

Aus dem Forschungs- und Technologiezentrum Westküste
der Christian-Albrechts-Universität zu Kiel

Habitat selection and foraging ecology of seabirds in the Gulf of St. Lawrence

Dissertation

zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

Nils Guse

Kiel, April 2013

Erster Gutachter: PD Dr. Stefan Garthe

Zweiter Gutachter: Prof. Dr. Hans-Rudolf Bork

Tag der mündlichen Prüfung: 29.05.2013

Zum Druck genehmigt Kiel, 29.05.2013

Der Dekan

Contents

Contents

Summary	1
Zusammenfassung.....	3
General Introduction & Methods.....	5
Chapter 1: Distribution of seabirds and cetaceans in the Lower Estuary and Gulf of St. Lawrence during summer	11
Chapter 2: The influence of colony location and oceanography on seabird distribution in the Lower Estuary and Gulf of St. Lawrence during summer.....	59
Chapter 3: The influence of marine mammals on the distribution of Northern Gannets in the Lower Estuary and Gulf of St. Lawrence during summer.....	93
Chapter 4: The Daily Catch: Flight altitude and diving behaviour of Northern Gannets feeding on Atlantic Mackerel	113
General Discussion & Conclusions	127
References.....	136
Description of the individual scientific contributions to multiple-author papers.....	150
Danksagung/Acknowledgements.....	152
Erklärung	154

Summary

The Lower Estuary and Gulf of St. Lawrence in the Northwest Atlantic Ocean host a highly productive marine ecosystem which represents a hotspot for seabirds, marine mammals and other marine megafauna. This thesis fills important gaps regarding the at-sea distribution, habitat selection and foraging ecology of seabirds. Moreover, the study area is subjected to intensive and increasing anthropogenic utilization. Thus, the present study can serve as baseline information on seabird habitat requirements. These can be incorporated into marine spatial planning applications such as the designation of Marine Protected Areas (MPAs). The spatial and behavioural analyses conducted in this thesis are based on standardized ship-based surveys with simultaneous oceanographic sampling and the equipment of breeding birds with data loggers.

This thesis supplies new comprehensive information on recent at-sea distribution and abundance of the most common seabirds and cetaceans during summer. Northern Gannets have one of their most important breeding areas worldwide in these waters. This was reflected by our investigations. Gannets proved to be most abundant and occurred widespread in the entire study area, followed by Wilson's Storm-Petrels, Common Murres, Northern Fulmars, Razorbills and Blacklegged Kittiwakes. Estimated at-sea totals for the Southern Gulf proved regional and international importance. In Gannets these comprised up to 150,000 birds in mid- and 140,000 in late summer equivalent to 47% - 75% of the Canadian breeding population. With regard to the latter, the Southern Gulf also held significant at-sea totals of Razorbills, Common Murres, Black-legged Kittiwakes and Black Guillemots. Significant proportions at sea were also estimated for Herring Gulls, Great Black-backed Gulls and Common Loons relative to their biogeographic population.

This thesis revealed and confirmed important multispecies hotspots around the Gaspé Peninsula, in the Northwestern Gulf, along the Lower North Shore and west coast of Newfoundland, in Cabot Strait, around Cape Breton Island and the Magdalen Islands and west and east of Prince Edward Island. Importantly, new insights into the links between seabirds and these habitats could be gained by spatial modeling at a coarse to mesoscale. The influence of colony location as spatial constraint on distribution of breeding birds was investigated using generalized additive models (GAMs). Water mass indicators and primary productivity, as proxies for suitable foraging habitat, were additional analyzed predictors. Models for Common Murres, Herring Gulls and Northern Fulmars gained the best results. Besides distance to colony or land, sea surface salinity proved the largest influence on seabird distribution and abundance. Common Murres, Razorbills and Northern Fulmars were associated with waters of higher sea surface salinity, Herring and Great Black-backed Gulls on the opposite with lesser saline waters. The modeled ranges relative to distance to colony strongly corresponded to foraging ranges of breeding birds gained e.g. with GPS data loggers in other studies.

The Northern Gannet was selected as a focal species due to its importance in these waters. This enabled gaining new detailed information on its foraging behaviour. A substantial proportion of Gannets (21.6%, n=3,452 ind.) showed foraging behaviour related to natural phenomena. Most of

Summary

these birds occurred in groups associated with multi-species feeding associations (MSFAs) and/or marine mammals (15% of all). Cetaceans and particularly dolphins were main producers in natural feeding associations. On the opposite, Gannets were hardly associated with fishing vessels. They exhibited a very close spatial association with cetaceans and 25% of them occurred within 0.3km and 50% within 2.9km (=median distance, $n=8766$, 20km radius) to the nearest cetacean. This relationship was also supported by spatial modeling (GAM). Cetacean abundance had the strongest effect on Gannet abundance of all predictors investigated. These results underline the importance of local enhancement of prey for the foraging of Northern Gannets. Cetaceans may concentrate and keep elusive prey such as pelagic fish in water depths within reach of plunge-diving Gannets. This may be particularly important during reproduction when energetic demands are high. This study focused further on the foraging behaviour of parental Gannets from the largest colony at Bonaventure Island using data loggers during a period when birds almost exclusively fed on Atlantic Mackerel. The associated dives were short (mean duration: 6.3s), high speed (up to $194\text{km}\cdot\text{h}^{-1}$) and shallow (mean depth: 4.2m; maximum: 9.2m). Most plunge-dives were initiated at flight altitudes of 11-60m. Almost all dives were V-shaped, suggesting a high speed attack to be the most efficient strategy for Gannets when feeding on large and fast-swimming prey such as Mackerel. The latter was probably well available and trapped in water depths exploited by Gannets due to its thermal preferences and thermocline depth.

The present study supplies new and valuable general information on distribution and habitat selection for a wide range of species. Moreover, it improves our knowledge on details of the foraging behaviour of Northern Gannets. However, the study area is most likely undergoing severe changes with regard to ocean climate and food web structure with accompanied deterioration of breeding success of Northern Gannets. Thus, further in depth studies on the foraging ecology of breeding seabird species using integrated approaches are highly recommended. These should comprise simultaneous equipment of selected seabird species with data loggers alongside with ship-based surveys, oceanographic and hydroacoustic sampling. These could supply vital information on possible ecosystem perturbations affecting all trophic levels, including commercially important species.

Zusammenfassung

Der St. Lorenzgolf und das Untere Ästuar des St. Lorenz-Stromes im Nordwestatlantik, Kanada, beherbergen ein hoch produktives marines Ökosystem, welches einen Hotspot für Seevögel, Meeressäuger und andere marine Megafauna darstellt. Diese Doktorarbeit füllt wichtige Wissenslücken in Bezug zur Verbreitung, Habitatwahl und Nahrungsökologie von Seevögeln auf dem Meer. Das Untersuchungsgebiet ist zudem durch intensive und zunehmende menschliche Nutzung beeinflusst. Daher kann diese Studie Grundlageninformationen hinsichtlich der Habitatanforderungen von Seevögeln liefern. Diese können für Raumplanungen auf dem Meer wie z.B. die Ausweisung von Meeresschutzgebieten (MPAs) berücksichtigt werden. Die Analysen von räumlicher Verbreitung und Verhalten in dieser Studie basieren auf standardisierten schiffsgestützten Erfassungen mit gleichzeitiger meereskundlicher Beprobung sowie der Ausrüstung von Brutvögeln mit Datenloggern.

Die vorliegende Arbeit liefert neue umfassende Informationen zur aktuellen Verbreitung und Abundanz der häufigsten Seevögel und Wale während des Sommers. Basstölpel haben hier eines der weltweit wichtigsten Brutgebiete. Dieses spiegelte sich auch in den Untersuchungen wider. Basstölpel waren insgesamt am häufigsten und kamen weit verbreitet vor, gefolgt von Buntfuß-Sturmschwalben, Trottellummen, Eissturmvögeln, Tordalken und Dreizehenmöwen. Hochgerechete Seevogelbestände für den Südlichen Golf betonten dessen regionale und internationale Bedeutung. Bei Basstölpeln umfassten die Bestände bis zu 150.000 Vögel im Hoch- und 140.000 im Spätsommer, was 47% - 75% der kanadischen Brutpopulation entspricht. In Bezug auf Letztere konnten ebenfalls erhebliche Bestände von Tordalken, Trottellummen, Dreizehenmöwen und Gryllteisten im Südlichen Golf gefunden werden. Weitere erhebliche Bestände auf See in Bezug zur biogeografischen Population wurden für Silbermöwen, Mantelmöwen und Eistaucher gefunden.

Diese Doktorarbeit zeigte und bestätigte wichtige Hotspots für viele Arten um die Gaspé-Halbinsel herum, im nordwestlichen Golf, entlang des unteren Abschnitts der Nordküste des Golfs und der Westküste Neufundlands, in der Cabot-Straße, um die Kap-Breton-Insel und die Magdalenen-Inseln herum, sowie westlich und östlich der Prinz-Edward-Insel. Zudem konnten mit Hilfe räumlicher Modelle neue Einblicke in die Habitatbindungen von Seevögeln auf der Mesoskala gewonnen werden. Mit diesen Habitatmodellen (generalisierte additive Modelle=GAMs) wurde der Einfluss des Koloniestandortes als räumliche Begrenzung für Brutvögel untersucht. Wassermassenindikatoren und Primärproduktion wurden als Einflusswerte stellvertretend für geeignete Nahrungshabitate analysiert. Die Modelle für Trottellummen, Silbermöwen und Eissturmvögel lieferten die besten Resultate. Neben der Kolonie- oder Landentfernung zeigte die Salinität an der Meeroberfläche den größten Einfluss. Trottellummen, Tordalken und Eissturmvögel waren mit Gebieten höherer Salinität assoziiert, Silber- und Mantelmöwen dagegen mit Gebieten niedrigerer Salinität. Die modellierten Reichweiten in Bezug zur Kolonieentfernung ähnelten stark bekannten Reichweiten von Nahrungsflügen von Brutvögeln, die z.B. anhand von GPS-Datenlogger-Studien gewonnen wurden.

Zusammenfassung

Wegen seiner hohen Bedeutung im Untersuchungsgebiet wurde der Basstölpel zur Fokusart bestimmt. Dies ermöglichte, neue detaillierte Informationen zu dessen Nahrungssuche zu gewinnen. Ein erheblicher Anteil aller Basstölpel (21,6%; n=3.452 Ind.) zeigte Nahrungssuchverhalten im Zusammenhang mit natürlichen Phänomenen. Die meisten dieser Vögel (15% von allen) kamen in Gruppen vor und waren mit Multispezies-Fressgemeinschaften (MSFAs) und/oder Meeressäugern assoziiert. Wale und insbesondere Delfine gehörten zu den wichtigsten Produzenten dieser natürlichen Fressgemeinschaften. Im Gegensatz dazu waren Basstölpel kaum mit Fischereifahrzeugen assoziiert. Basstölpel zeigten einen sehr engen räumlichen Zusammenhang mit Walen und 25% von ihnen kamen in Entfernungen von 0,3km und 50% von 2,9km (=Median der Distanz, n=8.766, 20km Radius) zum nächsten Wal vor. Diese Beziehung wurde auch mit Hilfe eines räumlichen Modells (GAM) belegt. Die Walabundanz zeigte den größten Effekt auf die Basstölpelabundanz von allen untersuchten Einflusswerten. Diese Ergebnisse betonen die Bedeutung von lokaler Anreicherung (engl.: *local enhancement*) von Beuteorganismen für die Nahrungssuche von Basstölpeln. Durch Treibjagden können Wale flüchtige Beute wie pelagische Fische konzentrieren und in Wassertiefen halten, die von sturztauchenden Basstölpeln erreicht werden können. Dieses scheint insbesondere während der Brutzeit von Bedeutung zu sein, wenn die energetische Belastung hoch ist. Die Study befasste sich eingehender mit dem Nahrungssuchverhalten brütender Basstölpel der größten Kolonie (Bonaventure-Insel); in einer Periode, in der nahezu ausschließlich Makrelen erbeutet wurden. Die Analyse basierte auf Datenloggern. Die entsprechenden Tauchgänge waren kurz (Mittlere Dauer: 6,3Sek.), sehr schnell (bis zu 194km*h⁻¹) und flach (Mittlere Tiefe: 4.2m; Maximum: 9.2m) und die meisten Sturztauchgänge wurden in Flughöhen von 11-60m begonnen. Nahezu alle Tauchgänge zeigten ein V-Profil was nahelegt, dass ein Hochgeschwindigkeitsangriff die effektivste Strategie für Basstölpel ist, wenn sie große und schnell schwimmende Beute wie Makrelen erbeuten wollen. Letztere waren vermutlich gut verfügbar und wegen ihrer Temperaturpräferenz und der Tiefe der Thermokline gefangen in Wassertiefen, die von Basstölpeln erreicht werden.

Die vorliegende Studie liefert neue und wertvolle generelle Informationen zur Verbreitung und Habitatwahl für eine Vielzahl von Arten. Darüber hinaus verbessert sie unser Wissen über Details des Nahrungssuchverhaltens von Basstölpeln. Jedoch ist das Untersuchungsgebiet höchstwahrscheinlich aktuell von tiefgreifenden Veränderungen hinsichtlich des Ozeanklimas und der Struktur des Nahrungsnetzes betroffen, die mit einem sinkenden Bruterfolg von Basstölpeln einhergehen. Daher werden weitere detaillierte Studien der Nahrungsökologie von brütenden Seevogelarten mit integrierten Forschungsansätzen dringend empfohlen. Diese sollten die Ausrüstung von ausgewählten Seevogelarten mit Datenloggern umfassen und gleichzeitig mit schiffsgestützten Erfassungen inklusive ozeanografischer und hydroakustischer Beprobung durchgeführt werden. Solche Ansätze könnten essentielle Informationen zu möglichen Ökosystemstörungen liefern, die alle trophischen Stufen inklusive kommerziell wichtiger Arten betreffen.

General Introduction & Methods

Seabird ecology and its value for the marine environment

Seabirds have evolved to live in a very dynamic environment. The world's oceans, seas and estuaries are subjected to permanent change on very different scales. In this habitat mosaic, seabirds forage at varying levels of the food web but many species belong to the top predators in marine ecosystems and prey on pelagic fish and squid (Montevecchi 1993). They share this role with marine mammals, predatory fishes and humans. The survival of seabirds depends on finding sufficient prey, which often is patchily distributed in space and time (Longhurst & Pauly 1987). Thus, they have developed mechanisms to locate areas where prey likely aggregates (e.g. Davoren et al. 2010) and might be predictably available in space and time. Often they are attracted to certain bathymetric features (e.g. (Hunt et al. 1998, 1999), such as reefs or banks (e.g. Stevick et al. 2008), where prey might be abundant. Oceanographic phenomena such as upwelling (e.g. Ballance et al. 2006, Sydeman et al. 2006) or fronts (Schneider et al. 1987) have also shown to attract seabirds, as prey concentrates in these areas creating distinct hotspots of top predators. Hence, the distribution of seabirds in general has been successfully linked to oceanographic variables such as chlorophyll *a* as proxy for primary productivity (e.g. Bost et al. 2009, Scott et al. 2010) or sea surface salinity or temperature as indicators of certain water masses (e.g. Garthe 1997, Markones 2007). In addition, many seabird species have shown to respond opportunistically to processes that facilitate access to prey on a finer scale. Such mechanisms comprise anthropogenic activities such as fishing (Furness & Monaghan 1987) and discarding (e.g. Camphuysen et al. 1995, Garthe et al. 1996) or natural feeding associations, which might be evoked by other seabirds, fishes or marine mammals (e.g. Camphuysen & Webb 1999, Camphuysen 2011).

A high foraging efficiency is particularly important for parental birds, as these have to provision their offspring alongside with themselves (Orians & Pearson 1979). The related high energetic demands and constraints birds are confronted with during reproduction are severe (Stearns 1992). One aspect regarding spatial constraints is the necessity to regularly return to the nest site to share parental duties such as incubation or delivering food to the young and defending the nest site (e.g. Daunt et al. 2002). And, as most seabirds are colonial breeders and central place foragers during this period (Orians & Pearson 1979), they experience both the advantages and disadvantages of interactions with their conspecifics. Advantages comprise for example the reduced risk of predation and cues to locate profitable foraging grounds by watching conspecifics (e.g. Camphuysen 2011). Disadvantages comprise the competition for the most attractive breeding sites and food, which can result in longer foraging trips in larger colonies (e.g. Lewis et al. 2001, (Garthe et al. 2007a). The latter might be a consequence of the disturbance and resultant avoidance response of prey (e.g. Lewis et al. 2001, Camphuysen 2011). Belonging to the upper trophic levels, seabirds integrate processes at lower trophic levels and have been shown to respond to changes in oceanography and food webs (e.g. Gaston et al. 2009). In addition, seabirds are conspicuous, numerous and often relatively easy to access at their breeding sites. These features make them excellent sentinel organisms for the marine

environment (e.g. Cairns 1987, Furness & Greenwood 1993, Gaston et al. 2009). Thus, their role in monitoring and management (e.g. Boyd et al. 2006) reaches far beyond the study of seabirds themselves and they supply information, which is for example used in ecosystem-based management of fisheries (Einoder 2009). In addition, the world's oceans are subjected to severe and increasing climatic and anthropogenic pressures (e.g. Derraik 2002, Schreiber & Burger 2002, Parmesan 2006, Mendel 2012). The latter encompasses shipping, recreational use of coastal habitats, fishing and mariculture, hydrocarbon exploration and production, oiling, sand and gravel extraction, construction and maintenance of offshore wind farms and tidal power stations as well as various sources of pollution (e.g. Coe & Rogers 1997, Melvin & Parrish 2001, Derraik 2002, Schreiber & Burger 2002, Mendel 2012). Many of these factors alone or in combination with the others have the potential to severely affect not only seabirds but whole marine ecosystems (Gaston et al. 2009). A holistic analysis of these factors is so far lacking and seems hardly achievable. Even cumulative perspectives on single factors are rare (e.g. Busch et al. 2012), despite being crucial to properly assess the influence of climatic and human induced changes.

Moreover, seabirds themselves are organisms of conservation concern and currently represent the most threatened group of all bird species, with 47% of the species known or suspected to be in decline and 28% to be in the highest categories of risk (www.birdlife.org/action/science/species/seabirds/index.html). Particularly, the expansion of long-line fishing with associated by-catch of seabirds and the introduction of invasive alien species at seabird colonies are key threats (www.birdlife.org/action/science/species/seabirds/index.html). Moreover, seabirds have proved to be successfully used to designate Marine Protected Areas (MPAs) (e.g. Garthe et al. 2012, Lascelles et al. 2012). These could benefit a multitude of marine habitats and organisms and enable a more sustainable use of marine resources in addition to the protection of seabirds as monitors of ocean health. Thus, current and updated knowledge and monitoring of distribution, hotspots and links between seabirds and their marine environment are vital information required for various applications regarding current and future marine spatial planning (e.g. Hyrenbach et al. 2000, Schwemmer et al. 2011).

Study rationale & objectives

Having outlined the general aspects of seabird ecology and their scientific and practical value for studying the marine environment, I now concentrate on the objectives of my study and therefore, briefly introduce the study area, study species and applied methods. My approach combined different levels and methods of study. First general distributional patterns and links with the marine environment for a range of the most common seabird species in the study area (see below) are analyzed. Then the study concentrates on one focal species where relevant processes and foraging behaviour are investigated in more detail.

The study area is the Lower Estuary and Gulf of St. Lawrence on the east coast of Canada. It is a semi-enclosed shelf sea which constitutes one of the world's richest estuarine and marine habitats with regard to primary productivity, abundance of crustaceans, fishes, seabirds and marine mammals (White & Johns 1997, Dufour & Ouellet 2007, for details see Chapter 2). It features unique hydrographic and bathymetric traits and its ecosystem is markedly influenced by oceanic and climatic variation of the North Atlantic Ocean. This variation is influenced by the Labrador Current (Arctic influence) and by the Gulf Stream (Tropical influence, Dufour & Ouellet 2007). The study area is known to hold significant breeding colonies of Northern Gannets (*Morus bassanus*), Black-legged Kittiwakes (*Rissa tridactyla*) and several alcid species such as Razorbills (*Alca torda*), Common Murres (*Uria aalge*) and Black Guillemots (*Cepphus grylle*) (Cairns et al. 1991, Fifield et al. 2009). In these, as well as in adjacent waters, seabirds have been intensively surveyed with ship-based censuses within the PIROP (Programme intégré de recherches sur les oiseaux pélagiques) framework (Brown 1986, Brown et al. 1975). These efforts were mostly confined to the 1970s and 1980s, with little effort in the 1990s and an almost complete lack of surveys thereafter. In the adjacent waters of the Atlantic Provinces however, the censuses were restarted in 2005 within the Eastern Canadian Seabirds at Sea (ECSAS) program (Fifield et al. 2009) and new surveys were also intended for Québec waters (F. Bolduc CWS pers. comm.), but not yet started. We addressed this gap in Chapter 1 by answering the following question:

1) How are common seabird species and cetaceans distributed in the study area during summer and what is the significance of this site?

Most seabird studies in this area were related to colony based investigations on breeding ecology, population sizes and diet (e.g. Chapdelaine & Brousseau 1996, Chapdelaine & Rail 1997, Rail & Chapdelaine 1998). More recently, the foraging ecology of breeding Northern Gannets from on Bonaventure Island was studied with bird-borne data loggers (e.g. Garthe et al. 2007a). Such bird-borne devices have evolved quickly and are increasingly used to study flight and foraging behaviour (e.g. Garthe et al. 2000, Grémillet et al. 2004), simultaneously measuring physical variables of the marine environment (e.g. Wilson et al. 2002, Daunt et al. 2003). More recently these devices are used in conjunction with oceanographic variables gained by remote sensing (e.g. Grémillet et al. 2008, Catry et al. 2009, Kotzerka 2011), which enables modeling of seabird habitats (Wakefield et al. 2009). The strengths of these bird-borne investigations are the high-resolution data gained of individual birds. In addition, their breeding status (e.g. chick-rearing) and colony location is known. Standardized ship-based seabird censuses (for details see Chapter 1) have the advantage of sampling a large proportion of the local seabird population (*sensu* Markones 2007, Camphuysen 2011, Camphuysen et al. 2012). Moreover, these censuses allow to observe how seabirds behave at sea (e.g. if they participate in a feeding frenzy with marine mammals or are associated with fisheries operations). In addition, these surveys often allow *in situ* measurements of oceanographic variables, which enable further in depth studies of habitat selection at sea (e.g. Markones 2007, Scott et al. 2010, Cox et al. 2012) Within this research field, hardly any current information is available for the study area, except for a study on Dovekies (*Alle alle*) during spring and fall (Gjerdrum et al. 2008). For

other abundant top predators such as cetaceans, however, some studies have already revealed links between their abundance and oceanographic phenomena (e.g. Cotté & Simard 2005, Doniol-Valcroze et al. 2007), suggesting that similar variables and processes may also play a significant role for seabirds in these waters. We investigated this subject using spatial modelling in Chapter 2 by addressing the following question:

2) How are seabirds with and without spatial constraint linked with oceanographic variables?

As outlined above, Northern Gannets have large colonies in these waters and several of the following aspects made them a focal species for our study (Chapter 3 & 4). Their total breeding population in the three Gulf colonies comprised ca. 90,000 breeding pairs in 2009 (JF Rail, CWS unpubl. data). This renders the study area one of the most important sites for this species worldwide during summer. Consequently, Northern Gannets are one of the most abundant seabird species in these waters. Bonaventure Island is the largest colony and accounted for ca. 59,600 breeding pairs alone (JF Rail, CWS unpubl. data). Northern Gannets occur in the North Atlantic being the only sulid in these high latitudes. Its behavioural flexibility together with a reduced human persecution has probably been responsible for the large increase in populations during the last decades (Nelson 2002). Their foraging technique comprises plunge-diving and diving from the surface, as well as surface pecking and scooping up prey (Camphuysen 2011). They can have long foraging ranges (e.g. Garthe et al. 2007a) and feed mostly on pelagic fish and squid (e.g. Montevecchi 1993). The fish prey can be numerous and small, such as Capelin and sand lances or be a single large-bodied prey, such as Atlantic Herring or Mackerel. Gannets are highly opportunistic and often engaging in multi-species feeding associations including marine mammals (e.g. Camphuysen & Webb 1999, Davoren et al. 2010). The mechanism behind these associations is called local enhancement. Waterborne predators, such as marine mammals, can facilitate access to prey for aerial predators by driving prey towards the water surface and by blocking the avoidance response of prey (Camphuysen 2011). Hence, the prey is concentrated and held in water depth within the diving capacity of many seabirds, including Northern Gannets. Gannets are indeed known to preferentially track feeding cetaceans, as cues to profitable feeding grounds, rather than their primary prey (Davoren et al. 2010). They also take regularly advantage of anthropogenic food sources such as fisheries discards (Camphuysen 1995, Garthe et al. 1996). Due to their size and physical strength, they are often the strongest competitor of all seabird species in such associations (Camphuysen 2011). In addition to their importance in these waters, they are highly visible at sea enabling detailed observations of their behaviour. Moreover, Gannets were shown to be ideal candidates for bird-borne studies with electronic devices (e.g. Garthe et al. 2000, Hamer et al. 2001, Davoren et al. 2010), not least because of their large size and comparatively good accessibility at colonies. These birds are further known to adjust their aerial and underwater diving behaviour in response to different types of prey (Garthe et al. 2000). These characteristics enabled applying the results of Chapter 1 and 2 as basis for a further study focusing on Northern Gannets. Thus, we analyzed the additional relevant mechanisms for their foraging behaviour and their distribution using ship-based observations and spatial modelling in Chapter 3. Finally, in Chapter 4, we studied in detail the interaction between Gannets and their prey by

deploying data loggers on breeding birds from the Bonaventure colony. The following questions were investigated in Chapters 3 and 4, respectively:

3) How important is local enhancement of prey for the spatial distribution of a generalist avian predator?

4) How do avian predators adjust their diving behaviour in response to a certain type of prey?

Chapter outline

This thesis contains four Chapters that comprise the distribution and habitat selection of a range of common seabird species (Chapter 1 & 2) in the Lower Estuary and Gulf of St. Lawrence during summer. It focuses on the role of local enhancement of prey for Northern Gannets and analyzes their diving technique in response to a certain type of prey (Chapter 3 & 4).

In **Chapter 1: Distribution of seabirds and cetaceans in the Lower Estuary and Gulf of St. Lawrence during summer** detailed information is supplied on the current distribution patterns for the most common seabird species and cetaceans in the study area observed during ship-based censuses. We identify single and multi-species seabird hotspots and compare these with past patterns and recent results from adjacent waters. We estimate total numbers at sea for the most abundant seabird species for the Southern Gulf and compare these with their respective Canadian breeding population or biogeographic population.

In **Chapter 2: The influence of colony location and oceanography on seabird distribution in the Lower Estuary and Gulf of St. Lawrence during summer** we investigate by spatial modeling how the abundance patterns of nine common seabird species are linked with oceanographic variables measured during ship-based research cruises. These variables comprise primary productivity and water mass indicators in addition to distance to the nearest colony or land. We discuss which processes and features are responsible for observed hotspots for different seabird species in the study area. We compare the findings between species with and without spatial constraint and results of similar studies around the world.

