres. Ils sont contraints de se nourrir en mer, parfois assez loin de leur site de nidification : on dit des oiseaux marins

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[5] Global Location System

qu'ils sont des *central place foragers* (Orians & Pearson 1979). Cette séparation spatiale entre la colonie et le lieu de nourrissage entraine un coût énergétique d'autant plus élevé que la compétition intraspécifique, augmentant avec la taille des colonies, force les oiseaux à rechercher leur nourriture plus loin encore (Lewis et al. 2001; Ainley et al. 2003). Pour Ashmole (1963), les grandes agrégations d'oiseaux marins épuisent les ressources alimentaires aux abords des colonies. D'après Lack (1968), les traits d'histoire de vie, tels que la faible taille des pontes, la croissance lente et l'accumulation de graisse chez les poussins ou la taille des colonies, résulteraient de cette difficulté d'approvisionnement à proximité du site de nidification, celle-ci étant aggravée par un environnement marin imprévisible (« Energy-limitation theory »). Mais selon Schreiber et Burger (2001), si les traits d'histoire de vie des oiseaux marins sont certainement le produit de forces de sélection liées aux conditions environnementales, cette théorie n'explique pas forcément la démographie particulière des oiseaux marins. La distribution des ressources serait peut-être moins imprévisible et labile qu'on ne l'aurait crue (Weimerskirch 2007).

2.2 Le rôle central des processus d'acquisition d'énergie

La valeur sélective d'un individu[6] est définie par sa capacité à produire des descendants et à survivre. L'efficacité des stratégies d'acquisition de ressources conditionne la quantité d'énergie qui pourra être allouée à la reproduction, à la survie et à la croissance d'un individu (Boggs 1992). Le lien entre le succès reproducteur des oiseaux et leur capacité à trouver des proies en quantité suffisante pour couvrir leurs besoins énergétiques est donc étroit. Cette demande énergétique est particulièrement élevée pendant la saison de reproduction puisque qu'aux besoins de l'adulte pour sa propre maintenance s'ajoutent ceux d'un ou de plusieurs poussins en croissance (Shaffer, Costa, & Weimerskirch 2003; Markones, Dierschke, & Garthe 2010). A ce stade de leur cycle de vie, les oiseaux sont particulièrement sensibles aux variations environnementales et lorsque les conditions d'approvisionnement se dégradent, le succès reproducteur diminue. Ce phénomène a été observé chez plusieurs espèces comme la mouette tridactyle *Rissa trydactila* (Wanless et al. 2007), le fou du Cap *Morus capensis* (Pichegru et al. 2010b), le pétrel bleu *Halobaena caerulea* (Chastel, Weimerskirch, & Jouventin 1995b), le manchot du Cap *Spheniscus demersus* (Crawford et al. 2006). Pour un

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[6] ou *fitness* en anglais

individu adulte, le compromis d'allocation des ressources se joue entre la reproduction et la survie ; les traits d'histoire de vie des oiseaux marins montrent que la survie des adultes prime sur la reproduction d'une année. Ainsi, les adultes atteignant un seuil critique de masse corporelle vont abandonner la reproduction pour assurer leur survie (Chastel, Weimerskirch, & Jouventin 1995a). Les processus d'acquisition des ressources tiennent une place centrale entre l'environnement marin et la capacité des oiseaux à survivre et à se reproduire, dont dépend la dynamique des populations (Figure 1.6).

Les oiseaux marins sont soumis à des pressions de sélection, mais leur plasticité comportementale leur permet de développer différentes stratégies de recherche alimentaire pour s'adapter aux variations de la disponibilité des proies.

3. Les réponses comportementales des oiseaux marins à la variabilité environnementale

Les prédateurs marins peuvent faire preuve d'une grande plasticité dans leurs comportements alimentaires pour maximiser leurs chances de capturer des proies. Cette capacité de moduler la réponse comportementale permet de compenser, dans une certaine limite, les variations de la distribution et de l'abondance des proies. Les prédateurs opposent une réponse fonctionnelle sigmoïdale aux variations de densités de leurs proies (Figure 1.7) qui se caractérise par un seuil critique inférieur et un seuil supérieur (Hassell, Lawton, & Beddington 1977). Entre ces deux valeurs limites, les prédateurs peuvent répondre aux variations environnementales en modifiant leur effort de recherche alimentaire ou en adoptant toute stratégie qui peut compenser une diminution ou une augmentation des proies recherchées. En dessous du seuil minimal, les oiseaux marins voient leurs fonctions reproductrices et vitales menacées selon le compromis d'allocation des ressources que nous avons détaillé plus haut. Lorsque l'abondance des proies baisse fortement, les parents connaissent des difficultés pour nourrir leurs jeunes et le succès reproducteur chute (Furness & Tasker 2000; Frederiksen et al. 2004). Si les conditions environnementales se dégradent encore, alors la survie des adultes est menacée (Barbraud et al. 2000; Oro & Furness 2002).

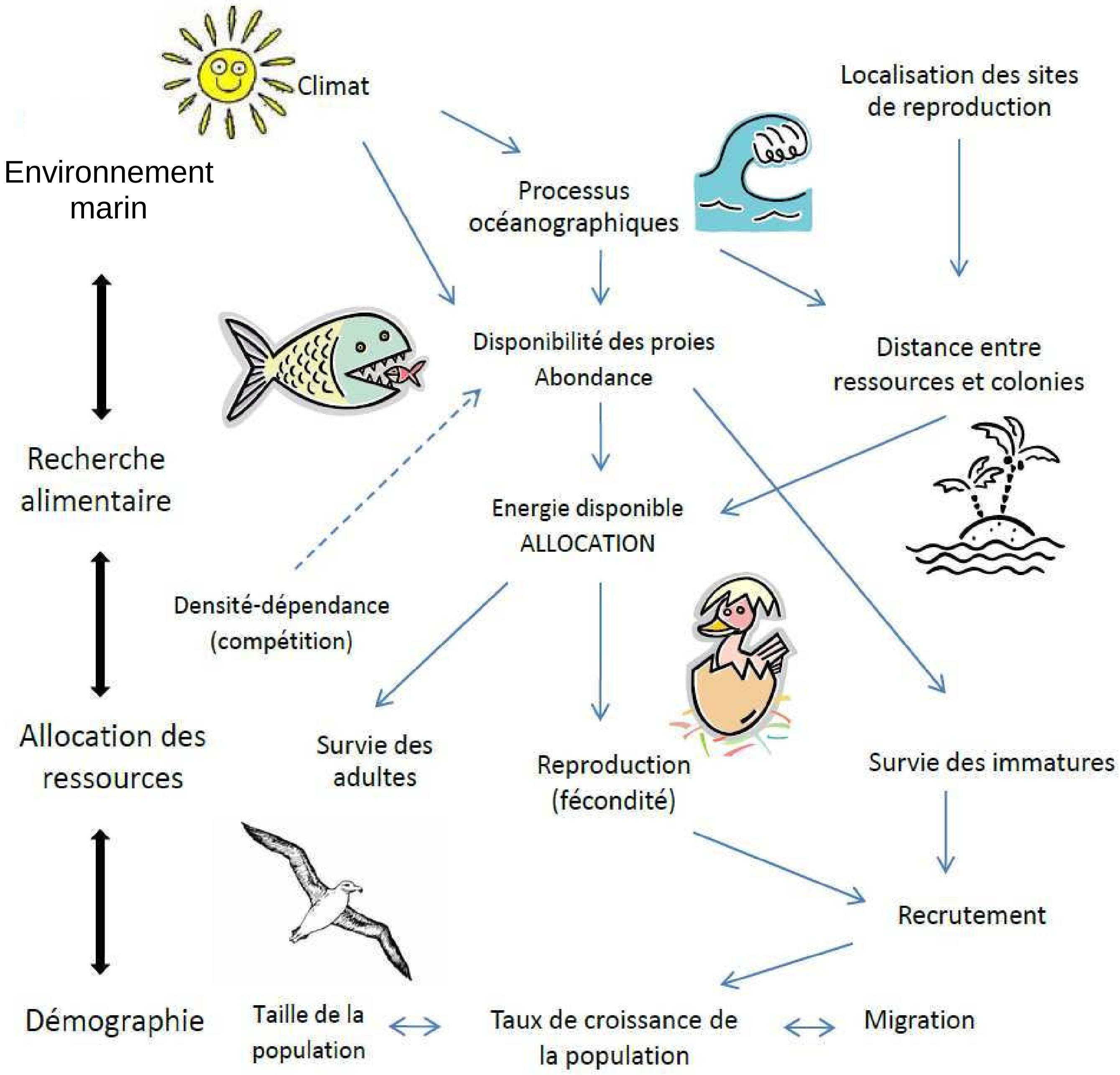

Figure 1.6 Représentation schématique des interactions entre environnement et démographie (adapté de Schreiber et Burger 2001)

La valeur de ce seuil varie d'une espèce à l'autre en fonction des coûts énergétiques liés aux déplacements des oiseaux, de leur rayon d'action, de leur performance prédatrice (Furness & Tasker 2000) mais également en fonction de la compétition intra et interspécifique pour les ressources et des risques liés à la prédation (Abrams 1991). A l'opposé, au-delà du seuil supérieur de densité des proies, les animaux n'accroissent plus leur effort de recherche alimentaire jusqu'à devenir *full and lazy*[7] (Jeschke 2007) et connaissent des conditions optimales pour leur reproduction (Furness 2007b).

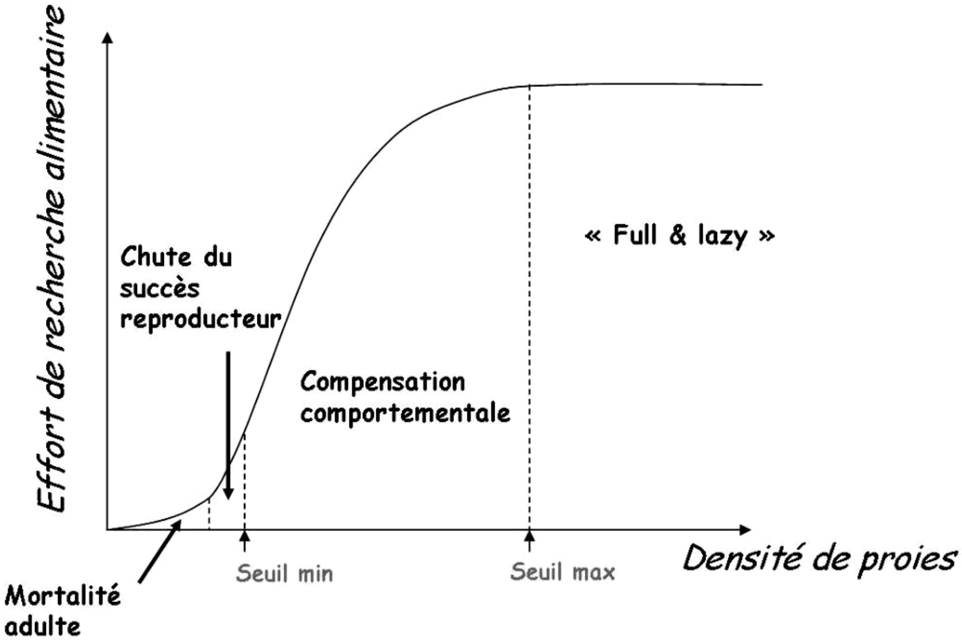

Figure 1.7 Réponse fonctionnelle des oiseaux marins à la densité de proies (tiré de Pichegru 2008)

La flexibilité comportementale permet dans certaines conditions aux oiseaux marins de compenser les variations environnementales en termes de ressources, mais le niveau de cette flexibilité est dépendant des caractéristiques l'espèce et du statut des individus. Le coût énergétique lié aux méthodes d'alimentation (Grémillet & Wilson 1999), la condition corporelle des parents et des poussins (Ochi, Oka, & Watanuki 2009), le statut de reproduction (Shaffer et al. 2003; Green et al. 2005) mais également l'expérience des oiseaux (Daunt et al. 2007) sont des déterminants essentiels de la réponse comportementale des

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[7] Rassasiés et paresseux

oiseaux. Au sein d'une population, tous les individus ne présentent donc pas la même capacité de réaction face aux changements environnementaux. C'est la capacité du plus grand nombre de reproducteurs à compenser ces variations de la disponibilité des proies qui influe sur les tendances populationnelles d'une colonie. Les oiseaux marins peuvent modifier leur comportement d'acquisition des ressources de différentes manières que nous allons détailler.

3.1 Varier le régime alimentaire

Dans des conditions environnementales contrastées, des individus de la même espèce, et vivant dans des colonies plus ou moins éloignées, peuvent avoir une alimentation différente. C'est le cas des manchots papous *Pygoscelis papua* de l'archipel des Kerguelen qui consomment des poissons démersaux ou des crustacés en fonction de la situation de la colonie sur une mer ouverte ou fermée (Lescroel & Bost 2005) ou des manchots de Magellan de Patagonie qui se nourrissent d'anchois *Engraulis anchoita* au nord et de sprat *Sprattus fuegensis* au sud (Wilson et al. 2005). Si les proies de prédilection deviennent moins abondantes, certains oiseaux marins se montrent très opportunistes dans leur régime alimentaire et consomment les proies de substitution disponibles (Litzow et al. 2002; Pinaud, Cherel, & Weimerskirch 2005). Avec le développement important des pêcheries industrielles, les déchets de pêche représentent également une alternative énergétique aux proies naturelles. Les fulmars boréaux *Fulmarus glacialis,* dont les effectifs ont significativement augmenté dans les dernières décennies, semblent avoir bénéficié de cet apport supplémentaire de nourriture dans certaines zones de leur distribution (Garthe, Camphuysen, & Furness 1996; Phillips et al. 1999). En revanche, d'autres espèces comme le fou du Cap *Morus capensis* subissent les effets de la valeur énergétique inférieure de ces déchets de pêche par rapport aux anchois et sardines habituellement consommés, avec pour conséquence un effondrement du succès reproducteur (Grémillet et al. 2008) mais un maintien de la survie adulte.

3.2 Moduler son budget temps

Les oiseaux marins peuvent également augmenter leur effort de recherche alimentaire en modulant le temps alloué aux différentes activités (budget-temps). Si les proies deviennent moins accessibles, ils consacrent plus de temps à la recherche alimentaire aux dépens du temps passé au nid (Ojowski, Eidtmann, & Furness 2001; Lewis et al. 2004). Cette modulation du budget-temps s’accompagne de différentes modifications du comportement de recherche alimentaire.

a) Modifier le comportement de plongée

Certaines espèces d’oiseaux marins accroissent leur effort de recherche alimentaire en adaptant leurs plongées en fonction de la profondeur des proies ou simplement du temps disponible pour pêcher. Les gorfous macaroni *Eudyptes chrysolophus* ainsi que les grands cormorans *Phalacrocorax carbo* augmentent le temps passé à plonger, la durée et le nombre des plongées pendant les jours d’hiver durant lesquels la lumière devient un facteur limitant (Green et al. 2005; Grémillet et al. 2005). Près de Terre-Neuve, les guillemots de Troïl *Uria aalge* suivent les capelans *Mallotus villosus* qui migrent plus en profondeur pendant le jour. Ces plongées sont énergétiquement plus coûteuses pour les oiseaux mais l’efficacité de prédation est meilleure dans ces eaux froides (proche de 0°C) où les poissons ectothermes se déplacent et fuient moins rapidement (Hedd et al. 2009).

b) Modifier la durée des voyages alimentaires

D’autres espèces modulent la durée des voyages alimentaires pour maximiser leurs chances de capturer des proies. Suite à la mise en place d’une zone d’exclusion de pêche aux abords de leur colonie, les manchots du Cap *Spheniscus demersus* de l’ile de Sainte Croix ont réduit la durée des voyages alimentaires tandis que ceux de la colonie voisine de Bird Island l’ont au contraire augmentée pour pallier à une diminution de la disponibilité des proies vraisemblablement liée à une pression de pêche plus forte à l’extérieur de l’aire marine protégée (Pichegru et al. 2010a). Cette augmentation de la durée des voyages alimentaires ne s’accompagnait pas dans ce cas précis d’une augmentation de la distance de recherche des proies.

3.3 Changer de zone d’alimentation

Il arrive que les proies se déplacent ou que leur densité diminue dans les zones les plus proches exploitées par les oiseaux. Ces derniers partent alors à la recherche de nouvelles zones d’alimentation plus éloignées, avec des contraintes qui varient selon les différents cas de figure.

a) Autour de la colonie

Pendant la saison de reproduction, les oiseaux sont soumis à des contraintes spatiales et temporelles plus fortes puisqu'ils doivent regagner leur nid régulièrement pour y relayer l'autre parent et nourrir leur poussin. Leur rayon d'action dépend donc de leur capacité de déplacement et du temps dont ils disposent avant que l'autre parent n'abandonne le nid ou que le poussin ne meure de faim. Les fous de Bassan de l'immense colonie de Bass Rock en Ecosse sont soumis à une compétition intraspécifique forte (Lewis et al. 2001). Selon les années, ils peuvent quasiment doubler la distance à la colonie pour gagner les zones de concentration des proies et se nourrir à plus de 360km de leur nid, sans voir leur succès reproducteur diminuer (Hamer et al. 2007).

b) Migration et zones d'hivernage

De la même manière qu'ils se déplacent plus loin pendant la saison de reproduction lorsque la nourriture vient à manquer, les oiseaux marins recherchent de zones d'hivernage profitables et se déplacent vers de nouveaux secteurs en réponse à une dégradation des conditions d'alimentation pendant la période hivernale (Ainley & Divoky 2001). Les contraintes spatiales sont moins fortes que lors de la saison de reproduction et les oiseaux marins ont de grandes capacités de déplacement. Le puffin fuligineux *Puffinus griseus* parcourt ainsi plusieurs dizaines de milliers de kilomètres dans l'Océan Pacifique pour gagner les zones océaniques les plus productives tout au long de l'hiver[8] (Shaffer et al. 2006).

c) Emigration

Lorsqu'ils sont reproducteurs, les oiseaux marins sont généralement très fidèles à leur colonie (Inchausti & Weimerskirch 2002). Cette fidélité leur permet entre autres de développer une bonne connaissance de leur environnement (Grémillet et al. 1999) et de retrouver facilement leur partenaire après la période hivernale (Wooller et al. 1989). Les cas d'émigration chez des oiseaux reproducteurs ont été peu décrits mais ils existent pourtant (Barrett 2008). Ils sont souvent liés à du dérangement humain (Anderson & Keith 1980) ou causé par des prédateurs (Jones et al. 2008). L'impact de mauvaises conditions alimentaires sur la fidélité aux sites de reproduction conduisant à une dispersion a été mis en évidence chez la mouette tridactyle

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[8] Comprendre ici toute la période qui sépare deux saisons de reproduction (*interbreeding* en anglais)

(Naves, Monnat, & Cam 2006). La baisse de fidélité au site était associée à des échecs répétés de la reproduction.

4. Les mécanismes de recherche des proies

Avant de pouvoir moduler son effort de recherche alimentaire, le prédateur marin doit pouvoir localiser les proies qu'il recherche dans un environnement marin qui semble fournir peu d'indices. Pourtant des processus permettent aux oiseaux marins d'accéder aux proies et d'en tirer assez d'énergie pour assurer leur survie et celle de leur descendance la plupart du temps, mais ils sont encore peu connus.

4.1 Anticiper la localisation des proies à distance

Avant de partir pour un nouveau voyage alimentaire, les oiseaux marins peuvent potentiellement obtenir des informations sur la localisation de la nourriture depuis le site de reproduction ou même en mer, à une certaine distance des sources de nourriture. Plusieurs mécanismes de détection des proies à distance sont décrits dans la littérature.

a) L'olfaction

La détection de nourriture à distance via l'olfaction a été mise en évidence chez plusieurs espèces de procellariiformes (pétrels, albatros). Ces oiseaux perçoivent et sont attirés par un composé volatile appelé sulfure de diméthyle (DMS). Cette molécule émise par le phytoplancton indique aux oiseaux les zones où la production primaire est élevée et potentiellement là où ils trouveront des proies (Nevitt & Bonadonna 2005; Nevitt, Losekoot, & Weimerskirch 2008). Le rôle de l'odorat via une réponse au DMS a également été révélé chez deux espèces de sphéniscidés, le manchot du Cap (Cunningham, Strauss, & Ryan 2008) et le manchot de Humboldt (Culik 2001).

b) Les signaux visuels

L'utilisation de signaux visuels comme la présence de congénères a été clairement mise en évidence chez les oiseaux marins (Davoren, Montevecchi, & Anderson 2003). A distance, il est certainement plus facile pour un oiseau de repérer le plumage blanc (ou partiellement blanc) caractéristique des oiseaux marins et le comportement d'un groupe d'oiseaux qui pêchent que d'apercevoir des proies sous l'eau (Shealer 2001). En mer, les groupes d'oiseaux regroupant souvent plusieurs espèces peuvent atteindre le million d'individus (Veit & Hunt 1991). Ce comportement, appelé *local enhancement* en anglais, consiste à s'associer à un groupe d'oiseaux ou de prédateurs ayant déjà repéré une source de nourriture. Ce comportement prévaut lorsque la ressource est agrégée en patches et labile et peut être envisagé comme une réponse adaptative au grégarisme des proies qui s'assemblent en bancs de poissons ou en « essaim »[9] pour le krill (Fauchald 2009).

Si le *local enhancement* est un moyen efficace pour localiser rapidement une zone de nourriture, il n'intervient qu'à une distance assez courte. Lorsqu'un individu quitte sa colonie, il peut éventuellement utiliser l'information visuelle induite par le retour de mer de congénères ou suivre des oiseaux plus expérimentés partant en voyage alimentaire. Cette hypothèse dite du « centre d'information » fait le postulat que des informations peuvent être échangées entre les individus à la colonie, sur la localisation de nourriture au-delà de la portée visuelle (Ward & Zahavi 1973; Danchin et al. 2004). Les cormorans de Bougainville *Phalacrocorax bougainvillii* qui se reproduisent le long des côtes péruviennes forment des radeaux[10] aux abords de la colonie, qui sont orientés suivant la direction des grands groupes d'oiseaux au retour de mer (Weimerskirch et al. 2010a). Les oiseaux entamant un voyage en mer rejoignent d'abord ces groupes posés devant la colonie et utiliseraient ce mécanisme d'information publique pour choisir direction à prendre afin de trouver de la nourriture.

c) La mémorisation de zones connues

La théorie de l'information publique a longtemps reçu peu de support de la part des études empiriques, laissant plutôt penser que les oiseaux utilisent leurs propres expériences et la mémorisation de zones riches pour orienter leurs nouveaux trajets en mer (Davoren et al. 2003). Les mouettes tridactyles *Rissa tridactyla* retournent fidèlement sur des sites déjà visités et semblent construire des cartes mentales à partir des voyages alimentaires précédents (Irons 1998). Cette faculté a également été montrée chez les guillemots de Troïl *Uria aalge* dont la fidélité aux sites d'alimentation n'exclut pas d'explorer de nouveaux sites (Wanless, Harris, & Morris 1990). Mémoriser des zones d'alimentation productives permet de réduire le temps de

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[9] *Swarm* en anglais

[10] Groupes d'oiseaux se reposant ou se nettoyant sur l'eau, souvent visibles aux abords des colonies ou en pleine mer

vol et de recherche alimentaire qui représente une forte dépense énergétique, particulièrement pendant la saison de reproduction (Birt-Friesen et al. 1989) et pour les espèces dont le vol est très coûteux en énergie.

4.2 Ajuster ses déplacements

a) Des mouvements ajustés à la densité des proies

Une fois en mer, les oiseaux marins disposent de nouvelles informations visuelles et peuvent détecter les proies recherchées. Ces dernières sont souvent agrégées en patches (exemple du banc de poisson) dont la distribution est spatialement hiérarchisée et dont la prévisibilité diminue avec l'échelle spatio-temporelle (Fauchald, Erikstad, & Skarsfjord 2000; Weimerskirch 2007). Cette structuration spatiale des proies entraine un ajustement des mouvements des prédateurs en fonction de la densité. Lorsque celle-ci est faible, l'animal aura tendance à augmenter sa vitesse et la linéarité de son déplacement pour trouver rapidement un patch de nourriture (Figure 1.8a). Lorsque la densité est forte, le prédateur ralentit et réalise des mouvements sinueux dans une zone restreinte (Benhamou 1992). Ce comportement de prospection est appelé *Area Restricted Search* ou ARS (Kareiva & Odell 1987) et vise à augmenter les chances de capture (Figure 1.8b).

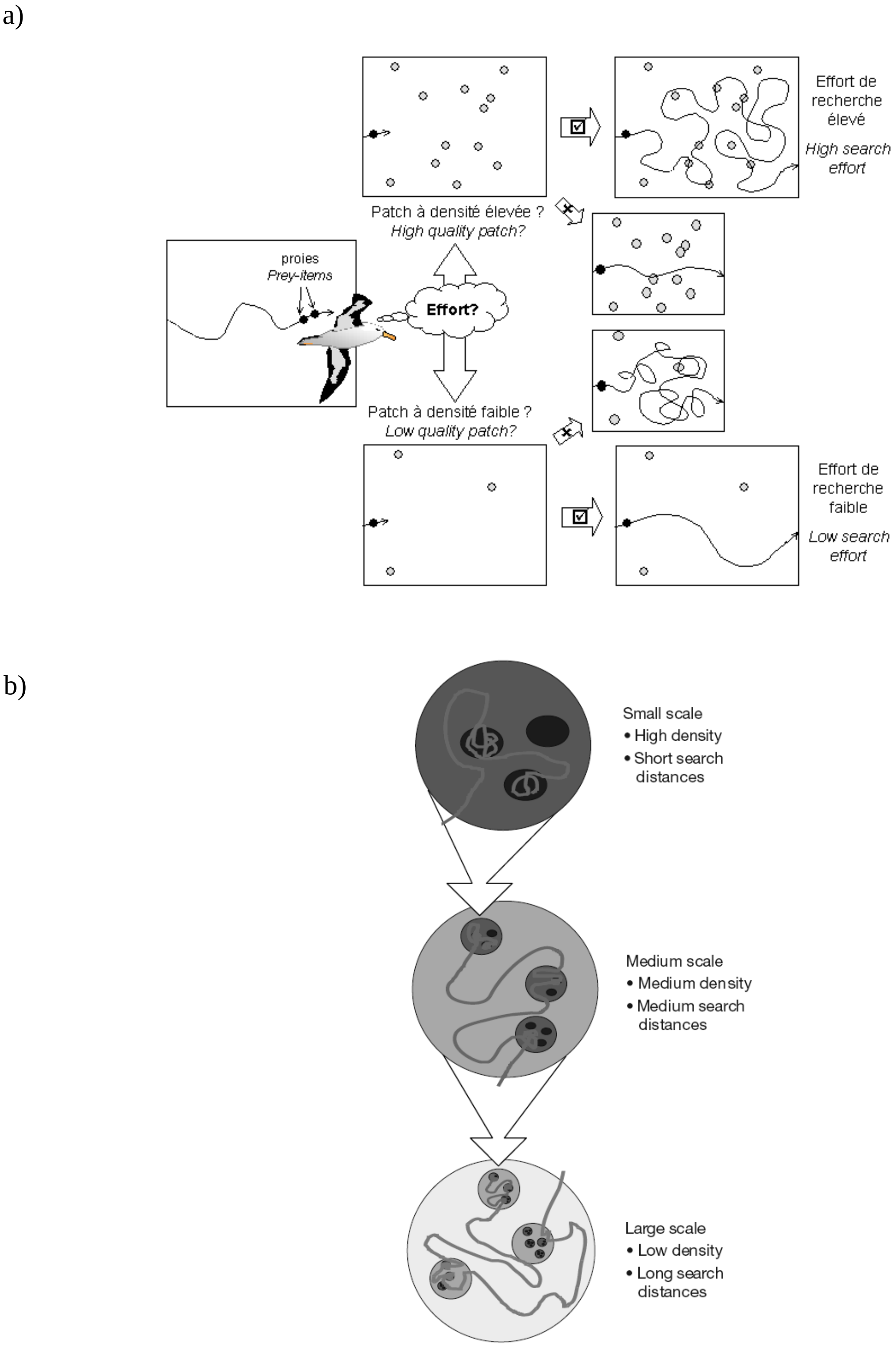

Figure 1.8 Ajustement du comportement de recherche en fonction de la densité des proies. a) Modification du déplacement en fonction des taux de rencontres (tiré dePinaud 2005) b) Adaptation du comportement de vol (vitesse et sinuosité) en fonction des échelles : plus la densité en proies est élevée, plus le trajet est sinueux (tiré de Weimerskirch 2007).

b) Profils de trajets alimentaires

Le développement d'enregistreurs miniaturisés a permis d'équiper de nombreuses espèces d'oiseaux marins et d'enregistrer leurs déplacements en mer avec une précision et une autonomie sans cesse croissantes (Wilson et al. 2002). En fonction des informations dont les oiseaux disposent sur la disponibilité des proies, les trajets alimentaires présentent un profil général variable. Les enregistrements des voyages alimentaires de 44 espèces d'oiseaux marins, réparties en 80 sous-population, ont été analysés (Weimerskirch 2007). Trois principaux profils se détachent, apparemment associés à un gradient de prévisibilité des proies. Le premier correspond à une recherche de type aléatoire, il n'est pratiquement pas représenté dans les espèces précitées (Figure 1.9a). Dans le second profil *looping trip* (Figure 1.9b), les oiseaux suivent une boucle ponctuée de phases de recherche alimentaire en fonction des proies rencontrées. La direction prise par les oiseaux au départ de la colonie n'est pas celle qui est observée lorsque l'animal revient de mer. Le troisième et dernier profil est appelé *commuting trip* (Figure 1.9c), que l'on peut décrire comme un voyage linéaire et rapide à l'aller entre la colonie et la zone de recherche alimentaire et au retour entre la dernière zone exploitée et la colonie. Dans l'étude de Weimerskirch (2007), 93% des sous-populations présentaient des déplacements en *commuting trip*. Il est intéressant de noter que le même individu peut alterner entre les deux dernières stratégies. La différence fondamentale entre les voyages en boucle et le commuting pourrait reposer sur la capacité de l'animal à anticiper la localisation de sa ressource et de l'atteindre directement. La proportion très élevée de voyages en *commuting* sous-tend l'idée que l'environnement marin n'est pas aussi imprévisible que la littérature l'a longtemps soutenu (Weimerskirch 2007), mais cela n'a pas été démontré empiriquement.

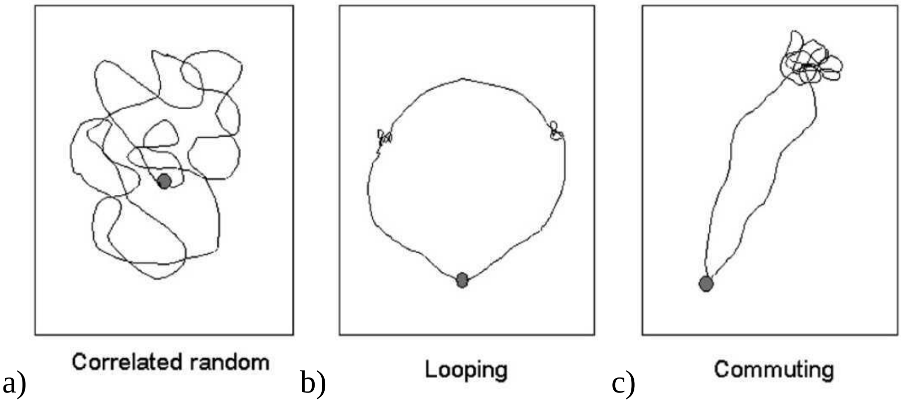

Figure 1.9 Profils type de trajet alimentaire chez les oiseaux marins a) aléatoire b) en looping ou boucle c) en commuting (tiré de Weimerskirch 2007)

Problématique et objectifs de la thèse

Les oiseaux marins évoluent dans un environnement où les processus physiques, chimiques et biologiques complexes génèrent une variabilité importante et peu prévisible de la disponibilité des ressources. L'acquisition des ressources dans cet environnement variable est un processus central qui conditionne la survie des individus et par conséquent des populations de l'avifaune marine. Au cours du temps, les oiseaux marins ont développé des traits évolutifs particuliers et des comportements de recherche alimentaire flexibles en réponse à cette variabilité. A travers l'étude de voyages alimentaires de fous de Bassan enregistrés à la fois pendant la saison de reproduction et en dehors de la saison de reproduction, nous essayerons de répondre à la question suivante :

« La plasticité comportementale permet-elle aux oiseaux marins de s'adapter à l'imprévisibilité spatio-temporelle de leurs ressources ? »

Le choix du fou de Bassan comme modèle biologique s'est imposé pour plusieurs raisons. La première est d'ordre technique. Les fous de Bassan sont des oiseaux dont la taille et le poids permettent le déploiement d'enregistreurs miniaturisés. Cette espèce n'est pas menacée et sa population mondiale est en croissance. Enfin, les fous sont relativement faciles à capturer sur leur nid sans que leur reproduction n'en soit menacée (pas d'abandons). La deuxième raison est liée à la grande flexibilité comportementale des fous. Ils sont très mobiles et peuvent parcourir de grandes distances. Ils sont également opportunistes et consomment facilement des proies variées (Montevecchi et al. 2009). En cas de nécessité, ils peuvent également augmenter leur effort alimentaire pour pallier à une diminution des proies localement (Hamer et al. 2007) ou adapter leur comportement alimentaire à des conditions environnementales contrastées (Garthe et al. 2006). Ces caractéristiques font du fou de Bassan un bon modèle pour étudier la variabilité et la plasticité comportementale chez les oiseaux marins.