In **Chapter 3: The influence of marine mammals on the distribution of Northern Gannets in the Lower Estuary and Gulf of St. Lawrence during summer** we study the role of natural multi-species feeding associations (MSFAs) for Northern Gannets compared with fisheries associations based on their foraging behaviour observed during ship-based surveys. We identify the other producers and main participants of these associations. We infer the spatial scale of association between Gannets

and cetaceans. We compare the influence between cetacean abundance, colony location and other variables on the general distribution of Gannets with spatial modeling.

In **Chapter 4: The Daily Catch: Flight altitude and diving behaviour of Northern Gannets feeding on Atlantic Mackerel** we analyze the diet of breeding birds and discuss the importance and characteristics of Mackerel as prey for an aerial diving seabird. We study the flight altitudes and diving profiles of Northern Gannets breeding on Bonaventure Island by using GPS data loggers and specifically designed altimeters. We investigate how Gannets adjust their diving depths and profile in response to preying exclusively on Atlantic Mackerel.

Chapter 1: Distribution of seabirds and cetaceans in the Lower Estuary and Gulf of St. Lawrence during summer



Chapter 1: Distribution of seabirds and cetaceans in the Lower Estuary and Gulf of St. Lawrence during summer

Nils Guse (1), Nele Markones (1), François Bolduc (2), Stefan Garthe (1)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Canadian Wildlife Service, Environment Canada, 801 - 1550, Avenue d'Estimauville, Québec, G1J 0C3, Canada

Abstract

Seabirds have systematically been surveyed at sea at least since the 1970s. Standardization and improvement of census techniques now enable generating reliable and comparable data on distribution and abundance applying distance sampling. We investigated the distribution and abundance patterns of a range of seabird and marine mammal species with ship-based surveys in the Lower Estuary and Gulf of St. Lawrence in the Northwest Atlantic Ocean during summer 2007, 2008 and 2009. For a range of seabird and cetacean species, this area is known to be of particular importance. We focused on common seabird species and compared their distribution and abundance between mid and late summer for the Southern Gulf, which was most intensively studied. Total numbers of a range of common seabird species were estimated in this sub-area for both summer periods. We related these totals to the biogeographic population or Canadian breeding population to highlight the importance of the Southern Gulf in a regional and international context for several seabird species. Survey effort was mostly available for waters >10m water depth. Gaps occurred in the central part and in the Northeastern Gulf. Northern Gannets were overall most abundant and occurred widespread. Their at sea estimate for the Southern Gulf of 150,000 birds in mid and 140,000 in late summer related to 47% - 75% of the Canadian breeding population, rendering the site one of the most important areas for this species worldwide. Wilson's Storm-Petrels, Common Murres, Northern Fulmars, Razorbills and Black-legged Kittiwakes were among the most abundant and widespread species in the entire study area, but with different areas of concentration. The at sea estimates for the Southern Gulf related to significant proportions of the Canadian breeding population in Razorbills (3 - 16%), Common Murres (3 - 6%), Black-legged Kittiwakes (2 - 4%) and Black Guillemots (1 - 2%). Relative to their biogeographic populations at sea, totals were also significant in Herring Gulls (3 - 4%), Great Black-backed Gulls (1 - 4%) and Common Loons (1 - 4%). Important multispecies hotspots occurred around the Gaspé Peninsula (Gannets, alcids, Kittiwakes, *Larus* gulls and cetaceans), in the Northwestern Gulf, along the Lower North Shore (near St. Mary's

Islands), along the west coast of Newfoundland (Bay of Islands to St. Georges Bay), in Cabot Strait, around Cape Breton Island and the Magdalen Islands, as well as west and east of Prince Edward Island. This study may serve as basis for analyses of habitat selection of seabirds as well as for marine spatial planning applications in these waters.

Introduction

For decades knowledge concerning seabird ecology has been restricted to the short time span these birds spend on land during reproduction. Since the 1960s, however, effort has been directed at surveying seabirds in their marine environment. Many questions regarding their distribution in time and space were addressed and some answered, resulting in detailed publications on seabird distribution and at-sea population numbers (e.g. Brown 1986, Brown et al. 1975, Skov et al. 1995, Sonntag et al. 2006, Garthe et al. 2007b). The methods for ship-based surveys have started with qualitative approaches, where data on relative abundance of seabirds was collected e.g. within the PIROP (Programme intégré de recherches sur les oiseaux pélagiques) framework (Brown 1986). Current methods apply distance sampling (Buckland et al. 2001) for clearly defined sampling units (e.g. adjusted line-transect) to account for imperfect detection of animals. These approaches enable estimating seabird abundance (e.g. Fifield et al. 2009) and seabird totals ('population estimates') for large marine areas (e.g. Sonntag et al. 2006, Garthe et al. 2007b). Standardization and improvement of survey methods (Tasker et al. 1984) lead to widely used and compatible protocols (e.g. Garthe et al. 2002, Camphuysen et al. 2004, Gjerdrum et al. 2012). We applied these methods to gain information on the current distribution patterns of the most common seabirds and cetaceans in the Lower Estuary and Gulf of St. Lawrence. These insights will form the basis for further in depth analysis of factors influencing the habitat selection of seabirds in these waters (see Chapter 3 and 4).

The study area is a highly productive marine area, holding important breeding colonies of Gannets, alcids and Kittiwakes (Fifield et al. 2009). It is also frequented by a large number of marine mammals (see Morissette et al. 2006). The area has been subjected to profound changes regarding the structure of the marine ecosystem, with fundamental effects on many fish species (e.g. Savenkoff et al. 2007a, b, Bundy et al. 2009) that represent important prey for a multitude of seabirds. Moreover, seabirds in this area were intensively surveyed at sea (PIROP) in the 1970s and 1980s (Brown 1986), with little effort thereafter and a total lack of current information. In addition, the efforts of the Eastern Canadian Seabirds at Sea (ECSAS) program in the adjacent waters of the Maritime Provinces have been restarted in 2005 (Fifield et al. 2009) and in the Gulf of St. Lawrence in 2006. This allowed for comparison of our results with past distributions (Brown 1986) in the study area and current information from adjacent sites (Fifield et al. 2009). Moreover, we estimated total numbers for common seabird species in the Southern Gulf to characterize its importance in a regional and international context.

Material & Methods

Study area

The Lower Estuary and Gulf of St. Lawrence in the Northwest Atlantic Ocean is a semi-enclosed shelf sea influenced by boreal and arctic climate. Its bathymetry and hydrography is highly complex and combines oceanic and estuarine traits (for details see Chapter 2). It is a hotspot for several species of seabirds, marine mammals and a variety of other marine life (White & Johns 1997, Dufour & Ouellet 2007).

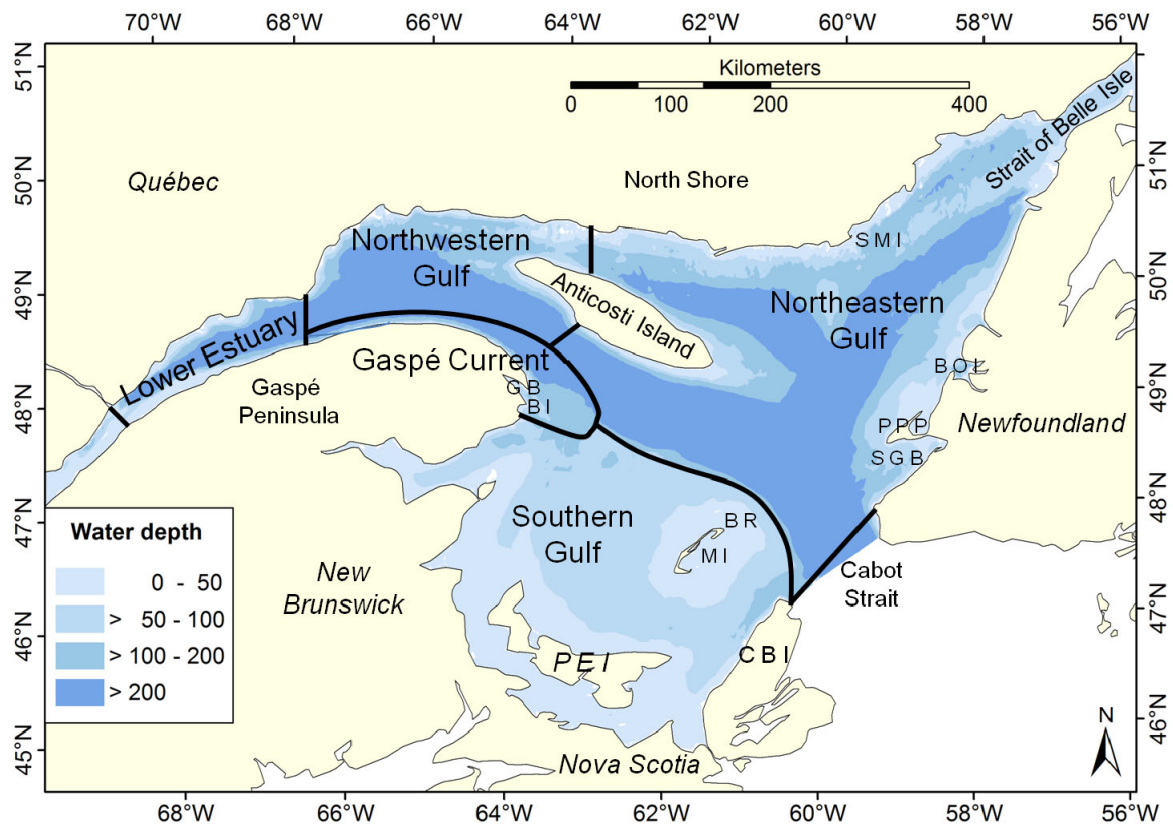


Fig. 1. Subdivisions of the Lower Estuary and Gulf of St. Lawrence modified after de Lafontaine et al. (1991) and Government of Canada (1991). Depicted are the five main marine subdivisions (Lower Estuary, Gaspé Current, Northwestern Gulf, Northeastern Gulf and Southern Gulf), the different provinces (in italics) and other locations mentioned in the text. Abbreviations: BI=Bonaventure Island, BOI=Bay of Islands, BR=Bird Rocks, CBI=Cape Breton Island, GB=Gaspé Bay, MI=Magdalen Islands, PEI=Prince Edward Island, PPP=Port au Port Peninsula, SGB=St. George's Bay, SMI=St. Mary's Islands.

Data on seabirds and marine mammals

We carried out seabird censuses including marine mammals and other marine megafauna during ship-based research surveys and along ferry routes. The surveys took place between June and September from 2007 to 2009 in cooperation with the Canadian Wildlife Service (CWS) in Québec

and scientists from both the Department of Fisheries and Oceans (DFO) of the Maurice Lamontagne Institute (MLI, Mont-Joli, QC) and the Gulf Fisheries Center (Moncton, NB). The bulk of the data was collected onboard the CCGS 'Teleost' during three oceanographic and two fisheries research cruises. The oceanographic surveys were part of the Atlantic Zone Monitoring Program (AZMP) in June 2007, 2008 and 2009 and covered the whole study area. The fisheries research cruises (Groundfish Survey) took place in August/September of 2008 and 2009 in the Southern Gulf (Fig. 1). The Southern Gulf study area was thus most intensely studied (Fig. 3) allowing further analysis (see below).

The counts were conducted by a single observer applying an adjusted line-transect count (Fig. 2) with a standardized protocol (Tasker et al. 1984, Garthe et al. 2002; Camphuysen et al. 2004). This method applies distance sampling (Buckland et al. 2001) and allows the calculation of seabird abundance as individuals per km² (hereafter: ind/km²), which is referred to as 'seabird density' in other publications (e.g. in Fifield et al. 2009). Distances of swimming birds are recorded in four spatial bins or distance bands (A-D) covering a distance of 300m perpendicular to the transect line. Swimming and flying birds are counted continuously. However, for calculating seabird abundance (ind/km²) only flying birds which are spatially 'inside transect' (bands A-D) during a snapshot may be used. This restriction should avoid overestimation of frequently or fast flying species. Usually a snapshot is conducted every minute. Each snapshot covers the area of the transect width multiplied by the distance the ship travels within a minute. The latter depends on the speed of the vessel. Birds and other megafauna observed spatially or temporally outside the transect, are used for abundance rates as individuals per km (hereafter ind./km). The latter is used for less frequently observed species (see below). The census method takes observational conditions (sea state), as well as behaviour (e.g. dipping, resting etc.) and associations with fishing vessels or visible fronts (etc.) of animals into account and applies the codes of (Camphuysen & Garthe 2004).

The surveys were carried out from outdoors providing unobstructed views ahead of 90° to 180° at 12m (range: 6 - 27m) above sea level with an average speed of 12knots (range: 4 - 21knots). Counts during fisheries research cruises were only conducted in periods between fishing operations when the vessel had regained its traveling speed and the number of ship-following birds was low and manageable. The overall survey effort totaled an area of 4,660km² and a distance of 15,532km during 116 days at sea. We calculated the abundance (ind./km²) for all common seabird species applying the distance sampling technique (Buckland et al. 2001) following the procedure described by Markones & Garthe (2012). Distance sampling accounts for the effect that the detection probability of birds decreases with increasing distance to the observer. Thus, the transect width is divided into four different distance bands measured by applying the formula of Heinemann (1981). At sea, these distances were measured with a ruler held in the hand, which was calibrated for the eye level of the observer above the sea surface and the observer's arm length (Gjerdrum et al. 2012). We calculated species-specific correction factors of detection probability for all species and species groups (Table 1) that comprised at least 50 observations within distance classes A, B, C or D (Fig. 2). These were multiplied with the number of birds inside transect to compensate for the proportion of birds that were probably missed on the outer transect bands, taking the size of bird clusters into account

(Buckland et al. 2001). We used the half-normal function with cosine smoothing of the DISTANCE software (version 5.0; www.ruwpa.st-and.ac.uk/distance/distanceabout.html) to calculate the 'effective strip width' (ESW). As flying individuals of a given bird species are assumed to be more easily detected than swimming individuals, only the latter were corrected. Storm-Petrels were the only species with corrections also of flying individuals. These birds almost always hover near the water surface, making it particularly hard to detect them due their small size and dark colour, thus resembling swimming birds from a census point of view. For Razorbills (*Alca torda*) and Common Murres (*Uria aalge*) common correction factor was calculated due to their similarity in size, colour and behaviour including all birds identified as 'Razormurres'. That is a mixed category comprising three species: Razorbills, Common Murres and Thick-billed Murres (*Uria lomvia*). Common Loons (*Gavia immer*) mostly showed escape reactions in response to the approaching survey vessel. They often swam or dived away from the transect line even at distances more than 1km ahead. This reaction to disturbance by the observation platform violates the critical assumption for distance sampling that *all* birds occurring at the transect line (i.e. in transect band A) are recorded perfectly ($g(0) = 1$). This led to a higher proportion of birds emerging in the outer transect bands C and D, thus supplying an erroneously low correction factor. We estimated a correction factor to account for the birds that were probably missed within transect to compensate for this effect. This correction factor was developed based on personal survey observations and by taking into account available distance correction factors for similar species from German Sea areas (Garthe et al. 2009, Markones et al. 2012). As the sea state influences detection probability, we used only census data collected during excellent to moderate conditions (sea states 0 to 4), which comprised more than 96% of the total effort (Table 2), to calculate abundance of different species. Only for highly visible and frequently flying species, such as all gull species, Northern Gannets (*Morus bassanus*) and Northern Fulmars (*Fulmarus glacialis*), we used the full data set. We calculated abundance as ind./km for rarely observed seabird species and cetaceans. This is quantitatively less precise compared with abundance as ind./km². The former includes all observations of a species along the transect line regardless if these were spatially and temporally (snapshot) 'inside transect' or not. The lower precision is due to the fact that observations 'inside transect' have priority and the observer has to focus on the 300m wide sampling unit. Thus, if many observations are made 'inside transect', time for observations or recording of animals 'outside transect' can be lacking. The data on ind./km is also more variable as highly visible species might still be detected at several km from the platform while smaller and less conspicuous species are hardly detected beyond the 300m boundary.

We used a grid based on a cell size of 10'*20' for mapping. For common species seasonal maps were produced. These were split into two periods: mid (June/July) and late summer (August/September). The first period additionally contained the 1st of August 2007 as this was the final day of a coherent July survey. The next survey effort was available from the 12th of August onwards. For less common species one map for the entire period was produced. All birds as well as all other marine megafauna (marine mammals, sea turtles, sharks, bony fishes) were identified to the lowest possible taxon (species, genus, family, order etc.). For (1) Leach's (*Oceanodroma leucorhoa*) and Wilson's Storm-Petrel (*Oceanites oceanicus*), (2) Common, Thick-billed Murre and Razorbill, and (3) Atlantic White-

sided (*Lagenorhynchus acutus*) and White-beaked Dolphin (*Lagenorhynchus albirostris*) the number of individuals not identified to species level (e.g. 'Razormurres') in each grid cell was divided between the two or three species in question (e.g. Common, Thick-billed Murre and Razorbill). This was conducted based on the ratio of animals identified to species level in the neighboring cells (Markones & Garthe 2011). With this approach the potential spatial differences of these species were taken into account. All birds of the mixed category 'Common/Yellow-billed Loon' (*Gavia immer*/*G. adamsii*) were treated as Common Loons as the Yellow-billed Loon was never identified at species level during the surveys. We included all known and potential seabird colonies since 1978 onwards into maps on distribution based on databases from Environment Canada ('Seabird and Waterbird database of Québec', status 13th July 2010 and 'Atlantic Waterbird Colony Database', status 10th July 2010, for details see Chapter 2). A full list of all observed taxa including their total number and scientific as well as North American names can be found in the Appendix (Appendix-Table 1).

Table 1. Correction factors for detection probability of common seabird species and species groups in the Lower Estuary and Gulf of St. Lawrence in summer 2007, 2008 and 2009 used for the calculation of abundance (ind./km²) and estimates of seabird totals. Derivation explains whether the correction factor was calculated by distance sampling for a single species or a species group or estimated otherwise (for details see text).

Taxon/Category	Correction Factor	Derivation
Common Loon (<i>Gavia immer</i>)	1.5	Estimate
Common/Yellow-billed Loon (<i>Gavia immer</i> / <i>G. adamsii</i>)	1.5	Estimate
Northern Fulmar (<i>Fulmarus glacialis</i>)	1.6	Calculation
Wilson's Storm-Petrel (<i>Oceanites oceanicus</i>)	1.6	Calculation for all swimming and flying storm-petrels
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	1.6	Calculation for all swimming and flying storm-petrels
Unidentified storm-petrel	1.6	Calculation for all swimming and flying storm-petrels
Northern Gannet (<i>Morus bassanus</i>)	1.2	Calculation
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	1.2	Calculation
Bonaparte's Gull (<i>Chroicocephalus philadelphia</i>)	1.2	Calculation
Ring-billed Gull (<i>Larus delawarensis</i>)	1.5	Calculation
Herring Gull (<i>Larus argentatus</i>)	1.2	Calculation
Great Black-backed Gull (<i>Larus marinus</i>)	1.0	Calculation
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	1.0	Calculation
Common Murre (<i>Uria aalge</i>)	1.6	Calculation
Razorbill (<i>Alca torda</i>)	1.6	Calculation for all alcids
Thick-billed Murre (<i>Uria lomvia</i>)	1.6	Calculation for all alcids
Unidentified alcid	1.8	Calculation for all unidentified alcids
Common/Thick-billed Murre (<i>Uria aalge</i> / <i>U. lomvia</i>)	1.8	Calculation for all unidentified alcids
Common/Thick-billed Murre/Razorbill (<i>Uria aalge</i> / <i>U. lomvia</i> / <i>Alca torda</i>)	1.8	Calculation for all unidentified alcids
Black Guillemot (<i>Cephus grylle</i>)	1.8	Calculation

Chapter 1 - Distribution & Abundance at sea

Table 2. Sea states and related census effort during seabird surveys in the Lower Estuary and Gulf of St. Lawrence in summer 2007, 2008 and 2009.

Sea state	Distance (km)	Area (km ²)	Proportion of total area (%)
0	191.1	57.6	1.2
1	1,856.8	557.6	12.0
2	4,718.7	1,417.2	30.4
3	5,330.8	1,599.6	34.3
4	2,835.7	851.0	18.2
5	557.8	167.2	3.6
6	44.7	13.6	0.3

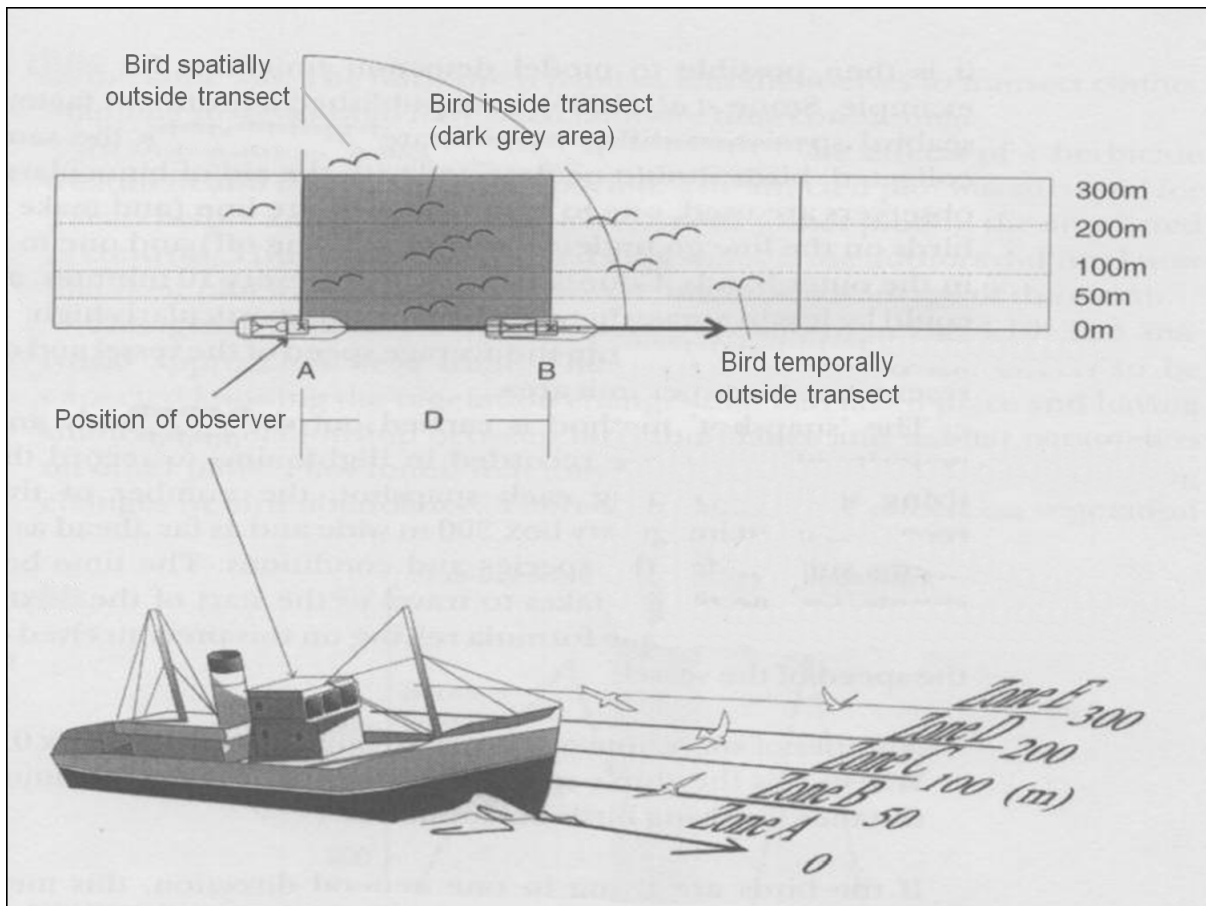


Fig. 2. Schematic illustration of the applied adjusted line-transect method for counting seabirds and other marine megafauna during ship-based surveys modified after Bibby et al. (1992). Depicted are the different distance bands (0-300m) subdividing the survey transect (upper image). The dark rectangle marks the area that is covered during a snapshot every minute. The size of the area results from transect width * distance (D) steamed by the vessel (from A-B) within a minute. Distance bands A-D (lower image) are inside transect and band E (>300m, =outside transect) lies beyond.

Estimating seabird totals for the Southern Gulf

For the vast majority of seabird species, the available census effort in the Southern Gulf (Table 3) between 2007 and 2009 was large enough to estimate their average total numbers during mid and late summer (monthly periods as above). We used the same sea state restrictions as for calculating abundance (ind./km²) resulting in slightly different available effort and therefore data basis for the different species (Table 3).

Table 3. Sea state restrictions and resultant survey effort for estimating seabird totals in the Southern Gulf of St. Lawrence and adjacent waters in summer 2007, 2008 and 2009. *The data set used for Northern Gannets in August/September comprised one additional survey leg where light conditions allowed a quantitatively survey only of this species.

Species	Sea state	Period	Area (km ²)	Distance (km)
Common Loon, Wilson's Storm-Petrel, Double-crested Cormorant, Black Guillemot, Common Murre, Razorbill	0-4	June/July	1,494	4,981
Northern Fulmar, Northern Gannet, Bonaparte's Gull, Ring-billed Gull, Herring Gull, Great Black-backed Gull, Black-legged Kittiwake	0-6	June/July	1,538	5,127
Common Loon, Wilson's Storm-Petrel, Double-crested Cormorant, Black Guillemot, Common Murre, Razorbill	0-4	August/September	1,769	5,898
Northern Fulmar, Bonaparte's Gull, Ring-billed Gull, Herring Gull, Great Black-backed Gull, Black-legged Kittiwake	0-6	August/September	1,849	6,163
Northern Gannet*	0-6	August/September	1,857	6,188

Beyond estimating the average at-sea total of a species we took the associated error (see below) into account following Markones & Garthe (2009). A bootstrap was applied which is a resampling approach. It is used if the probability distribution of a sample function or statistical test cannot be determined with appropriate effort (Efron 1979, Efron & Tibshirani 1993). By bootstrapping a random sample is selected out of the original data set which can be iterated a multitude of times. This generates large numbers of (pseudo) random data sets which are used to estimate the probability distribution and its dispersion parameters (Markones & Garthe 2009). We used a grid with a cell size of 10'*20' (as above) and calculated the distance-corrected mean abundance for each seabird species and grid cell. The overall mean abundance, its standard deviation and 95% confidence intervals were calculated by applying a bootstrap with 10,000 iterations. If a species

occurred frequently and the bootstrapped mean abundance showed a normal distribution, we multiplied the resultant overall mean abundance with the size of the reference area (104,064km²; Fig. 3) in the Southern Gulf to estimate its total number. Only for Black Guillemots and Common Murres during midsummer (June/July) we used a different approach. These occurred frequently but their abundance was highly skewed and their resultant bootstrapped mean abundance was not normally distributed. This would have lead to an erroneously high estimated total. In Black Guillemots the available survey effort did probably only partially overlap with their main concentration areas. The latter seemed to occur in close proximity to land (i.e. breeding sites) particularly around the Gaspé Peninsula. Thus, we calculated the estimated total number of Black Guillemots based on bootstrapping and excluded a single short survey leg inside the Gaspé Bay where abundance (ind./km²) was exceptionally high. We added the corrected total number on this survey leg to the total mean abundance estimate as well as to its lower and upper 95% confidence intervals. The abundance (ind./km²) of Common Murres at sea near the main colonies was magnitudes higher compared with areas further away. Thus, we defined two separate subareas (Fig. 4, Table 4, compare Garthe et al. 2007b) and calculated different total estimates for both subareas. The first subarea of high abundance comprised waters around the two main colonies (3,160km², subarea: 'near colony'). However, because the abundance was still so skewed, a bootstrap could not be applied. In this case, we calculated the median abundance (ind./km²) instead and multiplied it with the size of this subarea to generate an estimate (Table 4). The other subarea comprised the remaining waters (subarea: 'at sea') of the Southern Gulf (101,444km²). For the latter we calculated a total mean number and its 95% confidence intervals based on bootstrapping. Both estimates were added up to estimate the total mean number for the entire study area (Table 4). We rounded the estimated total number of the different seabird species and its confidence intervals according to Garthe, Sonntag, et al. (2007).