Après une description plus complète de l'espèce et des sites d'études (Chapitre 2), la thèse sera divisée en 4 chapitres constitués sur la base de publications scientifiques rédigées en langue anglaise (publiées ou en cours de soumission). Nous tenterons de répondre à la question générale de cette thèse en analysant le comportement de recherche alimentaire des fous **à des échelles spatio-temporelles croissantes** (Figure 1.10)**.**

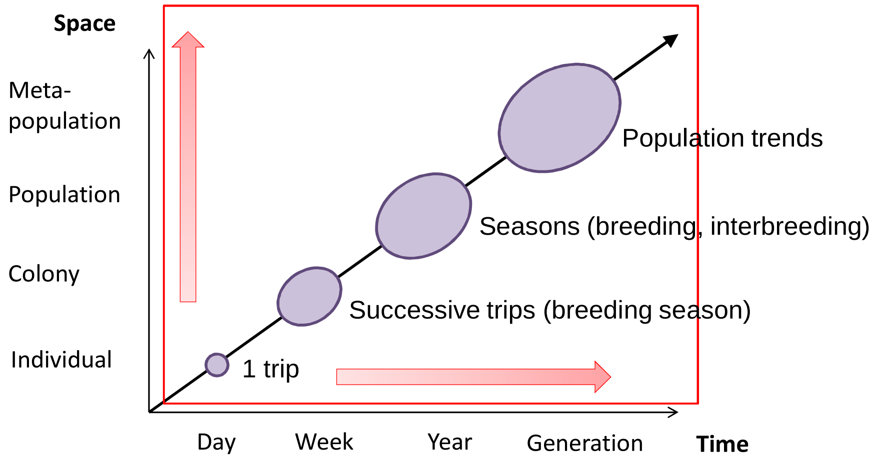

Figure 1.10 Analyse des comportements de recherche alimentaire des Fous de Bassan à des échelles spatio-temporelles croissantes

Dans le premier chapitre (Chapitre 3), nous mettrons en évidence l'anticipation de la localisation des proies par les fous de Bassan à la plus petite échelle spatio-temporelle, c'est-à-dire celle d'un voyage alimentaire.

Dans le deuxième chapitre (Chapitre 4), nous analyserons la variabilité des comportements de recherche alimentaires à l'échelle de plusieurs voyages successifs pour évaluer la plasticité comportementale des fous et les stratégies d'alimentation observées au sein de deux populations.

Dans le troisième chapitre (Chapitre 5), nous élargirons notre analyse de l'écologie alimentaire du fou de Bassan à la période hivernale et nous étudierons les variations de stratégies adoptées par différentes colonies en Europe pendant leur migration.

Dans le quatrième chapitre (Chapitre 6), nous essayerons de comprendre si des contraintes alimentaires en période de reproduction chez le fou de Bassan peuvent expliquer des tendances populationnelles locales.

En toute dernière partie (Chapitre 7), nous présenterons une synthèse des résultats de cette thèse, et nous discuterons des perspectives de ces résultats pour la compréhension de l'écologie spatiale des oiseaux marins.

Chapitre 2. Modèle biologique et sites d'études

1. Le modèle biologique : le fou de Bassan Morus bassanus

Le fou de Bassan *Morus bassanus* est le plus grand oiseau marin nichant dans l'Atlantique Nord. Il appartient à l'ordre des Pélécaniformes et à la famille des Sulidés. D'une envergure comprise entre 165 et 180cm, les adultes arborent un plumage blanc pur avec l'extrémité des ailes noires. La tête et le cou sont d'un jaune pâle à doré. Le puissant bec, très pâle et en forme de poignard, est souligné de lignes noires qui se prolongent en formant un masque noir autour des yeux clairs et cerclés d'un bleu vif. Océanique et vivant principalement en haute mer où il se nourrit de poissons, il se reproduit sur des îlots rocheux ou en falaise, au sein de colonies pouvant rassembler jusqu'à plusieurs dizaines de milliers de couples. Les adultes se reproduisent chaque année entre avril et septembre et sont fidèles à leur site de reproduction ainsi qu'à leur partenaire. Ils élèvent un unique poussin avec un succès reproducteur élevé, avoisinant fréquemment les 80%[11]. On observe, assez rarement, des nids contenant deux œufs ou deux poussins, mais il semble que ces couvées proviennent de deux femelles occupant le même nid (Nelson 2002). Le taux de survie annuel des adultes atteint les 95% et la longévité moyenne de 16 ans (Nelson 2002). La mortalité est forte (65%) durant la première année d'existence des jeunes. Après l'envol, ceux-ci se dispersent en mer. Ils n'atteindront l'âge de la maturité sexuelle que vers 4 ou 5 ans mais les oiseaux immatures âgés de 2 à 4 ans sont visibles aux abords des colonies durant la période de reproduction. Ils sont souvent philopatriques et retournent majoritairement nicher dans la colonie où ils sont nés. Le recrutement de juvéniles dans des sites éloignés de leur colonie de naissance n'est pas marginal et certaines colonies montrent des taux de croissance supérieurs à ce que peut expliquer le seul accroissement naturel. L'espèce connait une phase de forte expansion depuis le début du 20$^{\text{ème}}$ siècle (Figure 2.1), grâce aux mesures de protection interdisant ou limitant l'exploitation des œufs et la chasse (Wanless, Murray, & Harris 2005). Elle compte aujourd'hui environ 350 000 couples reproducteurs, répartis dans une quarantaine de colonies (contre 14 en 1913, cf Nelson 2002).

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[11] Entre 1961 et 1973, le succès reproducteur moyen de la ponte à l'envol était de 77, 7% (73-85) sur l'île écossaise de Bass Rock (Nelson 2002).

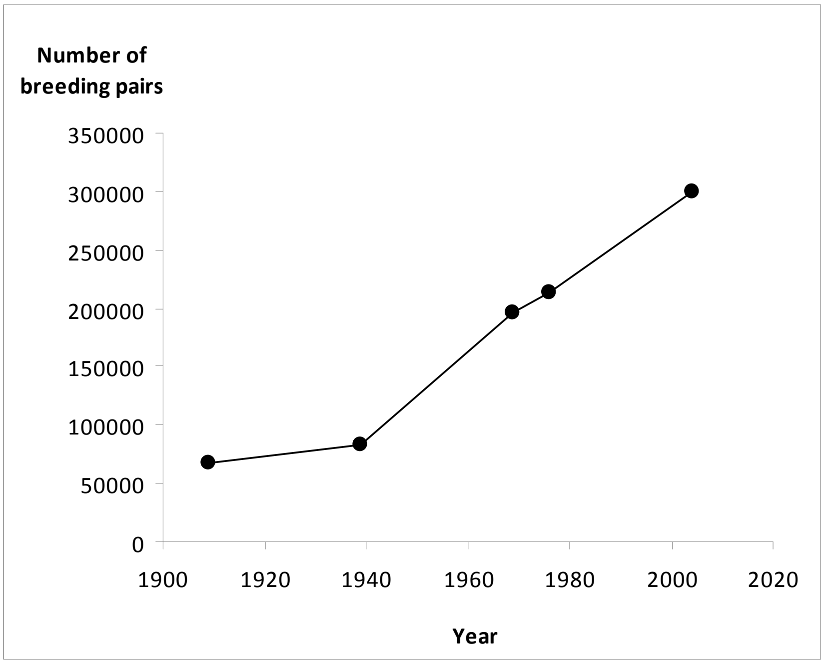

Figure 2.1 Evolution de la population mondiale des fous de Bassan Morus bassanus (d'après Nelson 2002 et Birdlife international 2011).

L’aire de répartition des fous occupe l’Atlantique nord (Figure 2.2). Les sites de reproduction sont concentrés dans les Iles Britanniques (20 colonies), l’Islande (8 colonies), la Norvège (entre 5 et 8 colonies), l’Allemagne, la France et les Iles Féroé et sur la côte est du Canada (6 colonies). L’Ecosse abrite à elle seule la moitié des couples reproducteurs (environ 172 000 d’après Nelson 2002) répartis dans 12 colonies dont la plus grande est Saint Kilda dans l’archipel des Hébrides extérieures. Cette colonie de fous est actuellement la plus importante au monde, elle compte plus de 60 000 nids. Lorsqu’elles sont établies, les colonies de fous de Bassan, rassemblent généralement plusieurs milliers d’individus. Dix d’entre elles abritent plus de 10 000 couples, bien que la compétition intraspécifique pour l’accès à la nourriture y soit plus forte que dans les petites colonies (Lewis et al. 2001), ce qui oblige les parents à couvrir de plus longues distances pour ramener les proies nécessaires à la croissance du poussin.

Pendant la saison de reproduction, il est contraint comme tous les oiseaux marins de revenir au nid pour nourrir son poussin et d’en assurer la garde pendant que son partenaire est en mer pour se nourrir à son tour. Il peut moduler son effort de recherche alimentaire mais également consommer une large gamme de proies (espèces et taille des proies). Parmi les plus communes, on peut citer entre autres le hareng *Clupea harengus*, le maquereau *Scomber scombrus*, le Lieu noir *Pollachius virens* ou encore le lançon *Ammodytes marinus* (Montevecchi & Barrett 1987; Hamer et al. 2000).

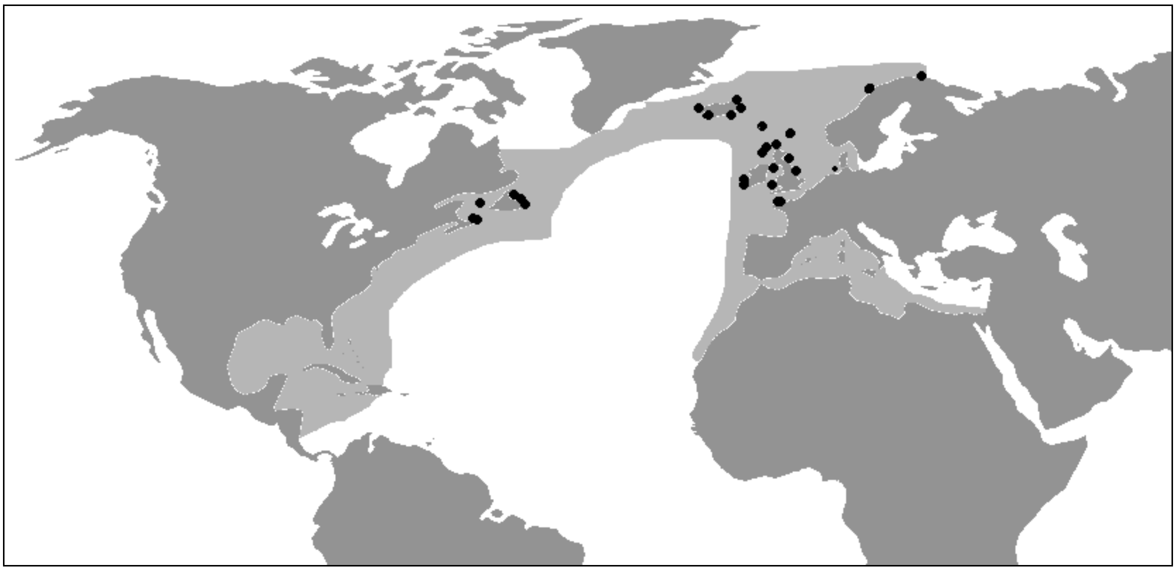

Figure 2.2 Distribution mondiale des Fous de Bassan (d'après Hornung, 2006), les sites de reproduction sont figurés par les points noirs et l'aire de distribution hivernale est représentée en gris clair.

Ce prédateur marin est particulièrement mobile et peut se déplacer jusqu'à plusieurs centaines de kilomètres de la colonie pour s'alimenter, sans altérer son succès reproducteur (Hamer et al. 2007). Lorsqu'il rencontre un banc de poissons, il entame un vol circulaire à une dizaine de mètres au-dessus de la surface avant de plonger de manière spectaculaire et d'entrer dans l'eau à la verticale le plus souvent, les ailes allongées en arrière et le cou tendu. Une fois sous la surface, il nage activement avec ses ailes et ses pattes et peut atteindre une profondeur supérieure à 20m bien que la plupart des plongées se limite aux 5 premiers mètres (Garthe, Benvenuti, & Montevecchi 2000). Les fous pêchent souvent en groupe. Lorsqu'un individu entame une série de plongée, il est généralement rapidement rejoint par des congénères, jusqu'à ce que le banc de proies se disperse.

2. Les sites d'études

Les données utilisées au cours de cette thèse sont de deux types : 1) un jeu de données collecté par nos soins au cours de campagnes de terrain en Norvège 2) des données collectées provenant d'autres colonies norvégiennes issues de collaborations. Le travail de terrain s'est déroulé en partenariat avec l'Institut Norvégien pour la Recherche sur la Nature (NINA) de Trondheim, avec la permission de la Direction norvégienne pour la gestion de la nature et des comtés du Nordland et du Finmark. Nous avons collecté des données au cours de 4 saisons estivales consécutives (entre 2007 à 2010) dans deux colonies.

Les deux sites sont les colonies de Store Ulvøyholmen dans l'archipel des Vesterålen en mer de Norvège et de Storstappen en mer de Barents (Figure 2.3). Chaque campagne a duré entre 7 et 9 semaines entre la mi-juin et le début d'août. Afin de collecter des données de voyages alimentaires pendant la reproduction, nous avons déployé des enregistreurs miniaturisés de type GPS pendant trois saisons consécutives à Storstappen et deux saisons à Store Ulvøyholmen. Des enregistreurs GLS ont été déployés sur 15 oiseaux dans les deux sites en 2008 et en 2009, afin d'enregistrer les mouvements hivernaux. Enfin, durant toute la durée de l'étude, nous avons réalisé des observations de 24 heures en continu pour d'une vingtaine de nids, collecté des régurgitats et réalisé des comptages des colonies.

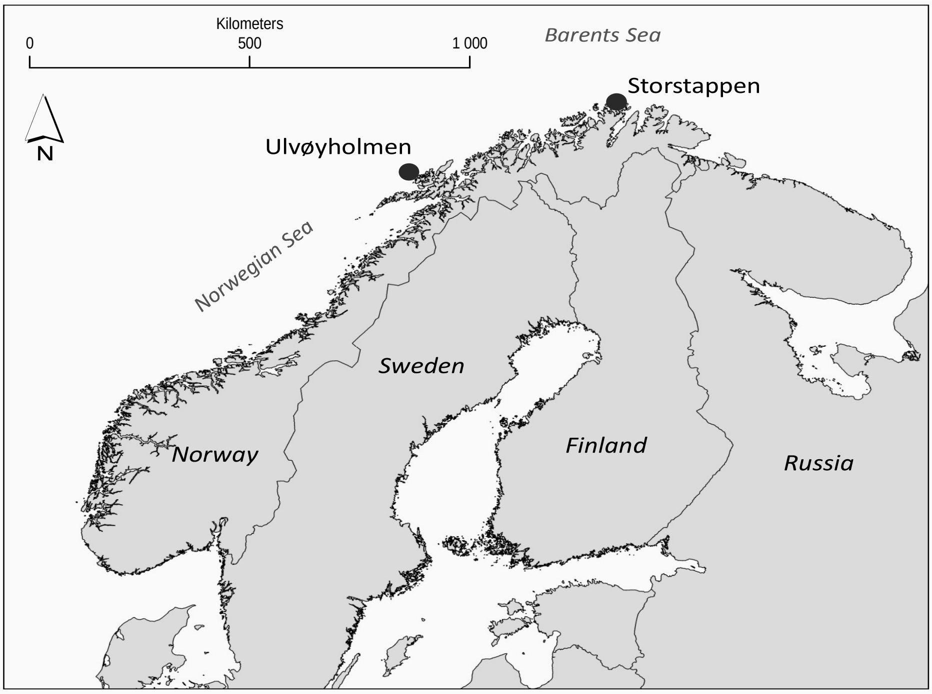

Figure 2.3 Localisation des sites d'études en Norvège de gauche à droite : Store Ulvøyholmen, Storstappen.

2.1 La mer de Norvège et la colonie Store Ulvøyholmen

La mer de Norvège est située entre l'Islande à l'ouest, l'Écosse au sud et la Norvège à l'est. Elle communique avec l'océan Atlantique et la mer du Nord au sud, la mer de Barents à l'est et la mer du Groenland (océan Arctique) au nord (Figure 2.3). Elle couvre une superficie d'environ 1,1 millions de km². Au contraire de la mer du Nord ou de la mer de Barents qui la jouxtent, la profondeur en mer de Norvège peut atteindre jusqu'à 4 000 mètres (profondeur moyenne de 1800m). La rencontre des eaux chaudes et salines de la Dérive Nord Atlantique venant avec les eaux froides et faiblement salines de l'Océan Arctique résulte en une forte productivité biologique, principalement au niveau du plateau continental (Loeng & Drinkwater 2007). De nombreuses espèces de poissons (maquereau, lieu noir, hareng) frayent le long des côtes norvégiennes et constituent la base alimentaire de grandes populations d'oiseaux marins (Figure 2.4a).

La colonie de Store Ulvøyholmen (68° 31' N, 14° 31' E) est située en limite nord de la mer de Norvège. Elle compte actuellement un peu plus de 300 couples et a été signalée occupée pour la première fois en 1997 (Barrett 2008). En 2004, 455 couples ont été recensés mais leur nombre est en diminution depuis lors. La colonie est située au sud de l'archipel des Vesterålen, sur un îlot plat dont le sommet se trouve à quelques mètres au-dessus de la surface de la mer (Figure 2.5).

Figure 2.5 Colonie de Store Ulvøyholmen dans l'archipel des Vesterålen (Norvège).

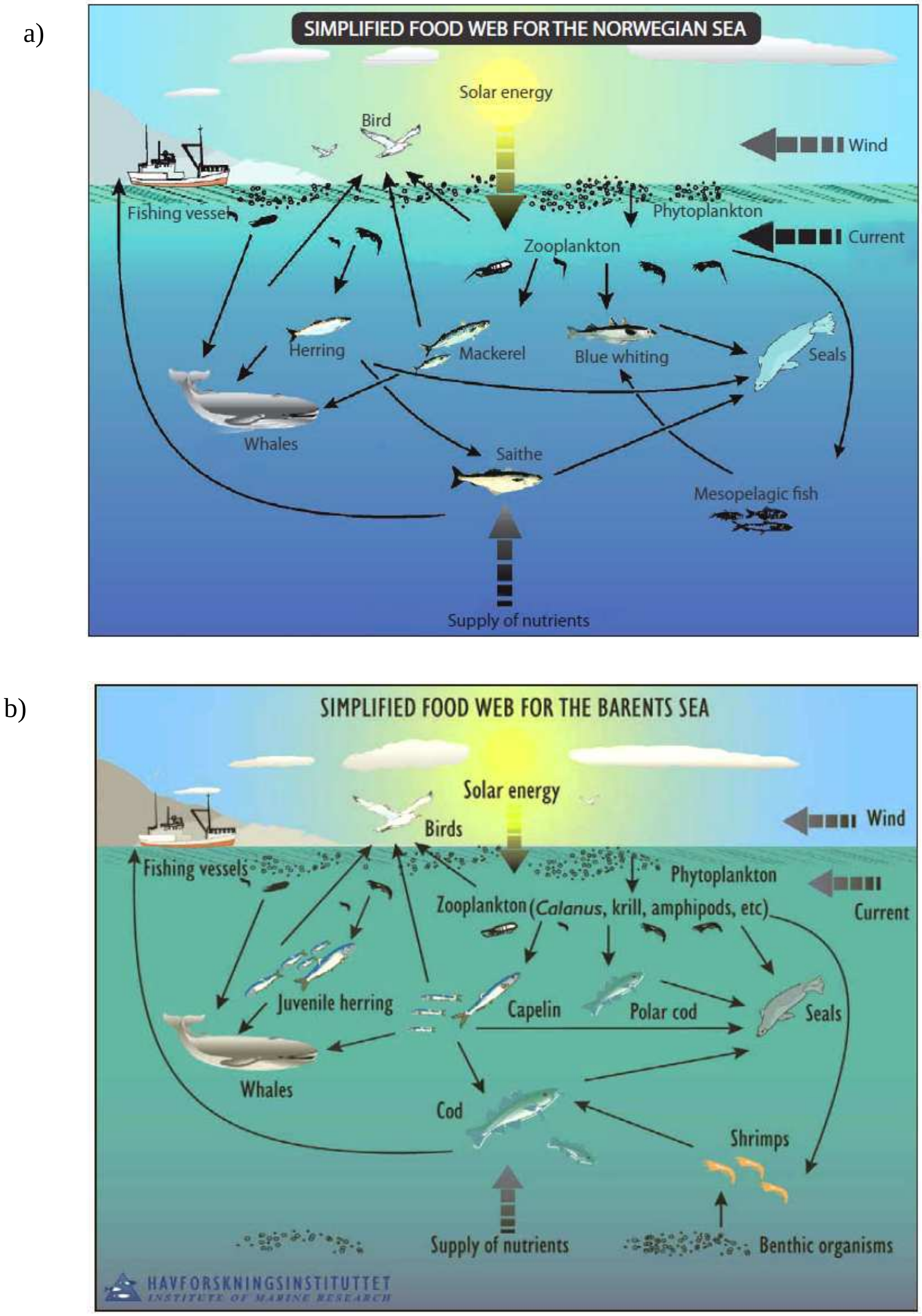

Figure 2.4 La chaine alimentaire simplifiée de a) la mer de Norvège et b) la mer de Barents (Institute of Marine Research - rapport au Parlement norvégien 2008-2009)

2.2 La mer de Barents et la colonie de Storstappen

La mer de Barents est située au nord de la Norvège et de la Russie occidentale. Elle est constituée d'un plateau d'une profondeur de 230 m en moyenne, délimitée par la mer de Norvège à l'ouest, le Spitzberg au nord-ouest, et les archipels François-Joseph et Nouvelle-Zemble au nord-est et est (Figure 2.3). Elle couvre une surface d'environ 1 400 000 km^2. Les eaux chaudes de l'océan Atlantique et de la Dérive Nord Atlantique y rencontrent les eaux froides de l'Océan arctique. La convergence de masses d'eaux chaudes et froides génère une importante productivité phyto- et zoo-planctonique au printemps. Cette nourriture abondante est à la base d'une chaine alimentaire assez courte. Les principales espèces de poissons (capelan et hareng) constituent une ressource majeure pour les nombreuses populations d'oiseaux et de mammifères marins (Figure 2.4b).

La colonie Storstappen (71°09'N, 25° 19' E) se trouve à l'ouest du Cap Nord dans la réserve ornithologique de Gjesvaerstappan, qui abrite environ 2,3 millions d'oiseaux marins nicheurs (Figure 2.6). Les premiers fous s'y sont établis en 1987 ; la colonie comptait déjà 500 couples en 1995 avant d'atteindre le nombre de 1200-1300 couples en 2008 (Barrett & Folkestad 1996; Barrett 2008).

Figure 2.6 Colonie de Storstappen près du Cap Nord (Norvège).

2.3 Les autres sites

Des données collectées par des collaborateurs ont été utilisées pour les chapitres 3 et 5 de cette thèse. Les effectifs et les localisations des colonies d'où proviennent des données analysées dans cette thèse sont présentées dans le tableau 2.1 ci-dessous.

Tableau 2.1 Caractéristiques des données issues des colonies françaises et britanniques

	Saison (reproduction/ non reproduction)	Type de donnée	Nb de couples reproducteurs	Géolocalisation	Pays
Rouzic	reproduction / non reproduction	GPS / GLS	env. 17 000	48°54'N, 3°26 W	France
Grassholm	non reproduction	GLS	env. 32 000	51°43'N, 5°28 W	Pays de Galles
Bass Rock	non reproduction	GLS	env. 48 000	56°04'N, 2°38 W	Ecosse

Chapitre 3. Anticipation de la localisation des proies à l'échelle d'un voyage alimentaire

En introduction de cette thèse, nous avons mis en évidence la forte variabilité environnementale qui caractérise les écosystèmes dans lesquels les oiseaux marins évoluent, ainsi que l'importance des stratégies de recherche alimentaire qu'ils ont développées pour compenser les variations de la disponibilité en nourriture.

Dans ce chapitre, nous testons l'hypothèse selon laquelle les Fous de Bassan *Morus bassanus* seraient en capacité d'anticiper la localisation de la première zone d'alimentation lorsqu'ils entament un nouveau voyage au départ de la colonie. Pour ce faire, nous avons analysé des trajets de recherche alimentaire effectués par des Fous de Bassan enregistrés à l'aide GPS miniaturisés pendant deux étés consécutifs dans la colonie de Rouzic (Réserve Naturelle des Sept Iles, Bretagne). Les Fous de Rouzic effectuent des trajets alimentaires que nous avons qualifiés plus haut (cf introduction) de *commuting trip*, c'est-à-dire que le vol est linéaire sur une longue section avant que l'oiseau ne commence à voler de manière très sinueuse et à pêcher, pour redevenir linéaire sur le trajet de retour vers le nid. Lorsqu'ils sont en mer, les oiseaux peuvent donc anticiper la localisation de la colonie à une distance qui ne permet pas un repérage visuel. Nous avons comparé les caractéristiques du vol (linéarité, vitesse, nombre d'arrêts sur l'eau, durée des arrêts) entre deux sections du voyage alimentaire : à l'aller depuis la colonie jusqu'à la première zone d'alimentation (reconnaissable au comportement d'*area restricted search* - ARS enregistré par le GPS) et au retour de la dernière zone d'alimentation ou de repos jusqu'à la colonie. Les deux sections de voyage présentent des caractéristiques similaires et la linéarité du tracé s'approche de la ligne droite, il est donc fort probable que les oiseaux anticipent la position de la zone de nourrissage à l'aller, de la même manière qu'ils anticipent la colonie au retour. Dans un second temps, nous avons également observé les azimuts suivis par les oiseaux au départ de la colonie et la variation au cours du temps de la différence angulaire entre le cap pris à un instant t et la direction que l'oiseau doit suivre pour atteindre sa première zone de pêche en suivant une ligne droite. Nos résultats montrent que cette différence angulaire diminue très fortement dans la première demi-heure de vol (pour des voyages d'une durée moyenne de 17 heures) et que les fous prennent rapidement le cap de leur futur site de pêche. Ces résultats soutiennent l'hypothèse d'une anticipation de la localisation des proies par les Fous de Bassan de Rouzic. Toutefois, d'autres investigations sont nécessaires pour comprendre les mécanismes sous-jacents à cette anticipation.

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Northern gannets anticipate the spatio–temporal occurrence of their prey

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SUMMARY

Seabirds, as other marine top predators, are often assumed to forage in an unpredictable environment. We challenge this concept and test the hypothesis that breeding Northern gannets (*Morus bassanus*) anticipate the spatio–temporal occurrence of their prey in the English Channel. We analyzed 23 foraging tracks of Northern gannets breeding on Rouzic Island (Brittany) that were recorded using GPS loggers during 2 consecutive years. All birds commuted between the breeding colony and foraging areas located at a mean distance of 85 km and 72 km (in 2005 and 2006, respectively) from the colony. Mean linearity indices of the outbound and inbound trips were between 0.83 and 0.87, approaching a beeline path to and from the foraging area. Additional parameters (flight speed, and number and duration of stopovers at sea) for the outbound and inbound trip were not statistically different, indicating that birds are capable of locating these feeding areas in the absence of visual clues, and to pin-point their breeding site when returning from the sea. Our bearing choice analysis also revealed that gannets anticipate the general direction of their foraging area during the first 30 min and the first 10 km of the trip. These results strongly suggest that birds anticipate prey location, rather than head into a random direction until encountering a profitable area. Further investigations are necessary to identify the mechanisms involved in seabird resource localization, such as sensorial abilities, memory effects, public information or a combination of these factors.

Key words: seabirds, *Morus bassanus*, GPS-tracking, orientation, optimal foraging.

INTRODUCTION

Spatio–temporal heterogeneity in the distribution of food resources is a major environmental constraint upon animals, which need to find resources to acquire energy. Time dedicated to foraging might change over the annual cycle, depending on the seasonal rhythm and the reproductive status of the animal (Rydell, 1993; McCafferty et al., 1998). For individuals commuting between feeding areas and breeding/shelter sites (called central places foragers), the energy needed is augmented by the energetic costs associated with commuting. During the reproductive period, energy and food requirements rise substantially, and foraging effort reaches a maximum, as adults collect food to fulfil their own requirements, as well as those of their offspring. Then, central place foragers experience increased constraints as their progeny requires feeding at regular intervals in order to avoid starvation and/or because the mate may abandon the young if its survival is threatened by starvation. For example, if not relieved by their partner, blue petrels (*Halobena caerulea*) leave the nest when their body mass reaches a minimum threshold (Chaurand and Weimerskirch, 1994).

Optimal foraging largely depends upon the animal's ability to find food within the accessible range (Bell, 1991). Individuals that successfully anticipate the spatio–temporal occurrence of profitable prey patches are most likely to optimize their foraging efficiency and their reproductive success, thereby increasing their fitness (Krebs and Davies, 1978). Locating profitable feeding areas may be a highly challenging task in an apparently poor or featureless environment, such as open seas exploited by foraging seabirds. The marine environment has long been considered as unpredictable, with a highly scattered, patchy distribution of resources (Ashmole, 1971). However, recent tracking results from biotelemetry studies clearly demonstrate that marine top predators do not search for prey randomly (Staniland et al., 2004; Weimerskirch, 2007). Physical features of ocean basins influence marine productivity. Upwelling areas, frontal zones and shelf edges are highly profitable areas that attract large number of marine predators (Hunt et al., 1999; Bost et al., 2009). These areas may provide clues exploited by marine predators to locate them. For example, several Procellariiform species are attracted by dimethyl sulphide (DMS), the concentration of which is particularly high in areas where primary productivity is enhanced (Nevitt and Bonadonna, 2005; Nevitt, 2008).

Beyond sensory abilities, individual experience, cognitive processes and information exchange between individuals (Ward and Zahavi, 1973) might help seabirds to find profitable areas and improve their foraging efficiency across successive foraging trips. The key role of experience and memory is supported by studies showing significant levels of foraging site fidelity in seabird species such as great cormorants *Phalacrocorax carbo* (Grémillet et al., 1999), black-browed albatrosses *Diomedea melanophris* (Weimerskirch, 2007) and Northern gannets *Morus bassanus* (Hamer et al., 2007).

Northern gannets are large seabirds that forage for pelagic fish in the North Atlantic, travelling tens to hundreds of kilometers away from their breeding sites (Hamer et al., 2000). Their reproductive success, therefore, largely relies upon their ability to identify profitable areas within a vast foraging range.

In this paper, by analyzing GPS-logged foraging tracks, we test the hypothesis that gannets anticipate the position of their first feeding patch and determine the bearing of their foraging location soon after leaving their nest sites.

MATERIALS AND METHODS

GPS deployments

Field work took place on Rouzic Island, Sept-Iles archipelago, Brittany (48°54′0″N, 3°26′11″W) under permits from the Réserve Naturelle des Sept Iles. Fourteen adults raising a chick and nine incubating adults were equipped with a GPS logger in July 2005 and June 2006, respectively. Birds were caught on the nest with a telescopic pole fitted with a noose, when both parents were present. We took great care to minimize the impact of our study and caught birds mainly at dawn to avoid heat stress (Hochscheid et al., 2002). Immediately after the changeover, the bird which was about to initiate a foraging trip was caught and equipped with a data logger, while its mate remained at the nest site attending the egg or chick. Handling lasted less than 10 min in all cases, during which time the bird's head was covered to reduce stress. Birds were only equipped for a single foraging trip not exceeding 38 h.

We used white Tesa (Hamburg, Germany) tape to attach the devices to the lower back of the birds. The tape, matching plumage colour, guaranteed a safe attachment during the whole trip at sea and a minimal damage to feathers upon removal (Wilson et al., 1997). A previous study at the same field site used these methods without noticeable impact on the birds (Grémillet et al., 2006).

We could not sex birds reliably during this study but assumed that random bird capture ensured a balanced sex ratio of our sample [validated in Lewis et al. (Lewis et al., 2002)]. In an expanding gannetry, the colony fringe consists almost entirely of young breeders (Nelson, 2002). To avoid any biases resulting from a site–age effect and to ensure a normal age distribution among the equipped birds, nests were selected randomly from the periphery to 10 m within the colony (i.e. the maximum length of the catching pole).

Data logger specifications and analysis of electronic data sets

We deployed GPS data loggers from Technosmart, Rome, Italy (95 mm×48 mm×24 mm; 65 g, i.e. 2.1% of the body mass of the birds) recording latitude, longitude and speed every 10 s. The GPS data loggers were removed from birds after a single foraging trip (Fig. 1). From GPS positions and speed values recorded off the colony, we calculated path lengths between two fixes, distances to the nest and the time spent flying – birds were assumed to fly when GPS speed exceeded 10 km h^{-1} (for details see Grémillet et al., 2004). In order to identify feeding areas for each bird, we used a path sinuosity index, defined as the ratio of the actual flight speed given by the GPS receiver to the velocity calculated from the distance travelled between every third fix (i.e. total displacement every 30 s). A bird circling around in a restricted area will have a lower calculated speed than the actual GPS speed, resulting in a higher sinuosity index. Such positions of high sinuosity have been shown to be associated with active feeding behaviour in gannets [for validation, see Grémillet et al. (Grémillet et al., 2006)]. Plotting all feeding locations as individual data points does not reveal the locations of the most intensively exploited areas within a home range. Following Wood et al. (Wood et al., 2000), we used kernel analysis to transform point distributions into density estimates of feeding positions. Analyses were conducted with the Kernel Density Estimate tool (Arcview GIS 3.2). The smoothing factor was chosen according to the Least Square Cross Validation method (Girard et al., 2002). This approach allows statistical analysis of distribution patterns and therefore highlights feeding hotspots.

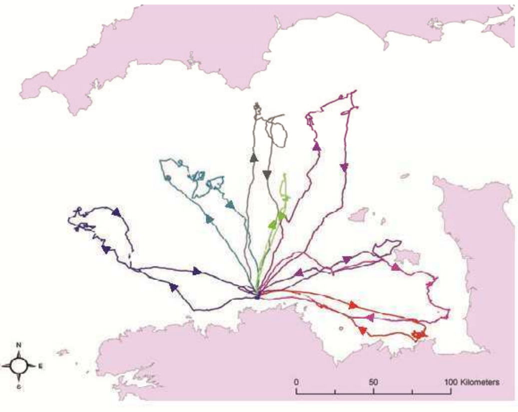

Fig. 1. *Morus bassanus*. Examples of GPS tracks recorded during the foraging trips of eight Northern gannets from the Sept-Iles in the western English Channel (2005 and 2006). Different colours show tracks from different birds, arrows show the outbound and inbound parts.

Comparison of outbound and inbound trip features

When gannets start a foraging trip at sea, different strategies may lead them to a profitable area, from a purely 'random walk' type path to an orientated path. There are three scenarios.

(1) Food is heterogeneously distributed and no information is available to the birds about the location of potential resource patches: a sinuous walk is then predicted to maximize chances to come across food (reviewed in Hawkes, 2009).

(2) Food is homogeneously distributed around the colony (with an extreme case whereby food is distributed along a 'ring' around the breeding site) and no information about the location of potential resource patches is available: the animal takes and keeps a random bearing and follows it in a beeline to reduce flight costs. It is important to note that this 'linear and random' strategy is entirely theoretical, and has never been observed in nature (Hawkes, 2009).

(3) Information about food distribution is available to the birds (e.g. from previous experience, public information or sensory cues), and a linear, goal-oriented trip towards the target is therefore expected (Hawkes, 2009). Animals then tend to follow a beeline, but potential errors in the orientation mechanisms induce deflections from this beeline and adjustments, that reduce path linearity.

Thus, if recorded paths show high linearity levels, we will have to determine whether gannets follow an anticipatory strategy or a 'linear and random' strategy during their foraging trips. We therefore hypothesised that the theoretical 'linear and random' trip will follow a perfect beeline, and that the characteristics of a goal-oriented trip are given by the inbound trip. Indeed, the location of the breeding site is known to the birds. We thus compared the outbound trip (between the colony and the main feeding area) to the inbound trip (return from offshore to the island). The end of the outbound trip, i.e. the area where birds foraged most intensively, was defined using a combination of three criteria: a high sinuosity index, an occurrence of drastic changes in the recorded flight speed (each dive induces a speed drop for a few seconds), and a visual assessment of the tracks using Arcgis 9.2 (Environmental Systems Research Institute). As our analyses confirmed that birds usually focused their foraging effort on one major foraging area, we assumed that it was the goal of their foraging trip.

To locate the start of the inbound journey, we analyzed the foraging track backwards, starting from the nest site towards the last intense foraging activity and/or overnight rest at sea [northern gannets spend nearly half of their time at sea resting at the water surface (Grémillet et al., 2006)]. For both trips, we calculated linearity index (i.e. the sum of the distances between each fix divided by the beeline distance between the breeding site and the foraging area), average flight speed, and the number and duration of stops at the sea surface along the track segment.

The colony is a predictable location that the gannets are able to anticipate. If gannets also anticipate the location of their foraging site, outbound and inbound journeys should show similar patterns. We therefore compared these indices for outbound and inbound sections of the foraging track using a paired-wise Wilcoxon test.

Data recorded in 2005 and 2006 were compared using non-parametric Mann–Whitney tests for each parameter. Values are presented as means ± s.d.

Bearing choice

After defining a main foraging area for each equipped bird (i.e. the area where birds foraged most intensively), we selected the position of the first diving event in the main foraging area (i.e. at the end of the outbound trip) and recorded it as ‘B’: the assumed goal of the bird. Using the geographical coordinates of the nest ‘A’ and the first foraging event ‘B’, we then calculated $\alpha(f)$, the theoretical bearing that birds should follow to reach the foraging area in a beeline (between 0 and 360°). Secondly, we calculated $\alpha(t)$, the angle between ‘A’ and each positional fix of the outbound trip. Finally, we calculated the angle Φ, which is the difference between $\alpha(f)$ and $\alpha(t)$ along the outbound trip, using the following equation (Fig. 2):

$$\Phi = \alpha(f) - \alpha(t)\,. \qquad (1)$$

The value of Φ in relation to flight duration and distance to the nest indicate the moment when gannets orientate their flight towards the foraging area. We assumed that birds headed towards the foraging area when Φ reached the asymptote.

RESULTS

All equipped birds bred normally after device deployment. In 2005, gannets encountered their first major fishing area within an average distance of 85±31 km (range: 35–133 km). They started their return journey to the breeding site from an average distance of 94±33 km (range: 36–145 km). Similarly in 2006, gannets foraged mainly within 72±25 km (range: 32–107 km) of the colony and travelled 71±26 km (range: 36–102 km) to get back to their nest.

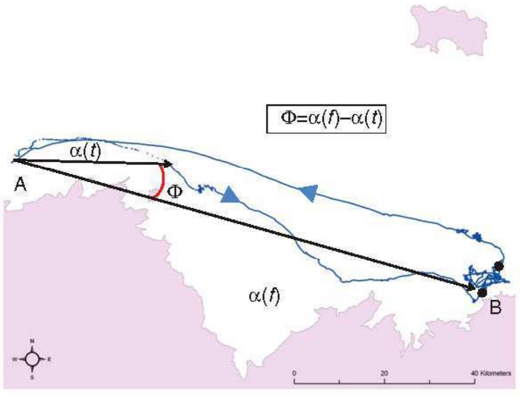

Fig. 2. *Morus bassanus*. GPS track recorded during the foraging trip of a Northern gannet from Rouzic Island. $\alpha(f)$ is the bearing between the nest site (A) and the foraging area (B). $\alpha(t)$ is the bearing between the nest site and each fix recorded at 10-second intervals along the outbound trip. Φ is the difference between $\alpha(f)$ and $\alpha(t)$. Arrows show the outbound and inbound parts, black dots show the end of outbound trip and the start of the inbound trip.

Birds spent the major part of their trip within a specific foraging area, either fishing or resting at sea. In fact, although total trip duration was 19.2±8.5 h in 2005 and 19.8±9.9 h in 2006, the duration of the outbound journey (2.7±2.3 h and 2.8±1.3 h in 2005 and 2006, respectively) and the homeward journey (2.4±0.8 h in 2005 and 1.8±0.6 h in 2006) accounted only for a small proportion of total trip duration: the sum of the outbound and return journey made up 26% and 23% of total foraging trip duration in 2005 and 2006, respectively. Summary statistics of foraging trip characteristics are given in the Table 1.

Density Kernel analyses of the foraging locations revealed that gannets were exclusively foraging in the Western English Channel (WEC) in both years (Fig. 3A,B). In 2005, gannets preferentially exploited the tidal front area situated in the central WEC, northwest of Guernsey, and coastal areas on both sides of the English Channel (Grémillet et al., 2006). In 2006, gannets mainly exploited the frontal zone of the WEC, north of the colony, as well as the French coastal area.

Comparison of the outbound and inbound trip features

Median linearity indexes in 2005 and in 2006 were between 0.83 and 0.87 (Fig. 4A), with the maximum value of 1 corresponding to a beeline trip. A Wilcoxon signed-rank test showed no significant differences between the linearity of the outbound and the inbound sections of the foraging path in both years (W=48, P=0.77 in 2005; W=14, P=0.31 in 2006).

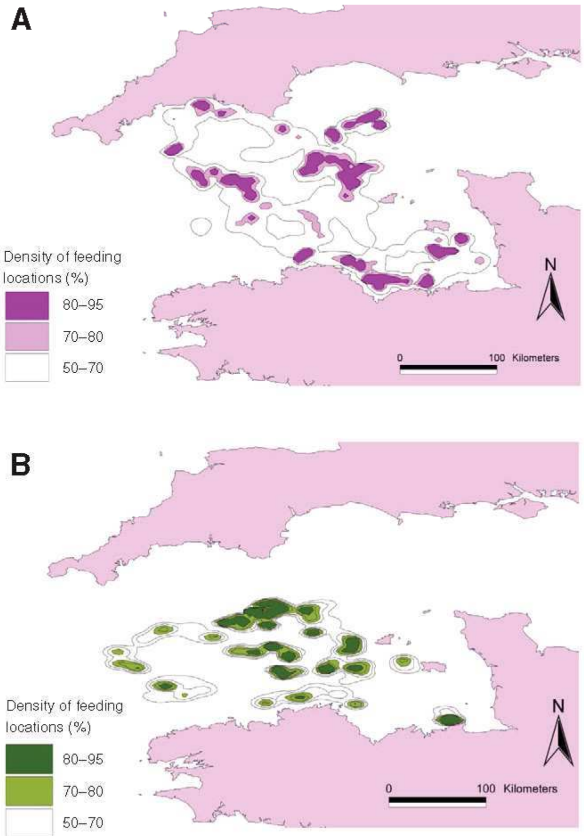

Fig. 3. *Morus bassanus*. Relative density of feeding locations in the Channel (from Kernel Density Estimate analysis, 50–70, 70–80, 80–95%): (A) in 2005 (N=20); (B) in 2006 (N=20).

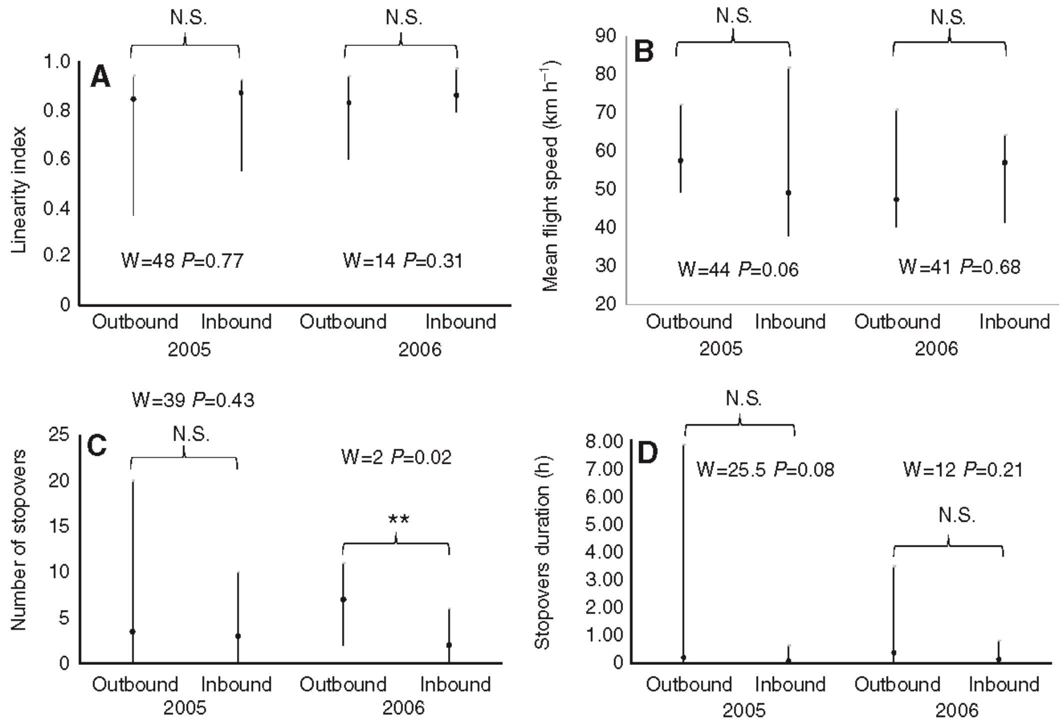

Fig. 4. *Morus bassanus*. Comparison of the outbound and the inbound section of foraging trips by breeding adults in 2005 (N=14) and 2006 (N=9) using a Wilcoxon signed-rank test (mean and range). (A) Linearity index. (B) Mean flight speed (km h^{-1}). (C) Number of stopovers at sea. (D) Stopover duration (hours).

When flying between nesting and foraging site, median speeds in 2005 and 2006 were between 47.4 km h^{-1} and 57.1 km h^{-1} (Fig. 4B). There was no significant difference between the outbound and return flight speeds in 2005 or in 2006 (Wilcoxon signed-rank test: W=44, P=0.06; W=41, P=0.68, respectively).

Birds showed a similar number of stop events during the outbound and the return trip in 2005 (Wilcoxon signed-rank test: W=39, P=0.43, see Fig. 4C). However, in 2006, birds stopped more frequently during the outbound section than during the return section (Wilcoxon signed-rank test: W=2, P=0.02, see Fig. 4C). There were no significant differences between the median duration of these stops for the outbound and inbound sections of foraging trips in either 2005 or 2006 (Wilcoxon signed-rank test W=25.5, P=0.08 in 2005; W=12, P=0.21 in 2006, see Fig. 4D).

Although, generally, all of these tests showed no significant differences between years, we nonetheless decided to analyze the 2 years separately, as birds were equipped at different stages of their reproductive cycle, during which they might potentially pursue different foraging strategies.

Bearing choice

Relationships between Φ and flight durations in 2005 and 2006 are shown in Fig. 5A,B. These relationships are best described by a logarithmic function, where the value of Φ drops rapidly after departure from the nest site and subsequently decreases more gradually towards zero as birds approach the foraging site. Crucially, the bearing followed by gannets after 15 and 9 min of flight (in 2005 and 2006, respectively) differed only by 20° from $\alpha(f)$, the ideal bearing to reach the foraging area in a beeline. The value of Φ decreased further to 14° and 13° after 30 min of flight (in 2005 and 2006, respectively).

Relationships between Φ and distance to the nest in 2005 and 2006 are shown in Fig. 5C,D. They are of similar shape as those between Φ and flight duration. In 2005, Φ dropped below 20° at a distance of 10 km from the nest site and reached 14.7° at a distance of 20 km from the nest (for a mean distance of 85 km between the nest site and the foraging area). In 2006, Φ dropped below 20° at a distance of 3 km from the nest site and reached 10.5° at a distance of 20 km from the nest (for a mean distance of 72 km between the nest site and the foraging area).

DISCUSSION

Movement patterns of foraging animals have been studied for decades in a broad range of species, from social insects such as bumble bees (Dukas and Real, 1993) and ants (Bovet et al., 1989; Müller and Wehner, 1988; Schmid-Hempel, 1984) to mammals (Loureiro et al., 2007). Weimerskirch (Weimerskirch, 2007) showed that marine predators do not forage randomly in an unpredictable environment at large and mesoscales, and numerous studies in seabirds focused on the identification of sinuous sections of the foraging trip, potentially associated with feeding activity (Area Restricted Search) (see Pinaud and Weimerskirch, 2007). However, recent work indicated that the ecological relevance of linear foraging tracks followed by seabirds has not been sufficiently explored (Trathan et al., 2008).

Our analysis of outbound and inbound paths from gannets foraging off Brittany revealed that birds followed equally straight paths on their way to the foraging area and when returning to their breeding site. All tracks showed similar patterns (see Fig. 1): (1) a

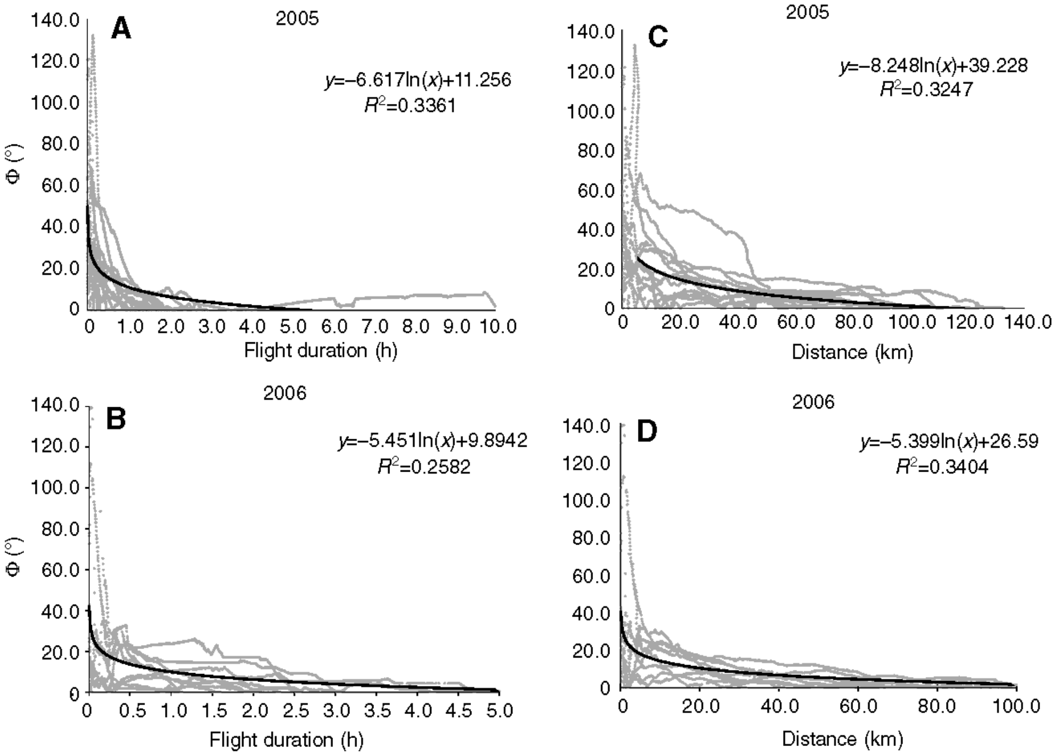

Fig. 5. *Morus bassanus*. Relationship between Φ (in degrees) and flight duration (in hours) during the outbound trip: (A) in 2005 (N=14); (B) in 2006 (N=9). Relationship between Φ (in degrees) and the distance to the nest site (in kilometers) during the outbound trip: (C) in 2005 (N=14); (D) in 2006 (N=9). Φ represents the difference between $\alpha(f)$, the bearing to the foraging area, and $\alpha(t)$, the bearing followed by the gannets at each fix (see Fig. 3). The solid black line represents the regression.

linear trajectory between the colony and the first foraging area (Fig. 4A); (2) a highly sinuous path in association with fishing activity, punctuated by resting periods at the sea surface; (3) a linear return trajectory to the nest (Fig. 4A). Travel time represented only a quarter of the total trip duration, with the remaining time being dedicated to fishing activity and resting at the sea surface within the foraging area (Table 1).

Gannets from Rouzic Island can therefore be defined as commuting foragers (*sensu* Nevitt, 2008), which travel rapidly towards a profitable area using navigation mechanisms yet to be investigated, and, once on site, engage in area-restricted search (ARS) (*sensu* Kareiva and Odell, 1987). They then rest and digest at the water surface (Ropert-Coudert et al., 2004) before flying straight back to their breeding site.

To compare outbound and inbound trips, we tested three additional parameters (Fig. 4B–D), which may reveal differential strategies adopted by gannets during these two phases. Median flight speed and stopover duration were not significantly different, supporting the anticipatory hypothesis. However, in 2006, the number of stopovers was higher during the outbound trip than during the return trip. As stopover numbers during outward and inward trip phases were not different in 2005, we think that the breeding status of the birds (chick rearing in 2005 and incubating in 2006) might explain this difference.

Table 1. Characteristics of foraging trips made by adult *Morus bassanus*

		Foraging trip duration (h)	Outbound distance (km)	Inbound distance (km)	Outbound flight duration (h)	Inbound flight duration (h)	Total path length (km)	Outbound path length (km)	Inbound path length (km)
2005	Mean	19.2	85	94	2.7	2.4	450	108	136
(N=14)	s.d.	8.5	31	33	2.3	0.8	224	40	106
	Min.	3.2	35	36	0.9	0.9	122	39	51
	Max.	28.2	133	145	10.1	3.9	856	166	487
2006	Mean	19.8	72	71	2.8	1.8	310	88	81
(N=9)	s.d.	9.9	25	26	1.3	0.6	116	33	29
	Min.	7.3	32	36	1.1	0.8	125	45	42
	Max.	36.7	107	102	5.2	2.8	509	136	120

Measurements were made during the incubation phase (N=9; 2006) and chick-rearing phase (N=14; 2005) on Rouzic Island, Réserve des Sept-Iles. Information derived from GPS data loggers.

However, the linearity index was not significantly different between incubating and chick-rearing gannets, suggesting that anticipation of the foraging site might occurs regardless of the stage of the reproductive cycle (Fig. 4A).

The fact that gannets foraged in one restricted area does not automatically induce an early anticipation of its location. We saw that the linearity index was high (LI=0.87 and LI=0.86 in 2005 and 2006, respectively) for the outbound trip, so that birds nearly followed a beeline trajectory towards the foraging site. Nevertheless, we have seen that two opposite and mutually exclusive strategies could generate this high path linearity.

(1) Birds randomly choose a bearing and keep flying in the same direction until they encounter a resource patch with a high degree of uncertainty. As alluded to earlier, it is important to note that this possibility has been largely excluded by theoretical work, and that it has so far never been observed in nature (Hawkes, 2009).

(2) Birds are anticipating the location of a profitable area when they start the foraging trip either by using sensory cues, public information (Ward and Zahavi, 1973) or their own experience gained during previous successful trips (Hamer et al., 2007). The latter strategy is the one expected for the inbound trip, from the feeding area towards the colony, the invariable position of which is obviously known to breeders from past experience.

Two further points support the idea that northern gannets foraging in the English Channel possess information about the position of the targeted prey patch.

(1) We compared the characteristics of outward *versus* homeward sections of the foraging trip. If a bird chooses a direction at random and follows it until encountering a prey patch, we would expect the path to be more linear than it would be for a bird that flies towards a known foraging area, gradually adjusting its bearing. In this case, if the gannets were following a 'linear and random' strategy, outbound trips would have been more linear than inbound trips, independent of distance, visibility and weather conditions, which occur randomly during the foraging trip. By contrast, our results show that the outbound and inbound linearity indexes are similar and the values (between 0.83 and 0.87) strongly support the theory that gannets succeed in orientating their flight to the foraging area and to their colony in an apparently featureless oceanic environment.

(2) Moreover, kernel analysis of the GPS positions of foraging gannets revealed that they exploited specific areas of the Western English Channel in both years, preferentially the area located to the north of the colony, which features a marked tidal front (Fig. 3A,B). This tidal front corresponds to a boundary layer between stratified Atlantic surface waters in the west and highly mixed surface Channel waters in the east (Southward et al., 2005). High productivity at this front favours aggregations of marine top predators (Sims et al., 2005), including northern gannets (Pingree et al., 1974; Siorat and Rocamora, 1992).

Clustered gannet foraging locations support the idea that prey distribution is not homogeneous in the vicinity of the colony and that it is advantageous for gannets to setup their own mental map of the profitable patches.

Our findings are in accordance with the conclusions of previous studies conducted in a wide range of foraging animals. For example, Bovet et al. (Bovet et al., 1989) analyzed movements in Serrastruma lujae ants and showed that the outbound trip was erratic and very sinuous, whereas the path towards the colony, of known location, was linear and directional.

These results could be further substantiated by recording a series of successive foraging trips for the same individuals. If single birds return time and again straight to the same feeding location, this will certainly be a clear sign that they anticipate its position. However, they might also use long-term experience for daily updates of the likely position of spatio–temporally labile food patches. In this case, an orientated trip of varying bearing will take them to a different feeding patch during each trip. Preliminary analysis of successive foraging trips conducted by northern gannets foraging off Norway supports this latter option (E.P., unpublished).

Bearing choice analysis supports the idea that gannets anticipate the direction towards the foraging area rapidly after starting the foraging trip (Fig. 5A–D). Indeed, the difference between the ideal bearing to the foraging area and the one actually followed by the gannets decreased dramatically during the first 30 min of the trip, and within the first 10 km from the nest site. At this point, gannets are not able to see the foraging area that they intend to visit, as the mean distance to the feeding site was >70 km in both years. For a seabird flying at 30 meters above the sea level, linear distance to the horizon does not exceed 20 km, independent of its visual capabilities. In this case, gannets that fly rather low when compared with other seabirds (Nelson, 2002), may rely upon further cues such as olfaction, public information and their own knowledge of the foraging grounds (the western English Channel in this case) to decide on a general orientation. They might later refine their navigation as additional information from the environment becomes available.

Previous studies investigating the foraging strategies of gannets have shown that changes in prey distribution might occur from one year to another and force birds to adapt their foraging behaviour (Hamer et al., 2007; Pichegru et al., 2007). In this context, three mechanisms can be envisaged.

(1) Main prey distribution does not vary significantly over time and gannets that return to a specific breeding area may use past experience to exploit these areas effectively from the start of the breeding season. Recurrent high productivity areas such as the mid-channel tidal front (see Grémillet et al., 2006) are typical examples of oceanic features that facilitate efficient seabird foraging in the long term.

(2) Main prey distribution changes significantly across breeding seasons: in this case gannets may engage in some form of random search early in the season while nest building and incubating. This will allow them to draw or update their own prey distribution map, to be efficiently exploited during the most demanding times of chick rearing.

(3) Finally, gannets may complement the first two strategies by fine-tuning their local knowledge of the most profitable foraging areas as they accumulate experience during the many foraging trips conducted during their extended breeding season (approximately 60 foraging trips over 4 months).

Such mechanisms are potentially applicable to a wide range of foraging animals. In the case of marine top predators, novel technologies now allow tracking the movements of individuals at a very fine spatial and temporal resolution, while assessing the biotic and abiotic parameters affecting their senses (Nevitt, 2008, Nevitt et al., 2008). These investigations will trigger a leap in our understanding of the cognitive abilities of marine animals and will most certainly demonstrate that these animals are very far from roaming in a featureless environment.

LIST OF SYMBOLS AND ABBREVIATIONS

GPS	global positioning system
s.d.	standard deviation
$\alpha(f)$	bearing between the nest 'A' and the foraging area 'B'
$\alpha(i)$	bearing between the nest 'A' and each positional fix of the outbound trip
Φ	measured difference between $\alpha(f)$ and $\alpha(i)$

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Chapitre 4. Variabilité des comportements de recherche alimentaire à des échelles spatio-temporelles multiples

Dans le chapitre 3, nous avons montré que les fous de Bassan nichant dans la colonie de Rouzic anticipent la localisation des proies recherchées. En allant se nourrir à plusieurs dizaines de kilomètres de leur nid, ils empruntent une route linéaire et prennent rapidement le cap en direction de leur première zone de pêche. Dans cette étude, l’absence d’enregistrement de voyages successifs ne permettait cependant pas de déterminer si les fous bénéficient de leur expérience, ou bien s’ils obtiennent d’autres informations au moment de l’envol pour identifier les zones d’alimentation. Le développement perpétuel des techniques de télémétrie permet désormais l’enregistrement des voyages successifs d’un animal dans son environnement naturel. Dans ce nouveau chapitre, nous avons voulu comprendre comment les prédateurs marins peuvent répondre à la variabilité de disponibilité et de distribution de leurs ressources en nous plaçant à une échelle spatio-temporelle un peu plus large. Pour ce faire, nous avons analysé les voyages successifs de fous de Bassan dans deux colonies norvégiennes distantes de 500 km, durant trois saisons de reproduction. Nous avons testé l’hypothèse que la variabilité des comportements alimentaire repose majoritairement sur une forte plasticité individuelle. L’analyse de variance (modèle mixte linéaire généralisé) et les analyses spatiales ont mis en évidence une forte variabilité individuelle des tactiques de recherche alimentaire. D’un voyage à l’autre, les oiseaux retournent sur des aires d’alimentation connues mais ils alternent entre elles. Au niveau interindividuel, des routes et des zones d’alimentation sont nettement privilégiées, et ce, dans les deux colonies. Des variations interannuelles ont été également observées dans la colonie du Cap Nord et la durée des voyages et les distances des zones d’alimentation ont augmenté au cours de notre étude. Les oiseaux prospectent largement autour de leur colonie, mais le domaine vital est huit fois plus grand dans la colonie où les oiseaux sont les plus nombreux. Ceci peut être le fait d’une compétition intraspécifique pour l’accès aux proies ou peut tout simplement refléter des différences environnementales entre les deux colonies étudiées. Notre étude confirme que les fous de Bassan font preuve d’une forte plasticité individuelle qui leur permet de moduler leurs efforts de recherche alimentaire et d’exploiter efficacement l’environnement marin. La somme des réponses individuelles se traduit par une importante variabilité des comportements de recherche alimentaire au sein des colonies, ce qui apporte certainement un avantage adaptatif aux fous lorsque la disponibilité des proies diminue dans les zones d’alimentation à proximité immédiate de la colonie.

Multi-scale foraging variability in a marine predator, the northern gannet (*Morus bassanus*)

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Abstract

In a variable environment, marine predators must respond to rapid changes in prey distribution by plasticity in their foraging tactics. We hypothesized that variability in the foraging behaviour of seabirds is mainly expressed at the individual level. Using miniaturized GPS recorders during three consecutive breeding seasons, we collected data over 341 foraging trips for 101 birds from two Norwegian northern gannet colonies. Using spatial analyses and generalized linear mixed models, we determined the effect of year, colony, intra- and inter-individual variability on foraging strategies. This information supported our hypothesis and revealed strong individual variability between foraging trips, with high plasticity in foraging effort, and switching between a panel of different fishing areas. At the inter-individual level, preferred commuting routes, flight bearings and feeding hotspots clearly emerged for individuals from both colonies. At the inter-colony level, home ranges were larger and foraging areas more numerous off the largest colony. Finally, inter-annual variation in feeding hotspots and foraging ranges occurred off the North Cape colony, but was not observed off the Vesterålen colony. Our study demonstrates that individual marine predators such as norther Gannets may show substantial foraging plasticity, which probably greatly facilitates their adaptation to current environmental change.

Key words: seabird, intra and inter-individual variation, successive foraging trips, GPS

1. Introduction

Ecosystems are consistently exposed to natural environmental variations. Spatio-temporal modifications of abiotic conditions impact living organisms and challenge food web stability. Primary productivity, which is strongly related to abiotic parameters, notably varies in time and space and affects resource distribution and its accessibility to consumers (Coe, Cumming, & Phillipson 1976; Olff, Ritchie, & Prins 2002; Townsend, Begon, & Harper 2003; Brown et al. 2010). Pollution, habitat destruction and climate changes are additional, anthropogenic perturbations that potentially increase environmental stochasticity (Lande 1998; Worm et al. 2006). In a context of global and long-lasting deterioration of ecosystems, behavioural plasticity of individuals plays a key role in a population’s adaptation to rapid environmental changes (Nussey, Wilson, & Brommer 2007), particularly in long-lived species whose microevolutionary response is too slow (Wingfield 2003). The ability to handle low food availability depends on the variety of individual foraging tactics responding to multiscale spatio-temporal changes in prey distribution. Ultimately intra- and inter-individual foraging plasticity might affect whole population trends.

Within marine ecosystems, sea temperature, currents, nutrient flow and turbidity strongly affect phytoplankton production and the microbial loop, and thus, the whole marine food web. As a consequence, spatio-temporal occurrence of prey available to predators varies greatly, and marine predators therefore have developed suites of flexible foraging strategies in order to survive and to breed (Thayer & Sydeman 2007). In their review, Grémillet and Boulinier (2009) describe the three possible responses of seabirds to rapid changes in their environment, which can be extrapolated to other marine predator species. (1) To cope with a modified distribution of their prey, organisms may operate a range shift to follow their natural prey either by increasing foraging range during breeding period (McCafferty et al. 1998; Miller, Karnovsky, & Trivelpiece 2009) or by modifying their distribution area during non-breeding period (Veit, Pyle, & McGowan 1996). (2) If they cannot move to buffer environmental changes, they might modify their feeding ecology and opportunistically exploit alternative prey (Baird 1990; Lawson & Stenson 1995; Fea, Harcourt, & Lalas 1999) or new food resources like fish discards (Camphuysen & Garthe 1997; Phillips et al. 1999; Tasker et al. 2000). Nevertheless, studies also indicate that behavioural plasticity does not always compensate for the consequences of prey decline on breeding success (Barrett & Krasnov

1996) or population trends (Pichegru et al. 2010b). This may occur when substitute prey (e.g. fishery waste) is not sufficiently energy-rich (Wanless et al. 2005) or if the usual prey is located beyond the maximum foraging range of a given species (Pichegru et al. 2007). (3) In the most severe case, populations that do not exhibit geographic plasticity or viable substitution prey might be led to extinction (Becker, Peery, & Beissinger 2007).