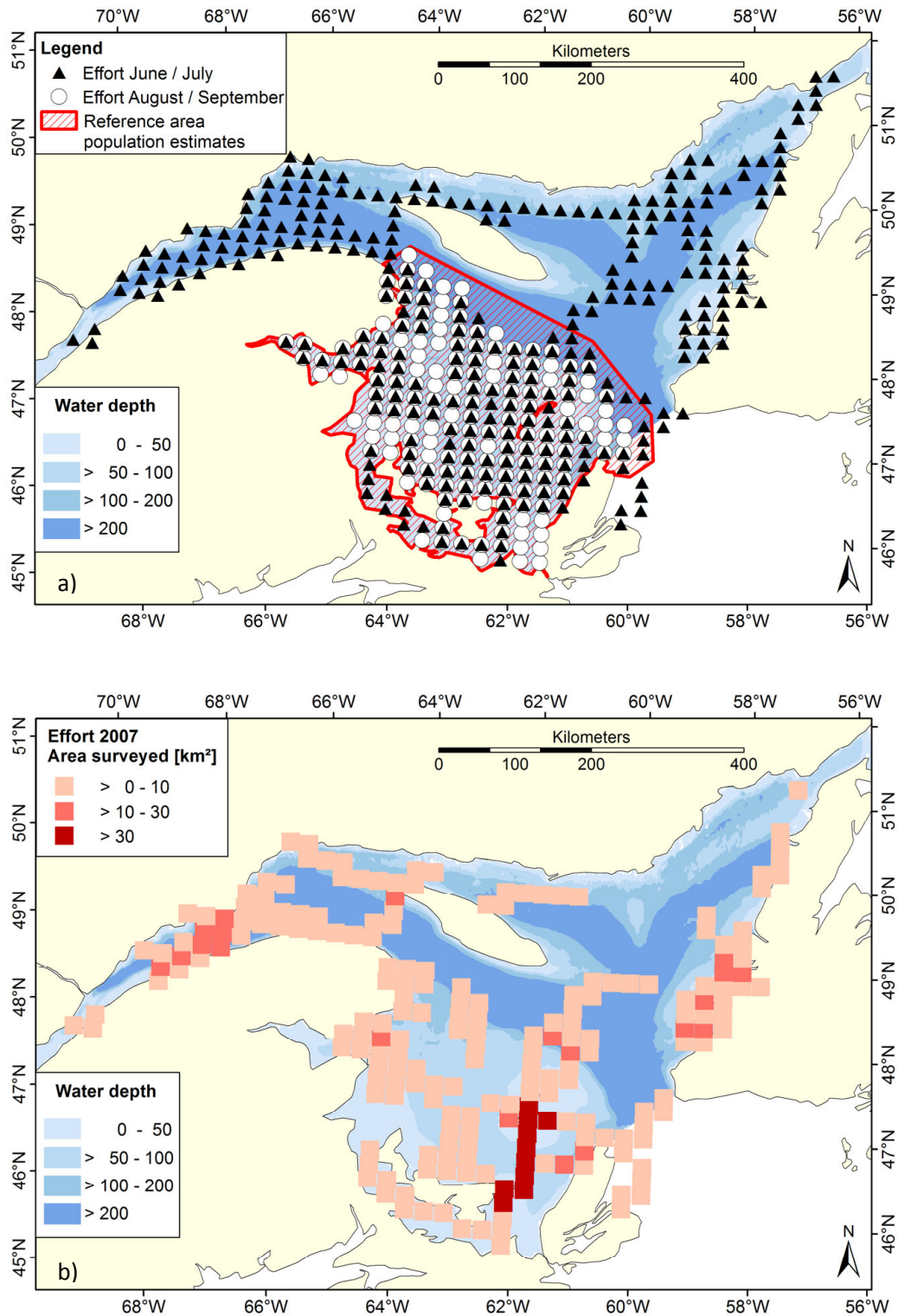


Fig. 3. (a) Reference area (hatched in red) of estimated seabird totals in the Southern Gulf and adjacent waters. The underlying seasonal survey effort in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 is depicted for 10'x20' grid cells. Black triangles and white circles show grid cells in which seabird census data were collected during June and July or August and September, respectively. The annual seabird survey effort is depicted for 10'x20' grid cells separately for (b) 2007, (c) 2008 and (d) 2009.

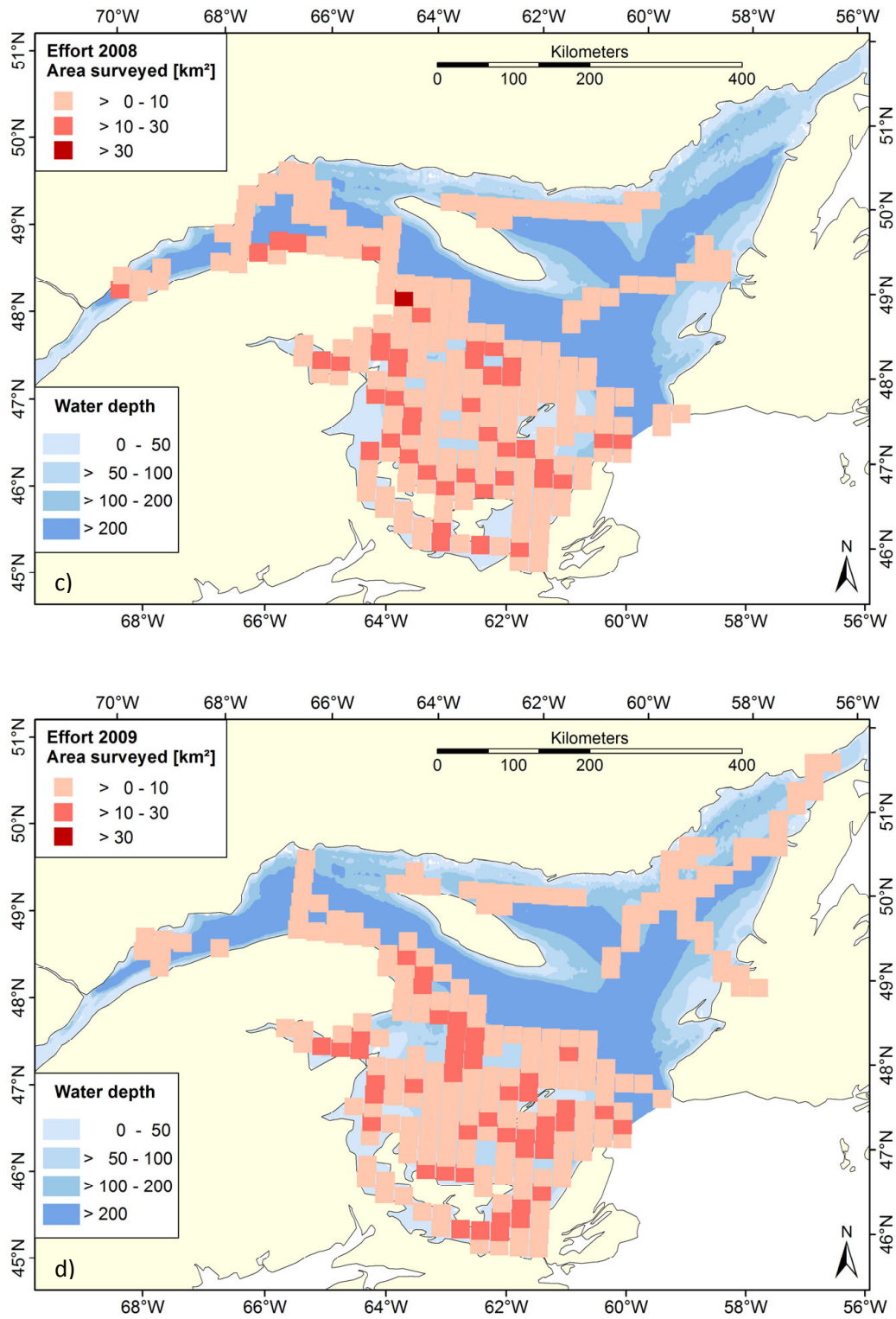


Fig. 3. Continued.

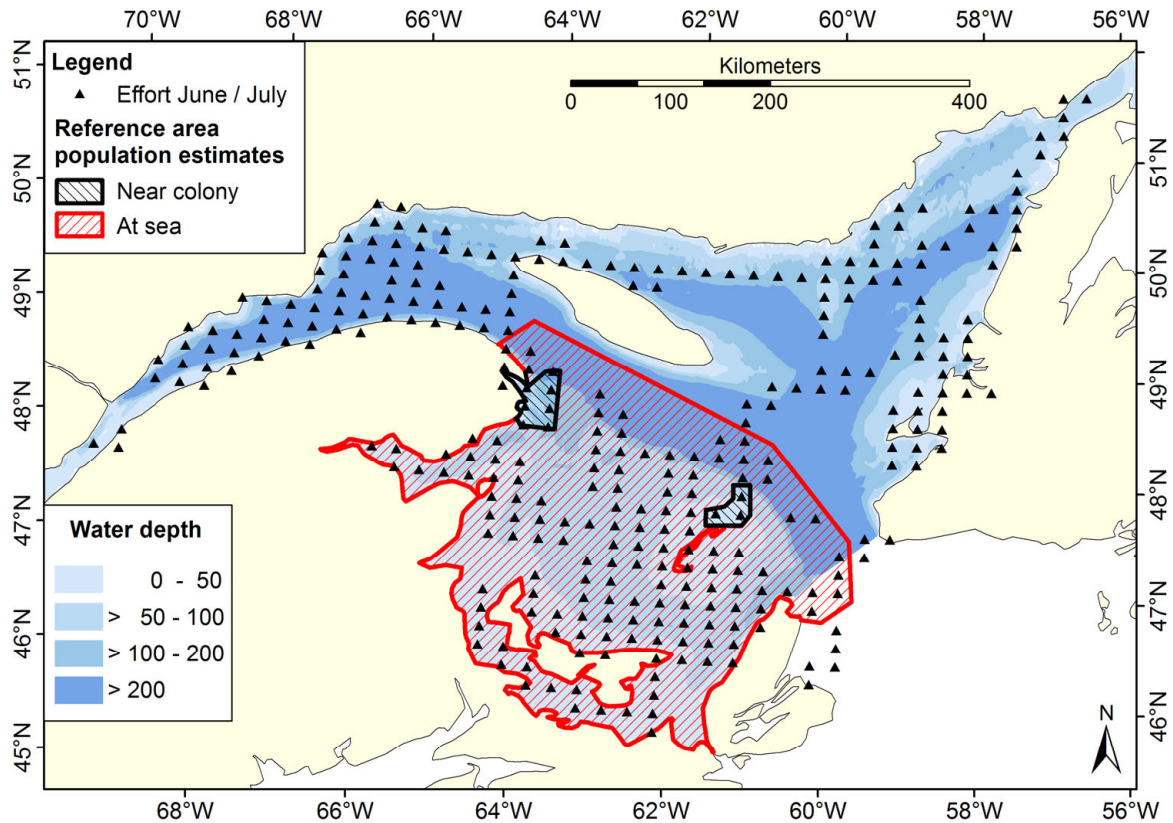


Fig. 4. Reference areas of Common Murre estimated totals in the Southern Gulf and adjacent waters in midsummer. The underlying seasonal survey effort (black triangles) in the Lower Estuary and Gulf of St. Lawrence in June and July of 2007, 2008 and 2009 is depicted for 10'x20' grid cells.

Results

Seabird distribution, abundance and estimated totals

Pronounced differences in their distribution both within and across species could be observed in the Lower Estuary and Gulf of St. Lawrence. Northern Gannets were most abundant and occurred both in coastal as well as offshore waters (Fig. 13, Fig. 14). The Southern Gulf and the distal part of Gaspé Current held highest concentrations. A total of 140,000 to 150,000 Gannets persistently occurred in these waters during the entire summer period (Table 4).

Common Murres were also very abundant and widespread (Fig. 29, Fig. 30). A particularly high abundance was observed in the Northeastern and Northwestern Gulf, in the Gaspé Current and around the Magdalen Islands. With a total of 57,000 individuals Common Murres were among the most numerous species in the Southern Gulf in midsummer (Table 4). Apart from the western part of the Southern Gulf fewer birds were observed in late summer.

The overall patterns in distribution of Thick-billed Murres (Fig. 31) and Razorbills (Fig. 32, Fig. 33) resembled those for Common Murres but with much lower abundance and total numbers (Table 4) and some regional differences. Thick-billed Murres were not observed in the Southern Gulf in late summer. Razorbills were particularly concentrated in the Lower Estuary and along the Lower North Shore in the Northeastern Gulf. In contrast to all other alcids they were more numerous in the Southern Gulf in late summer compared to midsummer.

Black Guillemots showed the strongest link to coastal waters of all alcid species (Fig. 27, Fig. 28). They were most abundant along the west coast of Newfoundland and the Gaspé Peninsula during midsummer. Regarded at the family level alcids were abundant and widespread (Fig. 34, Fig. 35) during the whole period with some clear areas of concentration.

Pelagic species such as Wilson's Storm-Petrels and Northern Fulmars were amongst the most numerous seabird species in the Southern Gulf in midsummer with an estimated total of 65,000 and 36,000 individuals, respectively (Table 4). Northern Fulmars were most abundant in the Northwestern and Northeastern Gulf and along the rim of the Southern Gulf during midsummer (Fig. 7), but less abundant in this area later in the season (Fig. 8). This paralleled the seasonal occurrence of Wilson's Storm-Petrel in these waters. The offshore distribution of Leach's Storm-Petrels (Fig. 11, Fig. 12) resembled that of Wilson's (Fig. 9, Fig. 10) while the latter was much more abundant.

Herring Gulls and Great Black-backed Gulls were also abundant and widespread in the study area showing similar patterns. Both species showed a stronger link to coastal waters during midsummer (Fig. 21, Fig. 23) and occurred more widespread and in larger numbers (Table 4) in the Southern Gulf in late summer (Fig. 22, Fig. 24). The distribution of Black-legged Kittiwakes during midsummer was more pelagic compared with the latter species (Fig. 25). Both the abundance and total number of Kittiwakes decreased markedly in the Southern Gulf in late summer (Fig. 26).

Several species such as Common Loon (Fig. 5, Fig. 6), Double-crested Cormorant (Fig. 15, Fig. 16), Bonaparte's Gull (Fig. 17, Fig. 18) and Ring-billed Gull (Fig. 19, Fig. 20) were restricted to certain areas and were largely low to moderate abundant in coastal waters. The first three species showed a higher abundance and total numbers in the Southern Gulf in late compared with midsummer. Ring-billed Gulls were consistently rare in these waters throughout the summer (Table 4).

Seaducks, phalaropes and shearwaters occurred comparatively seldom. Seaducks frequented rather shallow coastal waters in the Lower Estuary, Northwestern and western part of the Southern Gulf (Fig. 36). Shearwaters were mostly found in Cabot Strait, offshore in the Northeastern Gulf and along the west coast of Newfoundland (Fig. 37). Phalaropes were also found frequently further from shore but showed highest abundance along the Gaspé Peninsula and in the Southern Gulf (Fig. 38).

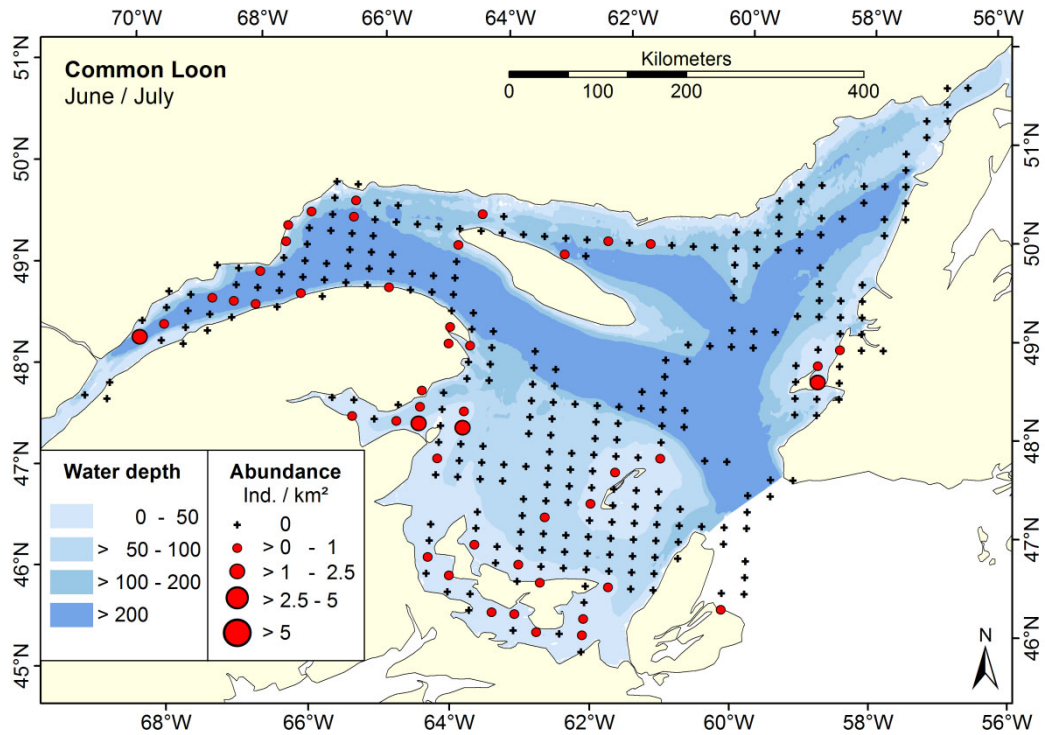


Fig. 5. Distribution and abundance of Common Loons (*Gavia immer*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

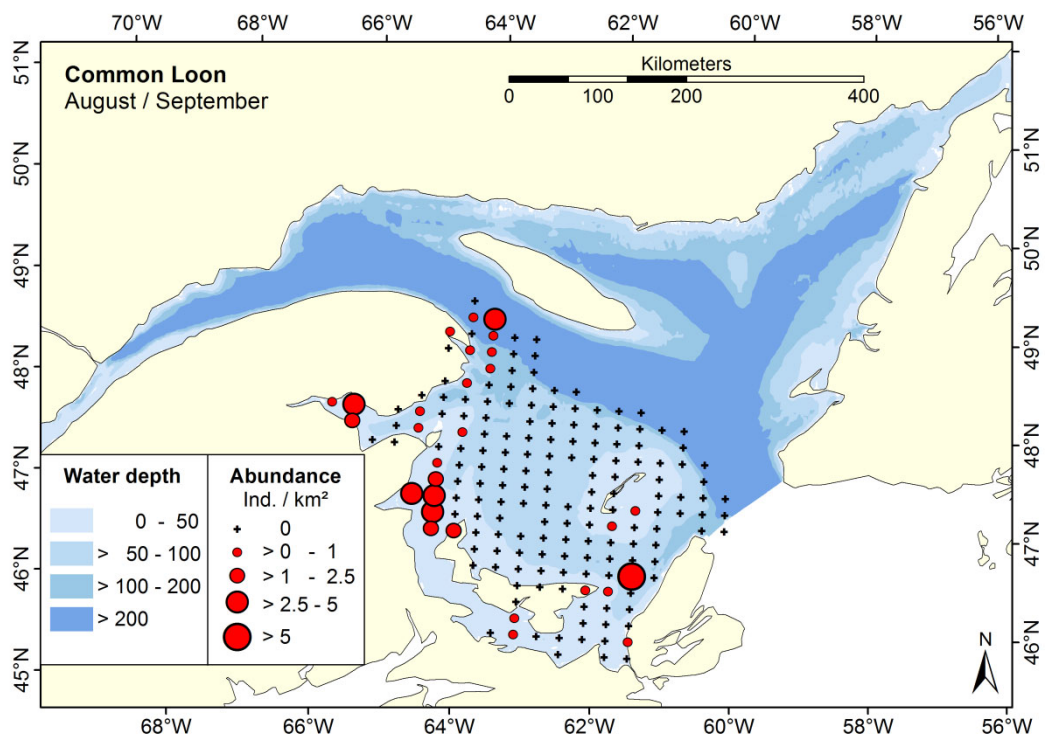


Fig. 6. Distribution and abundance of Common Loons (*Gavia immer*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

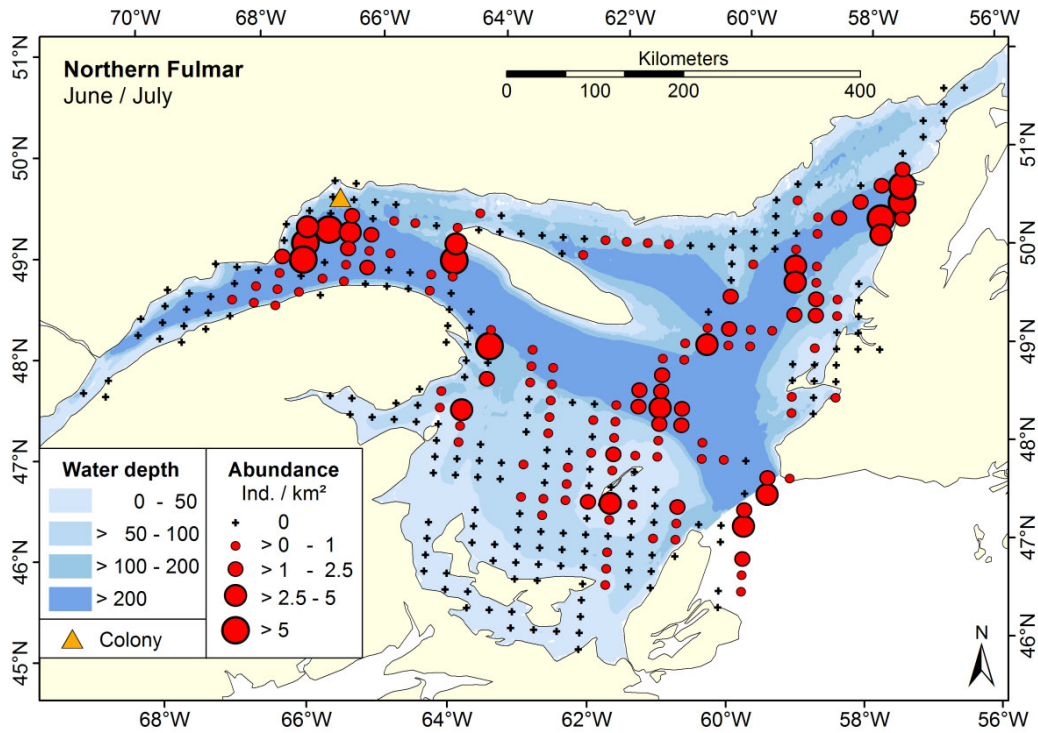


Fig. 7. Distribution and abundance of Northern Fulmars (*Fulmarus glacialis*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

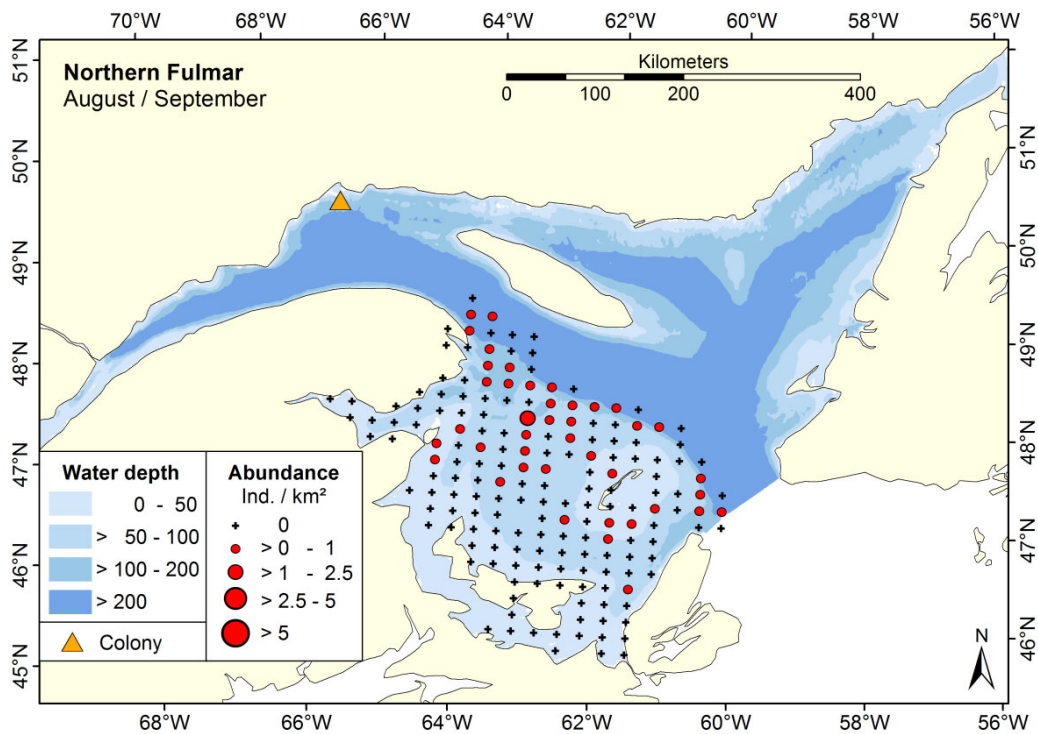


Fig. 8. Distribution and abundance of Northern Fulmars (*Fulmarus glacialis*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