During breeding the northern gannet (*Morus bassanus*, hereafter termed gannets) is a central place forager constrained to return to the colony to feed its single chick at short intervals. Gannets are large seabirds that can travel hundreds of kilometers from their breeding site and which feed on a broad spectrum of species and size of prey (Montevecchi & Barrett 1987; Hamer et al. 2000). Such mobility, and a broad diet, enable northern gannets to buffer environmental variability (Montevecchi et al. 2009). Previous studies have highlighted their ability to face inter-annual variations in prey availability, as well as a consistency in foraging behaviour and foraging area fidelity at an intra-individual level (Hamer et al. 2007), but also contrasted foraging tactics between colonies (Hamer et al. 2001). However, to our knowledge, no multi-scale analysis of their foraging plasticity had yet been performed. We therefore aimed at exploring how variability in gannet foraging response is partitioned at both the intra- and inter-individual levels, as well as the importance of inter-annual and inter-colonial variations. Considering the recent recovery of northern gannet population, and the rapid expansion of their distribution area with the establishment of new colonies (Nelson 2002), we hypothesized that variability in their foraging behaviour is largely expressed at an individual level. Individuals may develop foraging plasticity to face environmental variation and changes in food distribution. However, additional flexibility may emerge from groups of individuals (i.e. the colony), thereby extending the variety of foraging patterns. We predicted that the variability in foraging behaviour will occur at both the intra- and the inter-individual levels, as well as at inter-annual and inter-colony levels. In order to investigate such foraging plasticity in gannets, we analyzed GPS tracks from successive foraging trips for birds from two distant colonies in 3 consecutive years.

2. Materials and methods

2.1 GPS deployments

Fieldwork took place in two Norwegian colonies: 1) Store Ulvøyholmen (68°51 ’N, 14°51’ E) a small islet in the Vesterålen archipelago and 2) Storstappen (71°14’N, 25°30’E) in the Gjesvaer archipelago, near the North Cape. (Figure 4.1). Permission to enter the colonies were issued by the County Governors of Nordland and Finmark, while permissions to handle the birds was given by the Norwegian Directorate for Nature Management and the Norwegian Animal Research Authority. The field work was conducted in July 2008 and 2009 on Store Ulvøyholmen, and in July 2007, 2008 and 2009 on Storstappen.

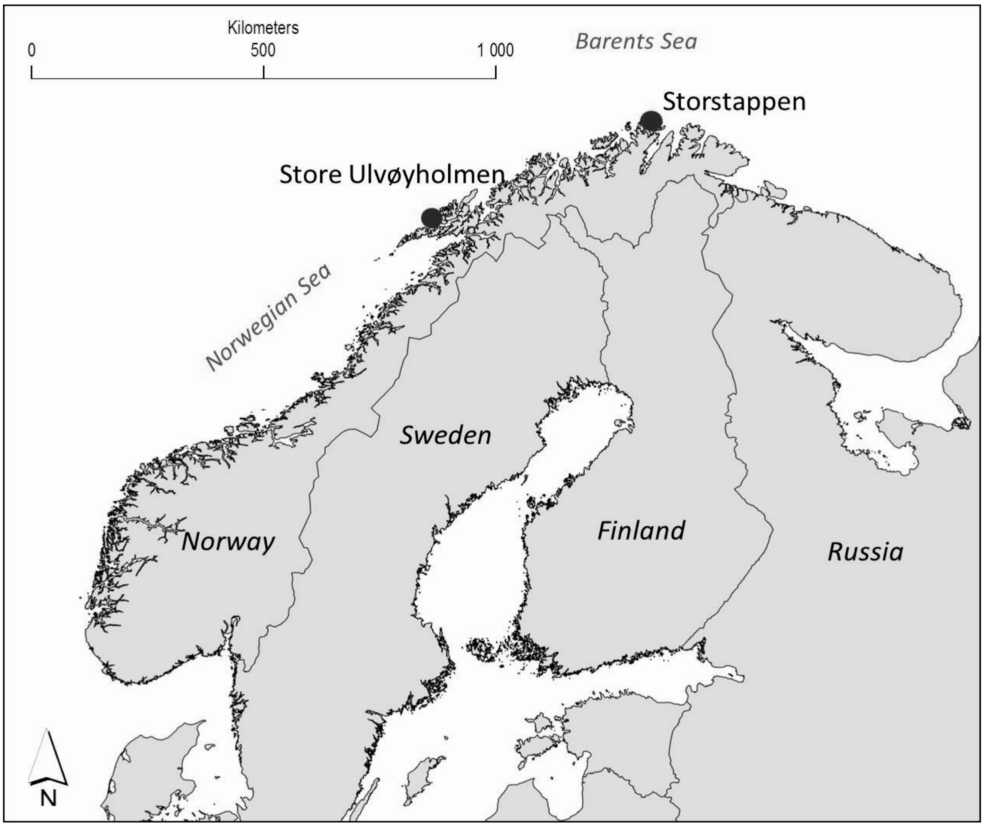


Figure 4.1 Localization of the two studied colonies along the Norwegian coast: Store Ulvøyholmen and Storstappen.

We deployed GPS data loggers on breeding adults rearing 2-5 week-old chicks. Individual birds were caught using a noose pole. This was performed when both parents were present at the nest, and we selected the bird which was about to leave for a foraging trip. Handling and attachment of the GPS data logger lasted less than 10 min in all cases, during which time the bird's head was covered to reduce stress. The devices were attached to the lower back of the birds using white Tesa tape (Hamburg, Germany) to match plumage colour. These methods have been used in several previous studies without noticeable impact on birds (Grémillet et al. 2006). In 2007 and 2008, devices were deployed for maximum 48 hours and recorded at least one foraging trip. In 2009, devices were deployed for 5 to 6 days, recording at least three consecutive foraging trips for each bird. All birds returned to their nest after the deployment and continued to breed. We caught birds at random within the first 10-meter fringe of the colony to avoid any bias in sex ratio and age (Lewis et al. 2002). Several birds caught that way at both colonies had been ringed as chicks, indicating that old birds also bred in the area accessible with the pole (mean age of ringed birds in both colonies (N = 25) was 16,3 years old – 8 birds were more than 20 years old). We therefore assume that working on the fringe of the colony did not bias the age structure of our sample towards young/inexperienced birds (Nelson 2002).

2.2 GPS specifications and data filtering

Two different models of GPS data loggers from Technosmart (Rome, Italy) were deployed. In 2007 and 2008, the first model of GPS (95 mm x 48 mm x 24 mm; 65 g, i.e. 2 % of adult body mass) was set to record the position every 10 seconds for a maximum duration of 48 hours. In 2009, we used GPS 'Gipsy 2' encapsulated in heat-shrink tubing (110x45x25 mm; mass 50 g, i.e. 1.6% of adult body mass), which were recording every 10 seconds during 5 consecutive days. Successive trips recorded in 2009 (i.e. on a 5 days period) were used to describe repeatability at the individual level. Using direct observations, we determined that birds returning from foraging trips lasting less than 30 min brought back nest material gathered at sea and did not feed. Trips < 30 min were therefore excluded from the analysis. Using the output data from the GPS's we calculated the distance between two consecutive positions, the distance to the nest, the time spent flying (i.e. when speed > 10km.h^{-1}) and a path sinuosity index to identify fishing events and locate feeding locations (see Grémillet et al. 2004; 2006 for details and validation).

2.3 Statistical analyses of foraging path characteristics

Statistical analyses were performed using R 2.11.1 (http://www.r-project.org). First, we addressed the level of foraging variability at the intra- and inter-individual levels and the effect of spatio-temporal factors. A global analysis of variance was conducted using a comparison of generalized linear mixed models (GLMM) with year and colony as fixed effects and bird identity as random effect associated to an autocorrelation structure of order 1, to correct for potential pseudo-replication. A Principal Component Analysis (PCA) was performed to identify correlations between the 6 descriptive variables of the foraging trips: trip duration, total path length, maximum distance to the nest, speed, flying time and sinuosity. Candidate models were run on the two first components of the PCA separately, and we compared them two by two (Zuur et al. 2009) to select the best model. For each comparison, a one-way ANOVA (fixed effects) and LRT method (random effect) were used to determine the model best supported by the dataset. For each component of the PCA (Dim.1 and Dim.2), model selection highlighted the mechanisms and the factors influencing variability in foraging behaviour.

In a second phase, we analyzed variability in trip duration, path length, maximum distance and speed with GLMMs (year as fixed effect, identity as random effect associated to an autocorrelation structure of order 1) within each colony. The GLMM was compared to a null model (without year as fixed effect) using a one-way ANOVA. Inter-annual variability was tested using a one-way ANOVA and post-hoc Tukey tests.

2.4 Spatial analyses

To describe the spatial use of gannets and to understand how they respond to changes in prey distribution, foraging trips and feeding positions were plotted and analyzed using Arcgis 9.2 (ESRI, France) and Hawth's Tools 3.27 extension. We used Minimum Convex Polygons (100%) to define the home range for individual trips. The Kernel Density Estimate tool was used to transform feeding positions into density estimates (Wood et al. 2000) and to determine the most intensively exploited areas within the home range of each colony.

a) Intra-individual variability

We analyzed individual plasticity using three complementary methods on successive trips recorded in 2009.

- Home range repeatability

For every bird, we calculated a cumulative home range for each additional trip to determine how the prospected area increases over 5 days of recording. To assess repeatability at an intra-individual scale, we calculated the overlap percentage of each pair of consecutive trips and the overlap percentage of all trips. We then compared, for each colony, the ‘first trip’ home range calculated from the first trip of each bird to the ‘5-days’home calculated from all trips over 5 days.

- Bearing fidelity

We measured the bearings followed by birds when they left and returned to the nest, to examine bearing consistency across successive trips. Since tracks were not all linear, we measured the azimuth on the first linear part at a minimum distance of 3 km from the colony. Using circular statistics for paired samples (Zar 1998), we calculated for all pairs of two successive trips (1) the difference between the azimuth of the first outbound trip (O1) and the azimuth of the second outbound trip (O2) and (2) the difference between the azimuth of the first inbound (I1) trip and the azimuth of the second outbound trip (O2). A mean difference of angle was calculated for each bird. We then calculated differences of angles between foraging trips recorded from different individuals (outbound trip from bird 1 vs bird 2 etc…). Using two sample t-tests, we compared differences in angles from two successive trips of a single bird with differences in angles between two unrelated trips. If repeatability in bearing is high, then the difference in angles should be lower for successive trips of the same bird than for unrelated trips.

- Feeding areas fidelity

We determined for each bird the total number of distinct feeding areas (feeding events separated by a distance of 5 km) and the total number of feeding events. We also estimated the mean number of repeated visits to the same feeding areas.

b) Inter-individual variability

Inter-individual variability in spatial strategies was examined via an analysis of preferred directions, feeding locations and home range overlap amongst individuals of the same colony, for each colony. The cumulative home range for each additional bird was calculated for each colony.

c) Inter-annual variability

Kernel density estimates of an entire colony highlight inter-annual variability in feeding hotspots distribution. For each year, we calculated a total home range (MCP 100%) using the first trip performed by each bird. We compared the percentage of overlap area between home ranges of two consecutive years for each colony.

3. Results

3.1 Sample sizes

We obtained a total of 341 foraging trips performed by 101 birds (N = 21, 23 and 14 on Storstappen in 2007, 2008 and 2009, respectively; N = 23 and 20 on Store Ulvøyholmen in 2008 and 2009, respectively). Each bird performed 1 - 14 foraging trips and we recorded a minimum of 3 consecutive trips for 39 birds. Because several analyses are informative on multiple scales, results are given for each type of analysis. The four considered scales (intra-individual, inter-individual, inter-annual and inter-colony) will be addressed in the discussion. Values are presented as means ± s.e.

3.2 Global variance analysis

The PCA analysis revealed a strong positive correlation between total trip duration, path length, maximum distance to the nest and flying time, and a negative correlation between speed and sinuosity (Figure 4. 2). The two first components of the PCA explained 77.2 % of the variance. The first component ‘Dim.1’ aggregated four of the six variables in relation to the duration and distance to the nest during the foraging trip and explained 55.8 % of the variance. The second component ‘Dim.2’ (speed negatively correlated to sinuosity of the path) explained 21.4 % of the variance.

From the GLMMs (Table 4.1), we selected the following models:

Dim.1	Dim.1~ year + colony, identity
Dim.2	Dim.2 ~ year, identity, autocorr.

Fixed effects ‘year’ and ‘colony’ had a significant effect on the observed variability of Dim.1, as well as inter-individual variability (expressed in the model by the random effect ‘identity’). Intra-individual variability was high, meaning a weak correlation between two successive trips (autocorrelation factor Phi = 0.06). The correlation structure did then not improve the model significantly. The fixed effect ‘year’ and ‘identity’ had a significant effect on the observed variability of Dim.2. The correlation structure estimate (Phi = 0.55) indicated a positive autocorrelation in speed and sinuosity of foraging. The ‘colony’ effect did not influence variability of Dim.2. We could not test any interaction effect between year and colony on the foraging behaviour, because no data were available in 2007 for Store Ulvøyholmen. To examine the foraging variability in details, we pursued foraging behaviour analysis within colonies.

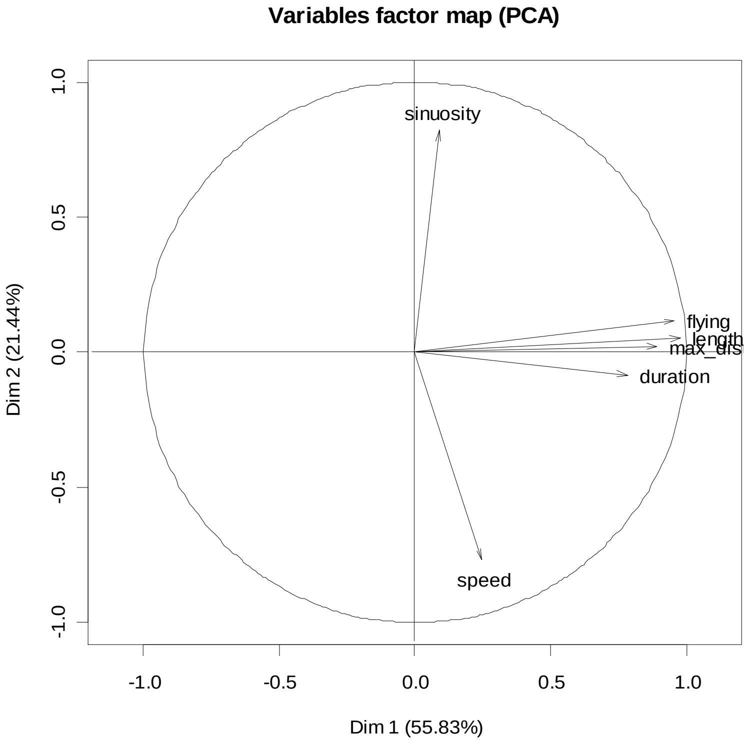


Figure 4.2 Morus bassanus. PCA analysis of 6 variables describing foraging trips in Northern gannets: duration, maximum distance to the nest, total path length, time flying, speed, and sinuosity.

Table 4.1 Comparison of different GLMM models testing the effect of variables on the two first components of the foraging trips PCA analysis: “year”, “colony” as fixed effect, bird “identity” as random effect and autocorrelation structure. Best models are written in bold letters.

	Model	AIC	Anova	p-value
Dim.1	**~Year + Colony, Identity**	**1307**	**-**	**-**
	Identity	1318	***	2^{e}-04
	Autocorr.	1308	N.S	0.45
	Colony	1332	***	<.0001
	Year	1332	***	<.0001
Dim.2	**~Year, Identity, autocorr.**	**981**	**-**	**-**
	Identity	1014	***	<.0001
	Autocorr.	1006	***	<.0001
	Colony	984	N.S	0.97
	Year	1016	***	<.0001

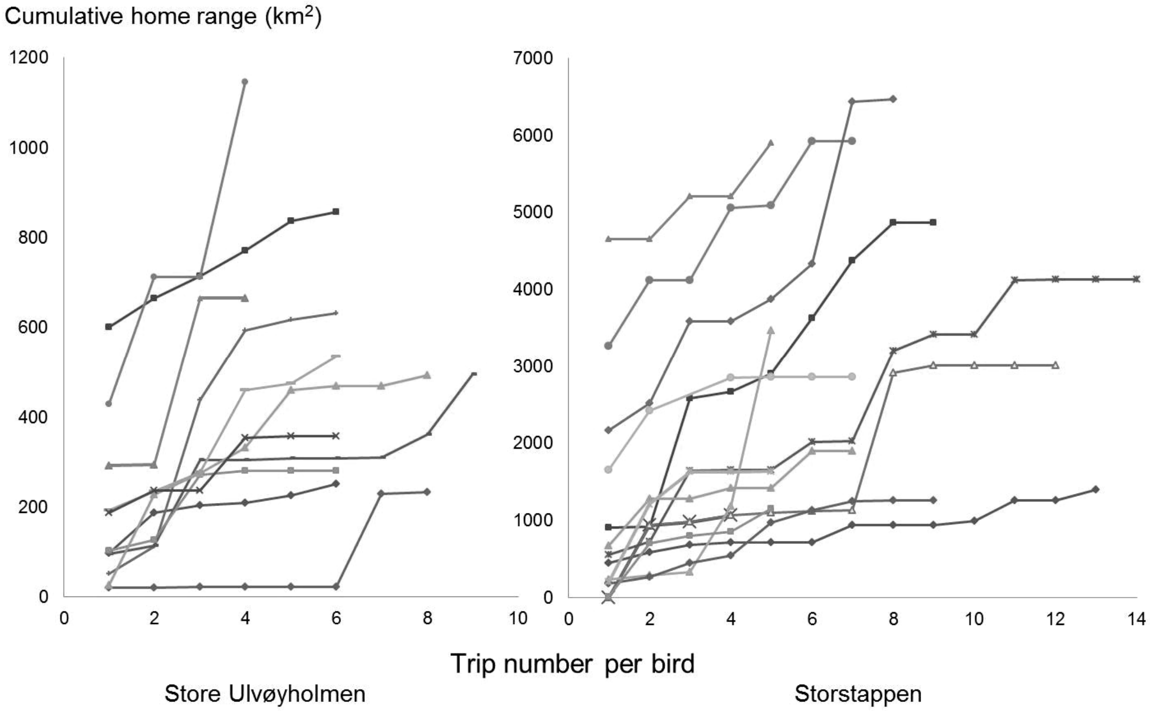


Figure 4.3 Cumulative home range per bird in relation with the number of foraging trips. Each solid line represents a single bird.

3.3 Spatial analyses

a) Intra- and inter-individual variability

On Store Ulvøyholmen, trip duration varied from 30 minutes to 22.8 hours, with maximum distance from the nest of 3 to 98 km and a total path length from 18 to 360 km. On Storstappen, foraging trip duration varied from 30 minutes to 23.5 hours, with maximum distances from the nest ranging from 5 to 132 km and a total path length from 18 to 595 km.

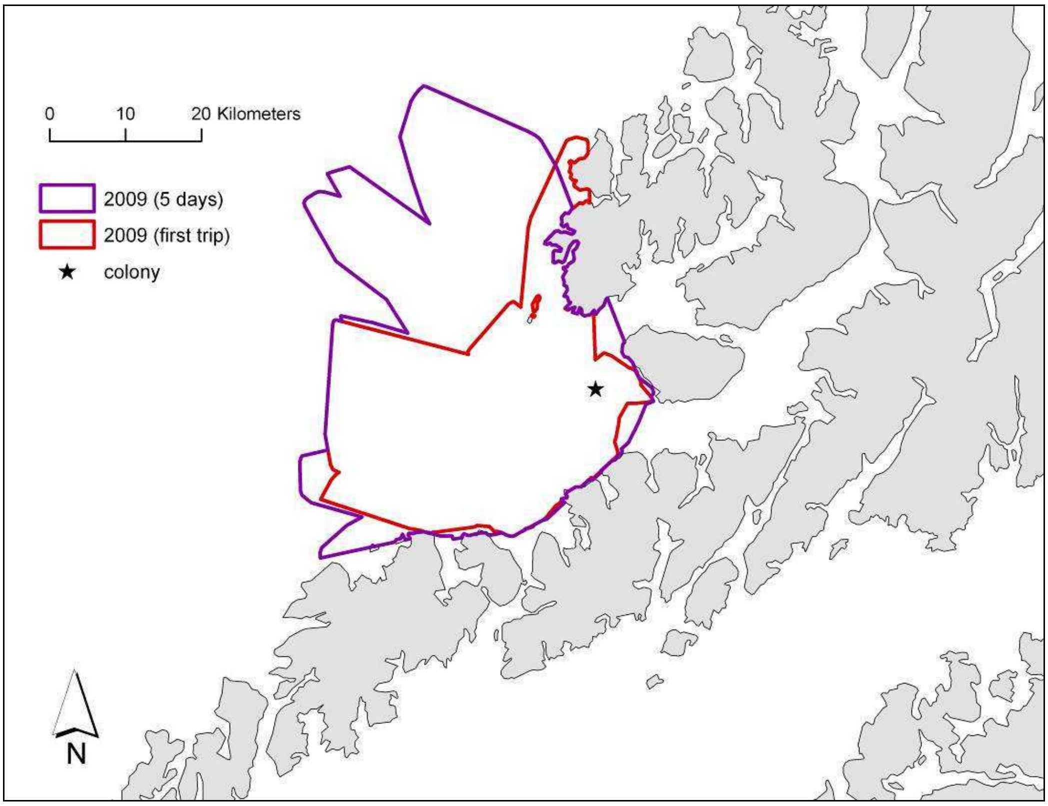
- Home range repeatability

Individual home ranges were increasing when new trips were recorded (Figure 4.3). On Store Ulvøyholmen, the size of most individual home range reached a plateau beyond four trips. On Storstappen, gannets seemed to prospect new areas at each new foraging trip, although the size of individual home ranges started to reach a plateau beyond seven trips (Figure 4.3). On Store Ulvøyholmen, the overlap between two successive trips of a single bird varied between 0-96 %, with a mean of 27 %. The overlap for all trips of a single bird varied between 5-56 %, with a mean of 27 %. On Storstappen, the overlap between two successive trips varied between 0-76 %, with a mean of 11 %. The overlap for all trips of a single bird varied between 1-55 %, with a mean of 12 %. At Store Ulvøyholmen, the home range increased from 1052 km2 to 1796 km2 if the first trip of each bird or all trips are considered (‘first trip’ vs ‘5-days’ home ranges, Table 4.2 Figure 4.4a). In the same way, the ‘first trip’ home range was 9672 km2 and the ‘5-days’ home range was 13856 km2 at Storstappen (Table 4.2, Figure 4.4b). Cumulative homes ranges (calculated for both ‘first trip’ and ‘5-days’) increased in the relation with the number of birds, but the home range size stopped increasing beyond six and seven birds at Store Ulvøyholmen and Storstappen respectively (Figure 4.5).

- Bearing repeatability

Differences in azimuths from successive trips were similar to azimuths from unrelated trips on Store Ulvøyholmen ($p = 0.22$ for O1 vs O2; $p = 0.70$ for I1 vs O2). On Storstappen, differences in azimuth between two unrelated trips was lower than the difference of azimuth between 2 successive trips ($p = 0.01$ for O1 vs O2; $p = 0.04$ for I1 vs O2). At the inter-individual level, a wide panel of bearings was used, but three mains routes were preferentially followed by gannets in both colonies (Figures 4.6a and 4.6b, page 88).

a)



b)

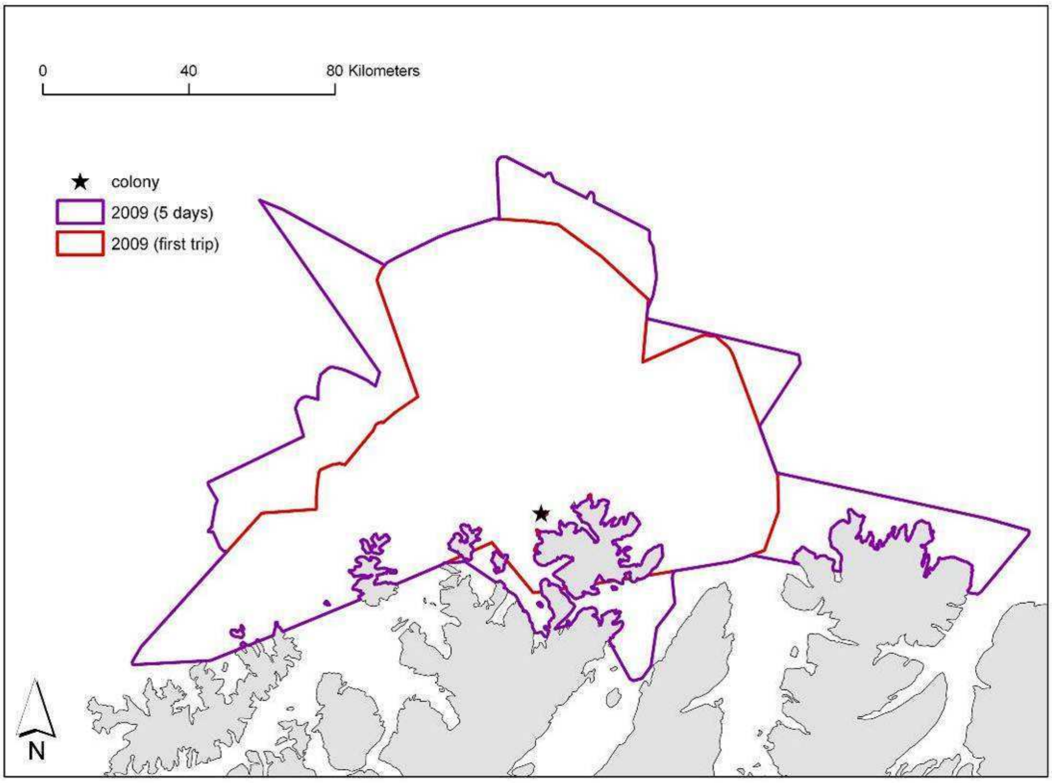
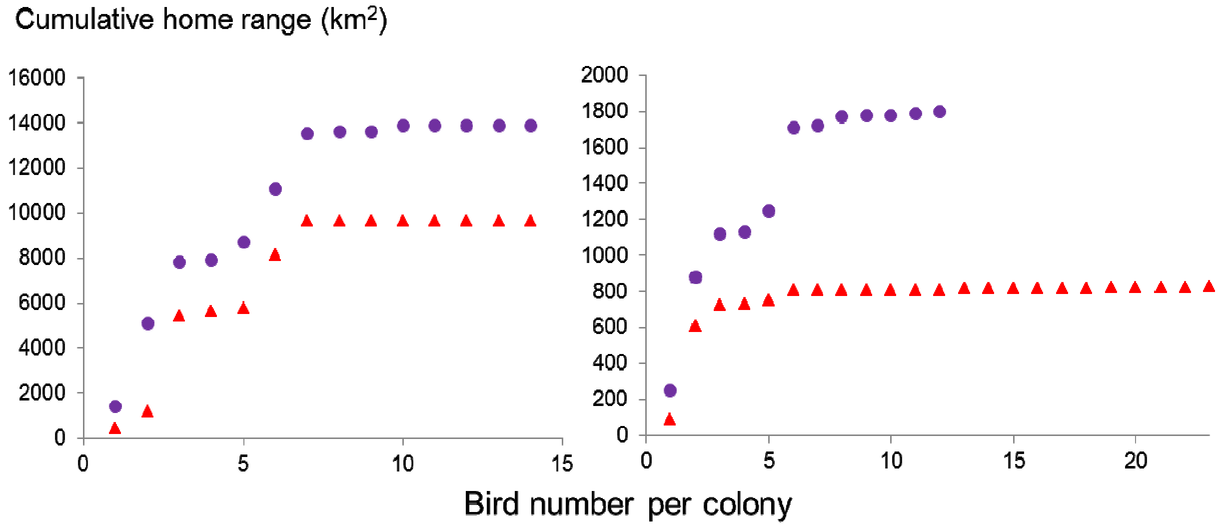


Figure 4.4 Home ranges calculated from the first trip (red line) and all trips on a 5-days period (purple) a) Storstappen (N= 14) b) Store Ulvøyholmen (N= 12).

Only one bird foraged farther north along the west coast of Andøya. Birds from Storstappen were travelled mainly westwards along the coast of Rolvsøya, southward to Kobbefjord and northwards off the North Cape (Figure 4.6b).

Table 4.2 Characteristics of foraging trips recorded with GPS loggers, of adults rearing chicks in two Norwegian colonies.

	Year	2007	2008	2009
Storstappen	N	21	23	14
	Duration (h)	4.5 ± 0.6	8.4 ± 1.2	6.6 ± 0.4
	Total length (km)	89.1 ± 9.4	190.6 ± 27.9	154.6 ± 9.0
	Maximum distance (km)	19.8 ± 2.2	53.8 ± 5.9	42.3 ± 2.5
	Speed (km.h^{-1})	47.0 ± 0.8	49.9 ± 0.7	48.4 ± 0.4
	Home range (km^2)	2841	8512	9672
Store Ulvøyholmen	N	-	23	20
	Duration	-	7.4 ± 0.9	6.3 ± 0.4
	Total length	-	114.8 ± 13.6	85.5 ± 4.4
	Maximum distance	-	25.3 ± 3.4	18.8 ± 1.1
	Speed	-	46.3 ± 0.6	47.9 ± 0.4
	Home range	-	1033	1052



Storstappen

Store Ulvøyholmen

Figure 4.5 Cumulative home range per colony in relation with the number of equipped birds and duration of GPS deployment. 5 days deployment (purple dots), 1 day deployment (red dots).

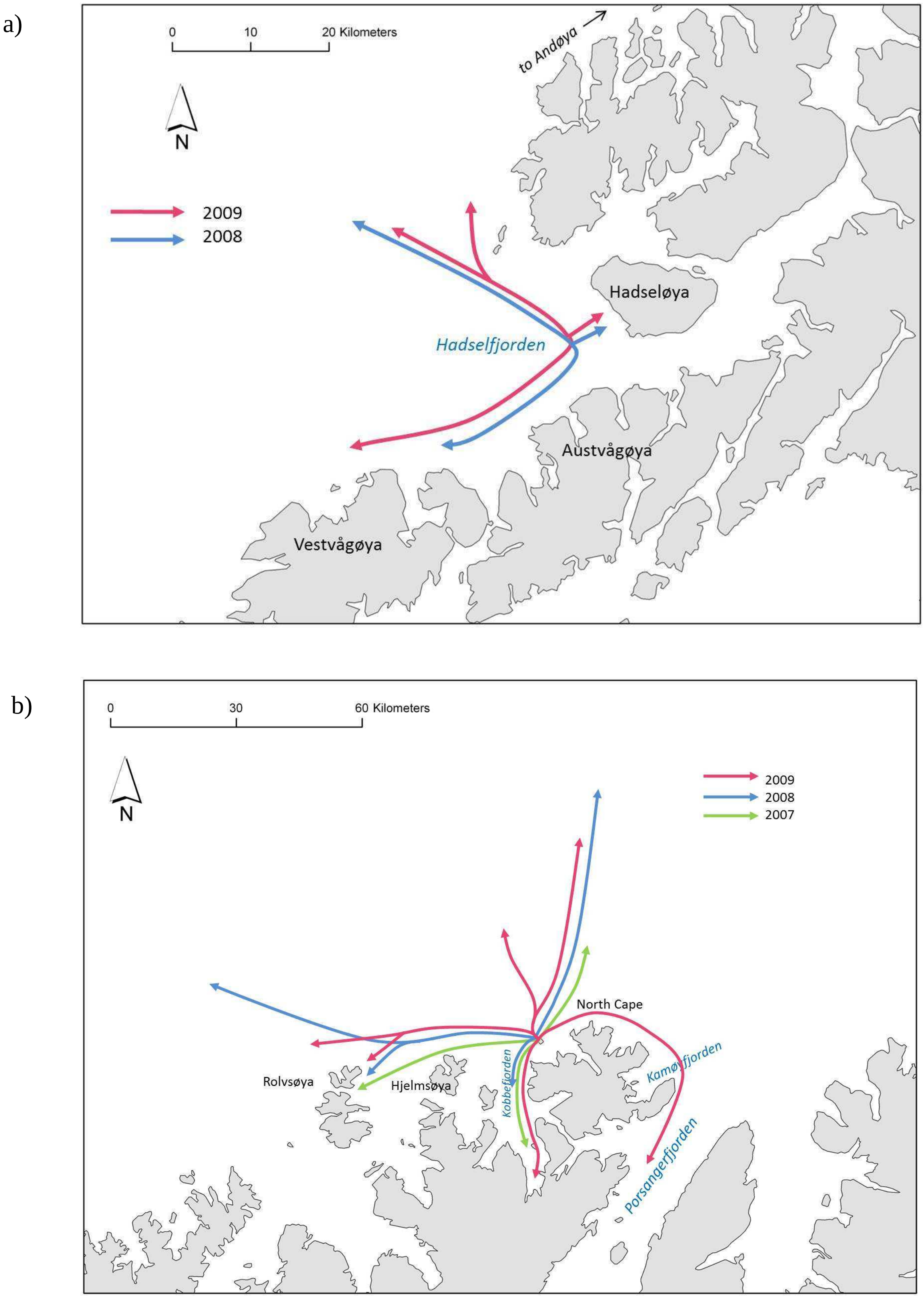


Figure. 4.6 Main foraging routes followed by northern gannets in 2007 (green line), 2008 (blue line) and 2009 (red line) in a) Store Ulvøyholmen b) Storstappen

- Feeding area fidelity

Individual gannets on Store Ulvøyholmen performed a mean of 6.3 ± 1.7 trips during 5 days of recording. Each bird foraged 8.8 ± 2.3 times in 3.9 ± 1.2 distinct areas. Each feeding area was visited twice by the same individual during the 5 day period. On Storstappen, each gannet performed an average of 8.3 ± 2.8 trips during 5 days of recording, it foraged 18.3 ± 5.2 times in 8.3 ± 2.1 distinct areas. Each feeding area was visited twice during 5 days.

At the inter-individual level, kernel density analyses revealed that, feeding on Store Ulvøyholmen was mainly off Hadseløya and along the northern coast of Lofoten (Figure 4.7a), rather close to the colony in both cases. On Storstappen, feeding hotspots were west-northwest of the colony, north off the North Cape and in the fjord south off the colony (Figure 4.7b).

b) Inter-annual variability

On Store Ulvøyholmen, no significant difference in the speed of flight, trip duration and the maximum distance to nest occurred between years (ANOVA: duration $p = 0.31$, max. distance $p = 0.17$, speed $p = 0.11$, Table 4.2) but path lengths were longer in 2008 than in 2009 (Tukey: $p = 0.05$, Table 4.2). On Storstappen, trip durations, path length, maximum distance to the nest and speed of flight were significantly different between years (ANOVA: duration $p = 0.003$, path length $p < 0.001$, max distance $p < 0.001$ and speed of flight $p = 0.034$). Trip durations were shorter in 2007 than in 2008 (Tukey: $p < 0.001$, Table 4.2) and in 2009 (Tukey: $p = 0.02$, Table 4.2). Maximum distance was significantly lower in 2007 than in 2008 (Tukey: $p < 0.001$, Table 4.2) and in 2009 (Tukey: $p < 0.001$, Table 4.2). Total path length was significantly different between all years (Tukey: 2007-2008 $p < 0.001$; 2007-2009 $p = 0.001$; 2008-2009 $p = 0.01$, Table 4.2). Speed of flight only differed between 2007 and 2008 (Tukey: $p = 0.005$, Table 4.2). During the three breeding seasons of the study, the gannets from both sites showed preferential routes (see above and Figures 4.6a, 4.6b), but marked inter-annual variations occurred on Storstappen. The gannets foraged within 20 km of the coast in 2007, while in 2008, they travelled further offshore in two main directions 50-100 km from the colony). In 2009, they foraged 40-80 km from the colony, following the 3 main routes as they did in 2007 (Figure 4.6b), though several birds also went around the North Cape peninsula and travelled southwards to Kamøyfjord and Porsangerfjord. Kernel density estimates showed variations in important feeding locations, although several feeding hotspots were consistent throughout the study period (Figure 4.7b). Gannets from Store Ulvøyholmen travelled in the same directions both years (Figure 4.6a). Feeding locations were also very similar, but were more tightly clustered in 2009 than in 2008 (Figure 4.7a).

c) Colony home range

We calculated the annual home for each colony as a Minimum Convex Polygon (100%) based on the first foraging trip of each bird. On Store Ulvøyholmen, 2008 and 2009 home ranges were of similar size (Table 4.2) and overlapped by 70% of the total area (Figure 4.8a). On Storstappen, home ranges were smaller in 2007 than in 2008 and 2009 (Table 4.2). Home ranges overlapped by 34% of the total area between 2007 and 2008 and by 75% of the total area between 2008 and 2009 (Figure 4.8b).

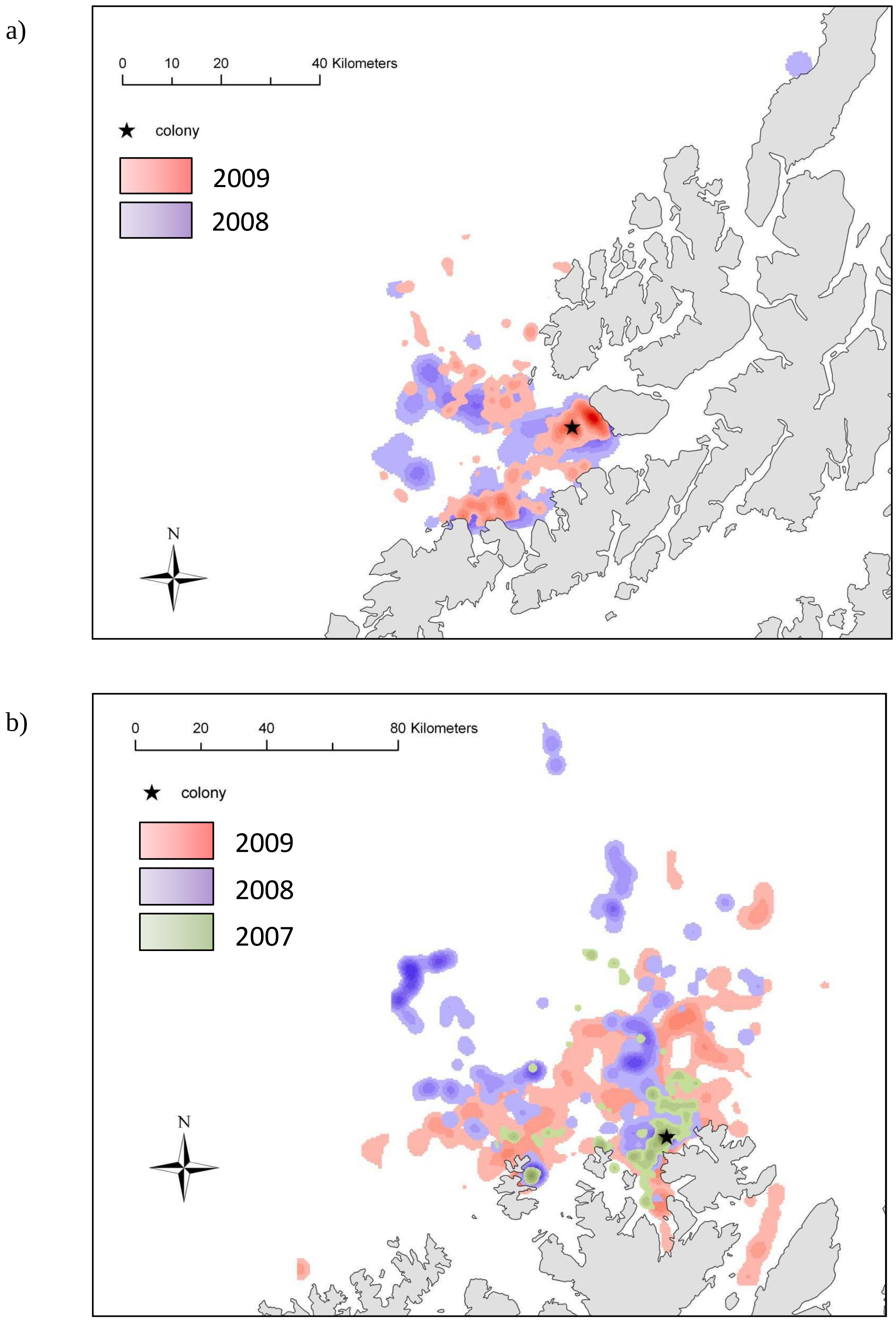
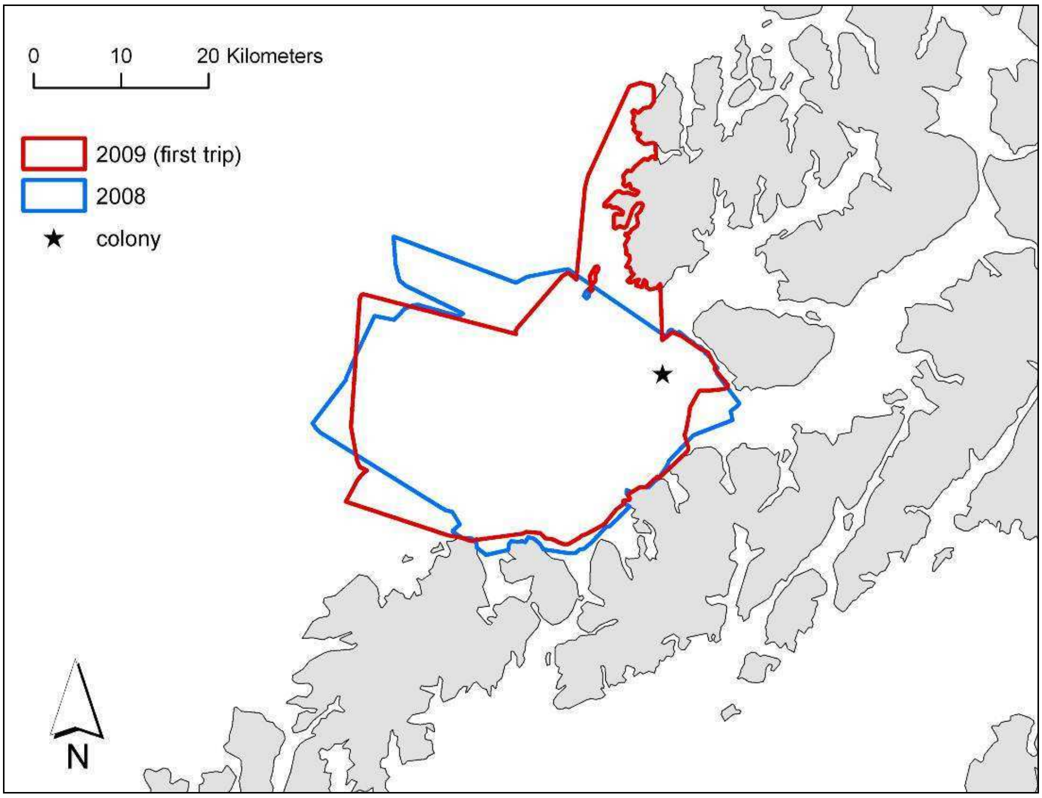


Figure 4.7 Relative density of feeding locations around the breeding sites in 2007 (green), 2008 (blue) and 2009 (red), from Kernel Density Estimate analysis, Jenks Natural thresholds. a) Store Ulvøyholmen (N= 23 and 20 in 2008 and 2009) b) Storstappen (N= 21, 23 and 14 in 2007, 2008 and 2009)

a)



b)

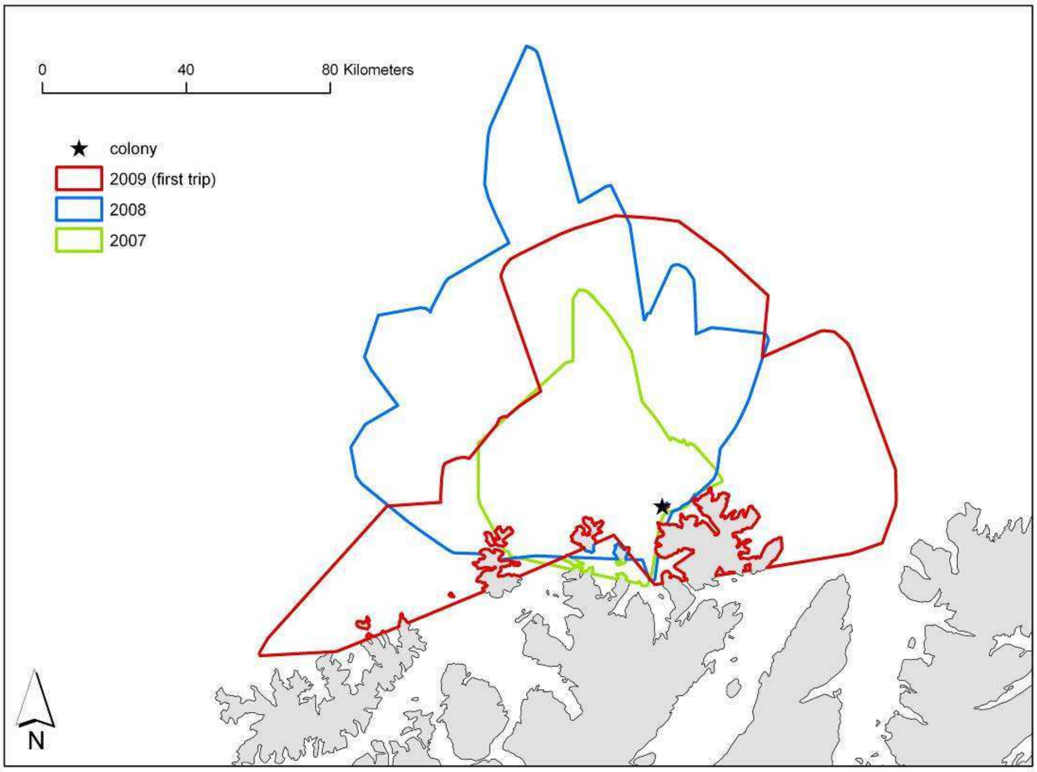


Figure 4.8 Annual home range in 2007 (green line), 2008 (blue line) and 2009 (red line), made from the sum of the first foraging trips of each bird A) Storstappen (N= 21, 23 and 14 in 2007, 2008 and 2009) B) Store Ulvøyholmen (N= 23 and 20 in 2008 and 2009).

4. Discussion

Behavioural plasticity plays a key role in the ability of organisms to adjust to environmental variability, and understanding its mechanisms and limits is crucial for predicting population viability (Komers 1997). In this study, we showed that Northern gannets exhibit high individual plasticity in their foraging behaviour, as well as substantial variability in foraging tactics at the inter-individual level. Both mechanisms reflect spatio-temporal variability in their foraging behaviour.

4.1 Individual plasticity

Individual plasticity of gannets is illustrated by the great variability in the quantitative and spatial features of their foraging trips. An individual bird may alternate long and short foraging trips remaining however consistent in flight speed and path sinuosity. Our data show a relatively low percentage of overlap between successive trips of the same individual. As a consequence, individual cumulative home ranges increase over successive trips (Figure 4.3), meaning that birds prospect in varied areas within a short time period. This has an impact on the home range of the colony, which is larger when considering the foraging trips of all birds over five days than when considering only one trip (the first recorded) per bird (Table 4.2, Figures 4.4a ,4.4b). However, some birds also showed repeatability in foraging tactics, returning on average twice (but up to 5 times) in a given feeding area before heading in a different direction during the next foraging trip. Analyses of flight compass bearings revealed that birds switch regularly between them, strongly suggesting that they could memorize profitable areas.

When foraging in the same area, foraging flights appeared very similar (Figures 4.6a, 4.6b), confirming the suggestion expressed in our previous work (Pettex et al. 2010) that prey-patch position may be anticipated by gannets. Gannets might thus use previous experiences gained during the breeding season to return to profitable areas (Hamer et al. 2007), as shown in other seabird species such as black-legged kittiwakes *Rissa tridactyla* (Irons 1998) and great cormorant *Phalacrocorax carbo* (Grémillet et al. 1999) or in other marine top predators such as southern elephant seals *Mirounga leonina* (Bradshaw et al. 2004) and Antarctic fur seals *Arctocephalus gazella* (Bonadonna et al. 2001).

In 2001, Hamer et al. showed marked differences in fidelity to foraging areas between two colonies from the North and the Celtic seas. At the Bass Rock colony, birds were following very similar bearing on successive trips, while those from Great Saltee were much less consistent. Here, we confirm and extend this result to Norwegian birds and show that individual northern gannets can be both consistent and flexible in the routes followed, in the exploited area and also in the duration and distances of foraging trips. How gannets decide to switch from a foraging area to another is unknown but public information may play a fundamental role in food patches localization (Weimerskirch et al. 2010a).

4.2 Inter-individual variability

Inter-individual variability in the foraging effort was shown by the variance analysis and the wide range of trip durations (from 30 min to 23 hours in both sites) and maximum distances from the nest (from < 5 kilometers to > 100 km). The bearing consistency also differs among individuals, from birds switching constantly between exploited foraging areas to birds following the same routes each time. Our results showed that equipped individuals prospected the whole area around their colony (Figures 4.8a, 4.8b). Cumulative home ranges revealed an inter-individual variability (Figure 4.5), but the spatial inter-individual variability is relatively low compared to the individual plasticity. In fact recording several trips of a limited number of birds was sufficient depict the whole home range of the colony. Our results consequently suggest that to show the “home range” of one colony it is more informative, and less invasive, tracking a small number of individuals for longer than a large number of individuals for just one foraging trip. A great consistency occurred among colonies in the choice of routes and feeding areas (Figures 4.6a, 4.6b, 4.7a, 4.7b). Indeed, gannets preferentially followed three directions and kernel analysis revealed an annual occurrence of feeding hotspots at both sites. Very productive feeding grounds are found along the northern part of the Norwegian coast (Sakshaug et al. 1994), thanks to the convergence of the low saline Norwegian Coastal Current and the warm saline North Atlantic Currents close to land off Vesterålen and North Cape area (Barrett, Lorentsen, & Anker-Nilssen 2006). This suggests that the marked colony-preferred routes and feeding sites observed might reflect a good predictability of prey at a small spatio-temporal scale. This is also concordant with the short foraging range observed at both sites (Table 4.2), compared to gannets’ ability to travel great distances to find prey (Hamer et al. 2007).

4.3 Inter-colony variability

Similarities and differences were observed in the foraging behaviour of gannets from Storstappen and Store Ulvøyholmen. If preferred routes and feeding hotspots (Figures 4.6 and 4.7) occurred at both sites, Storstappen birds exploited feeding areas twice as large as birds from Store Ulvøyholmen colony. Consistently, the percentage of overlap for two successive trips was much lower at Storstappen (11%) than at Store Ulvøyholmen (27%). It has been suggested that foraging effort and home range are positively correlated to the size of the colony (Lewis et al. 2001). Store Ulvøyholmen and Storstappen held, in 2008, 308 and 1244 breeding pairs respectively (Barrett 2008). Then, we might expect gannets from Storstappen to show a greater foraging effort than those from Store Ulvøyholmen, due to the effect of an intra-specific competition. In 2008 and 2009, gannets from Storstappen explored and foraged an area 8 times larger, performed longer foraging trips and travelled further than gannets from Store Ulvøyholmen (Table 4.2). However, the duration of foraging trip did not really differ between the two sites, meaning that gannets from Store Ulvøyholmen probably rested longer at sea-surface during their trips than their conspecifics from Storstappen. Gannets from both colonies might experiment good environmental conditions that limit competition. Differences in travelled distances and home ranges between both colonies could also reflect various distribution of prey. Variability in foraging behaviour in relation with contrasted environmental conditions between breeding sites have already been documented in northern gannets (Hamer et al. 2001; Garthe et al. 2006) and among marine predators: gentoo penguin *Pygoscelis papua* (Lescroel & Bost 2005), northern fur seals *Callorhinus ursinus* (Robson et al. 2004). Further work and additional sites would be necessary to draw any clear conclusion, nonetheless birds from the two breeding site behaved differently.

4.4 Inter-annual variability

Annual changes in food distribution can affect predator foraging behaviour, and animals should adapt their foraging effort or exploit different feeding grounds to find their prey (McCafferty et al. 1998; Hamer et al. 2007). Environmental conditions close to Store Ulvøyholmen were probably similar in 2008 and 2009, as gannets showed a very similar foraging behaviour. Home ranges were of identical size (ca 1000 km^2) and widely overlapped (Figure 4.8a). Gannets exhibited marked preferred areas and foraged in the close vicinity of the colony, suggesting favorable and stable prey availability conditions during our study.

Conversely, the gannets from Storstappen significantly increased their foraging effort (trip duration, maximum distance to the nest and distance travelled) and their home range between 2007 and 2009 (Table 4.2). Although several areas were continually exploited during the three breeding seasons, the general distribution of feeding hotspots varied between years. For instance, in 2008 the gannets foraged intensely in two areas located north and northwest off the colony (ca 80 km), while in 2009, most of the fishing activity was limited to a semi-circle 40 km from the breeding site, and to the Porsangerfjord (Figure 4.7b). This resulted in important variations in the 'colony' homes ranges overlap between 2007 and the two subsequent years (Table 4.2). These changes in the gannets foraging effort and foraged areas may be a response to variations in distribution and availability of their prey. Although the Barents Sea holds among the most productive grounds (Sakshaug, Johnsen, & Kovacs 2009), previous studies have highlighted pronounced interannual variations in the Barents Sea productivity and biomass in relation to the North Atlantic Oscillation (Drinkwater 2011). These changes resulted in important variation in the distribution of pelagic fish such as capelin *Mallotus villosus* and cod *Gadus morhua* (Loeng & Drinkwater 2007), but also herring *Clupea harengus* (Røttingen 1990) which is an important prey to Storstappen gannets (Montevecchi & Barrett 1987).

4.5 Ecological, conservation and methodological implications of plasticity in foraging

Our study shows that flexibility occurs in gannet foraging behaviour at the four considered levels, and that all derive from individual plasticity. Individual plasticity and as a consequence inter-individual variability may confer to northern gannets an advantageous ability to cope with environmental changes. The world population of northern gannets dramatically declined across the 19th century because of a massive exploitation of chicks and eggs (Wanless, Murray, & Harris 2005), but gannets positively and rapidly responded to protection measures during the 20th century, recovering and recolonizing a large part of their distribution area (Montevecchi & Hufthammer 1990; Wanless, Murray, et al. 2005). Young gannetries often experience a long latency period in their development, during which only a small number of pioneers settles, before becoming attractive for other individuals and growing fast (Nelson 2002). Pioneering individuals may not benefit of the presence of conspecifics to get information on profitable areas (Forbes & Kaiser 1994) either via local enhancement (Davoren, Montevecchi, & Anderson 2003) or public information (Ward & Zahavi 1973;

Weimerskirch et al. 2010a), but must rely upon individual plasticity to cope with the unpredictable marine environment. Thus the foraging plasticity of settlers might be essential to an efficient exploitation of resources and to ensure the durability of the colony during the first stage of its development. The rapid recovery of northern gannets during the last decades might be related to their highly plastic foraging behaviour and diet (Montevecchi et al. 2009).

Our results also showed that the distribution of foraging birds might differ among years (Figures 4.8). This must be considered in the design of conservation measures intended to marine predators. Among them, marine protected areas are increasingly implemented to protect pelagic habitats (Wood et al. 2008), but mobility of targeted species is a challenge to define suitable limits (Game et al. 2009). Tagging technologies have improved our knowledge of the spatial ecology of marine species (Ryan et al. 2004; Staniland, Reid, & Boyd 2004; Piatt et al. 2006; Burger & Shaffer 2008), and concurrently, the dynamic character of marine ecosystems needs to be considered by providing multi-year data to conservation managers.

The methodology of recording can also influence the quality of collected information. For organisms exhibiting a strong individual plasticity, it can be more informative to deploy a smaller number of loggers for a longer period than a larger number of loggers for a short period (Figures 4.5 and 4.6). Multi-sites studies might also be necessary to faithfully describe foraging behaviour at a regional scale and acquire a reliable overview of animal behaviour. These constraints should be taken into account in future studies and management decisions, to avoid a mismatch between the complexity of animal behaviour and conservation objectives.

Chapitre 5. Distribution et mouvements hivernaux à l’échelle méta-populationnelle

Dans les deux précédents chapitres, nous avons étudié le comportement alimentaire des fous pendant la période de reproduction, lorsqu'ils sont accessibles pour des observations et des poses d'appareils électroniques, mais aussi au moment où leur dépense énergétique est la plus forte. Les informations relatives à cette saison de reproduction sont désormais fournies, alors que l'écologie hivernale des oiseaux marins est généralement mal connue. A la fin de la saison de reproduction, les oiseaux quittent leurs colonies et débutent une migration importante qui les conduit parfois à plusieurs milliers de kilomètres de leur site de nidification. La recherche de conditions plus favorables, et notamment sur le plan alimentaire, pendant la mauvaise saison conditionne sans doute les mouvements et la distribution des oiseaux en mer. A l'aide d'enregistreurs de type GLS (*Global Location Sensor*), nous avons étudié les mouvements hivernaux d'individus issus de cinq colonies européennes distribuées le long d'un gradient latitudinal d'environ 2500 kilomètres. Les aires d'hivernage des fous de cette meta-population sont réparties entre deux zones hautement productives de l'Atlantique Nord Est : les côtes ouest africaines entre la Maroc et le Sénégal et celles des îles britanniques, de la France (hors Méditerranée dans notre étude) et du Portugal. Au sein de chaque colonie, plusieurs stratégies d'hivernage ont été observées, avec une ségrégation spatiale entre les oiseaux des différentes colonies. Les oiseaux norvégiens sont demeurés principalement en mer du Nord durant le mois de décembre, alors que les oiseaux des deux colonies britanniques avaient une distribution bimodale entre la Manche, le Golfe de Gascogne et les côtes mauritaniennes. Les fous de la colonie française ont principalement hiverné le long des côtes marocaines. Cette structuration de la distribution hivernale suggère l'existence d'une migration en chaine en fonction d'un gradient latitudinal des colonies. Peu d'oiseaux sont entrés en mer Méditerranée alors que les observations de fous en hiver y sont très nombreuses. Ces résultats montrent l'intérêt de réaliser des études à l'échelle méta-populationnelle afin de mieux comprendre l'écologie spatiale des oiseaux marins.

The Shetland – Senegal flyway: meta-population evidence of oriented migration in European northern gannets

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Abstract

Defining animal distribution is a major issue in ecology and evolutionary ecology. It aims at understanding how species interact with their environment, and how they respond to its variability. Until recently, understanding of individual seabird movements and distribution at sea was mainly restricted to the breeding season when birds are easy to observe and capture. Conversely, their migratory patterns and wintering hotspots remain poorly understood. Using miniaturized geolocators, we studied inter-breeding movements and winter distribution of European northern gannets (*Morus bassanus*). We focused on five major breeding colonies (in Norway, United Kingdom and France) distributed along a latitudinal gradient of ca. 2500 km including the southern- and the northernmost breeding sites. We showed that the overall inter-breeding distribution of the European meta-population is divided in two main areas situated in the European Seas and off Northwest Africa, in two of the most productive areas of the Northeast Atlantic. Nevertheless, smaller scale analyses highlighted important spatial segregations during winter, both within and between colonies. During this season, northern gannets breeding in Norway were mainly located in the North Sea. Conversely, birds breeding in two colonies of United Kingdom showed a bimodal winter distribution with a hotspot located in the English Channel and the Bay of Biscay, and another off the Islamic Republic of Mauritania. Finally, northern gannets breeding in France, at the lowest latitude, mainly wintered in the coastal area of Morocco. This structured winter distribution, linked to the latitude of the breeding colonies, strongly suggests a chain migration. Interestingly, while the eastern Mediterranean is usually considered as an important wintering ground for northern gannets, only a very few number of the birds tracked flew into this area. Overall, our study therefore shows the existence of a major northern gannet flyway along the coasts of Western

Europe and Africa, from the North Sea to Senegal, and highlights the benefit of meta-population studies in seabird species to accurately define and understand at-sea hotspots.

Keywords: avian conservation, dispersive migration, GLS, inter-breeding movements, migration corridor, seabird hotspots, winter distribution

1. Introduction

Defining animal movements and distribution in space and time is essential to understand how species interact with their environment, and how individuals respond to the environmental variability and heterogeneity (Lack 1968). Such knowledge is also important as many ecosystems are currently subject to rapid modifications and degradations which might challenge the survival of species unable to respond or adapt to these changes (Millennium Ecosystem Assessment 2005). Among these affected environments, marine ecosystems have a particular place. Indeed, marine regions hold some important resources and a large part of the Earth biodiversity, but are also subjected to the combined effects of climate change and anthropogenic stressors, which are bound to have strong deleterious impacts on the state of these sensitive systems (Halpern et al. 2008). For instance, there is growing evidence that climate change can lead to large-scale ecosystem shifts (Scheffer et al. 2001; Beaugrand 2004; Drinkwater 2006), with detrimental effects upon marine resources and biodiversity (Beaugrand, Edwards, & Legendre 2010). As for human activities, such as fisheries or offshore gas/oil extraction, they can also strongly impact regional marine communities and their dynamics at various levels of the food-web (Reid et al. 2000; Halpern et al. 2008; Bartumeus et al. 2010). Investigating the distribution of marine organisms is therefore a priority which might help future defining and setting-up of conservation actions (e.g. Schofield et al. 2007; Pichegru et al. 2010a).

Seabirds are in high abundance from pole to pole (Woehler & Croxall 1997; Barrett et al. 2006) where they exert a strong predatory pressure on lower trophic levels (Furness & Cooper 1982; Karnovsky & Hunt 2002) and therefore play a key role in marine ecosystems, worldwide. Seabirds are also the most threatened group of bird in the world (Butchart et al. 2004), and their protection is now a major concern (Birdlife International 2004). During summer, most of seabird species come to land to breed. They can then be observed, captured and equipped with miniaturised recorders allowing investigations of their at-sea movements and distribution at different temporal and spatial scales (Phillips et al. 2004; Weimerskirch et al. 2010b). Previous studies involved in conservation programs used this information to define and establish Important Birds Areas and/or Marine Protected Areas where seabird populations and/or other marine species became protected (Arcos, Rodríguez, & Ruiz 2009; Pichegru et al. 2010). Nevertheless, this use of the biotelemetry approach to determine and understand seabird distribution has essentially focused on the breeding season, and despite recent efforts to improve our knowledge of seabird inter-breeding movements (e.g. Shaffer et al. 2006; González-Solís et al. 2007; Bost et al. 2009; Egevang et al. 2010), the inter-breeding ecology of seabirds is still poorly understood. Moreover, while most studies focused on specific colonies, at a population scale only, there is growing evidence that seabird ecology should rather be investigated at a meta-population scale (Grémillet & Boulinier 2009). Indeed, different studies previously demonstrated that, within a same species, individuals from neighbouring colonies can occupy distinct and distant foraging areas, both during their breeding (e.g. Grémillet et al. 2004) and their wintering (e.g. Thiebot et al. 2011) season. Restricting studies to a specific colony or population might therefore limit our overall understanding of seabird distribution at sea and of hotspots areas, therefore calling for further, larger-scale studies. Further, seabird post-breeding movements are generally considered as dispersive migration (Newton 2010), yet recent investigations indicated that migration corridors might occur, even in oceanic birds (e.g. Shaffer et al. 2006, Egevang et al. 2010). It is therefore important to test whether, at the meta-population level, seabird winter movements are indeed oriented so as to feature migration similar to that of land birds.

In this paper, we focus on the northern gannet (*Morus bassanus*), a species widely distributed in the North Atlantic (del Hoyo 1992). On the eastern side of this ocean, where more than 80% of the world population breeds (Nelson 2002), northern gannets occupy four main breeding sites (United Kingdom, Norway, Iceland, and France; Nelson 2002), each of them consisting of colonies with hundreds to tens of thousands of breeding pairs (Anker-Nilssen 2000; Lewis et al. 2001). During their breeding season, the biology and foraging distribution of northern gannets has been the subject of many studies and is relatively well understood (e.g. Hamer et al. 2007; Skov et al. 2008; Pettex et al. 2010). However, our knowledge of their migratory patterns and winter areas remains limited. Over last decades, important ringing and at-sea survey programmes allowed to define some major staging areas for inter-breeding northern gannets (both for juveniles and adults) and therefore brought essential basal knowledge on their movements and distribution during this season (Barrett 1988; Stone et al. 1995; Nelson 2002; Veron & Lawlor 2009). However, determining the distribution of marine organisms from direct observations such as ring recoveries remains dependent on the recapture effort and the capacity to observe birds, and can therefore be biased spatially and temporally. Similarly, ship-based monitoring only allows community level observations rather than individual level observations (Tremblay et al. 2009). Only one study used biotelemetry to investigate the complete inter-breeding individual movements of northern gannets (Kubetzki et al. 2009). Focused on a unique colony in Scotland, it showed that this species can adopt various and very contrasting overwintering strategies, thereby confirming observations of ringing programs (Nelson et al 2002). However, several studies previously showed existing exchanges in northern gannets between colonies, within and between the main European sites (e.g. Barrett 2008; Votier et al. 2010a), strongly suggesting that this ‘European’ group should be rather considered at a meta-population scale.

The present study has therefore three main objectives: (1) bring new knowledge of migratory patterns and winter sites of European northern gannets at population and meta-population levels. (2) Identify hotspots for wintering northern gannets and potential migratory pathways between breeding and wintering sites. (3) Understand how the environment governs northern gannet winter distribution.

2. Materials and methods

2.1 Study sites and data collection

We studied over several years the inter-breeding distribution of 86 northern gannets breeding in five European colonies: Storstappen (71°14'N, 25°30'E; Norway; 2008/2009 - 2009/2010), Store Ulvøyholmen (68°51'N, 14°51'E; Norway; 2008/2009 - 2009/2010), Bass Rock (56º04'N, 2º38'W; Scotland, UK; 2002/2003 - 2003/2004), Grassholm (51º43’N, 5º28’W; Wales, UK; 2007/2008) and Rouzic (48º54'N, 3º26'W; France; 2006/2007). These colonies are distributed over the Northern Europe and along a latitudinal gradient, Storstappen being the northernmost, and Rouzic the southernmost, respectively (Figure 5.1), and can thus be considered as representative of the western and northern European meta-population. Hereafter, and for the sake of simplicity, these 5 colonies are referred to as NO1 and NO2 for the 2 Norwegian colonies, UK1 and UK2 for the 2 UK colonies and FR for the French colony (see Figure 5.1 and Table 5.1 for details). The Bass Rock data were analysed and published in Kubetzki et al. (2009).