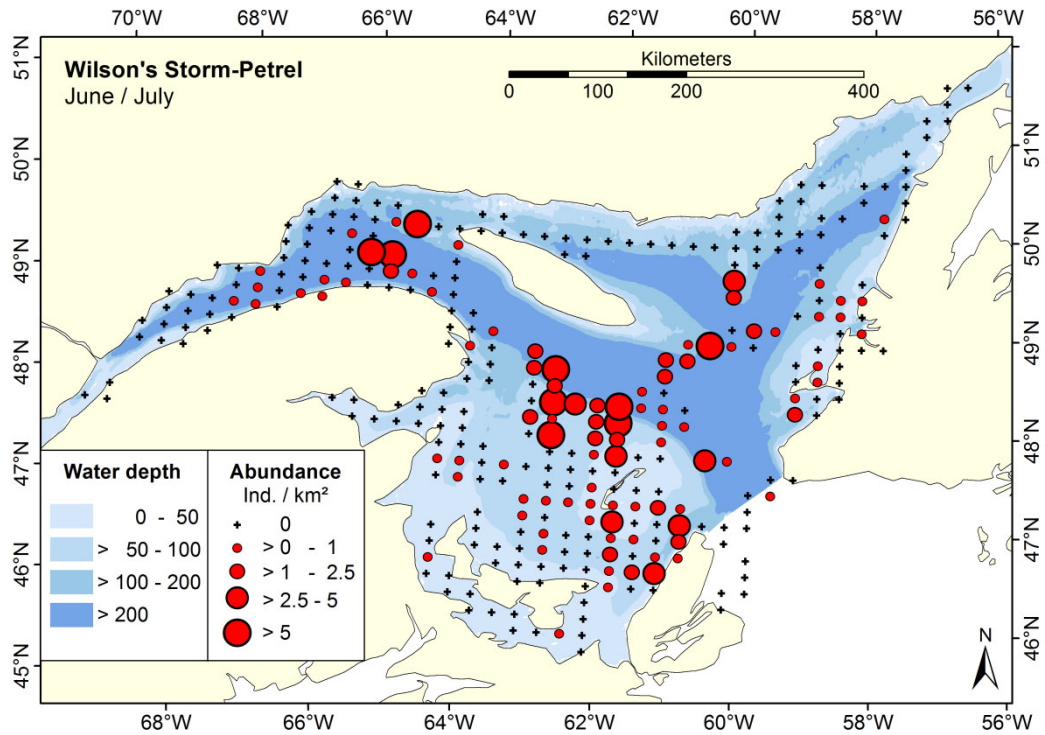


Fig. 9. Distribution and abundance of Wilson's Storm-Petrels (*Oceanites oceanicus*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

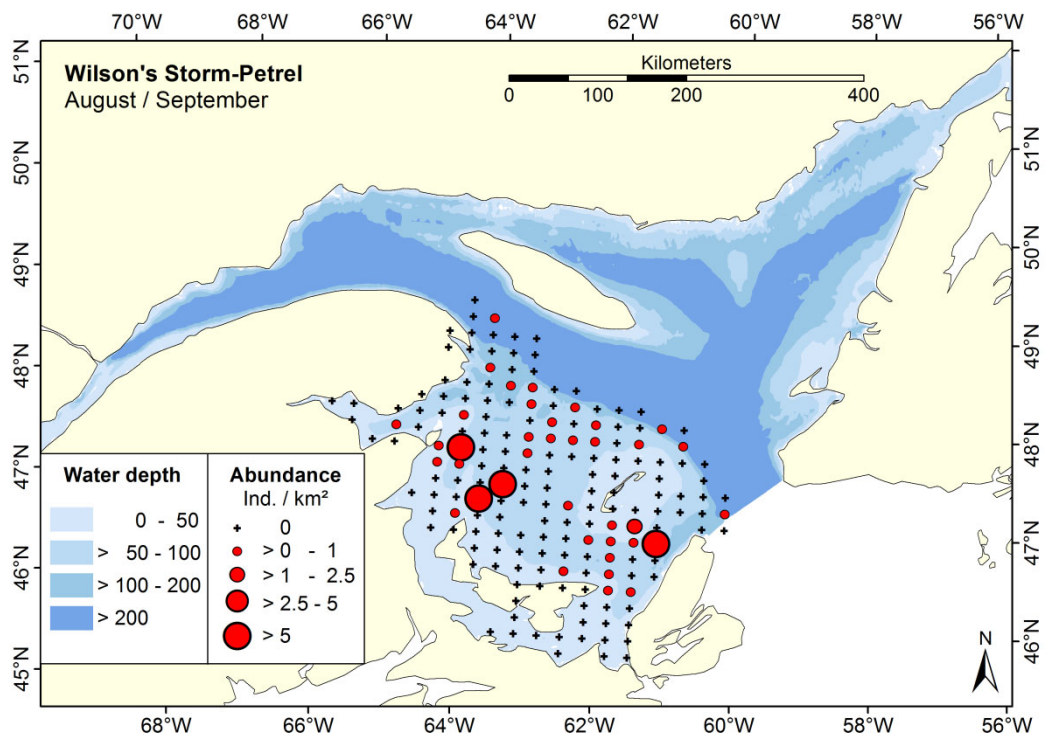


Fig. 10. Distribution and abundance of Wilson's Storm-Petrels (*Oceanites oceanicus*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

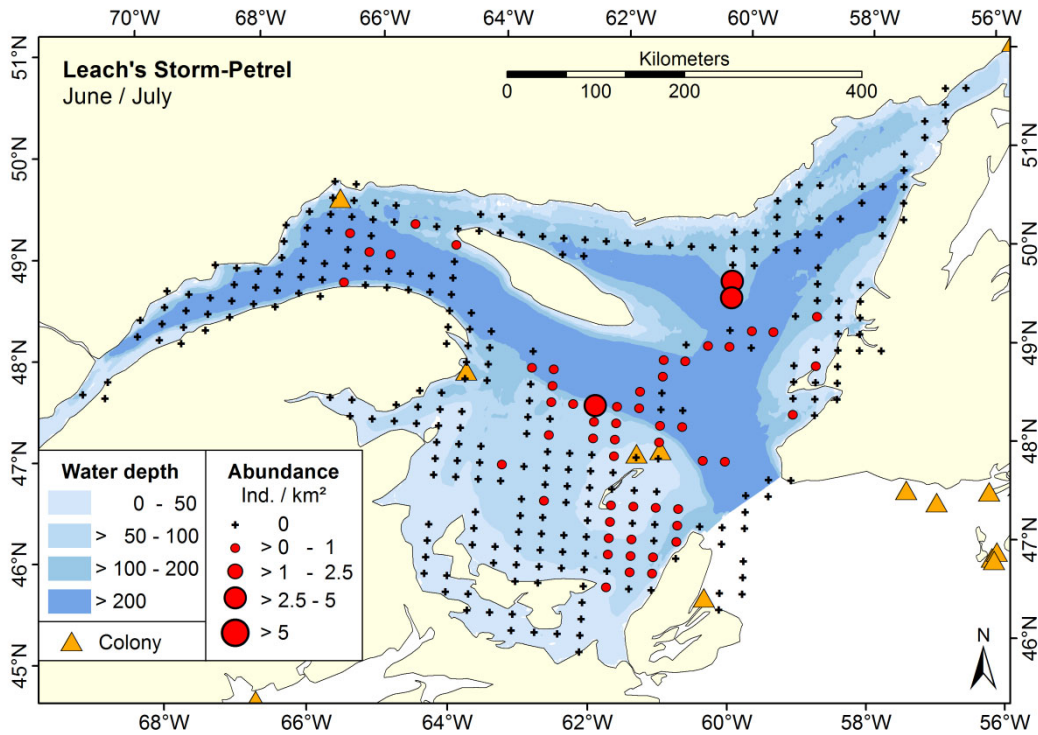


Fig. 11. Distribution and abundance of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

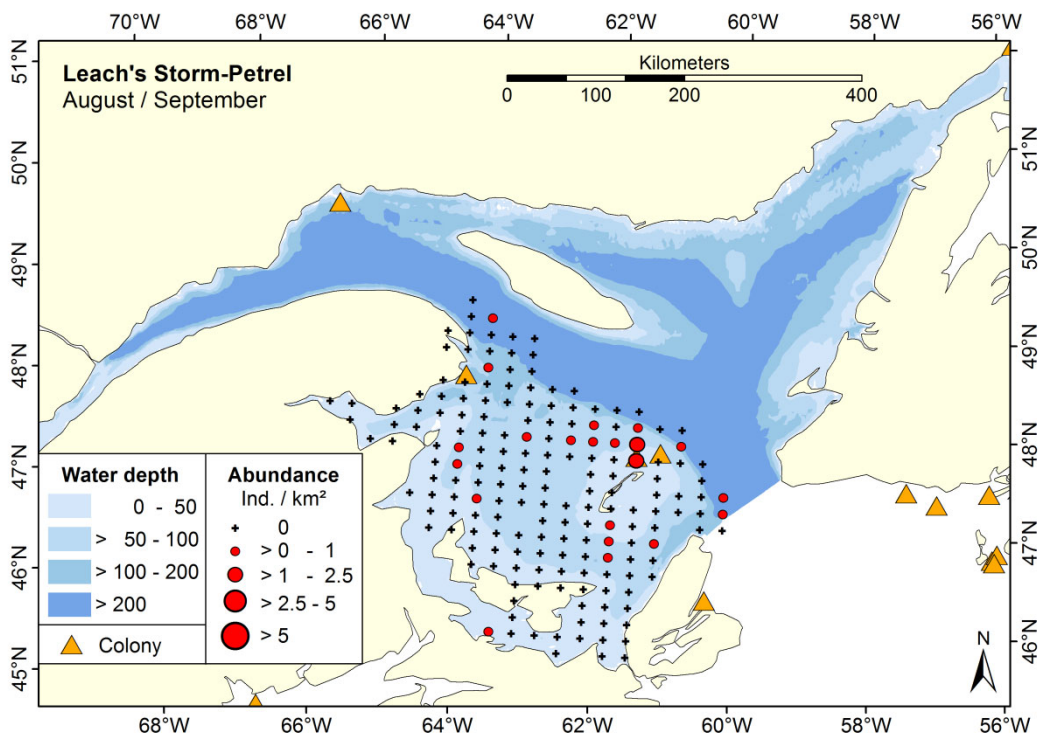


Fig. 12. Distribution and abundance of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

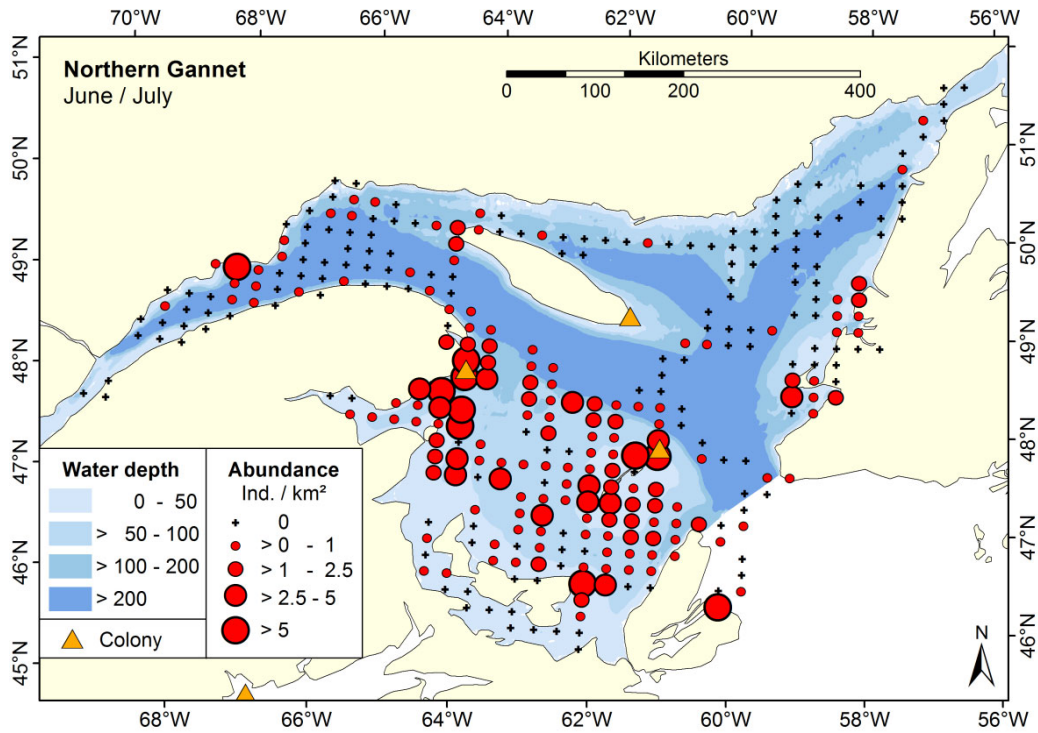


Fig. 13. Distribution and abundance of Northern Gannets (*Morus bassanus*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

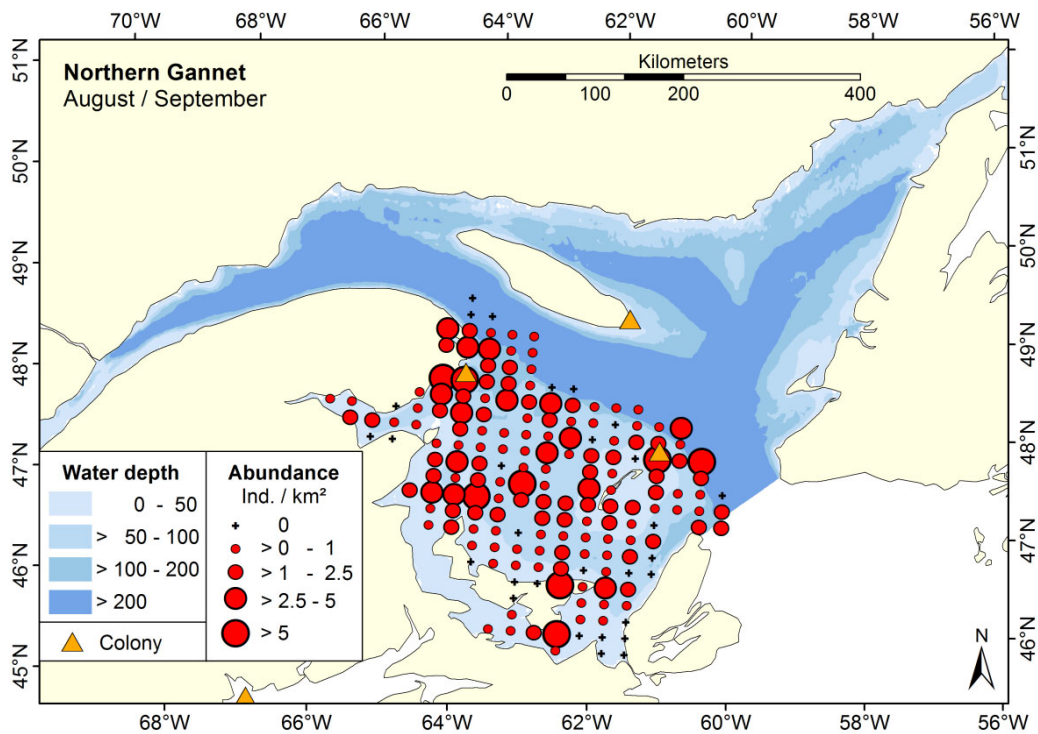


Fig. 14. Distribution and abundance of Northern Gannets (*Morus bassanus*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

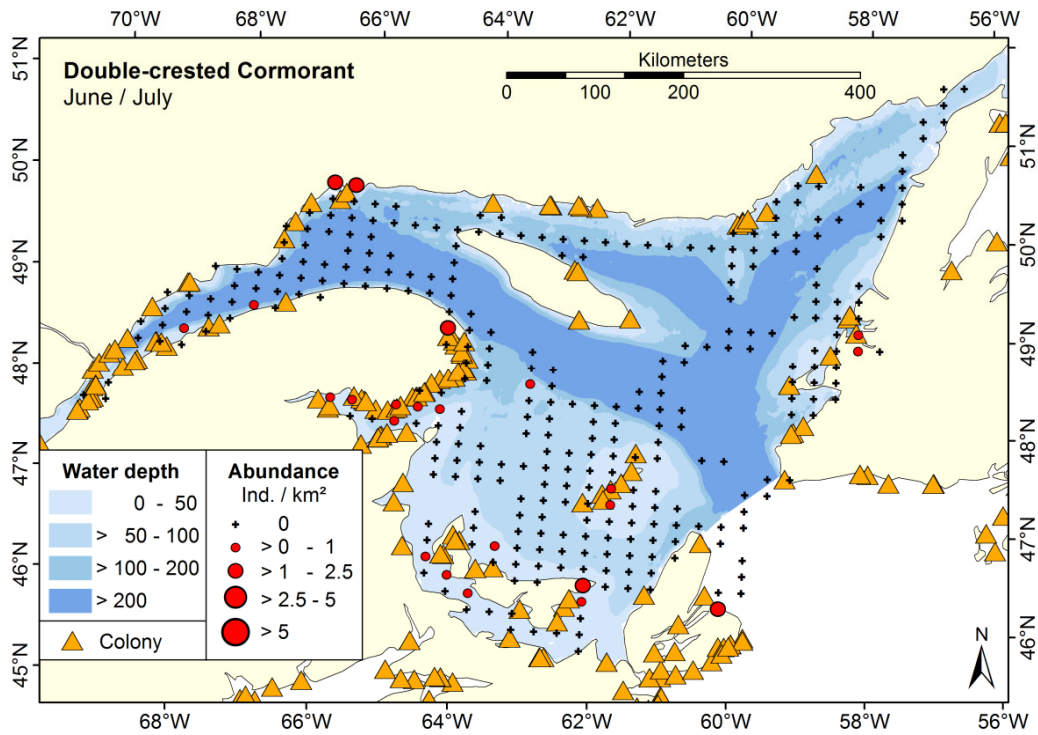


Fig. 15. Distribution and abundance of Double-crested Cormorants (*Phalacrocorax auritus*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

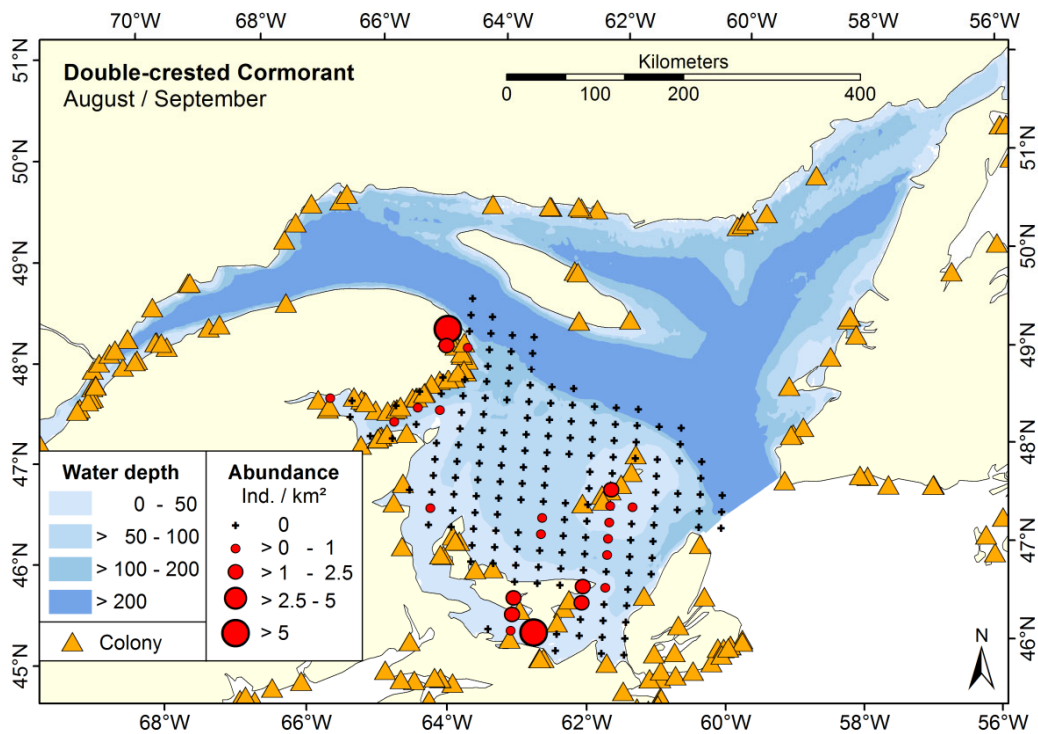


Fig. 16. Distribution and abundance of Double-crested Cormorants (*Phalacrocorax auritus*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

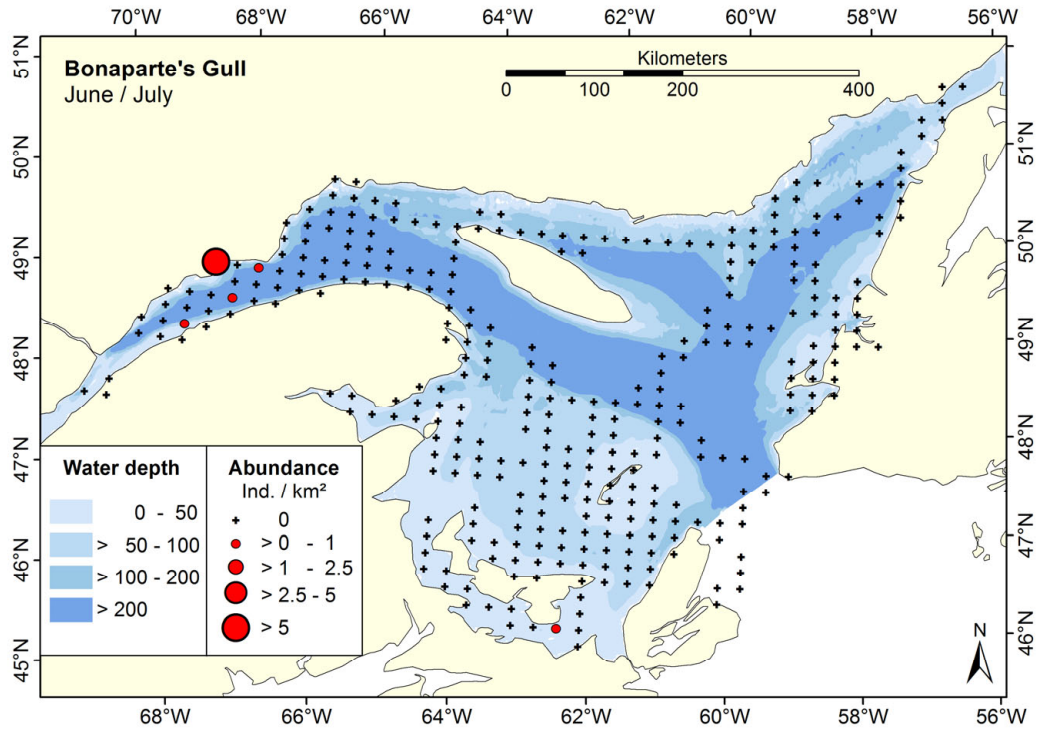


Fig. 17. Distribution and abundance of Bonaparte's Gulls (*Chroicocephalus philadelphia*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

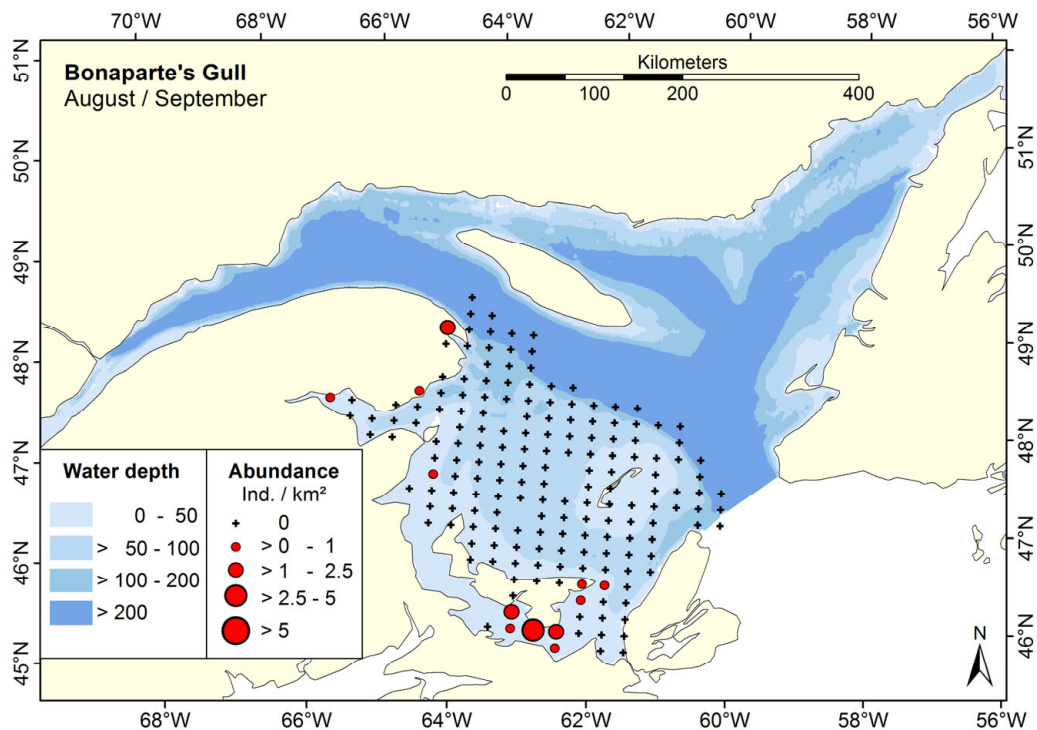


Fig. 18. Distribution and abundance of Bonaparte's Gulls (*Chroicocephalus philadelphia*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

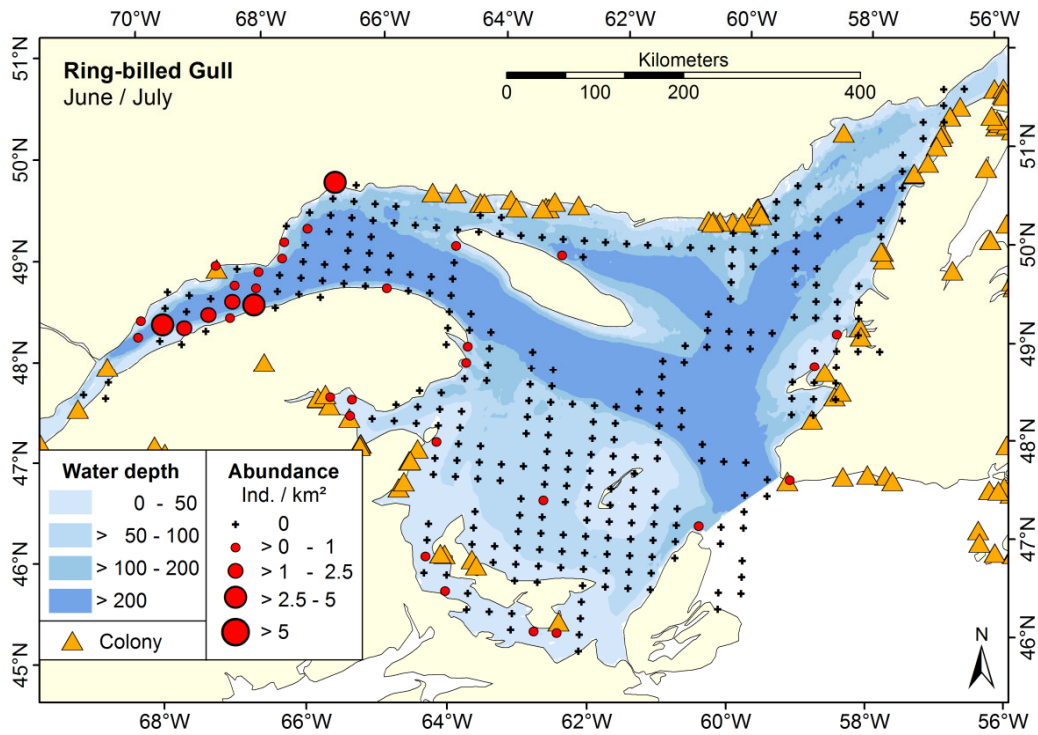


Fig. 19. Distribution and abundance of Ring-billed Gulls (*Larus delawarensis*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