At each colony, breeding northern gannets were fitted with a Global Location Sensor (GLS; Wilson et al. 1992) attached to a plastic or metal leg ring (see Table 5.1 for details). GLSs were programmed to record time, light levels and temperature throughout the non-breeding season. Because GLSs store recorded data, birds had to be recaptured and recorders recovered the following breeding season in order to secure and analyse the data (see below).

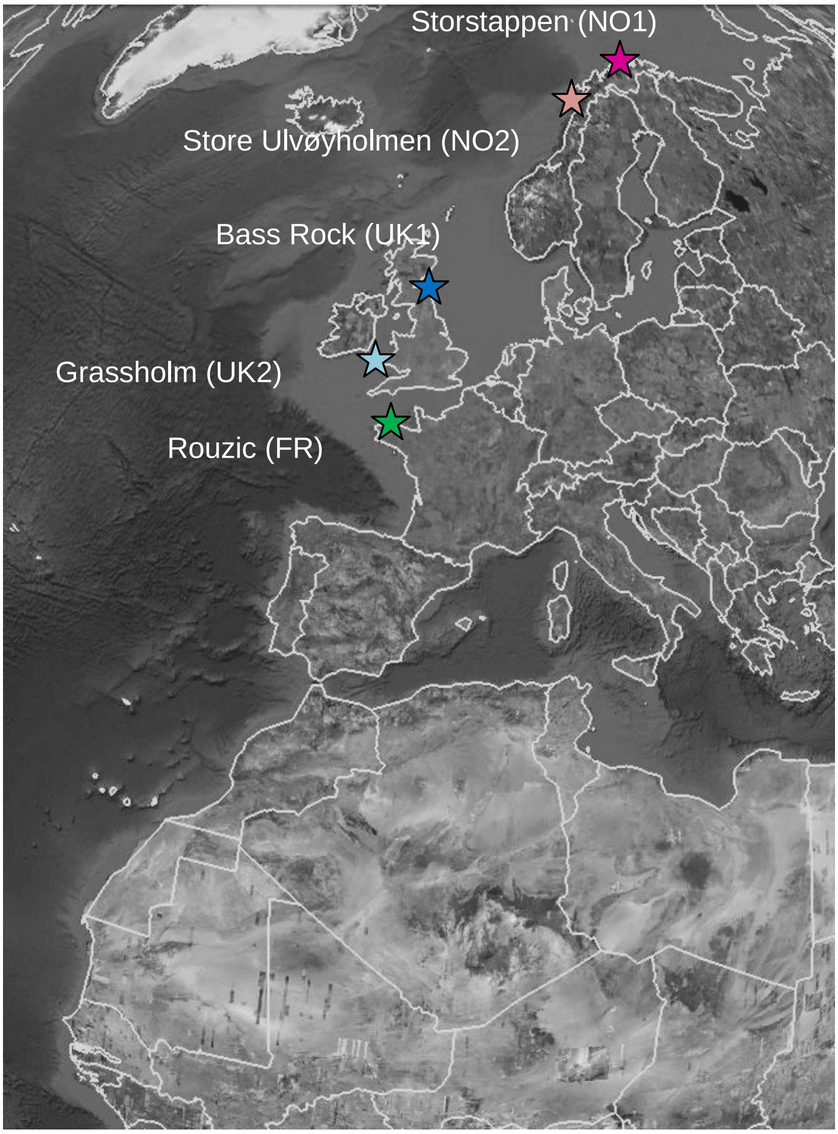

Figure 5.1 Studied northern gannet colonies, labelled as follows in the text: NO1 and NO2 for Norway, UK1 and UK2 for United Kingdom and FR for France. Geographical coordinates are given in Table 5.1

Table 5.1 European colonies where breeding northern gannets were equipped with miniaturised geolocators (GLS)

	Rouzic (48º54'N, 3º26'W)	Bass Rock (56º04'N, 2º38'W)		Grassholm (51º43'N, 5º28'W)	Storstappen (71°14'N, 25°30'E)		Store Ulvøyholmen (68°51'N, 14°51'E)	
	FR	UK1		UK2	NO1		NO2	
Recorded year	2006/2007	2002/2003	2003/2004	2007/2008	2008/2009	2009/2010	2008/2009	2009/2010
GLS type	GeoLT	GeoLT	GeoLT	GeoLT	Lotek LAT 2500	Lotek LAT 2500	Lotek LAT 2500	Lotek LAT 2500
Dates of deployments	21/07/2007	19/08/2002	02-03/09/2003	18/07/2007	16-25/07/2008	21-29/07/2009	05-20/07/2008	04-08/07/2009
Number of equipped birds	7	9	13	10	14	11	9	13

2.2 Data analyses

All analyses were conducted using Matlab R2010b (The MathWorks) and ArcGis 9.3 (ESRI Inc.).

a) Light-level data analysis

Light-level data were extracted and converted into geographic coordinates using MultiTrace Geolocation (Jensen Software System) for UK1, UK2 and FR data and using LAT Viewer Studio (Lotek fish & wildlife monitoring systems) for NO1 and NO2. Some of the raw spatial positions obtained from these extractions can contain some large errors (Phillips et al. 2004; Teo et al. 2004; Shaffer et al. 2005) because of the latitude (higher latitudes can have constant daylight or dark), of the period considered (equal day and night duration during equinoxes) or because of animal behaviours which might occasionally alter the quality of the light level readings. Therefore, and in order to take these errors into consideration, all raw positions were processed using Tremblay et al.'s (Tremblay, Robinson, & Costa 2009) method. The method consisted in transforming each estimate of position into a cloud of possible locations, distributed in relation to their potential error. Each of these locations (or particles) was then weighed in relation to a number of parameters such as being on land or not, having a good matching with the sea surface temperature (SST) at the same place or not. Indeed, SST experienced by individual birds were estimated from the raw temperature data recorded by the logger, as being stable successive readings of temperatures within a reasonable range of possible SST. These estimated SST were then compared to satellite-derived SST maps (Teo et al. 2004; Shaffer et al. 2005). From the cloud of locations obtained, we ran a number of biased random walks, each representing a possible path given the data collected. The whole set of paths embrace an average, most probable path. The most probable paths were used in subsequent calculation of distances and distributions. Random walks were computed with a time grain of 8 hours (3 points a day).

Different additional information were also extracted from the estimated non-breeding positions. The maximum distance to the colony of origin was calculated for the whole inter-breeding season and for each individual. Distances were computed as the great-circle distance on the Earth spheroid, thus taking into account the Earth's curvature but not accounting for coast avoidance. These estimations were assumed to represent the distance separating, for each bird, its colony and its wintering ground. Results were used to examine the inter-individual variations in the winter distribution among and between colonies.

b) Hotspots identifications

Kernel analyses were used to determine the areas preferentially occupied by European northern gannets during their inter-breeding season. These preferred areas were delimited using the 25% kernel density contours. Kernel Analyses were performed during 3 distinct periods defined as 1) pre-winter period (1-31 October; during which birds were assumed to migrate to their wintering site), 2) winter period (1-31 December; during which birds were observed to stay in a restricted area without any large-scale movements) and 3) post-winter period (1-28 February; during which birds were assumed to migrate back to their breeding site). Bird densities were computed using a 50 km grid. Only cells used by 2 individuals or more were taken into account, in order to avoid giving importance to zones used by only one individual. Further, the number of locations within one cell was multiplied by the total number of birds contributing to these locations. This transformation allows to favour zones used by many individuals over zones used for a long time by only a few individuals.

3. Results

Overwinter strategies adopted by European northern gannets were generally similar between years. Though these results are based on two successive years only and for three different colonies, they allowed us to pool multi-years data for each colony in order to increase our sample size and therefore our confidence in the determination of seabird hotspots.

3.1 Global inter-breeding movements of European northern gannets

After their breeding season, almost all northern gannets equipped with a GLS moved southwards. Overall, a strong inter-individual variability occurred and birds globally occupied a wide area ranging from the North Sea to Northwest Africa. Nevertheless, distances between colonies and wintering areas (defined from the individual maximum distances to the colony) revealed colony-specific strategies (Figure 5.2). During winter, northern gannets breeding at NO1 were continuously distributed between the North Sea and the northern part of Northwest Africa, with one individual reaching the coasts of the Islamic Republic of Mauritania. Birds from NO2 presented a more restricted and bimodal distribution with most birds remaining in European waters (in the North Sea, the English Channel and the Bay of Biscay), and three other individuals located much further south in northwest African waters and western Mediterranean (Figure 5.2). Birds from UK1 showed a wide distribution between the North Sea and the Senegal coasts in Northwest Africa (Figure 5.2). One bird also wintered in the Mediterranean Sea, between Tunisia and Sicilia. Similarly to the previous UK colony, birds from UK2 were widely distributed between European Seas and Northwest Africa. Nevertheless, three narrow main areas were occupied; in the Bay of Biscay, off the west coasts of Portugal, and off Northwest Africa (Figure 5.2). The winter distribution of northern gannets breeding at FR was also very restricted with almost all birds reaching the northwest African coast, one bird wintering in the Irish Sea while another stayed off the Portuguese coasts (Figure 5.2). Importantly, only 1 of the birds tracked wintered far into the Mediterranean Sea (Figure 5.2). For the whole European meta-population, maximum distances from the colony ranged from 1105 to 6677 km (Table 5.2).

3.2 Hotspots for inter-breeding northern gannets : intra- and inter-colony variations

a) Pre-winter period

In October, kernel analyses show that the core areas (25% kernels) occupied by northern gannets were all concentrated in seas around the UK, with large overlaps between the five study populations (Figure 5.3a). However, despite this overall common distribution, different pre-winter strategies were observed between and among colonies. First, birds distribution revealed that the timing of the autumn migration and the arrival on winter sites were completely dissimilar between Norwegian colonies and the others.

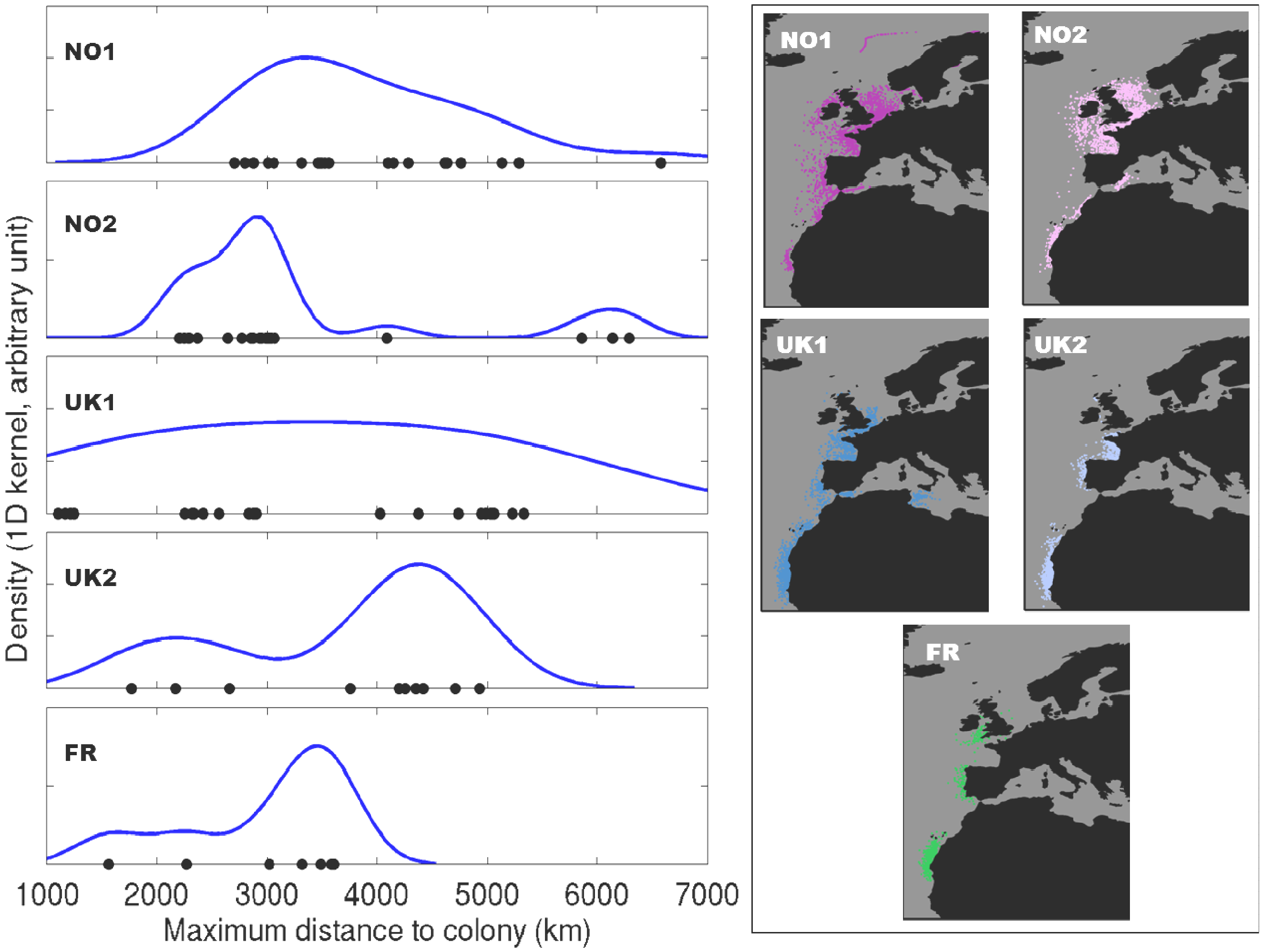

Figure 5.2 Left panel. Maximum distances to the colony (in kilometres) reached by each individuals (black circles) from the five studied colonies. Blue lines represent for each colony the kernel smoothing density estimate. Right panel. Winter (December) positions estimated by the model for all individuals and at each colony.

Indeed, in October, birds from the two Norwegian colonies had already migrated and reached their wintering sites (see below), while birds from other colonies were still mainly distributed around their breeding places (Figure 5.3a). Moreover, birds from UK2 and FR adopted a similar pre-winter strategy, with birds mainly distributed in the Irish Sea. Conversely, the main distribution of birds from NO2 is located in the southern part of the North Sea. Gannets breeding at UK1 and NO1 adopted very similar distributions in October, with in each case, a distribution divided in 2 main areas, one located in the North Sea overlapping the NO2 distribution, and one located in the Bay of Biscay. Surprisingly, while FR birds winter far south from their colony (see below), they initially moved northward after their breeding season, a strategy which is specific to this colony (Figure 5.3a).

Table 5.2 Average maximal distances (in kilometres) reached by birds from the different studied colonies

	Maximal distance from the breeding colony (km)
FR	2979 (min=1562, max=3608)
UK1	3362 (min=1105, max=5330
UK2	3721 (min=1769, max=4926)
NO1	3290 (min=2699, max=6577)
NO2	3872 (min=2202, max=6291)
Mean	3444.8

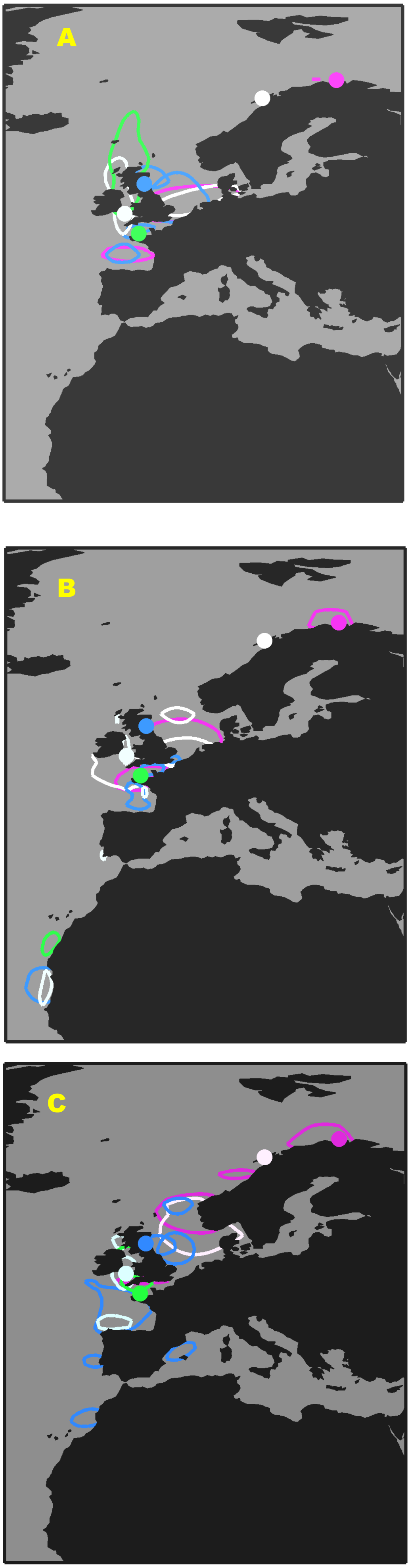

Figure 5.3 Main areas occupied by European northern gannets during the inter-breeding season, represented by 25% kernel density contours. (A) pre-winter (October) distribution, (B) winter (December) distribution, (C) post-winter (February) distribution. On each map, plain-colour dots represent the different breeding colonies (see Figure 5.1), a same colony-specific colour being associated with the kernel density contours.

b) Winter period

European northern gannets clearly adopted two distinct and contrasting winter strategies, split in two main distribution areas: one located in Northern Europe and one off the coasts of Northwest Africa (Figure 5.3b). Overall, there were again large overlaps between the main winter areas occupied by birds from the five study colonies. Nevertheless, smaller spatial-scale segregations also appeared during the winter season, between and among colonies. Norwegian birds (NO1 and NO2) were mainly distributed in the North Sea and the English Channel, with a very similar spatial distribution between these two colonies. Contrary to the autumn, birds from these two colonies were the only ones wintering in the North Sea. French birds (FR) also had a single major distribution during winter, located in Northwest Africa. Conversely, the UK colonies presented a main distribution divided among two zones, some birds spending the winter in Northern Europe (Irish Sea, English Channel and Bay of Biscay) while the others overwintered in Northwest Africa. Interestingly, in northwest African waters, there was a spatial segregation between birds from France and from the UK (UK1 and UK2). Indeed, the main distribution of French gannets were located off Morocco, while those of UK colonies were very similar and located further south, off the Islamic Republic of Mauritania and Senegal (Figure 5.3b). It should also be noted that in December, two individuals from NO1 were back at their breeding site, while all other birds remained at their wintering site (Figure 5.3b).

c) Post-winter period

Kernel analyses revealed a strong heterogeneity of birds’ main distribution (25% kernels) in February, both among and between colonies. There was an important segregation between Norwegian birds and those from France and UK, with only few individuals from UK1 located in the North Sea and sharing main areas with Norwegian birds (Figure 5.3c). Divergent distributions were also observed in western Europe waters, with birds from FR mainly distributed in the English Channel, birds from UK2 restricted to the Irish Sea and to an area along the north coast of Spain, and birds from UK1 distributed widely in other places, mainly the Bay of Biscay, the Portuguese coast, the Mediterranean and Northwest Africa (Figure 5.3c).

It is worth noting that the timing of the spring migration was very variable among sites. On average, birds from UK1, UK2 and FR left their winter sites in January (see Table 5.3), earlier than Norwegian birds (NO1 and NO2) which start their northward spring migration in late-February and March, respectively (Table 5.3). In February birds from NO2 were still very close to their wintering site with a single main area occupied in the North Sea (Figure 5.3c). Conversely, birds from FR had completed their spring migration and were mainly distributed around their breeding colony. Gannets from NO1, UK1 and to a lesser extent UK2 show a main distribution dispersed between their wintering and breeding sites, strongly suggesting various individual strategies, with some birds migrating while some others already reached their colony (Figure 5.3c). On average birds from FR and UK2 arrived early-February in the vicinity of their colony, while birds from NO1, NO2 and UK1 didn't arrived before early-March (Table 5.3). Overall, despite individual and population differences, our analyses reveal the existence of a gannet winter flyway ranging from the northern North Sea to the tip of West Africa.

Table 5.3 Timing of spring migration movements of individuals from the different studied colonies.

Colony	Start date of the spring migration	Arrival date at the breeding site
FR	04/01	02/02
UK1	19/01	> 01/03
UK2	11/01	03/02
NO1	21/02	> 01/03
NO2	> 01/03	> 01/03

4. Discussion

By focusing on five representative European breeding colonies distributed along a latitudinal gradient of ca. 2500 km including the southern- and the northernmost breeding sites, the present study investigated for the first time the inter-breeding movements and winter distribution of European northern gannets at a meta-population scale. The GLS method (sensu Wilson et al. 1992), based on light-level recordings, is essential to track small/medium-sized animals over large time scales. However, this method also entails a large error of 100-200 km which limits its use to the study of wide-scale movements (Phillips et al. 2004; Teo et al. 2004). Though we used a refined model taking into account potential biases of the method to predict individual positions more accurately (Tremblay, Robinson, & Costa 2009), we wish to stress that small-scale results should be interpreted carefully.

One of the main outcomes of this study is the high variability of winter distribution observed both at the individual and inter-colony levels. Several studies investigating seabird movements previously showed that individuals from a common colony can segregate during winter and use contrasting wintering sites (Shaffer et al. 2006; González-Solís et al. 2007; Catry et al. 2009). In the case of European northern gannets, such segregation also exists at a meta-population scale, with two main and distinct areas occupied in the Northern Europe seas and off the coast of Northwest Africa. Despite its long distance from the breeding sites, the use of the latter zone by northern gannets confirms that it is an important ground for wintering seabirds (Wernham et al. 2002; Camphuysen & van der Meer 2005; González-Solís et al. 2007). The coastal area off Northwest Africa is indeed one of the 4 major upwelling zones in the world, extending between 10°N and 22°N during winter and holding high densities of resource for marine predators (Mittelstaedt 1983). Overall, a simple comparison between winter chlorophyll a concentrations and birds distribution (Figures 5.3b and 5.4) shows that northern gannets were distributed in the most chlorophyll-rich areas, where the maximum abundance of prey (large pelagic fish; Hamer et al. 2007) can be expected. The Baltic Sea, a large and highly productive area, was nonetheless completely excluded by all northern gannets and during all years. The Baltic Sea is a nontidal, brackish environment characterised by a low salinity, a pronounced density stratification and small funnel-like connections to the North Sea, and might therefore represent a non-profitable habitat for wintering northern gannets and other pelagic seabirds (Österblom et al. 2007). Further, fluctuating sea-ice conditions might also explain this exclusion. Indeed, even if the Baltic Sea is usually largely free of ice year-round, ice can have an unusual large extent in the Danish Straits during severe winters and disconnect the Baltic Sea from the North Sea until spring, which could affect seabird survival (e.g. McFarlane Tranquilla et al. 2010). Therefore, the Baltic might appear too risky for inter-breeding northern gannets. Further, only a very few number of the birds tracked flew into the Mediterranean, which is very surprising since substantial numbers of northern gannets are being observed in the eastern Mediterranean, especially in the Gulf of Lyon during the winter months (Hashmi 1993; Nelson 2002). However, based upon its limited winter primary productivity (Figure 5.4), this marine area does appear as only marginally attractive in comparison with the North Sea and West Africa.

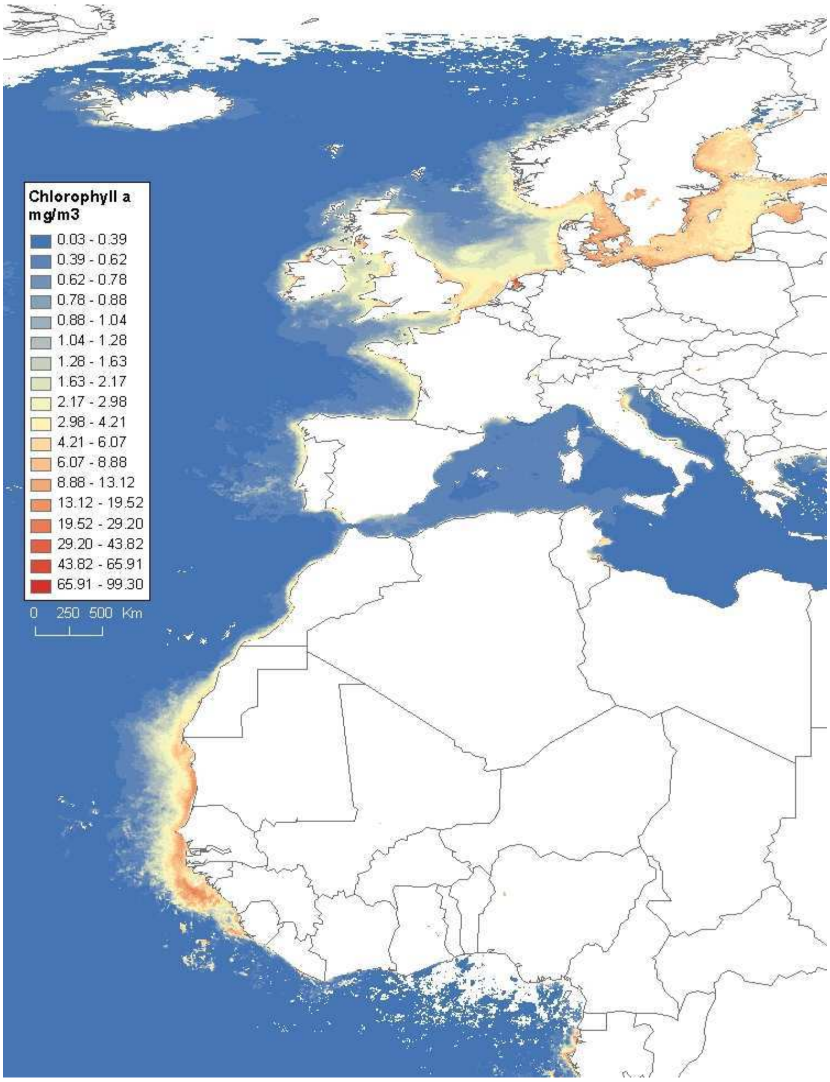

*Figure 5.4 Average winter chlorophyll a concentration. This concentration was calculated for a period ranging from December 21th to March 20th and for the years 2002-2010. These chlorophyll data were based on level 3 data from the MODIS Aqua satellite sensor and downloaded from OceanColorWeb (http://oceancolor.gsfc.nasa.gov). The spatial resolution used was 4 km, and 16-bit satellite readings were converted to chlorophyll concentrations using the equation: Chl (mg/m3) = exp10((0.00005813776*scaledreading)-2).*

The position of commercial fishing boats releasing large amounts of discards at sea might also influence gannets' distribution. Indeed, these discards can represent a large source of food for northern gannets (Votier et al. 2010b). Such relationship between the distribution of fishery discards and wintering northern gannets has already been shown for individuals breeding at UK1 (Kubetzki et al. 2009), and should now be tested for the entire European meta-population.

The distribution patterns observed for each colony were obtained in different years and should therefore be compared carefully. Nevertheless, European Northern gannets from all sites globally share common places during their inter-breeding season located in the Northern Europe and the north-western coasts of Africa. These results are important as they reveal possible exchanges during the inter-breeding season between individuals from different colonies. After being extensively hunted for decades until the end of the twentieth century (Wanless et al. 2005), northern gannets are now in a phase of expansion and recolonization (Nelson 2002). This recolonization phenomenon is clearly visible in Norway where several new settlements were established and a steady increase of breeding birds was observed during the last decades (Montevecchi et al. 1987, Barrett 2008). In this context, Votier et al. (2010a) demonstrated that immature birds can prospect surrounding areas during the breeding season at a scale of up to ~1000km. Here, we show that exchanges of information might also concern birds from very distant colonies (for instance between Norway and UK), with large consequences for these population processes. These results are confirmed by existing ring recoveries which notably identified birds previously breeding in UK, currently breeding in Norway (Barrett 2008).

Beyond the overall bimodal distribution strategy adopted by the European meta-population, differences arose between colonies at smaller spatial scale in the main wintering areas (estimated from 25% kernels analysis). These differences seem to be linked to colonies latitudes, and strongly suggest chain migration (sensu Salomonsen 1955). Indeed, Norwegian birds breeding at higher latitudes were restricted to Northern Europe, whereas those breeding at intermediate latitudes (UK birds) showed a bimodal main distribution between Northern Europe and Northwest Africa, and French birds breeding at lower latitudes were exclusively distributed off Northwest Africa. Previous studies demonstrated that seabirds can travel impressive distances of thousands of kilometres to reach their winter sites (e.g. Egevang et al. 2010, Frederiksen unpublished). It is also the case for Northern gannets which travel to up to 7000 km from their colony after breeding. Nevertheless, the similarity observed between colonies in the average maximum distance travelled from breeding sites (3445 ± 355 km SD; min = 2979 km for FR; max = 3871 km for NO1; see Table 3) suggests that northern gannets might also be limited by distance in their overwintering strategy. This is surprising since, in great contrast to passerines migrating over water, gannets are entirely at home offshore where they can rest and feed *en route*.

Moreover, the bimodal strategy used by UK birds is intriguing and merits further investigations to understand the reason why these birds do not adopt a uniform strategy. Recently, Bogdanova and colleagues showed that black-legged kittiwakes (*Rissa tridactyla*) breeding performance affects their winter distribution and demonstrated that individuals experiencing a breeding failure tend to overwinter in different (farther) places than other birds (Bogdanova et al. 2011). Therefore, the important inter-individual variability observed in UK colonies could be explained by different individual breeding history, and further studies are now necessary to understand the underlying mechanisms of decisions regarding wintering grounds and potential consequences for the population dynamics.

Finally, kernel analyses showed an important spatial segregation during winter between the core-distributions (25% kernels) of UK (UK1 and 2) and French colonies off Northwest Africa. Indeed, in this area, birds from FR were mainly distributed off Morocco, while UK birds showed a common main distribution off Senegal and the Islamic Republic of Mauritania (Figure 5. 2b). Though these segregations are difficult to interpret (the upwelling region off the northwest African coast is expected to hold sufficient resources to avoid inter-individual competition), this result nonetheless confirms the importance to work at meta-population scales rather than restrict studies to populations. Such information might indeed be crucial for studies directly aiming at defining important bird areas at sea, and further conservation actions.

5. Conclusion

Conservation of avian biodiversity is now a priority, with seabirds, the most threatened group of birds in the world, being the first concerned. To this end, it is essential to understand how species are distributed in their environment and how this distribution changes through time, and according to environmental variations. In this context, our study highlighted the main hotspots occupied by wintering European northern gannets. It notably demonstrated that strongly contrasting overwintering strategies can be adopted by seabird species with important variations between colonies, and thereby highlighted the necessity for meta-population studies. Crucially, it confirms that Northern gannet post-breeding movements can certainly not be assimilated to dispersive migration or vagrancy, and that a major Northern gannet flyway exists along the coasts of Western Europe and Africa, from the North Sea to Senegal.

Furthermore, defining factors governing observed animal distribution is also essential in order to understand how species respond to particular environmental conditions and therefore to investigate future impact of environmental changes. However, only a very few recent studies investigated this problematic in wintering seabirds (e.g. Pinet et al. 2011, Fort et al. subm.), and the development of further studies is now required. Additional detailed analyses will be necessary to accurately define the relationship existing between European northern gannets' distribution and the productivity of their environment, but our observations are essential and highlight that information on habitat preference is key to identifying critical areas for marine conservation.

Chapitre 6. Tendances populationnelles et disponibilité alimentaire

Les processus d’acquisition d’énergie tiennent un rôle majeur pour la survie des individus et leur reproduction. A long terme, il est évident que ces processus peuvent influencer les tendances populationnelles si un grand nombre d’individus ne parvient pas à nourrir sa progéniture et si le succès reproducteur est limité par l’accès aux ressources. Dans les chapitres précédents, nous avons étudié la variabilité des comportements de recherche alimentaire des fous de Bassan pendant et en dehors de la période de reproduction et à des échelles spatiales croissantes. Dans un environnement soumis à des variations physiques et biologiques importantes, la plasticité comportementale joue un rôle important dans la capacité des individus à faire face aux changements de distribution et de disponibilité des proies. En hiver, les fous de Bassan peuvent parcourir des milliers de kilomètres pour rejoindre des zones poissonneuses, mais en été, ils sont soumis à une forte contrainte spatio-temporelle pour assurer la survie de leur jeune. Dans ce chapitre, nous avons testé l’hypothèse d’une contrainte de disponibilité alimentaire pour expliquer les tendances populationnelles contrastées observées dans les deux colonies norvégiennes étudiées. Pour ce faire, nous avons analysé la durée des voyages alimentaires et le temps passé par les deux parents au nid et nous avons comparé ces valeurs à celles mesurées dans plusieurs colonies des îles britanniques, ainsi qu’en Manche. Malgré des variations interannuelles, la durée des voyages alimentaires dans les colonies norvégiennes est inférieure ou n’excède pas les valeurs enregistrées dans des colonies britanniques en croissance et de taille similaire. La collecte de régurgitats a montré que les oiseaux norvégiens se nourrissent de grandes proies à forte valeur énergétique. L’alimentation ne semble donc pas expliquer la disparition de plusieurs colonies dans la région des Lofoten depuis la fin des années 90 et l’émigration de nombreux individus vers le nord mise en évidence par les reprises de bagues. D’autres facteurs pourraient expliquer l’effondrement des effectifs et parmi eux, un potentiel dérangement provoqué par une population croissante de pygargues à queue blanche *Haliaeetus albicilla*.