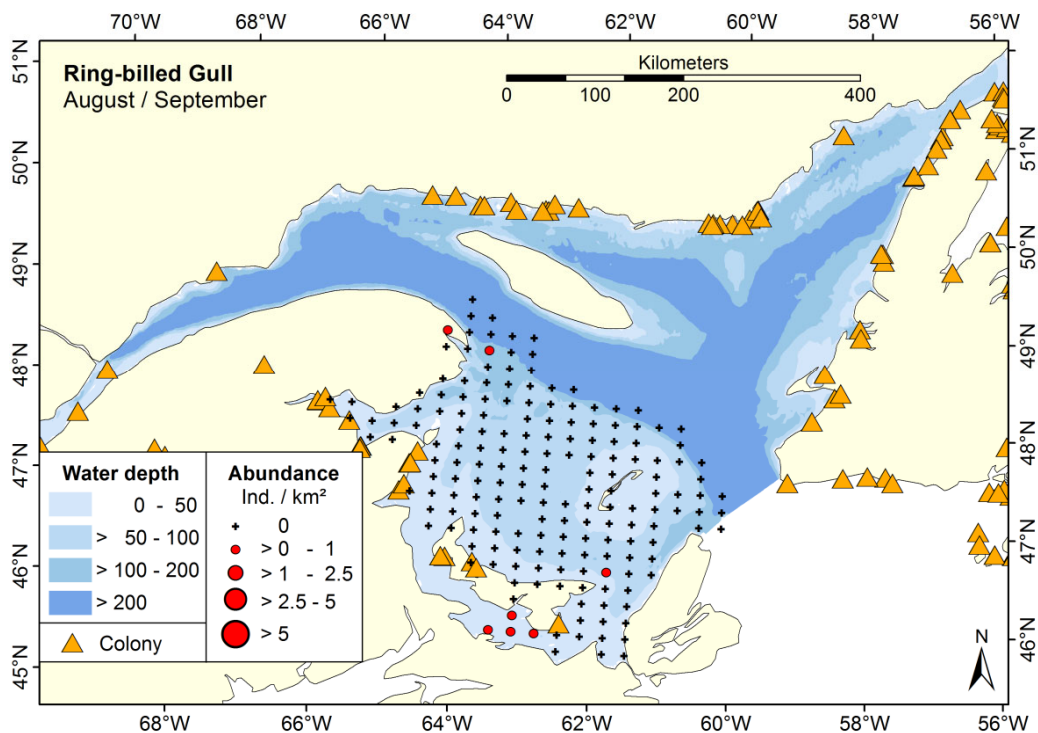


Fig. 20. Distribution and abundance of Ring-billed Gulls (*Larus delawarensis*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

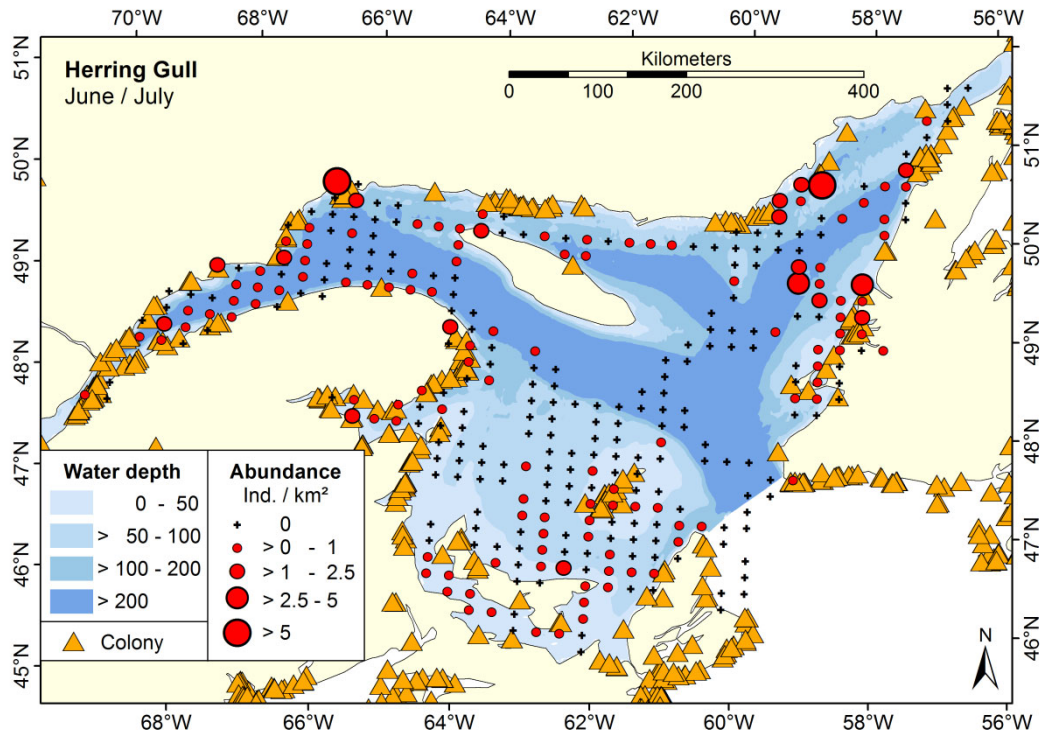


Fig. 21. Distribution and abundance of Herring Gulls (*Larus argentatus*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

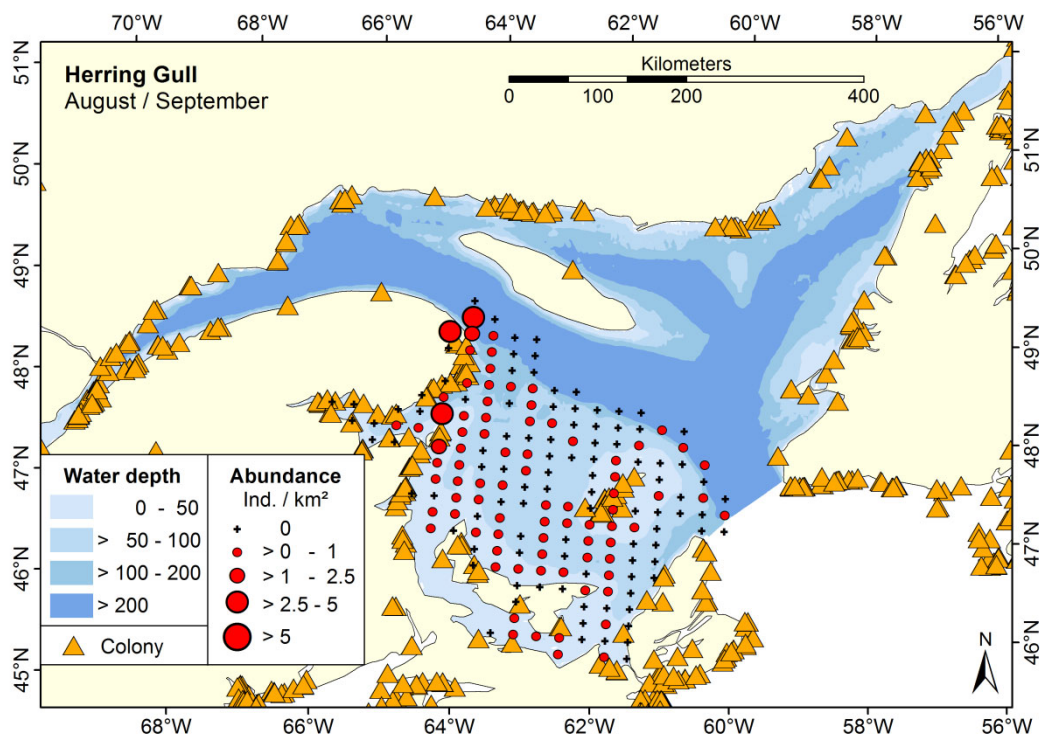


Fig. 22. Distribution and abundance of Herring Gulls (*Larus argentatus*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

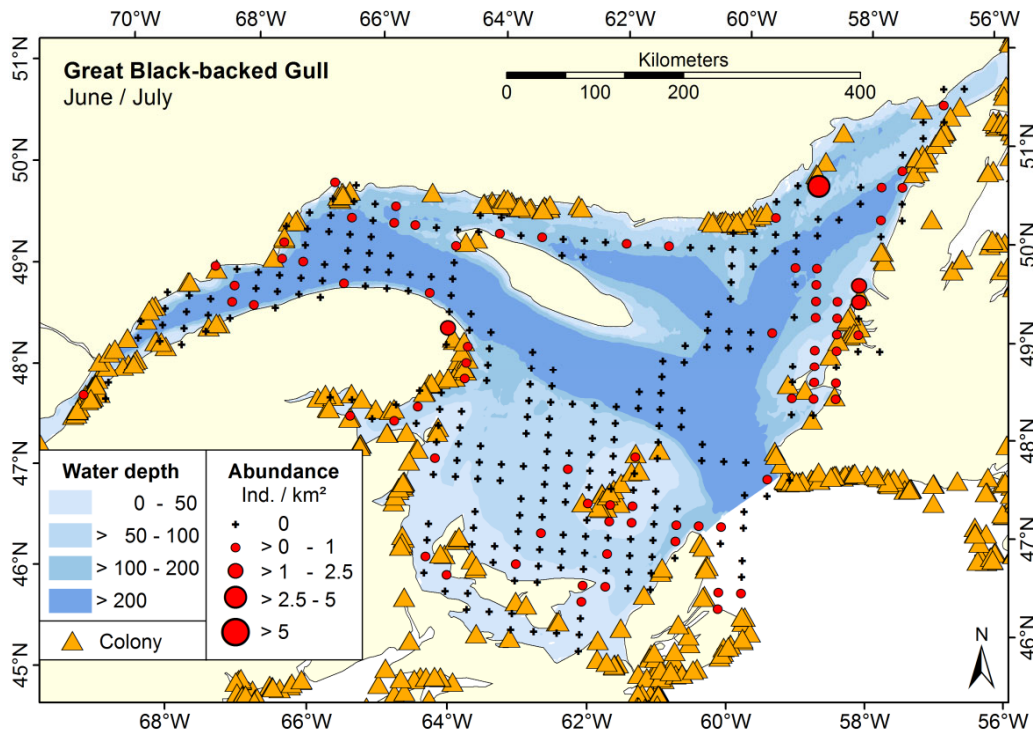


Fig. 23. Distribution and abundance of Great Black-backed Gulls (*Larus marinus*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

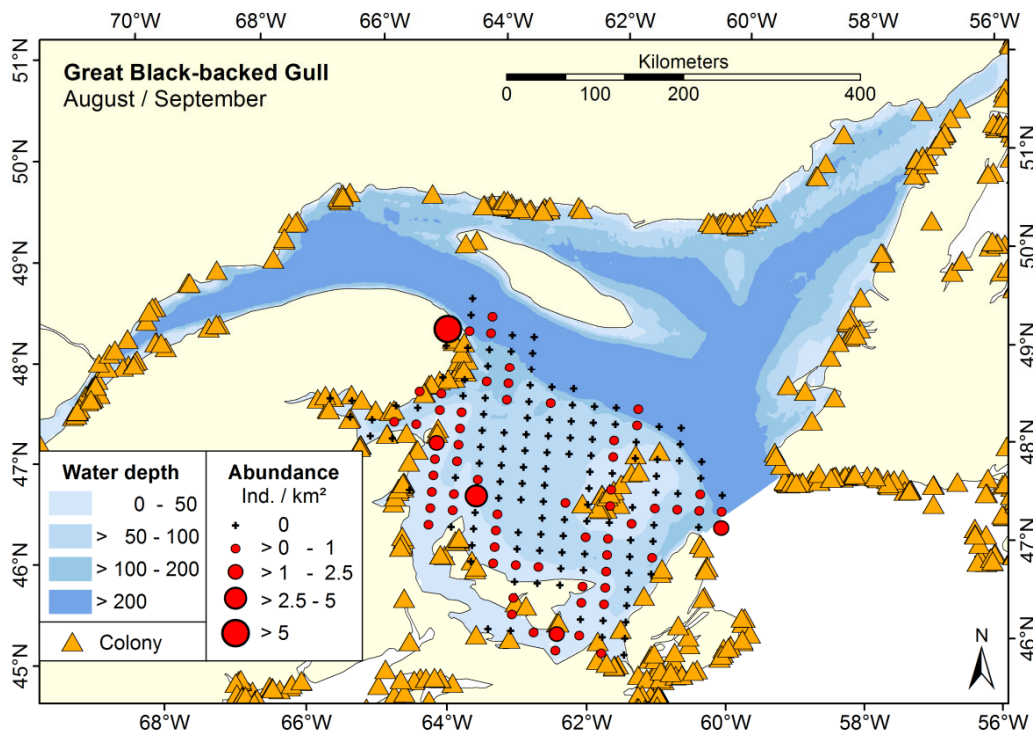


Fig. 24. Distribution and abundance of Great Black-backed Gulls (*Larus marinus*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

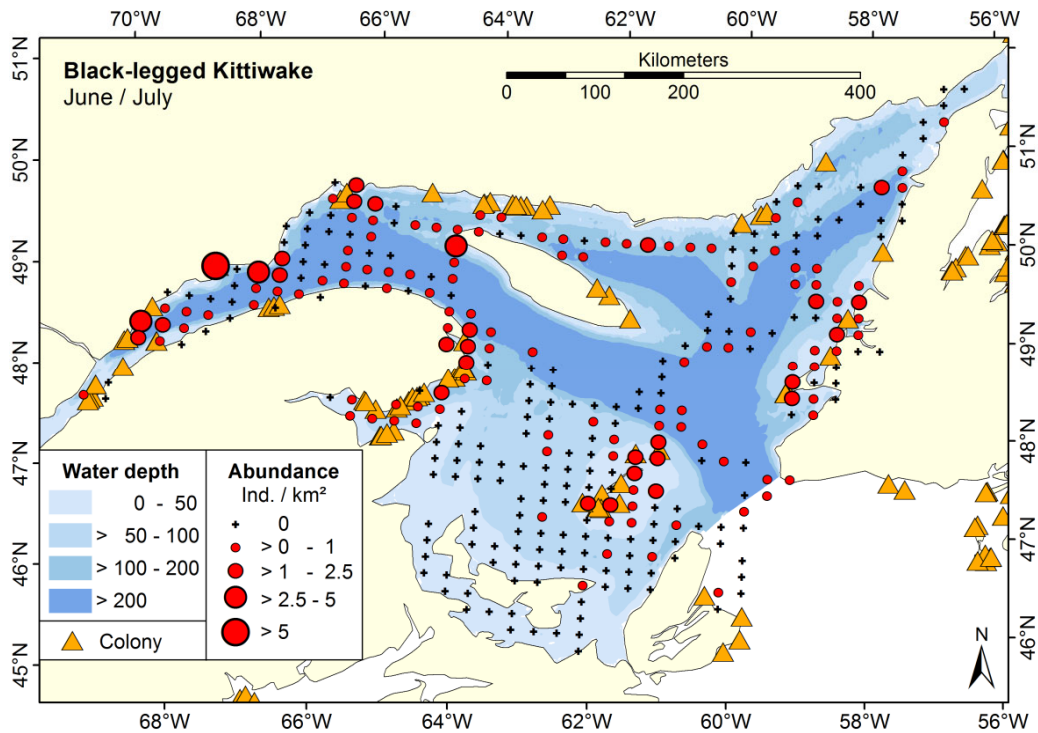


Fig. 25. Distribution and abundance of Black-legged Kittiwakes (*Rissa tridactyla*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

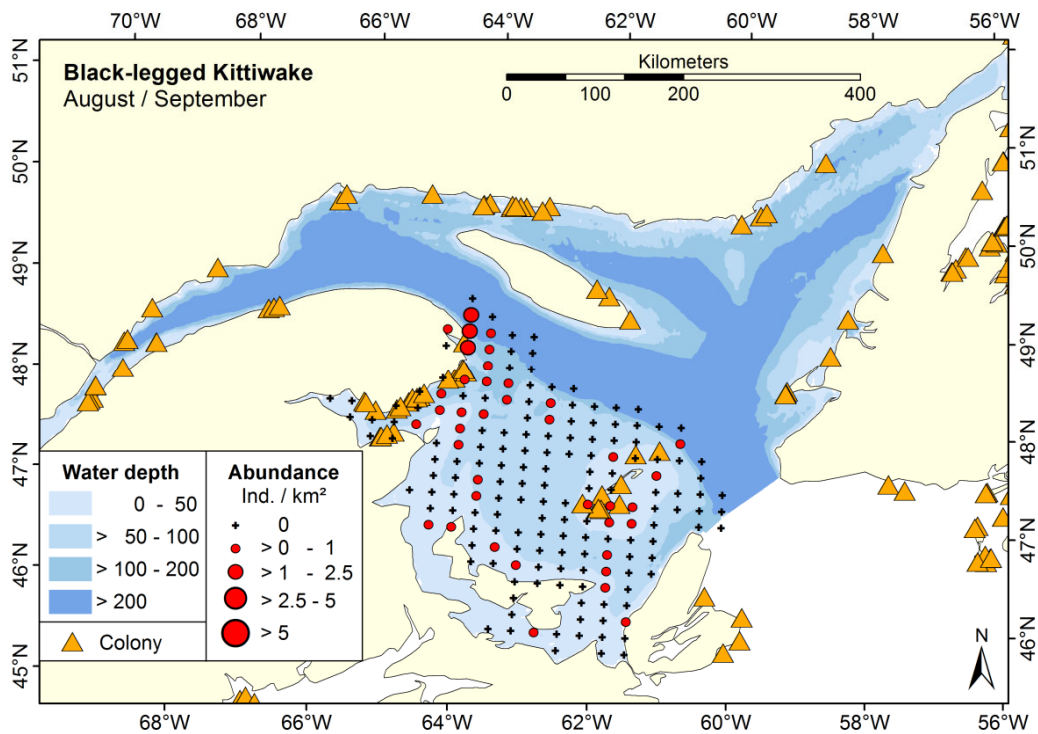


Fig. 26. Distribution and abundance of Black-legged Kittiwakes (*Rissa tridactyla*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

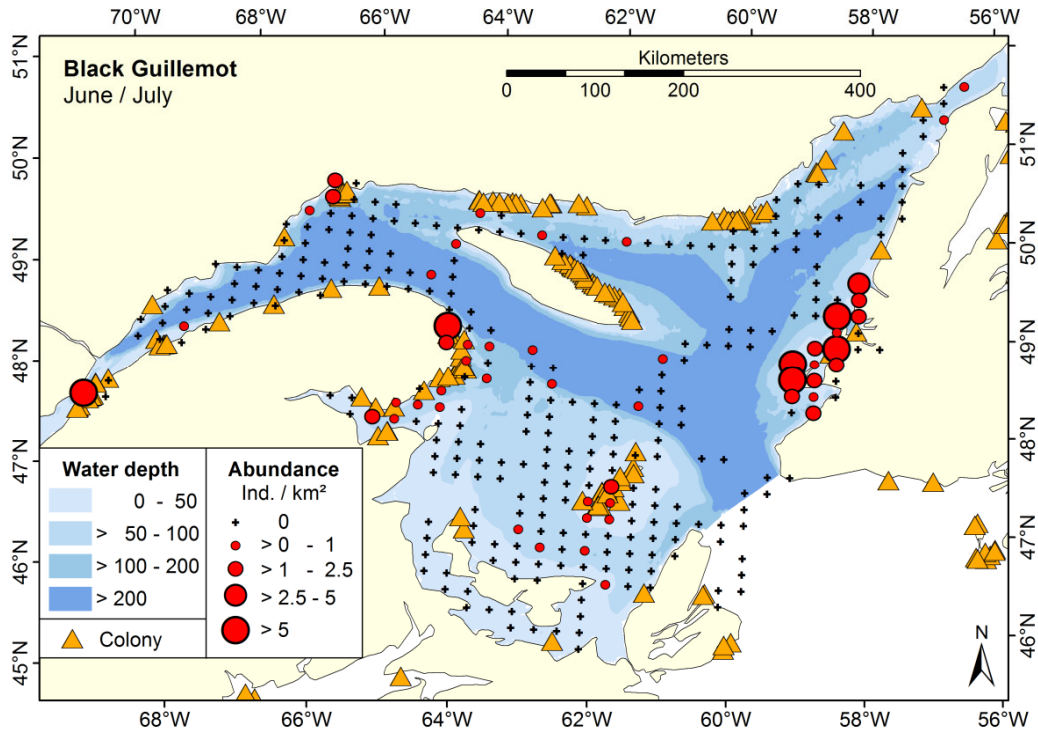


Fig. 27. Distribution and abundance of Black Guillemots (*Cepphus grylle*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

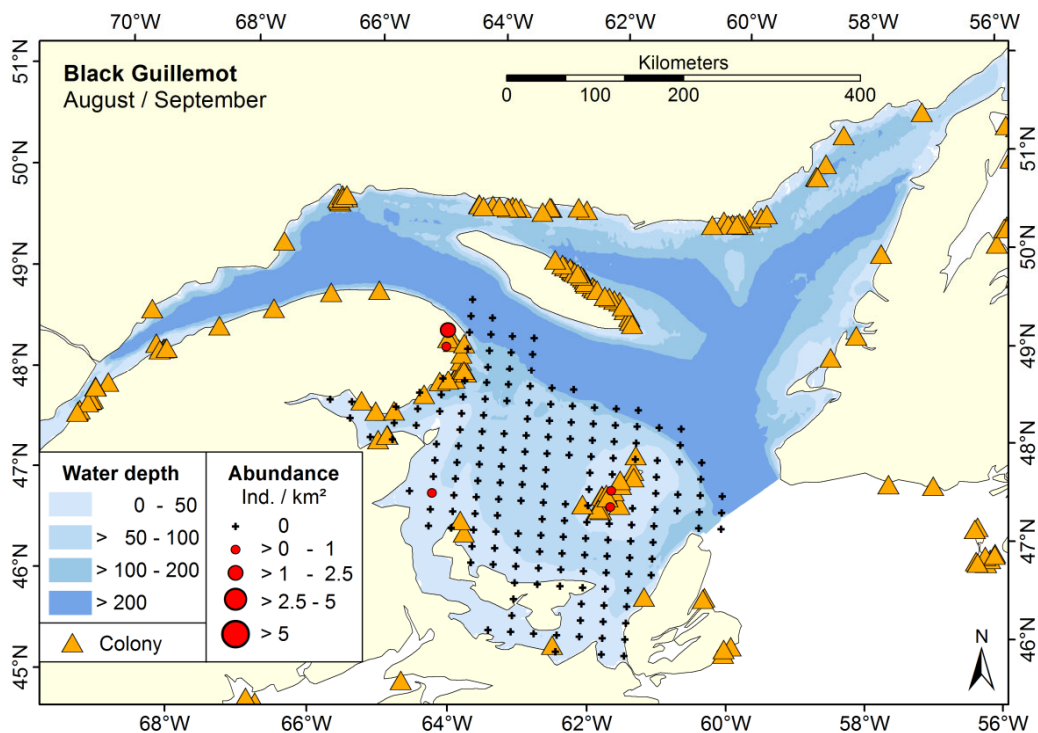


Fig. 28. Distribution and abundance of Black Guillemots (*Cepphus grylle*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

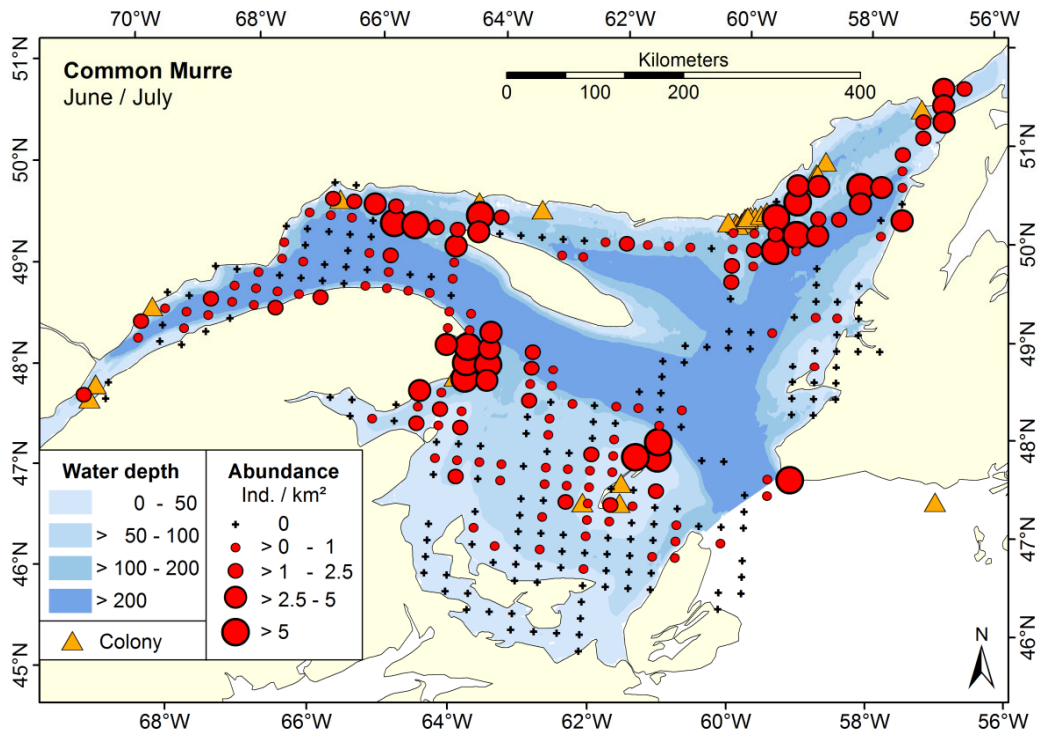


Fig. 29. Distribution and abundance of Common Murres (*Uria aalge*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

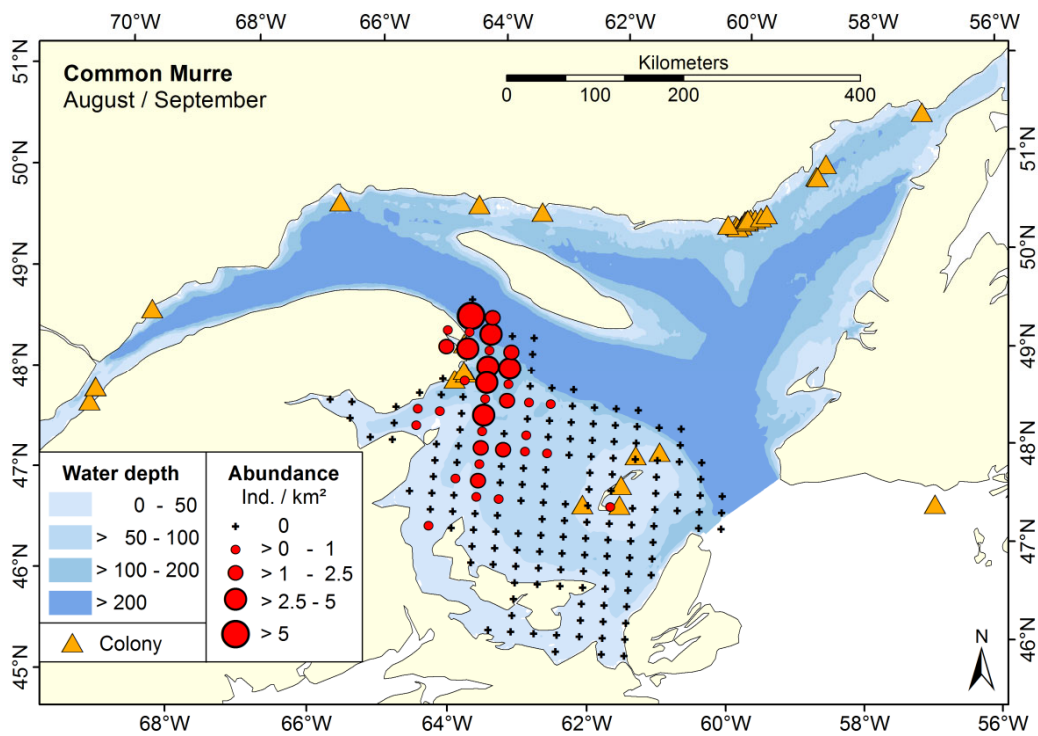


Fig. 30. Distribution and abundance of Common Murres (*Uria aalge*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

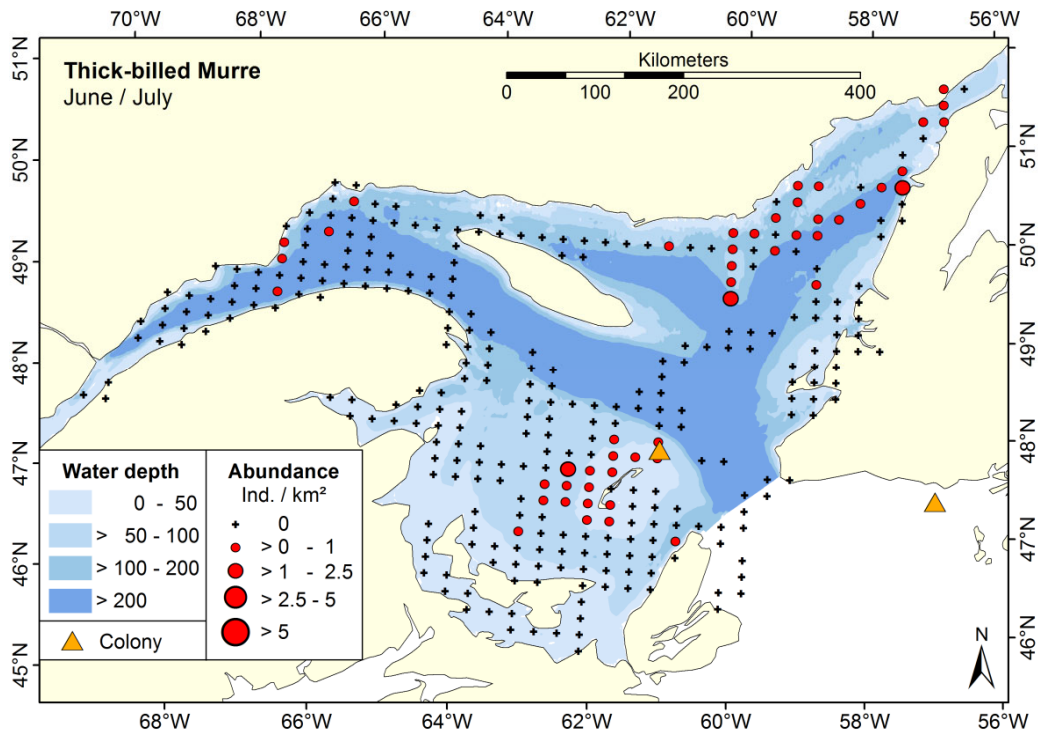


Fig. 31. Distribution and abundance of Thick-billed Murres (*Uria lomvia*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

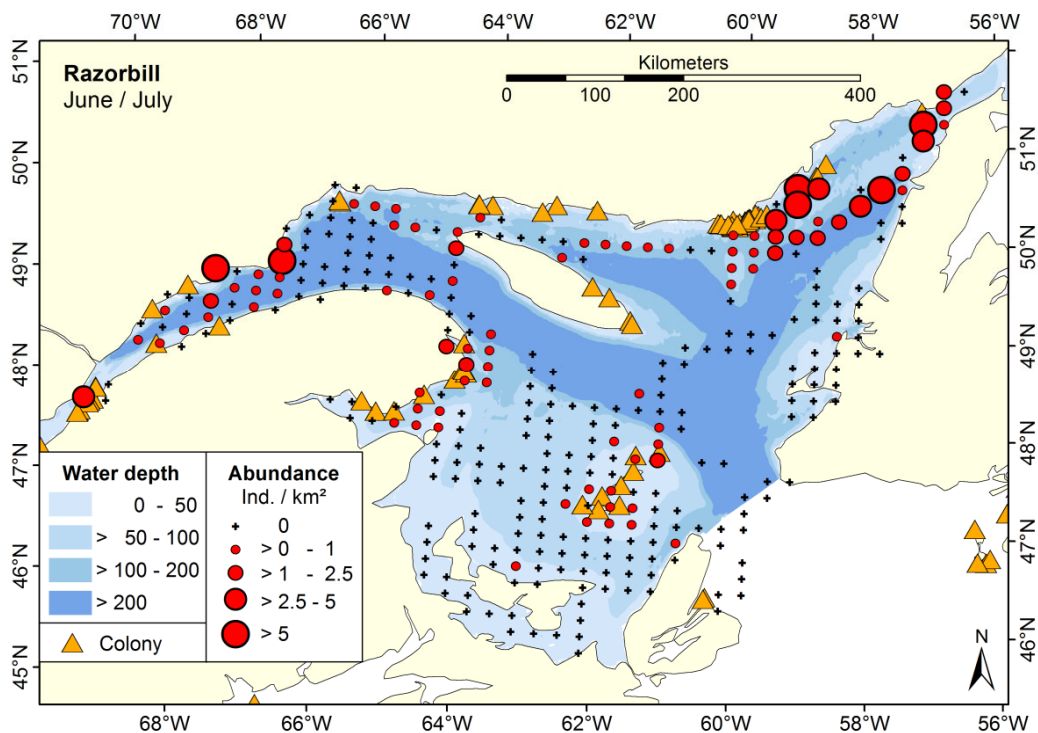


Fig. 32. Distribution and abundance of Razorbills (*Alca torda*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

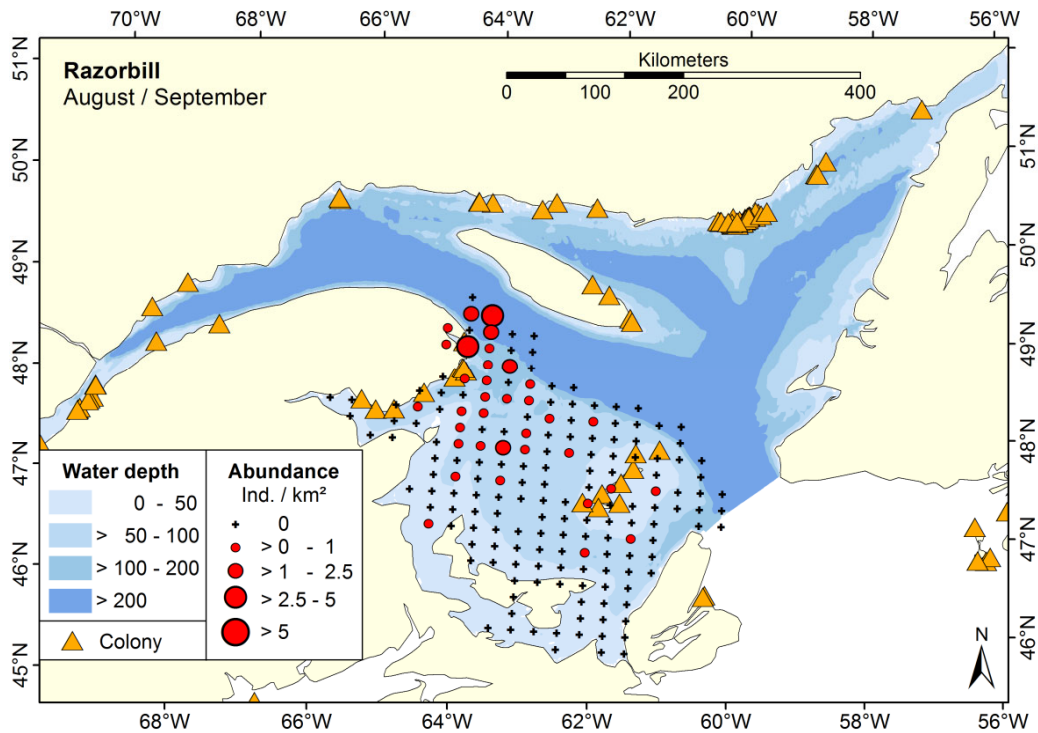


Fig. 33. Distribution and abundance of Razorbills (*Alca torda*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

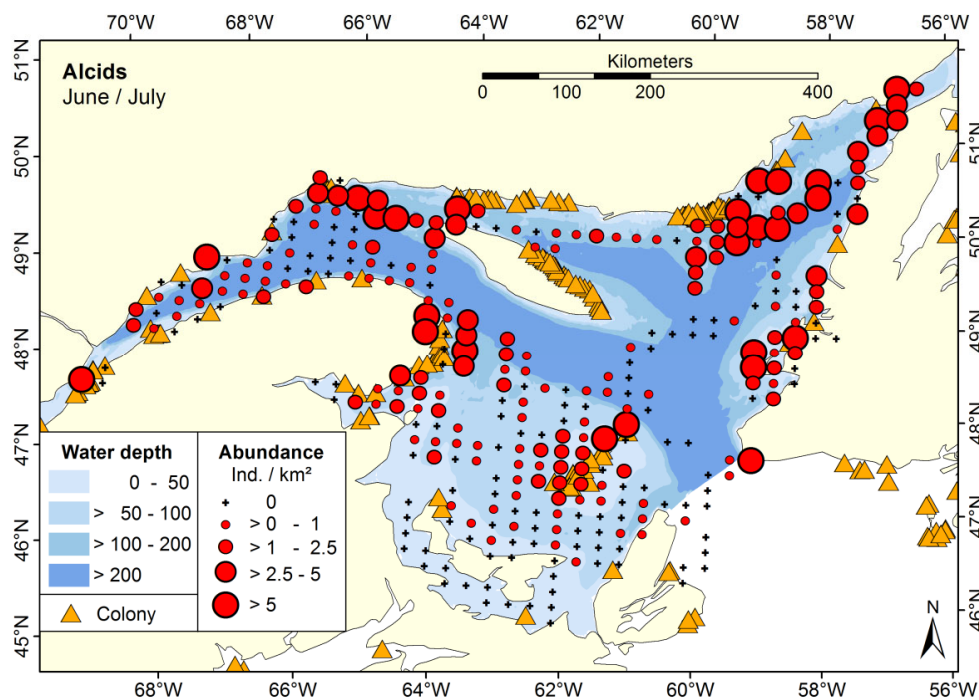


Fig. 34. Distribution and abundance of alcids comprising Common Murres (*Uria aalge*), Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), Atlantic Puffins (*Fratercula arctica*) and mixed categories (for taxonomic details see Appendix) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

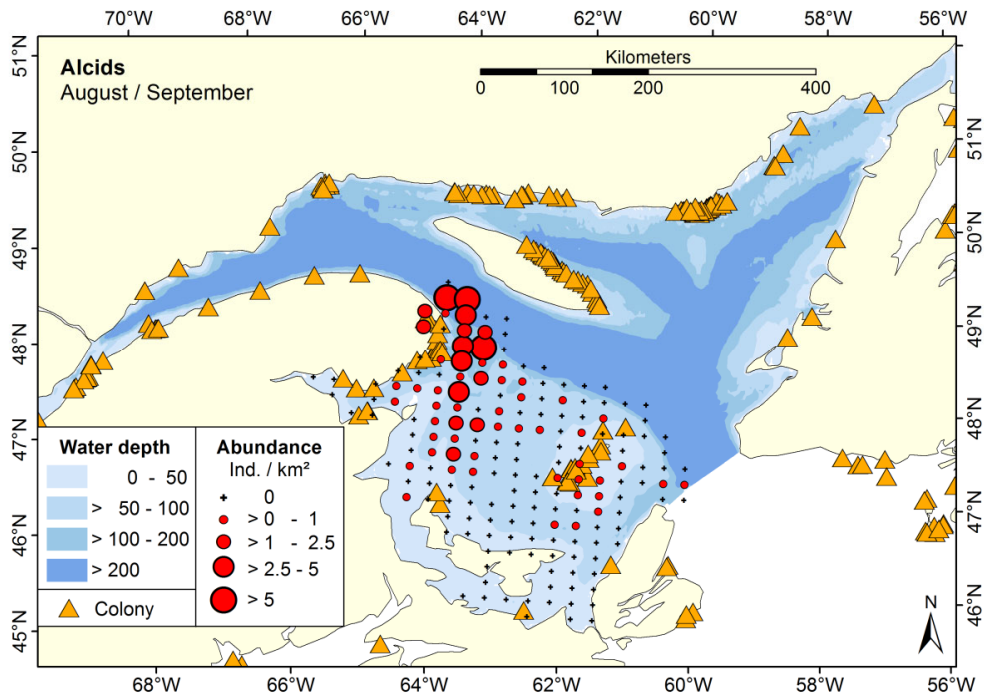


Fig. 35. Distribution and abundance of alcids comprising Common Murres (*Uria aalge*), Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), Atlantic Puffins (*Fratercula arctica*) and mixed categories (for taxonomic details see Appendix) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

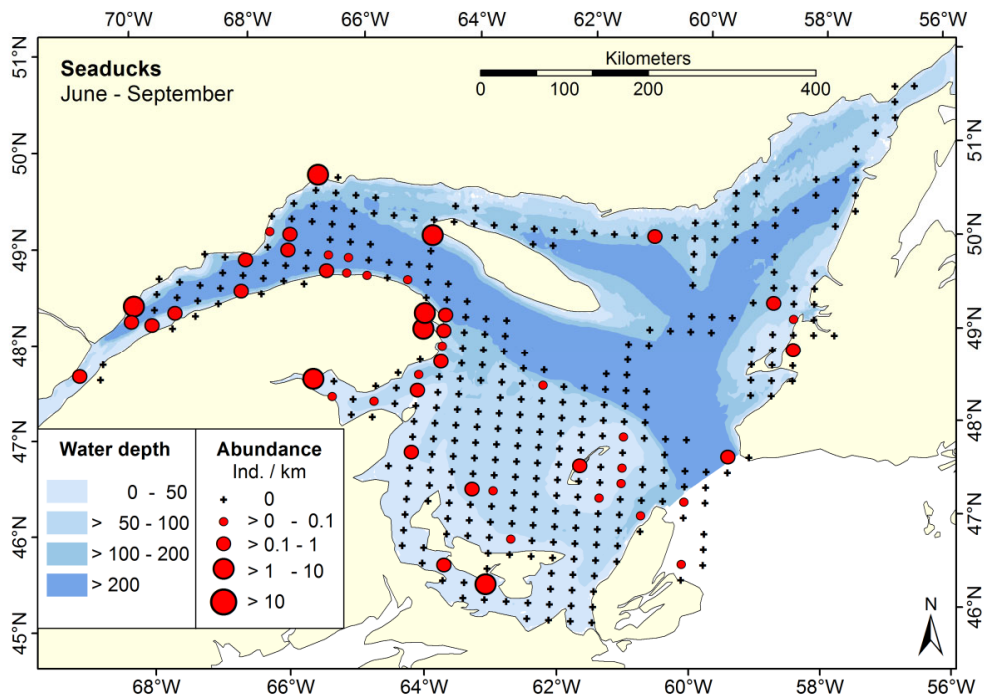


Fig. 36. Distribution and abundance of seaducks comprising Surf Scoters (*Melanitta perspicillata*), Black Scoters (*M. americana*), White-winged Scoters (*M. fusca*), Common Eiders (*Somateria mollissima*), Long-tailed Ducks (*Clangula hyemalis*) and mixed categories (for taxonomic details see Appendix) in the Lower Estuary and Gulf of St. Lawrence during summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

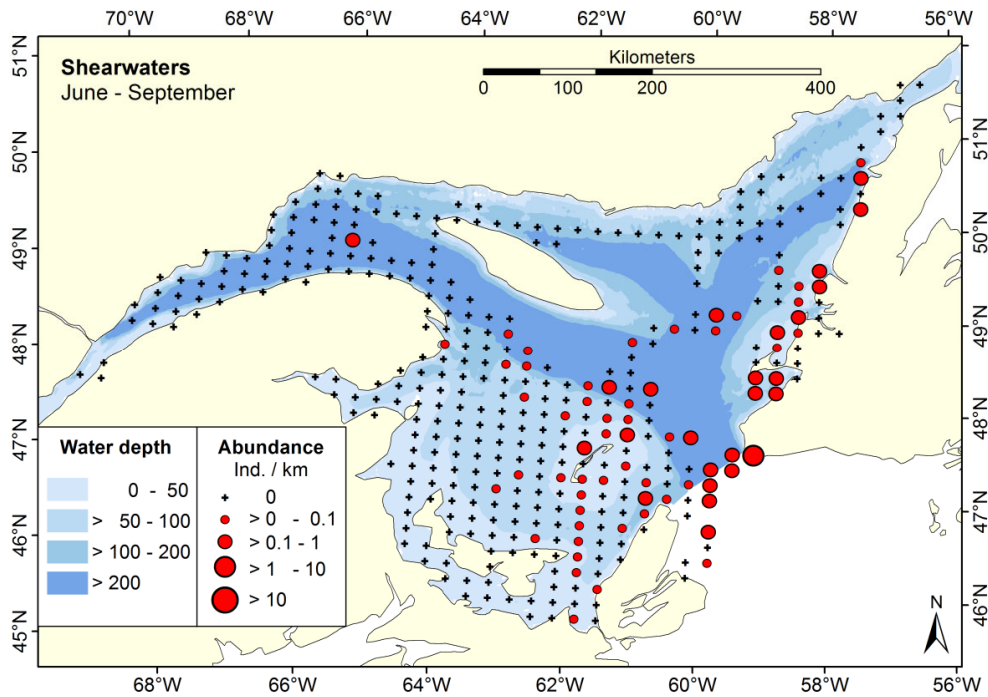


Fig. 37. Distribution and abundance of shearwaters comprising Great Shearwater (*Puffinus gravis*), Sooty Shearwater (*Puffinus griseus*), Manx Shearwater (*Puffinus puffinus*) and mixed categories (for taxonomic details see Appendix) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

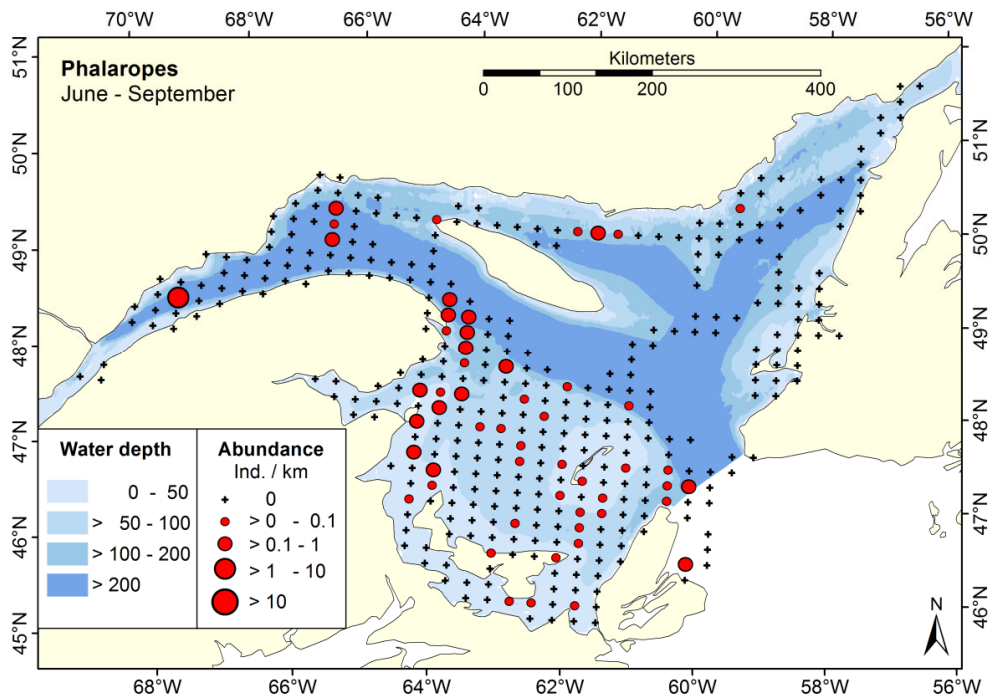


Fig. 38. Distribution and abundance of phalaropes comprising Red-necked Phalarope (*Phalaropus lobatus*), Red Phalarope (*Phalaropus fulicarius*) and mixed category (for taxonomic details see Appendix) in the Lower Estuary and Gulf of St. Lawrence during summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10'x20' grid cells.

Chapter 1 - Distribution & Abundance at sea

Table 4. Estimated totals of common seabird species in the Southern Gulf of St. Lawrence and adjacent waters in mid (June/July) and late summer (August/September) of 2007, 2008 and 2009. Depicted is the estimated average total number and its lower and upper limits of the 95% confidence intervals (=CI) calculated by bootstrapping. For Black Guillemot* and Common Murre** another method was used (for details see Methods); X=no value calculated due to low occurrence; NA=nonapplicable i.e. confidence intervals could not be calculated. The numbers were rounded according to Garthe, Sonntag, et al. (2007): 50–500: to the nearest 10; 500–1,000: to the nearest 50; 1,000–5,000: to the nearest 100; 5,000–20,000: to the nearest 500; 20,000–100,000: to the nearest 1,000; more than 100,000: to the nearest 5,000.

Species	Period	Estimated total	95% CI (lower)	95% CI (upper)
Common Loon	June/July	7,500	3,500	12,000
Common Loon	August/September	26,000	4,700	47,000
Northern Fulmar	June/July	36,000	20,000	51,000
Northern Fulmar	August/September	6,500	4,200	9,500
Wilson's Storm-Petrel	June/July	65,000	37,000	93,000
Wilson's Storm-Petrel	August/September	28,000	8,000	48,000
Northern Gannet	June/July	150,000	90,000	205,000
Northern Gannet	August/September	140,000	110,000	170,000
Double-crested Cormorant	June/July	4,700	950	8,500
Double-crested Cormorant	August/September	13,500	1,400	26,000
Bonaparte's Gull	June/July	X	X	X
Bonaparte's Gull	August/September	6,000	1,300	10,500
Ring-billed Gull	June/July	1,600	650	2,500
Ring-billed Gull	August/September	1,200	0	2,400
Herring Gull	June/July	11,500	7,000	16,000
Herring Gull	August/September	17,500	10,500	24,000
Great Black-backed Gull	June/July	4,600	1,600	7,500
Great Black-backed Gull	August/September	18,000	8,000	27,000
Black-legged Kittiwake	June/July	19,000	12,000	26,000
Black-legged Kittiwake	August/September	7,500	3,700	11,000
Black Guillemot*	June/July	6,500*	2,500*	10,500*
Black Guillemot	August/September	X	X	X
Common Murre** (near colony)	June/July	29,000	NA	NA
Common Murre** (at sea)	June/July	28,000	18,500	36,000
Common Murre** (total)	June/July	57,000	NA	NA
Common Murre	August/September	27,000	14,000	39,000
Razorbill	June/July	6,000	2,700	9,500
Razorbill	August/September	12,000	4,700	19,500

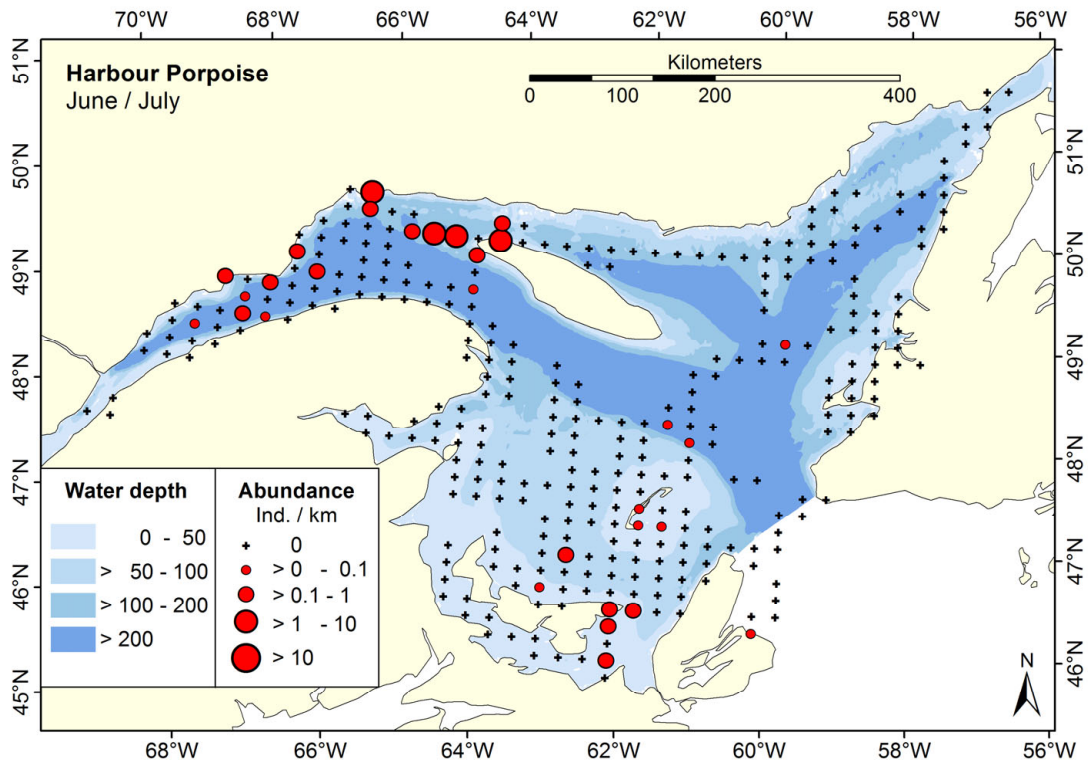


Fig. 39. Distribution and abundance of Harbour Porpoises (*Phocoena phocoena*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

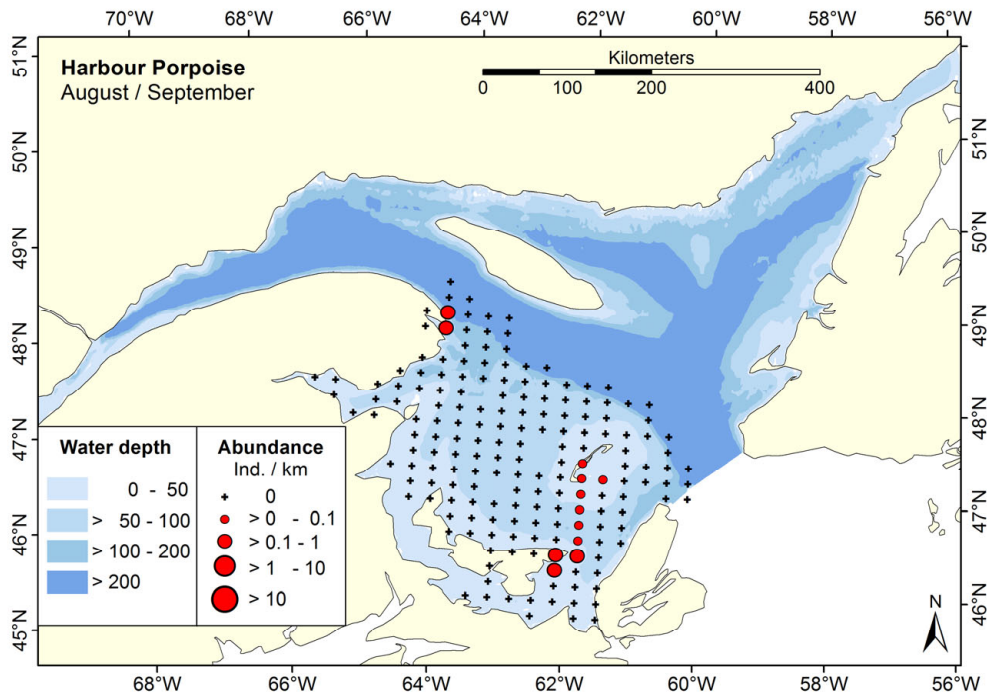


Fig. 40. Distribution and abundance of Harbour Porpoises (*Phocoena phocoena*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