Decreasing trends at Norwegian Northern gannet colonies are independent from food availability during the breeding season

Emeline Pettex, Robert T. Barrett, Svein-Håkon Lorentsen, Francesco Bonadonna, Lorien Pichegru, Jean-Baptiste Pons, David Grémillet.

Abstract:

Norwegian northern gannet populations exhibit contrasted trends at a regional scale and several colony extinctions occurred in recent decades. In an attempt to understand the ecological drivers of such variability, we tested whether resource availability is a factor limiting the current development of gannetries in the Lofoten/Vesterålen area. Between 2007 and 2010, we recorded arrival and departure times of breeding gannets from two 500 km distant colonies showing contrasting population growth rates. We also recorded the duration of joint attendances by gannet parents at the nest, and performed opportunistic diet sampling. Finally we compiled ring recoveries over a 30-year period to assess inter-colony movements. Norwegian gannet parents spent the longest time attending their chick together, and performed the shortest foraging trips. Compared to growing British and French colonies of similar size, the foraging effort adults from the two Norwegian colonies was therefore relatively low, despite annual variations. Gannets ringed as chicks in the Lofoten area, as well as breeders from extinct Lofoten colonies subsequently established in the growing colony close the North Cape, 500km further northeast. Diet samples were mainly composed of large herring, mackerel, saithe, which are prey of relatively high energetic value, and this resource is relatively abundant within the study area. Food availability therefore does not seem to be the limiting factor potentially explaining successive extinctions and re-colonisations of breeding sites in Lofoten/Vesterålen. Further investigations are required to investigate the suspected impact of the growing population of white-tailed eagles *Haliaeetus albicilla* upon colonies of Norwegian northern gannets.

Key words: Northern gannets, foraging effort, population trends

1. Introduction

Seabirds populations from the North East Atlantic have increased since the early 1900s (Grandgeorge et al. 2008), benefiting from protection measures that reduced human hunting and harvesting (Wanless et al. 2005). They probably also benefited from a positive and indirect impact of predatory fish harvest, which reduces competition for prey between the birds and these fish (Tasker et al. 2000), or supplies extra food in the form of fishery discards and offal (Garthe et al. 1996). However, commercial fisheries may also compete with seabirds for small pelagic fish (Furness 2007a). During summer, central place foraging seabirds are constrained to return regularly on land to feed their chick and to attend their nest (Orians & Pearson 1979) and are hence sensitive to low food availability during their breeding cycle.

Seabirds evolved to buffer environmental variability (i.e. the seabird syndrome see Gaston 2004), and foraging ranges can vary between species from tens to hundreds of kilometers from the breeding site (Wanless et al. 1990; Jouventin & Weimerskirch 1990). Local prey depletion can, however, have major consequences on demography and population dynamics of seabirds by altering the breeding success (Frederiksen et al. 2004; Grémillet et al. 2008), adult survival (Harris et al. 1997), recruitment (Oro & Pradel 2000) and emigration (Montevecchi et al. 1987). Whereas negative population trends are often attributed to poor environmental conditions, many other possible factors may lead to seabird colony extinction, such as hunting, human disturbance, pollution or the consequences of climate change.

The northern gannet Morus bassanus is a large, mobile and opportunistic seabird breeding in the North Altantic from Murman Coast in Russia to Québec (Wanless et al. 2006). The world population of gannets rose from 50 000 breeding pairs in the early 20th century (Gurney 1913) to more than 350 000 in 2004 (Birdlife International 2011). In Norway, Northern gannets occurred along the coasts for several millennia, but the species was absent from the region during the last centuries (Montevecchi & Hufthammer 1990). A re-colonization started at Runde, Møre and Romsdal in 1946 (Valeur 1947) and the population subsequently increased rapidly during the next 20 years (rate > 20% per annum) probably assisted by immigration of birds from British and Icelandic colonies (Brun 1972; Moss, Wanless, & Harris 2002; Barrett 2008). Gannets spread northwards and established several colonies along the Norwegian Sea and the Barents Sea coasts (Montevecchi et al. 1987). However, the population dynamic pattern has varied from one region to another, and contrasted trends have been observed in Finnmark and Lofoten/Vesterålen colonies since the 1990s. While the colonies in Troms/Finnmark have continued to increase after their settlement, Lofoten/Vesterålen colonies decreased between 1990 and 2004 with several extinction events.

In this study, we aimed at testing whether resource availability is a limiting factor to the current development of the Norwegian gannetries, and if poor feeding conditions may explain negative population trends in the Lofoten/ Vesterålen area. Previous studies showed a strong positive relationship between foraging trip duration and maximum foraging distance in northern gannets (Hamer et al. 2001). Therefore, following Lewis et al. (2001), we used foraging trip durations as a proxy for foraging effort, and compared this effort for two Norwegian colonies showing contrasted population trends, as well as with those recorded at British, Irish and French colonies. If food availability is a limiting factor to the development of Norwegian gannetries especially in the Lofoten/Vesterålen area, we predicted that: 1) Norwegian gannets would show a higher foraging effort than gannets breeding at more successful colonies of similar size in other European countries. 2) Chick would be left along at the nest more often in Norway than at gannetries of similar size elsewhere in Europe, because food limitation forces paired males and females Norwegian gannets to abandon the nest to forage simultaneously.

2. Materials and methods

2.1 Foraging trip duration and joint attendance

Fieldwork took place at two of the Norwegian gannet colonies between 2007 and 2010, under permits from the Nature Directorate of Norway and from the Counties of Nordland and Finnmark (Figure 6.1): 1) Store Ulvøyholmen (68°51’ N, 14°51’ E) in the Vesterålen archipelago, 2) Storstappen (71°14’ N, 25°30’ E) in the North Cape area. Data were collected during the chick-rearing period in June and July 2007, 2008, 2009 and 2010. At this time of the year, daylight is continuous and gannets were consistently flying from and towards the sea. At each colony, we observed continuously a mean of 20 nests (range 17-24) with chicks (2-5 weeks-old) for periods of 24 hours. We observed the time of departure and arrival of each parent, and deducted the duration of each foraging trip and the amount of time that parents spent together at the nest attending their chick. Grand means of foraging trip duration for each colony were calculated from means for each nest. Using direct observations, we determined that birds returning from foraging trips lasting less than 30 min brought back nest material gathered at sea and did not feed. Trips < 30 min were therefore excluded from the analysis. We also summed the time spent jointly at the nest by parents over 24 hours. One-way ANOVA and post hoc Tukey tests (using Statistica 6.1) were used to measure differences in mean foraging trip duration and joint attendance in Storstappen and Store Ulvøyholmen each year. Trip durations of birds from British, Irish and French colonies were derived from published data (Lewis et al. 2001; Grémillet et al. 2006). We plotted the mean foraging trip duration (in hours) versus the square root of colony size for each site (see Lewis et al. 2001; Grémillet et al. 2006 for details).

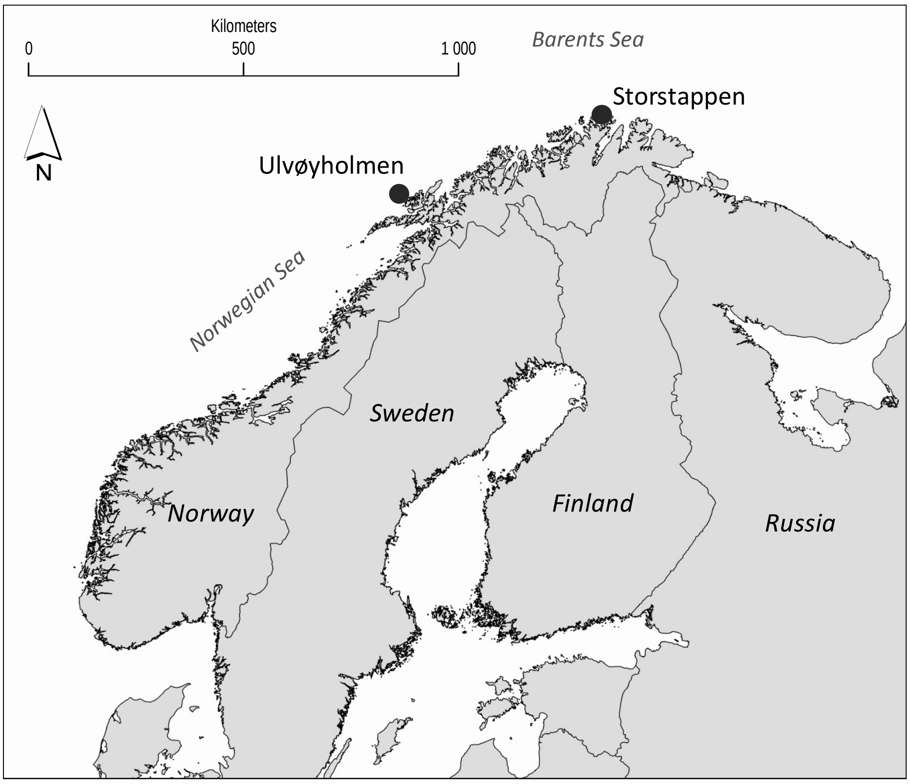

Figure 6.1 Localization of the two studied colonies along the Norwegian coast: Store Ulvøyholmen and Storstappen.

2.2 Diet samples

Diet samples from adults and chicks were collected at the periphery of the colony. When handled, birds often regurgitated spontaneously. In 2007 and 2008, regurgitates were collected and identified in the field when possible. Food remains from 2009 and 2010 were collected individually, stored in a plastic bag, weighed, marked and deep frozen for later analysis. After thawing, a preliminary identification to the lowest possible taxon was performed. Skeletal remains (including vertebrae and heads) were then digested in a saturated solution of biological washing powder (Biotex ©) in an oven at 50° C for at least 24 h. The remaining hard parts (mainly otoliths, vertebrae and pro-otic bullae (characteristic for Herring *Clupea harengus*) in the samples were identified after Härkonen (1986), Watt et al. (1997) and our own reference collection. The taxonomic composition of each load was determined by the estimated mass (%) of each taxon.

2.3 Population censuses and ring recoveries

Northern gannet colonies in Norway were counted at regular intervals (1- 4 years), using different methods according to accessibility and logistical constraints (see Barrett 2008 for details). Data prior to 2008 was gleaned from Montevecchi et al. 1987 and Barrett 2008. Later counts made in Lofoten/Vesterålen followed the same procedures as described in (Barrett, 2008). In the two studied colonies, apparently occupied nests (AON, defined as a site attended by a pair or a single parent where nest material is observed) were also counted either from the ground (Store Ulvøyholmen, 2009 and 2010), or from photographs taken from cliffs above the colony (Storstappen, 2009).

AON numbers were log-transformed to calculate growth rates from the slopes of the regression ln (AON) versus year. We calculated growth rates for the two studied colonies, for all colonies in Norway, for colonies in the Lofoten/Vesterålen area (10 colonies: Hovsflesa, Skarvklakken, Skittenskarvholmen, Store Ulvøyholmen, Utflesøyan, Kvalnesflesa, Fyllingen, Buholmene, Oddskjaeren and L. Forøya) and for colonies in the Troms/Finnmark area (Storstappen, Syltefjord, Kvitvaer). We also used data from gannets ringed as chicks or adults between 1971 and 1999 at Store Ulvøyholmen, Skarvklakken and Hovsflesa (Lofoten/Vesterålen) and at Storstappen (Finnmark). Rings were recorded during visits to the colonies between 1973 and 2009, and the data were used to analyze movements between the colonies.

3. Results

3.1 Foraging trip duration and joint attendance

We recorded arrivals and departures for a total of 154 nests and a total of 426 trips (Table 6.1). Mean foraging trip duration never exceeded 8.3 hours at the two Norwegian colonies. Foraging trip duration at Storstappen increased significantly during survey period (ANOVA: *F3, 73* = 6.14, p < 0.001), and was significantly shorter in 2007 than in 2009 (Tukey, p = 0.012) and 2010 (Tukey, p = 0.001). At Store Ulvøyholmen, mean foraging duration varied among years (ANOVA: *F3, 73* = 3.57, p = 0.018). Trip duration was longer in 2010 than in 2008 (Tukey, p = 0.035) and in 2009 (Tukey, p = 0.043). As Norwegian gannets performed rather short foraging trips, parents often attended their chick together (Table 6.1). The range of the mean time spent together varied from an average of 4 h (Storstappen in 2010) to 11 h (Store Ulvøyholmen in 2008). Joint attendance in Storstappen decreased significantly during the study period (ANOVA: *F3, 72* = 4.71, p = 0.004). Gannets from Storstappen spent significantly more time together in 2007 than in 2009 (Tukey, p = 0.019) and than in 2010 (Tukey, p = 0.004). One-way ANOVA showed no difference in mean joint attendance between years in Store Ulvøyholmen (*F3, 73* = 4.71, p = 0.105), despite the difference in foraging trip duration between years.

Table 6.1 Foraging trip duration and joint attendance at two North Norwegian gannet colonies. Values are presented as means ±s.e.

		Storstappen				Store Ulvøyholmen			
	year	2007	2008	2009	2010	2007	2008	2009	2010
Trip duration (hours)	n	18	20	21	18	21	19	17	20
	mean	3.4 ± 0.4	5.3 ± 0.6	7.2 ± 1.0	8.3 ± 1.1	6.3 ± 0.5	4.5 ± 0.7	4.5 ± 0.5	7.6 ± 1.2
	range	1.1 - 7.8	1.8 - 11.5	2.6 - 23.6	2.0 - 20.1	2.2 - 11.4	1 - 11.9	2.1 - 8.2	0.7 - 18.2
Joint attendance (hours)	n	18	20	20	18	21	18	17	21
	mean	10.3 ± 1.3	6.9 ± 1.1	5.3 ± 1.1	4.3 ± 1.1	7.0 ± 1.0	11.4 ± 1.6	9.6 ± 1.1	9.2 ± 1.3
	range	0.8 - 19.9	0.1 - 15.5	0.2 - 16.9	0.2 - 15.5	0.4 - 19	0.1 - 21.4	0.9 - 16.6	0.2 - 21.5

3.2 Comparison to British and French colonies

Compared to the UK & Ireland sites of equivalent population size (Figure 6.2), mean foraging trip durations from Store Ulvøyholmen gannets were lower in 2008 and 2009, similar in 2007 and slightly higher in 2010. Even though foraging effort increased in Storstappen during the study, only that recorded in 2010 slightly exceeded the British regression line for gannet foraging trip duration versus colony size.

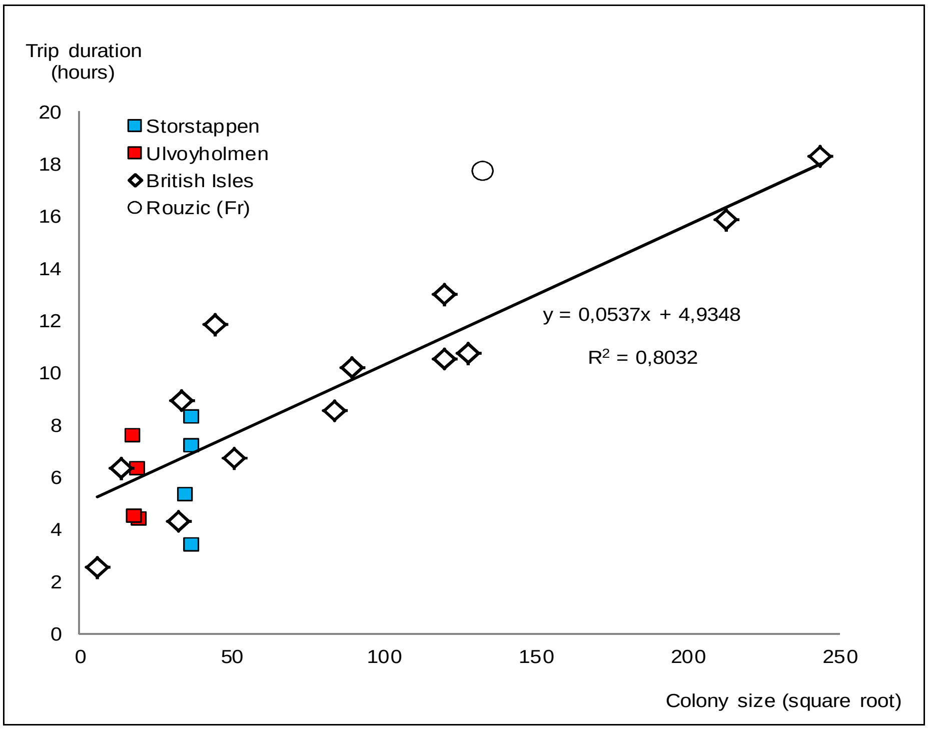

Figure 6.2 Comparison of foraging trip duration in relation with the colony among northern gannet colonies from Norway, British Isles and France.

3.3 Diet samples

Storstappen: In 2007, food samples (N = 24) were composed of 87.5% herring (N = 21) and 12.5% garfish *Belone belone* (N = 3). In 2008, two of the three samples we obtained were herring *Clupea harengus* and one was Atlantic salmon *Salmo salar*. In 2009, the food composition was 92.9% herring and 7.1% gadids (saithe *Pollachius virens* and cod *Gadus morhua*, N=39). Herrings size was between 25-30 cm. In 2010, gannets ate 30.8% herring, 54.2% mackerel *Scomber scombrus*, 12.7% sandeel (Ammodytidae**)**, 1.9% garfish, 0.4% saithe (N=50). Herrings were approximately 10-20 cm long, mackerel 35-40 cm, sand eels 12-16 cm and one saithe 22,5 cm long.

Store Ulvøyholmen: In 2007, the two samples collected were both mackerel. In 2008, four samples were collected, three contained mackerel and one sandeel. In 2009, the diet consisted of 45% saithe, 37% herring, 14% mackerel and 4% sandeel (N=35). At least three of the herring were gravid and contained roe. Herring measured approximately 30-35 cm and saithe ca. 20 cm. One mackerel was whole and was ca 35 cm long.

3.4 Population censuses

The latest counts gave a total of 4721 breeding pairs in Norway in 2008, 1844 pairs in Troms/Finnmark, also in 2008 and 794 pairs in Lofoten/Vesterålen in 2010. The Norwegian population of breeding gannets has increased steadily (Figure 6.3) since the first settlement at Runde in 1946 (Montevecchi et al. 1987; Barrett 2008).

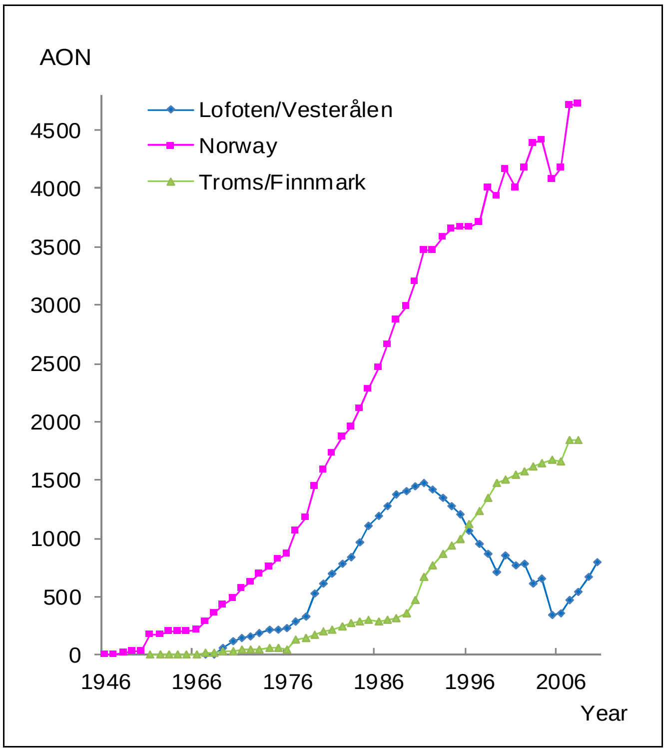

Figure 6.3 Numbers of northern gannets (Apparently Occupied Nests) from Norway (pink line), Lofoten/Vesterålen area (blue line), Troms/Finnmark area (green line).

In the 1960's, gannets moved northwards and colonized several breeding sites in the Lofoten/Vesterålen and Finnmark areas. Until 1971, colonies of both regions increased rapidly (+148% per annum in Lofoten/Vesterålen and +39.3% per annum in Finnmark), before growth slowed to 14.1% and 13% per annum respectively. In 1990-2004, the gannet population in Lofoten/Vesterålen decreased at a rate of 7.8% per annum. Colonies from Finnmark continued their rapid progression until 1997, before slowing down to a growth rate of 2.7% during 1997-2008. The population trend in Lofoten/Vesterålen reversed again in 2005 and increased at 17% per annum until 2010. Both colonies of Storstappen and Store Ulvøyholmen showed the same three-step development pattern (Figure 6.4): 1) an exponential increase in numbers soon after establishment, 2) a period of rapid growth and 3) a stabilization of the growth at Storstappen and a small decrease at Store Ulvøyholmen.

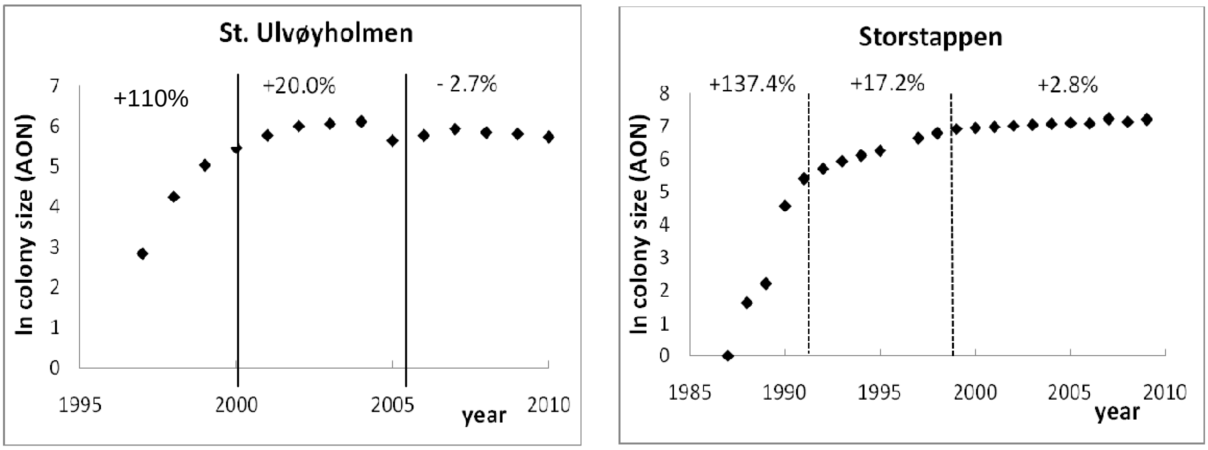

Figure 6.4 Growth rate per annum of two northern gannet colonies (Apparently Occupied Nests) in North Norway

3.5 Ring recoveries

A total of 310 rings were read since 1979 at Storstappen, Skarvklakken, Store Ulvøyholmen and Hovsflesa. At Storstappen, 82 of the 107 (77%) ringed birds were allopatric (Figure 6.5) with 75 (70%) originating from Lofoten/Vesterålen. At Skarvklakken, only four (2%) of the 164 ringed birds were allopatric. All rings found on Store Ulvøyholmen (n=20) were from two extinct colonies in Lofoten/Vesterålen; 12 (60%) were ringed on Hovsflesa and eight (40%) on Skarvklakken. Twelve of the allopatric birds had been ringed as chicks in the UK (including Channel Islands) and Iceland.

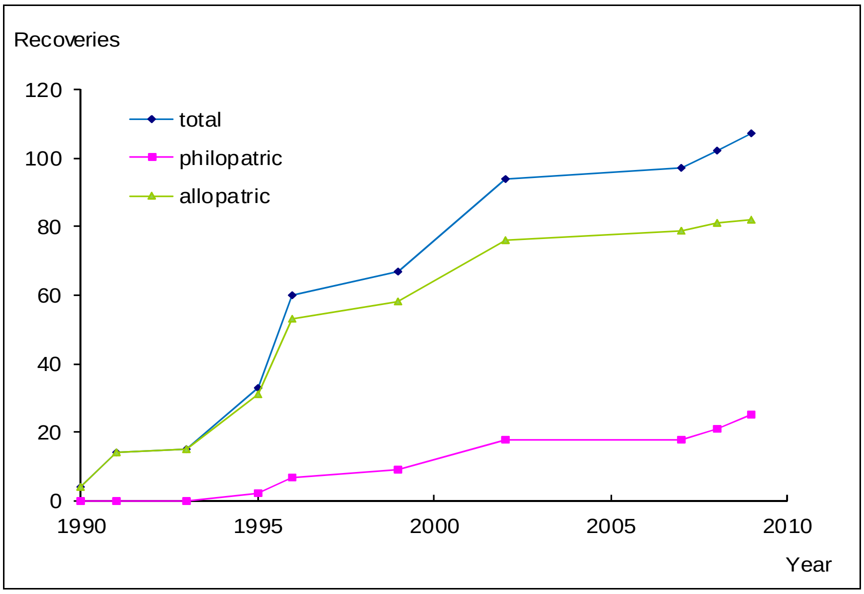

Figure 6.5 Origins of the ringed a northern gannet adults (n=107) caught at Storstappen. Blue line: cumulative total in time, Green line: cumulative number of allopatric birds, Pink: cumulative number of philopatric birds.

4. Discussion

Several studies have shown that limitation of resources can modify the time budget of seabirds through increase in foraging activity and reduction in resting time at the breeding site (Monaghan et al. 1994; Hamer et al. 2000; Litzow & Piatt 2003). However, flexibility in foraging behaviour might not compensate for poor environmental conditions that influence long-term seabird populations through breeding failures (Wanless et al. 2005), higher rates of emigration (Oro et al. 2004) or adult survival (Oro & Furness 2002). Lewis et al. (2006) used behavioural and state variables from five sub-populations of Cape Gannets *Morus capensis* to show the relationship between food availability and growth rates. They demonstrated that these variables were informative to understand extrinsic drivers of population trends. Using the same rationale, our study brings evidence that current population trends in Norway are most probably not driven by limited food availability. This is supported by the, comparatively, short foraging trip durations of Norwegian gannets (Figure 6.2), yet these values must be discussed in the perspective of colony size, to take into account the effect of a potential intraspecific competition (Lewis et al. 2001). Indeed, gannets breeding in larger colonies perform longer trips to feed their chick than parents from smaller colonies. Compared to growing British and French colonies of similar size, the foraging effort adults in both Norwegian colonies was relatively low, despite annual variations (Figure 6.2). This comparison demonstrates that Norwegian gannets did not work any harder than British gannets to find sufficient resources and rear their chick.

Further, joint attendance is considered as a buffer of foraging activity, which varies with food availability (Monaghan et al. 1994). Duration of joint attendance was inversely proportional to foraging trip duration, as illustrated by the constant decrease in joint attendance associated to a constant increase in the foraging trip duration at Storstappen (Table 6.1). Reduction in nest attendance in relation with low environmental conditions has been shown in black-legged kittiwakes *Rissa tridactyla* (Hamer et al. 1993) and common guillemots *Uria aalge* (Zador & Piatt 1999). Norwegian gannets spent hours resting together at the nest and no chick was seen unattended, while in the large colony of Bass Rock (Scotland), breeding parents often leave chicks alone in order to increase foraging duration (Lewis et al. 2004). Long periods of joint attendance in Norwegian gannets might therefore be interpreted as a sign of relatively abundant resources in the vicinity of their breeding sites.

Diet samples collected in this study are qualitative, must be taken carefully, and only serve the purpose of defining broad dietary preferences in Norwegian gannets. Yet they show that gannets from Storstappen mainly consumed large herring, mackerel, saithe, which are prey-items of relatively high energetic value (Hislop, Harris, & Smith 1991). In 2009, birds from Store Ulvøyholmen fed on a mixture of fish, which was similar to the diet of the extinct colonies of Skarvklakken and Hovsflesa in Lofoten in 1985 and 1986 (Montevecchi & Barrett 1987). No diet data are available for the time period when these two colonies started to decline in the early 1990s, but fish stock data from this region (ICES 2009) revealed no changes in saithe and mackerel stocks, and even indicate a strong increase in the total herring stock in the late 1980s and the early 2000s (Figure 6.6). Storstappen and Store Ulvøyholmen are located in the Barents Sea and Norwegian Sea respectively, both of which are among the most productive oceanic waters of the world, that benefit to millions of seabirds (Sakshaug et al. 1994; Barrett et al. 2006). However, overfishing led to a collapse of spawning herrings from western and northern coasts of Norway in the 1960s (Røttingen 1990).

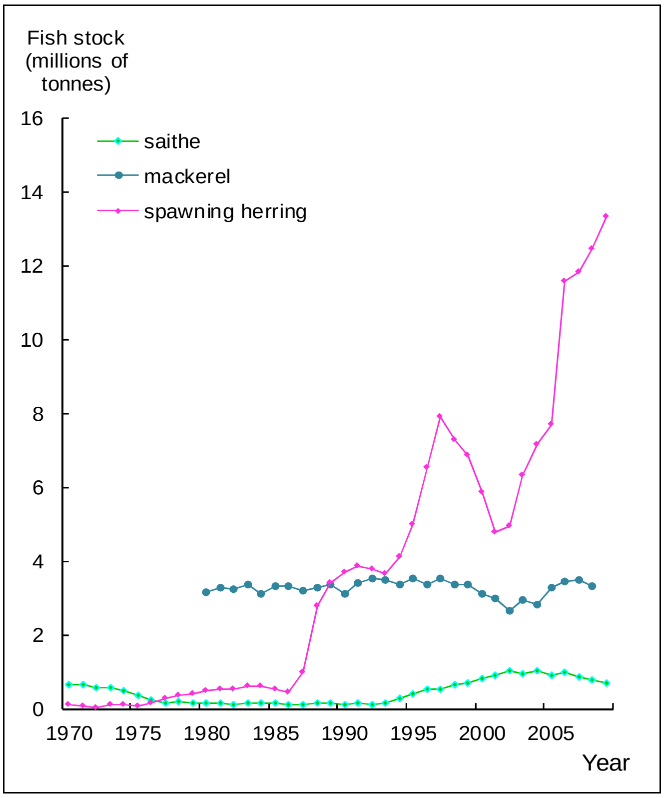

Figure 6.6 Estimates of stock sizes of pelagic fish from the Norwegian and Barents Sea (ICES2009).

Gannets established colonies in the Lofoten/Vesterålen region while herring stocks were very low and one would have expected them to benefit from the recent recovery of the stock (Figure 6.6). Since the first breeding gannets were recorded in 1967 in Lofoten/ Vesterålen, ten colonies were established, of which five have later become extinct and an attempts of re-colonization were observed at Skarvklakken and Fyllingen. The two largest colonies of Hovsflesa and Skarvklakken were flourishing before a sudden reversal of their demographic trend in 1988 and 1990, respectively, and an inexorable decrease until extinction (Figure 6.7a). The establishment and growth of the colony at Storstappen (Fig. 6.7b) was concomitant to the decrease of Hovsflesa and Skarvklakken, and recoveries of ringed adults documented a significant emigration from Lofoten/Vesterålen to Finnmark at this time (Barrett 2008).