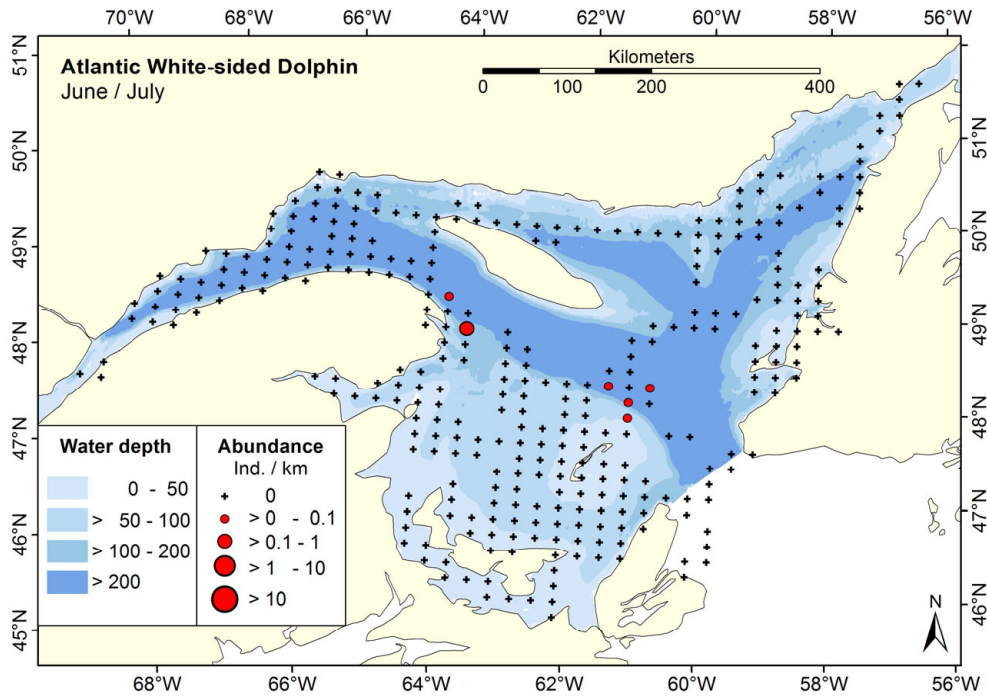


Fig. 41. Distribution and abundance of Atlantic White-sided Dolphins (*Lagenorhynchus acutus*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

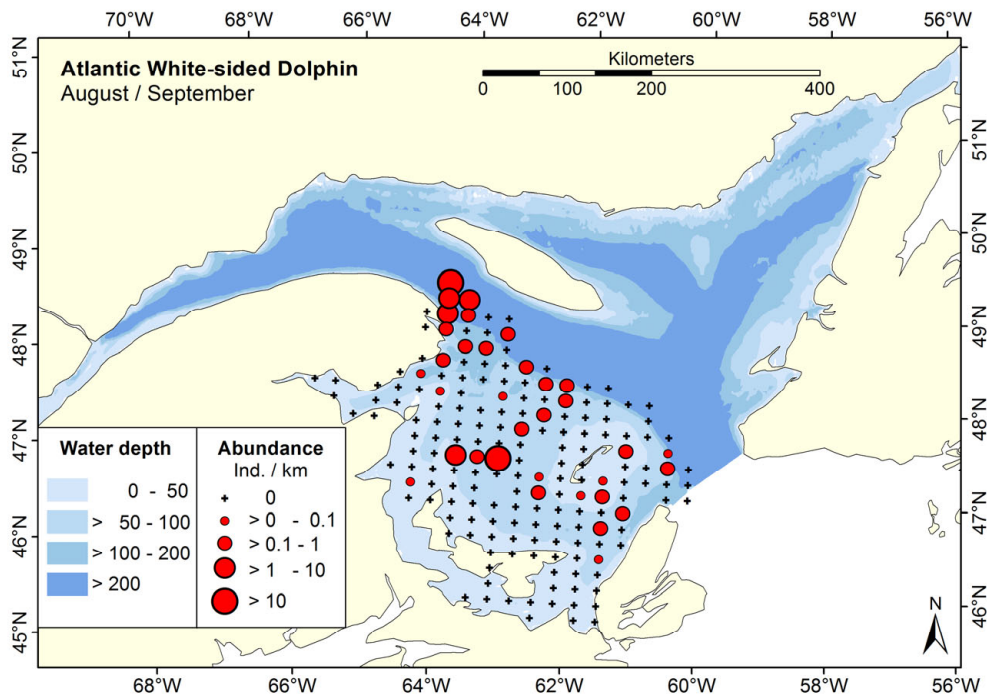


Fig. 42. Distribution and abundance of Atlantic White-sided Dolphins (*Lagenorhynchus acutus*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

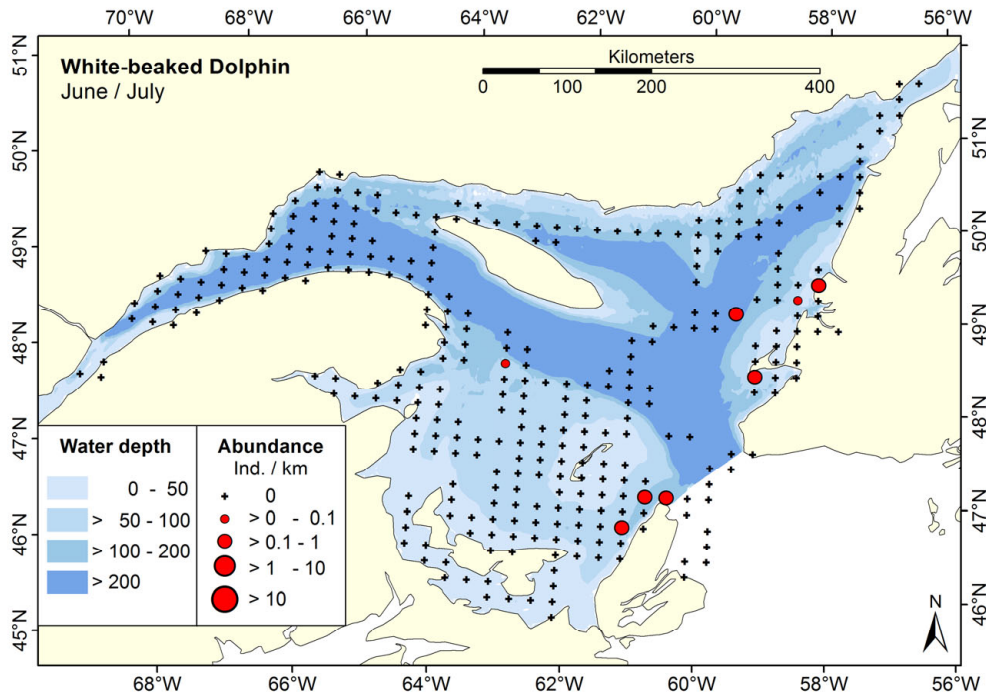


Fig. 43. Distribution and abundance of White-beaked Dolphins (*Lagenorhynchus albirostris*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

Distribution and abundance of marine mammals

Cetaceans occurred widespread and frequently throughout the study area over the whole summer period (Fig. 46, Fig. 47). Atlantic White-sided Dolphins were the most abundant cetaceans. They were most frequently recorded in the Gaspé Current and Southern Gulf in late summer (Fig. 41, Fig. 42). White-beaked Dolphins were less abundant and only observed in midsummer, particularly around Cape Breton Island and along the west coast of Newfoundland (Fig. 43). Harbour Porpoises were second in overall abundance found mostly in the Lower Estuary, Northwestern Gulf and around Prince Edward Island (Fig. 39, Fig. 40). Minke Whales were widespread in low to moderate abundance throughout the summer and occurred mostly in shallower waters (Fig. 44, Fig. 45).

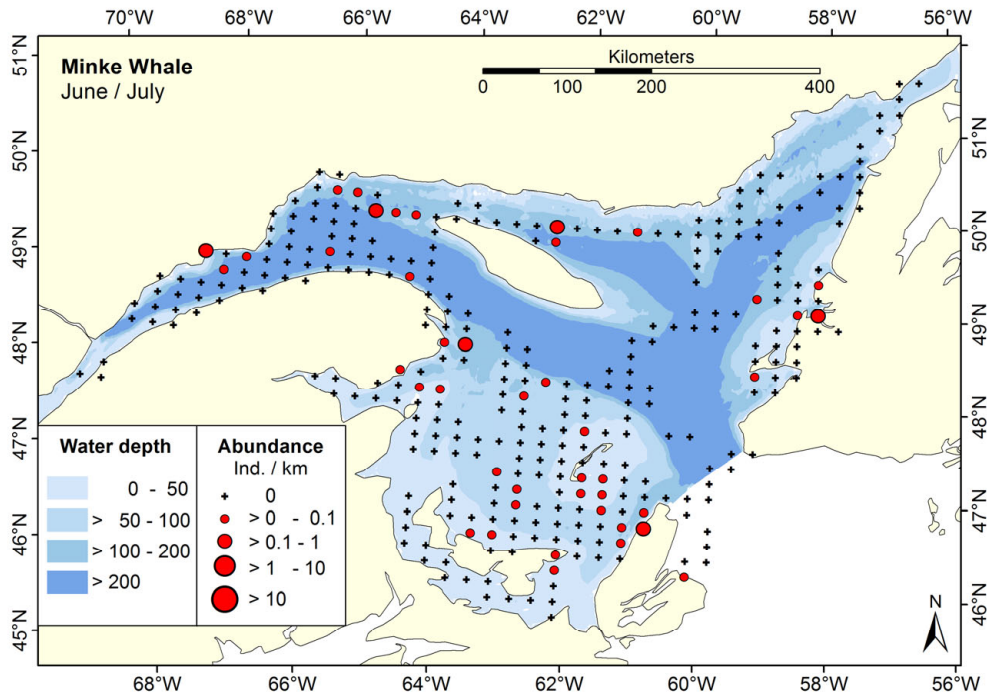


Fig. 44. Distribution and abundance of Northern Minke Whales (*Balaenoptera acutorostrata*) in the Lower Estuary and Gulf of St. Lawrence during midsummer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

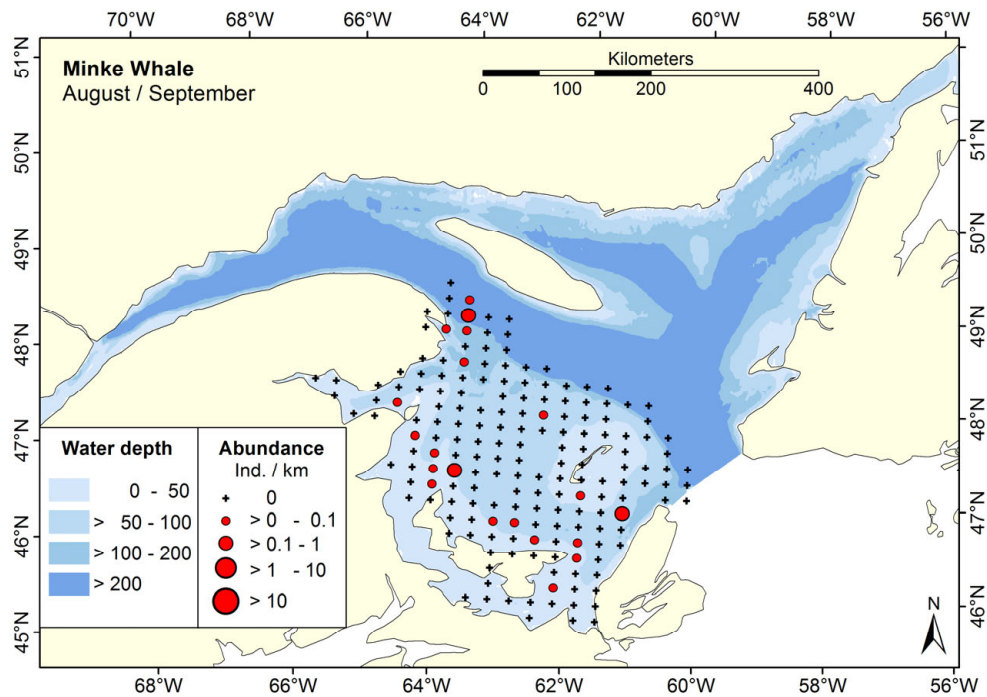


Fig. 45. Distribution and abundance of Northern Minke Whales (*Balaenoptera acutorostrata*) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

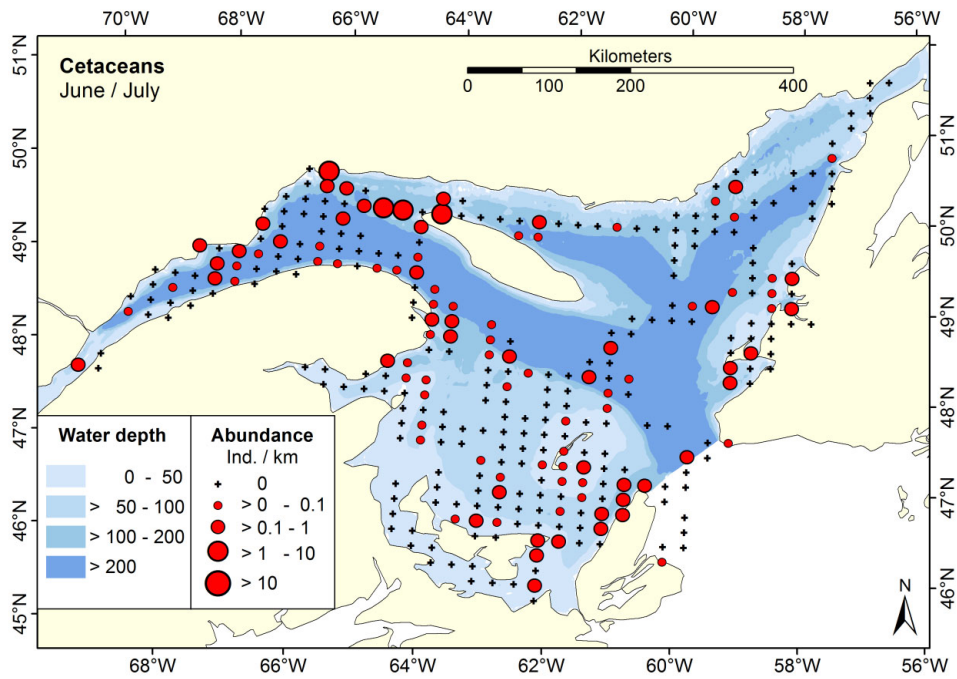


Fig. 46. Distribution and abundance of cetaceans comprising Sperm Whales (*Physeter macrocephalus*), Humpback Whales (*Megaptera novaeangliae*), Blue Whales (*Balaenoptera musculus*), Fin Whales (*Balaenoptera physalus*), Sei Whale (*Balaenoptera borealis*), Minke Whales (*Balaenoptera acutorostrata*), Long-finned Pilot Whales (*Globicephala melas*), Belugas (*Delphinapterus leucas*), White-beaked Dolphins (*Lagenorhynchus albirostris*), Atlantic White-sided Dolphins (*Lagenorhynchus acutus*), Harbour Porpoises (*Phocoena phocoena*) and mixed categories (for taxonomic details see Appendix) in the Lower Estuary and Gulf of St. Lawrence during midsummer of 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

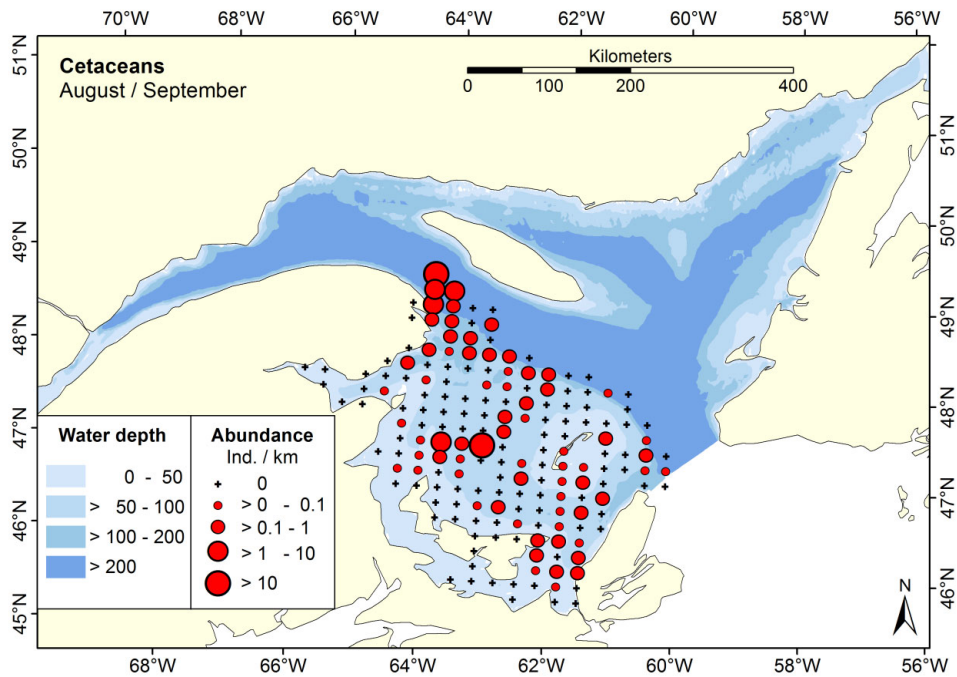


Fig. 47. Distribution and abundance of cetaceans (species list see Fig. 46) in the Southern Gulf of St. Lawrence and adjacent waters during late summer 2007, 2008 and 2009 based on ship-based surveys depicted in 10' * 20' grid cells.

Discussion

Census technique, abundance and estimated totals

Generating reliable results on abundance and numbers by surveying highly mobile species in a dynamic environment from a mobile platform might seem a rather challenging task. However, the methods for counting seabirds have evolved and matured from relative abundance (see Brown 1986) to an abundance (ind./km²) based on distance sampling (Buckland et al. 2001). The latter takes the incomplete detectability of seabirds at sea into account (Fifield et al. 2009). Despite the great advances in standardizing survey techniques (Tasker et al. 1984) and reducing many problems and pitfalls there are still some limitations of these methods.

One problem is that with our method we can only correct perpendicular to the side of the vessel for birds that are not detected. And we have to assume that we detect 100% of birds being ahead of the platform. In distance sampling this would relate to $g(0)=1$ which is an important assumption for the reliability of abundance calculations (see Bächler & Liechti 2007) that we cannot verify with our method. However, our protocol is widely used in European waters and the standard method applied in the North Sea (Camphuysen 2011). Moreover, it is compatible with the protocol of the eastern Canada pelagic seabird monitoring program (ECSAS, Fifield et al. 2009) which was restarted in 2005 and applies the methods described by Gjerdrum et al. (2012). This allows for comparisons of our study with effort in adjacent waters as well as with waters in the Northeast Atlantic Ocean. This is a great advantage as the applications for multi-jurisdictional areas increase (Fifield et al. 2009).

The results of our study show both the strengths and weaknesses of our technique. An advantage of our dataset is its homogeneity as the entire census data were collected by one experienced observer. This comprised experience in the survey method as well as in the identification of species. Thus, inter-observer variability regarding detection probability or identification skills could be fully excluded for our dataset.

The correction factors we calculated were all low compared with studies from adjacent waters (Fifield et al. 2009) or from the North Sea (Garthe et al. 2007b). One likely explanation might be that the bulk of our census data was collected on a large research vessel with an eye level of 13m above the sea surface. This high outlook probably enabled many seabirds to be detected in the outer transect bands. Moreover, the weather conditions and associated sea states were mostly excellent to moderate further increasing detection probability.

However, ideally individual seabirds would not react to the platform as it approaches but many individuals do and some species are particularly prone to either attraction or escape. Regarding the latter response loons are known to react particularly sensitive (Garthe & Hüppop 2004, Bellebaum et al. 2006) and the majority of Common Loons during our surveys tried to escape from the approaching vessel often more than 1km ahead. Thus, their distribution inside our transect was biased by their behavioural reaction (e.g. Hyrenbach et al. 2007). This probably led to a correction factor calculated with distance sampling that underestimated the proportion of birds actually missed. We tried to

circumvent this problem by conservatively estimating how many Common Loons were missed. However, loons in general might be more appropriately counted by aerial surveys (Garthe et al. 2007b, Markones & Garthe 2012). All alcids and several of the other species also frequently showed escape reactions and distraction but these were hardly as pronounced as in loons. Generally, flushing up or escape diving of alcids and other species occurred when the distance to the vessel was shorter. Thus, the distance judgment was unlikely to be biased substantially.

As our data were collected on ships of opportunity some gaps in our dataset exist. These occurred particularly in the central and northeastern part of the Gulf. In addition, surveys were mostly conducted in waters beyond 10m depth due to the size of most vessels. Thus, for some groups like seaducks and terns for example which have important colonies in the study area (CWS unpubl. data) their main habitat could not be quantitatively surveyed. For these groups dedicated surveys in coastal waters would be needed. For other species, especially for Common Loons, Black Guillemots, Razorbills and *Larus* gulls, the precision of abundance estimates might also be improved by incorporating dedicated surveys in selected areas, particularly during midsummer. The estimated total number of Black Guillemots in the Southern Gulf during midsummer thus only represents a minimum number, as important areas in close proximity to land were only rarely surveyed. For alcids the Northeastern Gulf is known to host important colonies. An increased effort in these waters would promise a wider basis for calculating abundance in this area and allow for the calculation of reliable at-sea totals.

As seabird distribution patterns can change within short time spans (e.g. Markones et al. 2008), it is important to have sufficient spatial and temporal survey effort in an area before calculating total numbers. Thus, we only generated estimates for the Southern Gulf which was most intensively surveyed during the three years of our study. The calculation of seabird totals is more reproducible when a bootstrap can be applied than an estimate based on defining areas of different abundance (Markones & Garthe 2012). In Black Guillemots and Common Murres however, we had to alter methods due to the extreme differences in abundance (see Methods). For Common Murres we selected a combination of both methods. In support of this approach, very similar results were gained when comparing estimated totals for Little Gulls (*Hydrocoloeus minutus*) by applying a bootstrap for the entire study area or separately for two subareas of different abundance (Markones & Garthe 2012). Thus, the results on estimates of Common Murres and Black Guillemots in midsummer are most likely comparable with the other estimates despite the difference in methods.

Hotspots

Species with significant breeding colonies in the study area, particularly Northern Gannets, Common Murres, Razorbills, Black Guillemots and Black-legged Kittiwakes, contributed substantially to the local seabird community during summer (Cairns et al. 1991, Fifield et al. 2009). Several areas seemed of particular importance for single or multiple species and some changed with the progression of summer whereas others were visited during the whole period. Many of these hotspots were already

identified in the past despite methodological differences (see Brown 1986). Hotspots occurred in all subdivisions but some of these persistently stood out and were often related to oceanographic and bathymetric peculiarities. The distal part of the Gaspé Current was one such hotspot where deep nutrient rich waters from the St. Lawrence River meet warmer and shallower waters of the Southern Gulf, resulting in extremely high productivity (see Chapter 2). As a consequence, a range of seabirds such as Gannets, alcids and Kittiwakes, have significant colonies in this area. Herring and Great Black-backed Gulls were also highly abundant.

Bonaventure Island is one of the largest colonies in the whole study area. For Northern Gannets it represents one of the two world's largest colonies with close to 60,000 breeding pairs in 2009 (JF Rail, CWS unpubl. data). Regarding alcids, only the adjacent waters of the Gaspé Current held high concentrations during the whole summer period. The significance of this area was also underlined by the high abundance of cetaceans. Particularly Blue and Fin Whales alongside with Atlantic White-sided Dolphins were most abundant in these waters. Consequently, an AOI (Area of Interest) for a Marine Protected Area has been announced for a part of this area (see www.dfo-mpo.gc.ca/oceans/marineareas-zonesmarines/mpa-zpm/index-eng.htm#).

Other multispecies hotspots occurred during midsummer along the northern rim of the Lower Estuary, in the Sept Iles region, west and north of the Anticosti Gyre in the Northwestern Gulf and along the Lower North Shore near the St. Mary's Islands towards the Strait of Belle Isle (where particularly alcids were abundant). Another multispecies hotspot occurred along the west coast of Newfoundland from the Bay of Islands area south around the Port au Port Peninsula into St. George's Bay. Cabot Strait represented a hotspot for various species, which was already observed in fall by Fifield et al. (2009). These authors attributed the strong currents and large concentrations of zooplankton (Head & Pepin 2007), which might support a high availability of different types of prey (see Gjerdrum et al. 2008), as likely drivers behind these patterns. Other hotspots were observed around Cape Breton Island and the Magdalen Islands, as well as west and east of Prince Edward Island where frontal structures could frequently be observed.

Comparison of distributional patterns

When comparing our results with those of similar studies in this region some limitations arise because of differences in methods, spatial scale and seasonal splits. These methodological differences are rather pronounced compared with the past survey effort within the PIROP framework (see Brown 1986, Fifield et al. 2009). Recent survey effort in the Atlantic Provinces however, was based on an approach that differed only in minor details (see Gjerdrum et al. 2012). Although the distribution patterns shown by Brown (1986) mostly comprised data collected in the 1970s and 1980s, which were based on relative abundance of seabirds rather than abundance as ind./km², some species showed similar distribution and concentration patterns. These were e.g. Northern Fulmars, Leach's Storm-Petrels, Northern Gannets and Great-Black-backed Gulls. Wilson's Storm-Petrels on the opposite were far less abundant in the past compared with our surveys. This species

was one of the most numerous in the Southern Gulf during midsummer and also very abundant in other areas such as the Northwestern and Central Gulf. This partly contradicts Brown's statement (1986) that the Gulf is not frequented by large numbers of trans-oceanic and trans-equatorial migrants. Regarding shearwaters however, our findings are in line with his description of highest abundance occurring in Cabot Strait and a rather low overall abundance compared to the adjacent open Atlantic waters off Newfoundland and Nova Scotia. Recent survey effort in the latter area also confirmed this pattern (see Fifield et al. 2009). The distribution of Common Murres though, differed between our results and earlier studies, particularly in the Southern Gulf. In this area we found highest abundance around the two main colonies of Bonaventure Island in the distal part of the Gaspé Current and near Bird Rocks northeast of the Magdalen Islands. Brown (1986) conversely recorded the main concentrations at greater distances from these colonies. For Kittiwakes we also observed some important differences and found a higher abundance in the Lower Estuary compared to earlier findings. Some of these differences can presumably be attributed to the different seasonal splits applied and different spatial coverage. Our midsummer distribution covered the breeding season for most species (see Québec Breeding Bird Atlas, www.atlas-oiseaux.qc.ca/donneesqc/calendrier.jsp?lang=en), but during late summer many species will leave their colonies, accompany their young at sea and start migration. In Brown's atlas (1986) the period April to June comprised patterns of pre-breeding and breeding. Consequently, concentrations further away from colonies might well belong to the earlier period. For future analyses of seabird distribution in this area, the definition of species-specific seasons (see Garthe et al. 2007b) might be valuable. As the phenology and related usage and function of particular marine areas differs between species.