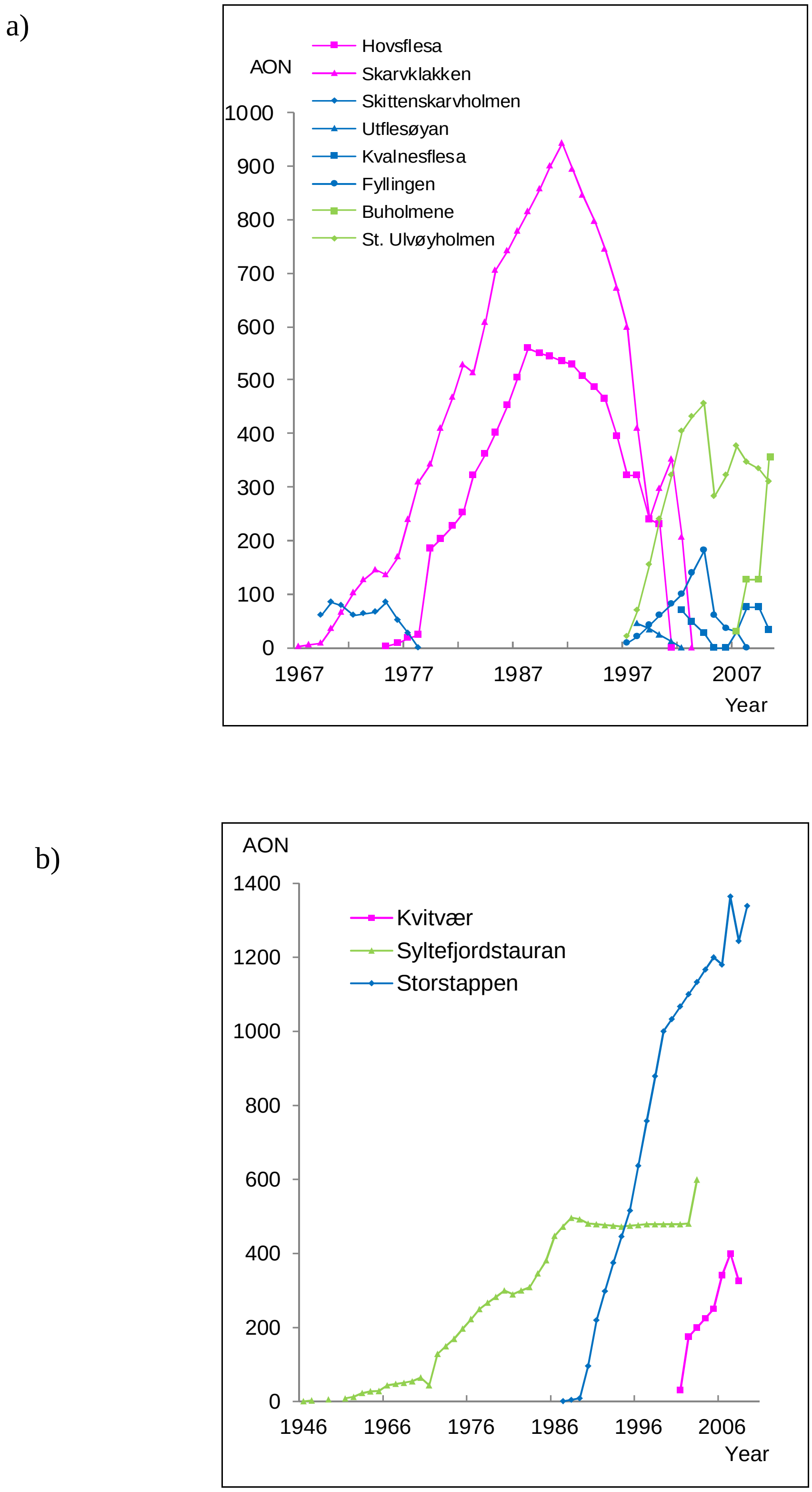

Figure 6.7 Numbers of northern gannets (Apparently Occupied Nests) breeding in North Norway: a) in Lofoten/Vesterålen (pink line: main extinct colonies, blue line: small extinct or nearly extinct colonies, green line: current colonies) b) in Troms/Finnmark.

Store Ulvøyholmen also recruited young breeders ringed as chicks from these two colonies, showing that several tactics of dispersal occurred at declining colonies. The number of breeding pairs on Store Ulvøyholmen keeps decreasing since 2004 despite the foraging effort of breeding parents revealing no real difficulty for parents to provide prey to their chick. Furthermore, a new colony in Buholmene was established in 2007, suggesting local disturbance further north and the need to look for more profitable places to breed.

If food is not a limiting factor for gannets in the Lofoten/Vesterålen area, what generates this dynamic system enough to force gannets from reasonably large colonies to emigrate to new sites (locally or much farther in Finnmark)? Among several factors that could be involved, Barrett (2008) suggested that White-tailed Eagle (*Haliaeetus albicilla*) harassment and predation on adults and/or chicks might have caused the decline in the colonies and forced the gannets to search for new breeding sites. After a dramatic decline during the 20th century, the European white-tailed eagle population has recovered steadily since the late 1960s, thanks to intense protection measures (Hailer et al. 2006). At Røst (Lofoten), common guillemots and black-legged kittiwakes have also been negatively impacted by disturbance by white-tailed eagles (Anker-Nilssen 2006). Their impact on the gannets has not been measured but observations of predation on chicks have been made (Johnsen pers. comm.) and an unprecedented number of adult corpses have been found in the Lofoten/Vesterålen colonies (sensu Barrett, 2008). Parrish, Marvier, & Paine (2001) highlighted negative effects of Bald eagles (*Haliaeetus leucocephalus)* on NW American common guillemot populations, showing the difficulty of managing interacting species, and confirmed the importance of dispersal in the understanding of seabird population trends.

Overall, our study shows that the four studied Norwegian gannets’ colonies are currently not limited by food availability. Our findings therefore strongly suggest that resource availability was not responsible of the decline and the extinction of several gannetries in the Lofoten/Vesterålen area in the 1990s. As food availability is not the only limiting factor to a population development, we confirm that this single proxy is not always useful to explain complex dynamics in populations.

Chapitre 7. Synthèse et perspectives

Les écosystèmes marins sont plus dynamiques que les écosystèmes terrestres (Takahashi, Hargrave, & Parsons 1984) et les divers processus physiques, chimiques et biologiques entrainent des changements rapides des conditions environnementales dont dépendent les prédateurs marins. Ces derniers se sont adaptés aux spécificités du milieu marin au cours du temps et ont développé des traits d'histoire de vie particuliers. Au niveau individuel, cette capacité d'adaptation se traduit entre autres, par une modification des réponses comportementales. Lorsque la distribution ou la disponibilité des ressources varient, les oiseaux marins adaptent leur comportement de recherche alimentaire en fonction des informations dont ils disposent (expérience, information publique, *local enhanceme*nt). Au cours de cette thèse, nous avons étudié les comportements de recherche alimentaire des fous de Bassan à différentes échelles spatio-temporelles afin de déterminer si la flexibilité de ces comportements permet une adaptation à la variabilité environnementale. Les nouvelles techniques télémétriques nous ont permis d'enregistrer les mouvements en mer des fous aussi bien pendant la saison de reproduction que lors de la migration hivernale sur plusieurs saisons consécutives. Les résultats présentés précédemment confirment la flexibilité comportementale de cette espèce, qui s'exprime de manières variées, au niveau individuel comme au niveau populationnel.

1. Les fous utilisent un éventail de réponses comportementales variées

Les oiseaux marins ont développé plusieurs types de réponses comportementales pour parvenir à se nourrir malgré les contraintes spatiales et temporelles qui leur sont imposées. Dans cette thèse, nous avons montré que les fous de Bassan utilisent l'ensemble des stratégies énumérées en introduction pour varier leur réponse comportementale.

1.1 Un régime alimentaire flexible

Les échantillons alimentaires récoltés dans les deux colonies norvégiennes entre 2007 et 2010 varient dans leur composition d'une année sur l'autre et entre les colonies. Les fous de ces deux colonies pêchent des poissons pélagiques, en moyenne de grande taille, principalement des harengs, des maquereaux et du lieu noir (chapitre 6). Les oiseaux des deux sites étudiés disposent apparemment de bonnes conditions alimentaires et s'alimentent sur des proies naturelles de forte valeur énergétique, même si celle-ci varie en fonction de la saison et de la taille des proies (Hislop, Harris, & Smith 1991; Pedersen & Hislop 2001). Les fous de Bassan sont connus pour être particulièrement flexibles dans leur régime alimentaire. Plus de quarante espèces de poissons différentes ont été identifiées dans les bols alimentaires des fous, dans la région de l'est Atlantique (Nelson 2002). En 2007, Montevecchi a mis en évidence des changements de régime alimentaire chez les fous de Bassan après d'importantes modifications de la distribution des proies. A la suite d'une perturbation des températures de surface en 1991, les fous de l'île de Funk (Terre-Neuve) se sont nourris de petits capelans, typiques des eaux froides, en remplacement des grands poissons pélagiques d'eaux chaudes qui composaient leur régime alimentaire dans les années 70-80. De nouveau, au début des années 2000, la diminution des stocks de capelan *Mallotus villosus* a conduit les fous à s'alimenter plus loin en capturant des saumons atlantiques *Salmo salar* (Montevecchi et al. 2009), sans que leur succès reproducteur n'en soit modifié (Chardine 2000). Cette flexibilité dans la taille et le type de proies consommées confère sans doute aux fous un avantage adaptatif dans des systèmes marins perturbés par la surpêche et les changements climatiques (Grémillet & Charmantier 2010).

1.2 Allongement de la durée des voyages alimentaires

Malgré les coûts énergétiques élevés durant la période d'élevage du jeune (Enstipp et al. 2006), les fous peuvent augmenter leur effort de recherche alimentaire en allongeant la durée des voyages (Hamer et al. 2007). Dans les colonies de Store Ulvøyholmen et de Storstappen, la durée moyenne des voyages varie entre les années mais il faut aussi noter que les individus eux-mêmes alternent des voyages de durée parfois très variable (chapitre 4). L'allongement de la durée des voyages alimentaires est associé à l'exploitation de zones d'alimentation plus éloignées de la colonie (Hamer et al. 2000), et cette relation a été vérifiée également dans la colonie de Storstappen. Cependant, les conditions alimentaires favorables permettent aux fous norvégiens de se nourrir à une distance faible de leur site de nidification, sans que la compétition intraspécifique ne soit forte (chapitre 6). La principale conséquence de la proximité des proies, en particulier à Store Ulvøyholmen, est un temps important passé par les deux parents ensemble au nid. En cas de dégradation des conditions environnementales, les oiseaux peuvent utiliser cette réserve de temps pour aller chercher des proies plus loin. Si les fous norvégiens ne semblent pas devoir produire de trop grands efforts pour élever leur jeune, en revanche les oiseaux de Rouzic réalisent des voyages plus longs que ce que la seule compétition intraspécifique laisserait supposer (chapitre 6). Dans la colonie de Bass Rock, les parents laissent leur poussin sans surveillance dans 15 à 20% des voyages alimentaires, dès l'âge de 4 semaines, malgré les risques liés aux attaques de congénères ou au stress thermique (Lewis et al. 2004). Malgré la grande mobilité et la flexibilité comportementale des individus, les populations de fous de Bassan pourraient donc subir les effets d'une diminution de leurs ressources à proximité des colonies comme cela s'est produit pour les fous du Cap *Morus capensis* dont le succès reproducteur s'est effondré à la suite d'un déplacement des proies hors de leur rayon d'action et en raison d'une compétition avec les pêcheries (Pichegru et al. 2007; Pichegru et al. 2010b).

1.3 Exploitation maximale du domaine vital et mémorisation de zones alimentaires

En analysant les voyages alimentaires de plusieurs individus nicheurs dans les deux colonies norvégiennes, nous avons mis en évidence une dualité du comportement de recherche alimentaire au niveau populationnel. Dans les deux colonies étudiées, les oiseaux empruntent des routes privilégiées pour accéder aux sites d'alimentation (chapitre 4). Ces routes semblaient relativement stables pendant la durée de l'étude, malgré le fait que la distance moyenne entre les sites de nourrissage et la colonie ait augmenté entre 2007 et 2009 à Storstappen. Certaines zones étaient exploitées d'une année sur l'autre, signe d'une persistance de la présence des proies (chapitre 4). Pourtant, la fidélité à ces zones de pêche n'empêchait pas les oiseaux d'une colonie de prospecter largement le domaine vital autour de leur site de nidification. Au niveau individuel, l'équilibre entre fidélité aux zones profitables et large prospection est également montré par l'analyse de voyages alimentaires successifs. Les individus font preuve d'une importante plasticité comportementale dans le choix des directions suivies (chapitre 4). Ils peuvent retourner continuellement sur une zone ou alterner entre des zones qu'ils visitent en moyenne deux fois chacune. Il semble probable que les oiseaux retournent sur un site de pêche car ils en ont mémorisé la localisation (Irons 1998). La capacité de retourner directement et rapidement sur une zone poissonneuse permet aux individus d'augmenter leur efficacité prédatrice et de diminuer le coût énergétique lié au vol. Si les animaux sont confrontés à une forte compétition intraspécifique, ces processus cognitifs permettent à l'individu d'améliorer ses performances, mais cela implique une persistance suffisante des patches de nourriture dans des zones localisées et prévisibles (Davoren et al. 2003; Gende & Sigler 2006). L'analyse des trajets alimentaires des fous de Rouzic montre que les oiseaux cherchent à atteindre rapidement des aires d'alimentation dont ils anticipent la localisation (chapitre 3). Les données recueillies dans les colonies norvégiennes confirment cette fidélité au site d'alimentation, probablement liée aux expériences précédentes de l'oiseau (chapitre 4). La fidélité aux sites de recherche alimentaire a été montrée chez de nombreux prédateurs marins (Hamer et al. 2001; Ropert-Coudert et al. 2003; Bradshaw et al. 2004; Call et al. 2008), ce qui confirme que les prédateurs marins ont une perception très fine de leur environnement, et que les ressources marines sont plus prévisibles qu'on ne l'a longtemps supposé (Weimerskirch 2007).

1.4 Une grande mobilité hivernale

A la fin de la période de reproduction, les oiseaux marins sont libérés de la forte contrainte spatio-temporelle du *central place foraging* (approvisionnement depuis un point central). La dégradation des conditions climatiques les conduit à quitter leur colonie pour gagner des zones d'hivernage plus favorables. Là encore, l'étude des mouvements hivernaux à l'échelle méta-populationnelle nous montre la flexibilité comportementale et la mobilité des fous de Bassan (chapitre 5). Les individus suivis ont parcouru plusieurs milliers de kilomètres en moyenne pour regagner les zones d'hivernage où la production primaire est la plus forte. Les oiseaux des cinq colonies étudiées se sont répartis en deux grandes zones : les mers du nord de l'Europe (mer du Nord, Manche, Golfe de Gascogne) et les côtes de l'Afrique de l'Ouest (du Maroc au Sénégal). Les oiseaux d'une même colonie peuvent hiverner dans des sites différents (Kubetzki et al. 2009), cependant nos résultats montrent l'existence de tactiques majoritaires au sein de chaque colonie, qui conduisent à une ségrégation spatiale des colonies pendant l'hiver (chapitre 5). Il est intéressant de noter que cette structuration spatiale de la distribution hivernale semble corrélée au gradient latitudinal des colonies. Les oiseaux des deux colonies norvégiennes hivernent plus au nord que les oiseaux des iles britanniques ou françaises. Toutefois, quelques individus norvégiens ont séjourné le long des côtes sénégalaises. Une limitation de la capacité de migration des fous pourrait être la cause d'une migration en chaine. Le vol battu des fous est coûteux en énergie (Birt-Friesen et al. 1989) et pourrait être un facteur limitant aux mouvements hivernaux, qui restent modestes en comparaison aux dizaines de milliers de kilomètres parcourus par les puffins fuligineux (Shaffer et al. 2003), les puffins cendrés *Calonectris diomedea* (González-Solís et al. 2007) ou les sternes arctiques (Egevang et al. 2010) pendant la période hivernale.

1.5 La capacité d'émigrer

Bien que la philopatrie soit forte chez la plupart des oiseaux marins et qu'elle contribue à un succès reproducteur élevé, l'émigration peut également être une stratégie adaptative en réponse à des ressources insuffisantes (Naves et al. 2006) ou à tout autre facteur qui mettrait la survie des adultes ou leur succès reproducteur en péril (Anderson & Keith 1980; Jones et al. 2008). La disparition de plusieurs colonies dans la région des Lofoten à la fin des années 90, alors que la population globale norvégienne n'a jamais cessé de croître, traduit un dérangement dont la véritable cause est inconnue, bien que nos résultats tendent à éliminer un facteur alimentaire (chapitre 6). Les bagues retrouvées à Store Ulvøyholmen et à Storstappen indiquent une double stratégie d'émigration parmi les oiseaux issus des colonies éteintes (Barrett 2008). Les multiples tentatives de recolonisation de sites dans les Lofoten/Vesterålen indiquent qu'une part des oiseaux cherche d'autres sites de reproduction à proximité de la colonie éteinte, tandis que l'expansion rapide de Storstappen (contemporaine aux extinctions) révèle que les fous peuvent aussi prospecter bien au-delà de leur région d'origine (chapitre 6). Un parallèle intéressant peut être fait avec les fous du Cap du Benguela, une espèce pourtant proche des fous de Bassan, dont les effectifs ont chuté suite à la disparition de leurs proies à proximité des colonies et qui se sont révélés incapables d'émigrer vers d'autres sites de nidification (Crawford 1999).

Les résultats présentés dans cette thèse confirment la forte plasticité des comportements de recherche alimentaire observée chez les fous de Bassan. Nous avons montré que les individus peuvent faire varier plusieurs paramètres de leur recherche alimentaire pour garantir leur efficacité prédatrice. Au niveau populationnel, cette plasticité se traduit par des tactiques alimentaires variables, car dépendantes de paramètres environnementaux qui divergent d'une colonie à l'autre.

2. Conséquences populationnelles de la plasticité comportementale et perspectives de conservation des fous de Bassan

2.1 Le rôle positif de la plasticité comportementale sur la démographie

Parce qu'elle contraint l'accès aux ressources des individus, la variabilité environnementale compte parmi les facteurs qui affectent le plus la croissance et la viabilité des populations

(Soulé 1987; Caughley & Sinclair 1994). Il est généralement admis que le degré de plasticité phénotypique augmente avec le niveau de variabilité de l'environnement (de Jong 1995). La plasticité comportementale est une des composantes de la plasticité phénotypique. Elle présente la particularité d'apporter des réponses immédiates et réversibles aux variations de l'environnement (West-Eberhard 1989). La capacité de survie des populations dans des environnements marins perturbés par les activités humaines est donc fortement liée au degré de plasticité comportementale des individus (Caughley 1994; Halpern et al. 2008). En introduction, nous avons identifié le rôle central des processus d'acquisition d'énergie pour les processus démographiques des populations d'oiseaux marins. L'allocation d'énergie destinée au poussin conditionne le succès reproducteur et par conséquent les tendances démographiques. Bien qu'il varie d'une colonie à l'autre et en fonctions des années, le succès reproducteur des fous de Bassan est particulièrement élevé, surtout si on le compare à celui d'autres espèces d'oiseaux marins telles que les guillemots *Uria aalge* et les mouettes tridactyles *Rissa tridactyla* (Nelson 2002). Pour illustration, dans les colonies de Bass Rock, Ailsa Craig et Bempton, la probabilité d'envol d'un poussin à partir d'un œuf pondu était comprise entre 74 et 78% sur une durée de 5 à 12 ans (Nelson 2002). Nelson attribue ce fort succès reproducteur à l'exploitation d'une niche écologique favorable et à la capacité d'aller se nourrir loin en mer lorsque les proies de prédilection (hareng, lieu, maquereau) diminuent. Les résultats de notre étude montrent que c'est probablement tout l'éventail de comportements alimentaires que les fous ont à leur disposition et leur forte plasticité individuelle qui expliquent ce succès démographique observé depuis un siècle. L'espèce a été longtemps exploitée par les populations humaines pour leur alimentation (Montevecchi & Hufthammer 1990; Wanless, Harris, et al. 2005), au point qu'en 1913, le premier comptage mondial ne faisait état que de 55 000 couples (Gurney 1913). A peine cent ans plus tard, la population a été multipliée par sept par le simple fait de la protection des colonies. Plus de 80% de la population mondiale se concentre entre l'Islande, les Iles Britanniques, la France et la Norvège, ce qui implique que les nouvelles colonies se sont établies et étendues en même temps que le développement industriel de la pêche dans les mers européennes et la dégradation des écosystèmes marins durant le siècle dernier (Halpern et al. 2008). Il est possible que les fous aient tiré profit de la quantité de nourriture apportée par les déchets de pêches (Garthe & Hüppop 1994; Votier et al. 2010b) mais les enregistrements de voyages alimentaires montrent qu'en Manche et en Mer du Nord où les pêcheries sont très actives, les oiseaux se nourrissent également de proies naturelles qu'ils vont chercher à une grande distance des colonies (Grémillet et al. 2006; Hamer et al. 2007). Quoiqu'il en soit, lorsque des individus s'établissent sur un nouveau site de nidification, ils doivent localiser rapidement les zones poissonneuses. Les quelques pionniers ne peuvent bénéficier d'un système d'information publique ou de *local enhancement* pour faciliter leurs recherches de proies et, dans ce cas précis, la plasticité comportementale joue un rôle important dans la viabilité de la nouvelle colonie (Komers 1997). Les tendances démographiques et l'expansion rapide de l'aire de distribution de l'espèce démontrent en tout cas, le succès des stratégies de recherche alimentaire des fous de Bassan. Devant l'apparente aisance des fous à trouver des proies et à se reproduire, on peut se demander pourquoi cette espèce n'élève qu'un unique poussin chaque année. Les expériences d'augmentation artificielle de taille de la couvée ont montré que les parents étaient capables nourrir deux poussins et que ceux-ci présentaient une croissance et un poids à l'envol comparable aux poussins uniques (Nelson 1964). Toutefois, le coût d'élevage d'un autre poussin pourrait avoir une incidence sur la condition corporelle des adultes et à long terme sur leur survie ; un facteur qui aurait pu contraindre la taille de ponte à un œuf unique.

2.2 Implications pour la conservation

La protection des sites de nidification est la condition *sine qua non* pour éviter le dérangement humain et donc pour la conservation des oiseaux marins. Cependant, les prélèvements importants réalisés par les pêcheries peuvent hypothéquer ces mesures préventives si les oiseaux ne parviennent plus à nourrir leurs jeunes. Les fous de Bassan sont suffisamment flexibles pour avoir pu compenser jusqu'à présent la diminution des proies accessibles et la dégradation des écosystèmes marins, mais les projections réalisées par les scientifiques sur l'avenir des stocks de poissons dans leur aire de répartition indiquent que les changements globaux pourraient bien compromettre cette belle réussite. Les fous sont très généralistes dans le choix des proies et peuvent choisir des espèces de substitution. Pourtant, le remplacement des proies peut se révéler néfaste au développement corporel et cognitif des poussins si la valeur nutritive est insuffisante (Batchelor & Ross 1984; Kitaysky et al. 2006), ce qui est le cas des déchets de pêche (Wanless et al. 2005; Grémillet et al. 2008) et on sait que les fous en consomment (Garthe & Hüppop 1994). Une étude récente a même montré une corrélation négative entre la condition corporelle des adultes et la proportion de déchets de pêche chez les fous de Bassan (Votier et al. 2010b).

Une solution existante pour protéger les ressources alimentaires consiste à mettre en place des Aires Marines Protégées (où la pêche est réglementée voire interdite), dans les zones correspondant aux sites d'alimentation des prédateurs marins. Le suivi des voyages alimentaires à l'aide des outils télémétriques (comme les GPS dans notre étude) permet d'identifier les habitats des oiseaux marins et de localiser les zones à protéger (Pichegru et al. 2010a). Ces méthodes permettent d'acquérir des données précises pour l'aide à la décision des gestionnaires, cependant il convient de tenir compte de la variabilité existante au plan individuel, populationnel et temporel. Nos résultats montrent que pour bien analyser les comportements alimentaires et définir les besoins d'une espèce, un nombre minimum d'individus est nécessaire, et que les mesures doivent être réalisées dans plusieurs colonies et sur un nombre d'années suffisant pour intégrer la variabilité environnementale (chapitre 4). Idéalement, il faudrait aussi collecter des données à différents stades de la reproduction (incubation, et tout au long de la croissance des poussins), car les besoins énergétiques varient. A l'exemple des fous de Bassan de Storstappen, on mesure la difficulté liée à la détermination d'un périmètre d'aire protégée pertinent dans le temps. Les fous norvégiens se nourrissent pourtant à une distance relativement faible de leur colonie respective, mais les variations interannuelles observées pourraient rendre caduque le périmètre établi. De plus, il faut considérer que la taille du domaine vital augmente avec celle de la colonie et que par conséquent la protection d'une grande colonie comme celle de Bass Rock entrainerait la mise en place d'une aire protégée très étendue (Pichegru et al. 2009). D'une part, cela pose un problème de moyens financiers et humains nécessaires pour une surveillance efficace de la zone, d'autre part les pertes économiques pour l'industrie de la pêche rendraient la décision politique difficile. Les aires marines protégées sont sans doute plus adaptées pour la conservation d'espèces moins mobiles que les fous (Pichegru et al. 2009).

En revanche, un respect strict des quotas et une gestion des pêches basée sur la dynamique écosystémique (*ecosystem based fishery management* Pikitch et al. 2004) qui intègre, entre autres, la protection et la restauration des habitats et la prise en compte de toutes les espèces non cibles, peuvent apporter des réponses à la préservation des ressources nécessaires aux prédateurs marins. La complexité et la dynamique des réseaux trophiques marins rendent cependant les projections difficiles. Les espèces d'oiseaux marins ne présentent pas toutes la même réponse fonctionnelle aux variations de disponibilité des proies, et certaines espèces dites sensibles vont réagir à des seuils de densité de proies plus élevés que ce que ne suggère leur consommation (Furness 2006). Les fous de Bassan ont la capacité de compenser une diminution de densité de proies que les guillemots de Troïl n'auront pas, par exemple. Ces espèces sensibles peuvent servir de sentinelles pour la définition des limites de biomasse nécessaire à la conservation de l'ensemble des prédateurs supérieurs (Furness 2007b).

3. Limites des méthodes télémétriques et perspectives

Au cours de la thèse, nous avons étudié les comportements de recherche alimentaire des fous de Bassan et les mouvements en mer associés pour comprendre comment les oiseaux marins intègrent la variabilité environnementale et s'y adaptent. Le comportement des fous se caractérise par une flexibilité qui s'exprime aux différentes échelles spatio-temporelles. Le succès démographique de l'espèce indique qu'ils parviennent à répondre aux variations de disponibilité des ressources.

Lors de ce travail, nous avons souhaité pouvoir associer des données sur la distribution des proies et sur leur abondance aux abords des colonies afin de pouvoir mettre en perspective les comportements de recherche alimentaire des fous. Ces données n'existent pas à l'échelle locale et nous n'avons pas pu conduire des études en mer en parallèle. Les travaux existants montrent l'importance de combiner plusieurs méthodes. Les systèmes de monitoring des bateaux de pêche (*Vessel Monitoring System*) apportent des informations sur les efforts de pêche qu'il est pertinent de mettre en relation avec les zones de pêches des oiseaux pour comprendre quel est l'impact de la pêche (Votier et al. 2010b). Connaitre la distribution des proies permet aussi d'estimer la persistance des patches et la variabilité de la disponibilité des ressources (Davoren et al. 2003) ou la capacité des oiseaux à détecter leurs proies à différentes échelles et de mettre en évidence l'efficacité d'évitement des proies ou de prédation des oiseaux (Fauchald et al. 2000; Grémillet et al. 2004). Les méthodes télémétriques ont beaucoup fait progresser les connaissances des comportements en mer des prédateurs marins, mais il est important de pouvoir les associer à d'autres méthodes qui apportent des informations sur les proies et l'efficacité réelle des prédateurs. De nombreuses questions restent encore en suspens en ce qui concerne les comportements alimentaires des oiseaux marins et des fous en particulier, et les perspectives de recherche sont nombreuses.

3.1 A l'échelle individuelle

a) Les mécanismes de localisation des zones d'alimentation

Les fous semblent anticiper la position des zones d'alimentation, mais les mécanismes qui conduisent à la décision de prendre une direction particulière restent inconnus. Les animaux retournent sur des zones de pêche déjà exploitées, ce qui laisse fortement penser qu'ils en ont mémorisé la localisation, mais ils pourraient également utiliser d'autres sources d'information à distance. Au moins trois mécanismes pourraient être testés et comparés chez les fous de Bassan. L'olfaction a été mise en évidence chez plusieurs espèces de Procellariiformes (Nevitt 2008) et Sphéniscidés (Cunningham et al. 2008), mais on ne sait pas si les fous de Bassan utilisent ce type d'information sensorielle à distance. L'information publique a également été testée chez les fous variés *Sula variegata* qui nichent sur les côtes péruviennes, mais sans pouvoir être mise en évidence (Weimerskirch et al. 2010a). Pour mesurer le poids des expériences de pêche précédentes dans le processus décisionnel, il faudrait également tester le lien entre le succès de capture rencontré lors d'un voyage et la direction prise lors du voyage suivant.

b) La connaissance du domaine vital et la variation de l'effort de recherche alimentaire en fonction du stade de reproduction

Il paraît essentiel de comprendre comment les fous appréhendent la richesse de leur domaine vital sur le plan sensoriel mais également cognitif. A ce titre, l'enregistrement de voyages tout au long de la saison de reproduction mettrait en évidence les tactiques exploratoires des fous lorsqu'ils retournent sur leur colonie et au fur et à mesure de la croissance du poussin. La demande énergétique varie aux différents stades et les contraintes aussi sont différentes entre le moment où les parents retournent sur la colonie et doivent s'investir dans la défense du nid, l'incubation, la première phase d'élevage où le poussin n'est pas autonome sur le plan thermique et la dernière période où les parents doivent nourrir un poussin plus gros qu'eux et qui constitue d'importantes réserves de graisse (Nelson 2002).

3.2 Au niveau populationnel et méta-populationnel

a) Les mécanismes d'émigration

La succession d'extinction et de recolonisation de sites dans la région des Lofoten / Vesterålen a mis en évidence les mécanismes d'émigration à petite ou grande échelle et l'existence d'une émigration des adultes déjà reproducteurs (Barrett 2008). Il serait pertinent de déterminer si les pygargues sont effectivement à l'origine des perturbations démographiques dans cette zone et quel est le seuil de tolérance des oiseaux avant de renoncer à se reproduire sur le site. Les pygargues sont également très nombreux à Storstappen, mais ils n'ont pas empêché la croissance rapide de la colonie de fous. Une comparaison de leur impact dans les deux sites permettrait de comprendre les facteurs qui limitent le dérangement à Storstappen.

b) La détermination des zones d'hivernage

Notre étude a mise en évidence une ségrégation spatiale entre les différentes colonies étudiées. Toutefois, au sein de chaque colonie, différentes zones d'hivernage sont exploitées et certains individus choisissent d'hiverner dans des sites différents que celui utilisé majoritairement par les oiseaux de la même colonie. Les premiers résultats laissent à penser qu'un gradient latitudinal régit les mouvements hivernaux chez les fous de Bassan. Il serait important de savoir quel mécanisme intervient au niveau individuel dans le choix de l'aire d'hivernage et quel mode de transmission intervient (vertical ou transversal). Nous avons vu que les colonies norvégiennes se sont développées grâce au recrutement d'oiseaux provenant de colonies britanniques et islandaises. Il paraît nécessaire de tester si l'origine des oiseaux peut influencer les mouvements hivernaux et l'existence éventuelle d'une culture coloniale dans le choix des aires d'hivernage.

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Résumé

L’environnement marin est soumis à un ensemble de processus physiques, chimiques et biologiques qui le rendent très dynamique. Les prédateurs tels que les oiseaux marins doivent donc ajuster leurs mouvements aux changements de disponibilité de leurs proies afin de survivre et de se reproduire. L’évolution de leur plasticité comportementale se traduit par la mise en place d’un éventail de tactiques de prédation. Nous avons étudié les comportements de recherche alimentaire chez le fou de Bassan *Morus bassanus* en Atlantique nord afin d’évaluer l’ampleur de leur plasticité comportementale au cours de leurs mouvements en mer. Ces analyses basées sur les enregistrements d’appareils électroniques miniaturisés portés par les oiseaux (GPS et géolocateurs) ont été effectuées à cinq échelles spatio-temporelles : individuelle, populationnelle, meta-populationnelle, saisonnière et interannuelle. La plasticité individuelle est forte et se traduit, principalement par le biais d’une modulation de la durée des voyages en mer et des zones d’alimentation exploitées. Ceci sous-entend une mémorisation de la position des zones de nourrissage les plus profitables et de leur variabilité spatio-temporelle ; postulat confirmé par nos analyses qui indiquent que les fous anticipent la position de leur aire de nourrissage dans les premiers kilomètres de leur voyage en mer, alors que celle-ci n’est pas encore en vue. Nous avons également identifié des différences inter-populationnelles notoires pour les mouvements en mer et pour les domaines vitaux des fous pendant la saison de reproduction, mais aussi pendant la période hivernale. A l’automne et au printemps, nos analyses nous ont en outre permis d’identifier un corridor migratoire emprunté par les fous entre les Shetland et l’Afrique de l’Ouest, alors qu’on considère généralement que cette espèce présente une dispersion non-orientée en dehors de la saison de reproduction. L’ensemble de nos résultats ont des implications majeures pour une meilleure compréhension de l’écologie spatiale des prédateurs marins confrontés à la variabilité naturelle et anthropique de leur environnement, ainsi que pour la gestion de leurs populations et la mise en place d’aires marines protégées ou de mesures conservatoires ajustées aux dynamiques spatio-temporelles.

Abstract

Physical, chemical and biological processes generate considerable variability in the distribution and abundance of marine organisms. In order to survive and successfully breed, marine predators, among them seabirds, must adjust their movements to changes in the availability of their prey. We studied the foraging behaviour of the northern gannet *Morus bassanus* in several European colonies to understand how a flexible predator manages environmental variability. We analysed records from miniaturized data loggers (GPS and geolocators) at five spatio-temporal scales: individual, populational, meta-populational, seasonal and inter-annual. These data revealed strong individual plasticity, which allows gannets to modulate the length and duration of their foraging trips and to exploit a panel of memorized feeding areas, for which they anticipate location from a distance. We identified differences in the movements at sea and in home range between colonies during the breeding and the interbreeding seasons. Although gannets were thought to follow a non-oriented dispersion during the interbreeding season; our results showed a clear migratory corridor from Shetland to the West African coast. These results have major implications for a better comprehension of spatial ecology of marine predators facing natural and anthropogenic variability of their environment, as well as for population management, the implementation of marine protected areas, and any conservation measures which depend on spatio-temporal dynamics.