Seabird totals in relation to population sizes

The significance of particular marine areas can be viewed from many different perspectives and scales. Here, we discuss our results on estimated seabird totals for a significant part of the entire study area – the Southern Gulf. This part of the Gulf hosts the most diverse zooplankton community and important nursery area for many species of fish such as Atlantic Mackerel (*Scomber scombrus*) and Atlantic Herring (*Clupea harengus*, Chapter 2). As a consequence of this variety of abundant prey, this area hosts large seabird colonies in addition to a range of cetaceans. Our study showed that at-sea abundance of several species amounts to considerable numbers in the Southern Gulf. For Northern Gannets it may be the most important area worldwide during summer. Their estimated total at sea relates to 83% (midsummer) and 78% (late summer) of the Gulf breeding population, which comprised approximately 180,000 birds in 2009. Even in relation to the estimated entire Canadian breeding population of 200,000 to 300,000 breeding birds in 2011 (www.ec.gc.ca/soc-sbc/oiseau-bird-eng.aspx?sY=2011&sL=e&sM=s&sB=NOGA), the Southern Gulf holds 47% to 75% of these numbers. However, 300,000 breeders seem a rather high estimate given that the other three Canadian colonies on the east coast of Newfoundland are significantly smaller than those at Bonaventure Island and Bird Rocks. The comparison of at-sea totals and breeding numbers is not

entirely correct as there was a range of non-breeders present in our estimate e.g. immature birds that were observed in changing proportions (N Guse unpubl. data). However, the breeding population currently constitutes the best available reference point as an estimate for the biogeographic population is lacking. We believe our data basis to be excellent for Gannets due to their frequent and widespread occurrence. In conclusion the magnitude of our estimate in relation to overall Gannet numbers seems realistic and underlines the high importance of this area during summer.

In Razorbills, a biogeographic population value was also not available and the estimated Canadian breeding population ranges from 76,000 (Fifield et al. 2009) to 100,000 to 200,000 breeding birds (www.ec.gc.ca/soc-sbc/oiseau-bird-eng.aspx?sY=2011&sL=e&sM=s&sB=RAZO). As a consequence, the Southern Gulf estimate for Razorbills at sea would comprise a population share from a minimum of 3% in midsummer to a maximum of 16% in late summer depending on source. However, as in Gannets, the proportion of non- or pre-breeders might be substantial (Cairns et al. 1991). During our surveys we indeed observed a range of parent-chick-pairs at sea. Still, the Southern Gulf waters most likely comprised a significant proportion of the entire North American Razorbill population during summer. The estimated totals for Common Murres and Black Guillemots were also only related to their respective Canadian breeding population, which is estimated at >1,000,000 (www.ec.gc.ca/soc-sbc/oiseau-bird-eng.aspx?sY=2011&sL=e&sM=s&sB=COMU) and 400,000 to 500,000 (www.ec.gc.ca/soc-sbc/oiseau-bird-eng.aspx?sY=2011&sL=e&sM=s&sB=BLGU) breeding birds, respectively. The at-sea numbers of Common Murres during mid and late summer in the Southern Gulf would thus equate to a maximum of 6 to 3% of the Canadian breeding population. The at-sea numbers of Black Guillemots would correspond to 1 - 2% of their respective breeding population.

Our at-sea estimate of Black-legged Kittiwakes relates to a minimum of 2% in midsummer to a maximum of 4% in late summer of the total Canadian breeding population (www.ec.gc.ca/soc-sbc/oiseau-bird-eng.aspx?sY=2011&sL=e&sM=s&sB=BLKI). For Herring and Black-backed Gulls, as well as Common Loons, available biogeographic population values allowed straightforward comparisons. For Herring Gulls the estimate for the Southern Gulf comprised 3% in midsummer and 4% in late summer of the total biogeographic population of the North American subspecies *Larus argentatus smithonianus* (Wetlands International 2012). For Great Black-backed Gulls and Common Loons the Southern Gulf was similarly important and comprised 1% in midsummer and 4% in late summer of their respective biogeographic population, which is the Northwest Atlantic for the Great Black-backed Gull and North American for the Common Loon (Wetlands International 2012). The estimated numbers of Common Loons for the Southern Gulf in late summer exceeded the total estimates of wintering individuals on the continental shelf of the Southeastern United States (Haney 1990), underlining the importance of the Gulf region for this species. Moreover, particularly the waters west and south of Prince Edward Island seemed to have an important function during this period. We often encountered groups of several Common Loons with visible differences in plumages. We assumed that these groups consisted of families or birds moulting together. Both the late chick rearing period before the young become fully independent, as well as moulting represent sensitive

periods for these birds. In conclusion, our findings demonstrate the presence of high proportions of biogeographic populations for several species in the study area and distinctly highlight the outstanding importance of the Southern Gulf region for seabirds in an international context which has not been described quantitatively so far.

Outlook

Beyond our scientific scope, data on seabird distribution, abundance and estimated totals may be more valuable than ever due to increased anthropogenic activities in the marine environment (Garthe et al. 2007b, Fifield et al. 2009) and related marine spatial planning applications (Hyrenbach 2007, Short 2011). These applications comprise for example hydrocarbon production and exploration, as well as the setup of Marine Protected Areas (MPAs, www.dfo-mpo.gc.ca/oceans/marineareas-zonesmarines/mpa-zpm/index-eng.htm), which are currently in progress in these waters. Thus, dedicated survey effort in areas such as along the North Shore and the Northeastern Gulf – where large spatial and seasonal gaps occur and important habitats for numerous seabirds occur or are suspected to – would be important to enable balancing future human pressures with the conservation of species and habitat.

Acknowledgements

We are sincerely grateful to Alain Gagné, Tom Hurlbut, François Grégoire, Charline Lévesque and their colleagues for the opportunity to join their research cruises. We thank the Crews of the ‘Teleost’ and other vessels we worked on for their support and cooperation during the surveys. We also thank Jean-François Rail and Carina Gjerdrum very much for providing data on seabird colonies as well as Esther Rickert for entering census data.

Appendix

Appendix-Table 1. All taxa recorded during ship-based seabird surveys in the Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Presented are seasonal sums separately for mid- and late summer (split of periods as in Methods) and the total sum of a taxon. The scientific and North American names are given. The scientific and North American nomenclature of birds follows the American Ornithologists' Union Checklist <http://checklist.aou.org/taxa/> (last accessed 8th April 2013). The scientific and North American names of other marine megafauna were retrieved from the Integrated Taxonomic Information System on-line database <http://www.itis.gov> (last accessed 8th April 2013). The table is sorted downwards by total sum.

Taxon/Scientific name	American English	June/July (n=ind.)	August/September (n=ind.)	Total (n=ind.)
<i>Morus bassanus</i>	Northern Gannet	5,500	10,504	16,004
<i>Uria aalge</i>	Common Murre	4,544	227	4,771
<i>Larus argentatus</i>	Herring Gull	1,614	740	2,354
<i>Fulmarus glacialis</i>	Northern Fulmar	2,078	255	2,333
<i>Rissa tridactyla</i>	Black-legged Kittiwake	1,866	340	2,206
<i>Alca torda/Uria aalge/lomvia</i>	Razorbill/Common/Thick-billed Murre	1,396	242	1,638
<i>Oceanites oceanicus</i>	Wilson's Storm-Petrel	948	365	1,313
<i>Larus marinus</i>	Great Black-backed Gull	503	718	1,221
<i>Hydrobatidae spec.</i>	unidentified storm-petrel	763	143	906
<i>Phalacrocorax auritus</i>	Double-crested Cormorant	252	587	839
<i>Alca torda</i>	Razorbill	674	105	779
<i>Cephus grylle</i>	Black Guillemot	611	37	648
<i>Gavia immer</i>	Common Loon	295	294	589
<i>Phocoena phocoena</i>	Harbour Porpoise	284	177	461
<i>unidentified large gull</i>	unidentified large gull	10	408	418
<i>Larus delawarensis</i>	Ring-billed Gull	326	33	359
<i>unidentified gull</i>	unidentified gull	205	126	331
<i>Melanitta perspicillata</i>	Surf Scoter	39	286	325
<i>Phalaropus spec.</i>	unidentified phalarope	90	200	290
<i>Chroicocephalus philadelphia</i>	Bonaparte's Gull	79	197	276
<i>unidentified dolphin</i>	unidentified dolphin	32	222	254
<i>Somateria mollissima</i>	Common Eider	236	10	246
<i>Sterna hirundo</i>	Common Tern	159	67	226
<i>Lagenorhynchus acutus</i>	Atlantic White-sided Dolphin	9	215	224
<i>Phalacrocorax carbo/auritus</i>	Great/Double-crested Cormorant	119	88	207
<i>Sterna hirundo/paradisaea</i>	Common/Arctic Tern	97	60	157
<i>Puffinus gravis</i>	Great Shearwater	148	7	155
<i>Melanitta americana/perspicillata</i>	Black/Surf Scoter	128	23	151
<i>Puffinus griseus</i>	Sooty Shearwater	145	2	147
<i>Oceanodroma leucorhoa</i>	Leach's Storm-Petrel	80	55	135

Chapter 1 - Distribution & Abundance at sea

Appendix-Table 1. Continued.

Taxon/Scientific name	American English	June/July (n=ind.)	August/September (n=ind.)	Total (n=ind.)
<i>Balaenoptera acutorostrata</i>	Minke Whale	86	42	128
<i>unidentified wader</i>	unidentified shorebird	57	67	124
<i>unidentified pinniped</i>	unidentified seal	95	10	105
<i>Gavia stellata</i>	Red-throated Loon	70	30	100
<i>Sterna paradisaea</i>	Arctic Tern	82	14	96
<i>Fratercula arctica</i>	Atlantic Puffin	70	26	96
<i>Alcidae spec.</i>	unidentified auk	56	40	96
<i>Melanitta fusca</i>	White-winged Scoter	64	30	94
<i>Phalaropus fulicarius</i>	Red Phalarope	5	77	82
<i>Gavia spec.</i>	unidentified loon	48	28	76
<i>Balaenoptera physalus</i>	Fin Whale	53	23	76
<i>Gavia immer/adamsii</i>	Common/Yellow-billed Loon	16	59	75
<i>Halichoerus grypus</i>	Grey Seal	37	32	69
<i>Uria lomvia</i>	Thick-billed Murre	65		65
<i>unidentified passerine</i>	unidentified passerine	8	51	59
<i>Globicephala melas</i>	Long-finned Pilot Whale	24	29	53
<i>Phalaropus lobatus</i>	Red-necked Phalarope	11	41	52
<i>unidentified large whale</i>	unidentified large whale	22	22	44
<i>unidentified whale</i>	unidentified whale	32	11	43
<i>unidentified marine mammal</i>	unidentified marine mammal	20	16	36
<i>unidentified bird</i>	unidentified bird	35		35
<i>Anser/Branta spec.</i>	unidentified goose		32	32
<i>Branta canadensis spp.</i>	Canada Goose	28	3	31
<i>Lagenorhynchus albirostris</i>	White-beaked Dolphin	29		29
<i>Uria aalge/lomvia</i>	Common/Thick-billed Murre	29		29
<i>unidentified cetacean</i>	unidentified cetacean	6	21	27
<i>Melanitta spec.</i>	unidentified scoter	19	7	26
<i>Lagenorhynchus acutus/albirostris</i>	Atlantic White-sided/White-beaked Dolphin		23	23
<i>Puffinus puffinus</i>	Manx Shearwater	18	3	21
<i>Balaenoptera musculus/physalus</i>	Blue/Fin Whale	12	5	17
<i>Megaptera novaeangliae</i>	Humpback Whale	11	4	15
<i>Ardea herodias</i>	Great Blue Heron	11	3	14
<i>Charadrius semipalmatus</i>	Semipalmated Plover		14	14
<i>Phalacrocorax carbo</i>	Great Cormorant	7	6	13
<i>Calidris maritima</i>	Purple Sandpiper		12	12
<i>Phoca vitulina</i>	Common Seal	10	2	12
<i>unidentified duck</i>	unidentified duck	11		11

Chapter 1 - Distribution & Abundance at sea

Appendix-Table 1. Continued.

Taxon/Scientific name	American English	June/July (n=ind.)	August/September (n=ind.)	Total (n=ind.)
<i>Stercorarius spec.</i>	unidentified jaeger		11	11
<i>Larus fuscus</i>	Lesser Black-backed Gull		11	11
<i>Balaenoptera musculus</i>	Blue Whale	8	2	10
<i>Stercorarius parasiticus</i>	Parasitic Jaeger	2	7	9
<i>Puffinus/Calonectris spec.</i>	unidentified shearwater	7	1	8
<i>Arenaria interpres</i>	Ruddy Turnstone		8	8
<i>Calidris spec.</i>	unidentified sandpiper		7	7
<i>Emberizidae spec.</i>	Emberizidae spec.	2	5	7
<i>Delphinapterus leucas</i>	Beluga	7		7
<i>Puffinus gravis/Calonectris diomedea</i>	Great/Cory's Shearwater	4	2	6
<i>Falco columbarius</i>	Merlin		6	6
<i>unidentified small cetacean</i>	unidentified small cetacean	6		6
<i>Pandion haliaetus</i>	Osprey	4	1	5
<i>unidentified swallow</i>	unidentified swallow	5		5
<i>Melanitta americana</i>	Black Scoter	4		4
<i>Calidris pusilla</i>	Semipalmated Sandpiper		4	4
<i>Numenius phaeopus</i>	Whimbrel	1	3	4
<i>Archilochus colubris</i>	Ruby-throated Hummingbird	4		4
<i>Physeter macrocephalus</i>	Sperm Whale	4		4
<i>Dermochelys coriacea</i>	Leatherback Turtle		4	4
<i>unidentified tuna</i>	unidentified tuna		4	4
<i>Clangula hyemalis</i>	Long-tailed Duck	2	1	3
<i>Falco peregrinus</i>	Peregrine Falcon		3	3
<i>Stercorarius pomarinus</i>	Pomarine Jaeger		3	3
<i>Cetorhinus maximus</i>	Basking Shark	2	1	3
<i>Balaenopteridae spec.</i>	unidentified rorqual whale	3		3
<i>Gavia pacifica</i>	Pacific Loon	2		2
<i>Podiceps nigricollis</i>	Eared Grebe		2	2
<i>Anas acuta</i>	Northern Pintail	2		2
<i>Pluvialis squatarola</i>	Black-bellied Plover		2	2
<i>Larus hyperboreus</i>	Glaucous Gull	2		2
<i>Mola mola</i>	Ocean Sunfish		2	2
<i>unidentified fish school</i>	unidentified fish school	1	1	2
<i>Tyrannidae spec.</i>	unidentified tyrant flycatcher	2		2
<i>Parulidae spec.</i>	unidentified wood warbler		2	2
<i>Podiceps grisegena</i>	Red-necked Grebe		1	1
<i>Haliaeetus leucocephalus</i>	Bald Eagle		1	1
<i>Circus cyaneus</i>	Northern Harrier		1	1

Chapter 1 - Distribution & Abundance at sea

Appendix-Table 1. Continued.

Taxon/Scientific name	American English	June/July (n=ind.)	August/September (n=ind.)	Total (n=ind.)
<i>Accipiter striatus</i>	Sharp-shinned Hawk		1	1
<i>Falco sparverius</i>	American Kestrel		1	1
<i>Tringa flavipes</i>	Lesser Yellowlegs	1		1
<i>Stercorarius skua</i>	Great Skua		1	1
<i>Larus atricilla</i>	Laughing Gull	1		1
<i>Xema sabini</i>	Sabine's Gull		1	1
<i>Hydroprogne caspia</i>	Caspian Tern		1	1
<i>Thalasseus sandvicensis</i>	Sandwich Tern	1		1
<i>Chlidonias niger</i>	Black Tern		1	1
<i>Columba livia</i>	Rock Pigeon		1	1
<i>Tachycineta bicolor</i>	Tree Swallow	1		1
<i>Troglodytes hiemalis</i>	Winter Wren		1	1
<i>Setophaga virens</i>	Black-throated Green Warbler		1	1
<i>Passerculus sandwichensis</i>	Savannah Sparrow		1	1
<i>Junco hyemalis</i>	Dark-eyed Junco		1	1
<i>large Balaenoptera spec.</i>	Blue/Fin/Sei Whale	1		1
<i>Balaenoptera borealis</i>	Sei Whale	1		1
<i>Cystophora cristata</i>	Hooded Seal	1		1
<i>unidentified shark</i>	unidentified shark		1	1

Chapter 2: The influence of colony location and oceanography on seabird distribution in the Lower Estuary and Gulf of St. Lawrence during summer



Chapter 2: The influence of colony location and oceanography on seabird distribution in the Lower Estuary and Gulf of St. Lawrence during summer

Nils Guse (1), Nele Markones (1), Sven Adler (2), Stefan Garthe (1)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Department of Forest Resource Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

Abstract

Marine predators respond to their changing environment at different spatio-temporal scales. Distribution and abundance of seabirds can be related to environmental and oceanographic variables that influence their foraging habitat. We studied habitat choice of nine common seabird species at a coarse to meso-scale in the Northwestern Atlantic (Lower Estuary and Gulf of St. Lawrence) in June 2008 and 2009. The study area is a hotspot for marine megafauna and subject to intense anthropogenic use. Several seabird species have significant colonies in the area. For Northern Gannets it is one of the most important sites worldwide. Seabird and oceanographic data were collected via ship-based surveys. We created spatial habitat models for seabird species with and without spatial constraint. Focus lay on water mass indicators, primary productivity and distance to nearest colony or land as explanatory variables. For all but one species significant variables were identified. Models for Common Murres, Herring Gulls and Northern Fulmars performed best. Distance to colony or land, respectively, and sea surface salinity were most important predictors. Modeled average ranges relative to distance to colony strongly paralleled foraging ranges of breeding birds described in other studies (e.g. with GPS data loggers). Northern Fulmars, Common Murres and Razorbills were associated with waters of higher sea surface salinity, Herring and Great Black-backed Gulls with lesser saline waters. Northern Fulmars and Wilson's Storm-Petrels were less frequent in coastal waters. Common Murres were significantly positively linked with stratified waters, whereas this relationship was negative for Razorbills and Northern Fulmars. Black-legged Kittiwakes, Herring Gulls, Razorbills and Common Murres were associated with waters of elevated primary productivity. We identified particularly important seabird habitats off the Gaspé Peninsula, around the Magdalen Islands, in the Northwestern Gulf and along the Québec North Shore. The Gulf and Estuary are recognized as Large Ocean Management Area (LOMA). Our results may serve as baseline information regarding habitat requirements of seabirds and can be used in marine spatial

planning applications such as designation of Marine Protected Areas (MPAs). Further studies combining ship-based seabird surveys with sampling of oceanographic variables and prey, as well as simultaneous equipment of breeding birds with data loggers are recommended to gain insight into processes and mechanistic links in selected areas.

Introduction

Seabirds are top predators living in a highly dynamic marine environment that shows variation at extremely different spatial and temporal scales. Seabird abundance and distribution has been successfully linked to environmental variables and oceanography (e.g. Hunt et al. 1999, Ballance et al. 2006, Sydeman et al. 2006, Ainley et al. 2009, Scott et al. 2010, Cox et al. 2012, Embling et al. 2012). Their foraging ecology responds at varying spatio-temporal scales to oceanographic processes that influence the distribution and abundance of plankton and other marine organisms (e.g. Hunt & Schneider 1987, Schneider 1993, Hunt et al. 1999). Several studies have emphasized the links between hydrographic phenomena such as fronts or convergences and concentrations of top predators such as seabirds (e.g. Schneider 1982, Follestad 1990, Decker & Hunt 1996, Ladd et al. 2005) or cetaceans (e.g. Doniol-Valcroze et al. 2007). At larger spatio-temporal scales seabird distribution has been connected to certain water masses that may differ in their physical and biological properties (e.g. Haney 1986, Garthe 1997).

Our study concentrated on the habitat choice of the dominant seabird species (see Methods) occurring in a semi-enclosed shelf sea - the Lower Estuary and Gulf of St. Lawrence in the Northwest Atlantic Ocean. This area exhibits unique oceanographic features (White & Johns 1997) and hosts a substantial and increasing number of breeding seabirds (Cairns et al. 1991). It is one of the most important sites worldwide for the Northern Gannet (*Morus bassanus*) (Seabird and Waterbird database of Québec, CWS unpubl. data). Our aim was to identify the relevant habitats and environmental variables during the breeding season at a coarse (1-100km) to meso-scale (100-1,000km) (Haury et al. 1978, Hunt & Schneider 1987) using a spatial modeling approach. Apart from a large scale study in the Northwest Atlantic (Huettmann & Diamond 2001), a detailed analysis for seabirds in the Lower Estuary and Gulf of St. Lawrence was lacking. We focused on a suite of seabird species that differ regarding foraging techniques, dietary niches and spatial constraint. We analyze the links between their distribution and environmental variables by concentrating on water mass indicators. We compare our findings with habitat choice of the respective seabird species described for other marine ecosystems.

With regard to the outstanding ecological importance of the Estuary and Gulf as Large Ocean Management Area (LOMA, Dufour & Ouellet 2007) such data can serve as baseline information. These enable incorporating the requirements of seabirds into marine spatial planning applications

(e.g. Hyrenbach et al. 2000, Busch et al. 2012), such as the designation of Marine Protected Areas (MPAs).

Material & Methods

The study area of the Lower Estuary and Gulf of St. Lawrence is a semi-enclosed shelf sea with two openings to the Northwest Atlantic Ocean – Cabot Strait and Strait of Belle Isle (Fig. 48). The Gulf has a size of 240,000km² (Dufour & Ouellet 2007) and a mean depth of 152m (Dickie & Trites 1983). Its bathymetry is highly variable and characterized by larger areas of lower water depth, particularly in the Southern Gulf which are rarely deeper than 80m (Fig. 48, Table 5). The Central and Northern Gulf is characterized by three deep troughs of several 100m depth – the Laurentian, the Esquiman and Anticosti Channel. The deepest and longest is the Laurentian Channel, which transports water masses from the deep ocean off the Scotian Shelf and Labrador Current into the Gulf and Estuary. The Laurentian Channel ends at the Saguenay Fjord, which is the upper limit of the Lower Estuary (Government of Canada 1991), where intense mixing occurs.

The Estuary exhibits features more typical for an ocean while the Gulf presents features of an extended estuary (White & Johns 1997). The freshwater discharge of the St. Lawrence River is huge with 424km³/y (Sutcliffe et al. 1976). At Cabot Strait the major outflow occurs on the western side around Cape Breton (Nova Scotia), whereas the inflow occurs predominantly at the eastern side around the southwestern part of Newfoundland (Fig. 49, Koutitonsky & Bugden 1991). The overall horizontal circulation in the Estuary and Gulf is counterclockwise.

During summer a warm shallow surface layer of lower salinity develops in the Lower Estuary and Gulf lying over cooler and deeper waters. Over waters beyond 150m depth the water column is separated into three distinct layers: the surface layer, the cold intermediate layer and the deep water layer (Dufour & Ouellet 2007). In the Laurentian Channel the shallow, warm surface layer of 10 to 30m depth has a salinity of 27 to 32psu. Underneath lies a cold intermediate layer which is on average below 1°C with a salinity of 31.5 to 33psu and reaches up to 150m depth (Drinkwater 1993, Gratton et al. 1994). Beneath begins the deep layer with 4 to 6°C and 33 to 34.6psu. There is a pronounced decrease in sea surface temperature during summer from up to 20°C in the Upper Estuary to 16°C in Cabot Strait and 11°C in the Northeastern Gulf.

The Lower Estuary is relatively productive in all types of plankton (de Lafontaine et al. 1991). Its production is mainly exported with the Gaspé Current into the Southern Gulf. The Southern Gulf is the most important spawning and nursery area for numerous fish species. The Northwestern Gulf is also very productive in phyto- and zooplankton and hosts a large abundance of juvenile Capelin. The Northeastern Gulf is very productive in shrimp and different commercial fish species can be found as well (de Lafontaine et al. 1991).

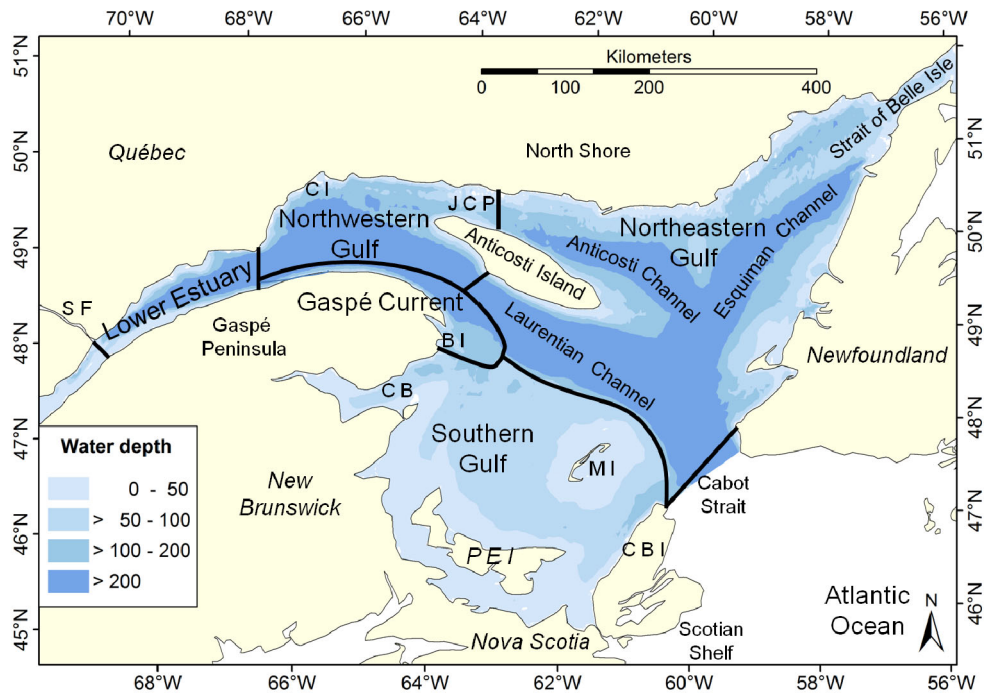


Fig. 48. Subdivisions of the Lower Estuary and Gulf of St. Lawrence modified after de Lafontaine et al. (1991) and Government of Canada (1991). Depicted are the five main marine subdivisions (Lower Estuary, Gaspé Current, Northwestern Gulf, Northeastern Gulf and Southern Gulf), the different provinces (in italics) and other locations mentioned in the text. Abbreviations: BI=Bonaventure Island, CB=Chaleur Bay, CI=Corossol Island, CBI=Cape Breton Island, JCP=Jaques Cartier Passage, MI=Magdalen Islands, PEI=Prince Edward Island, SF=Saguenay Fjord.

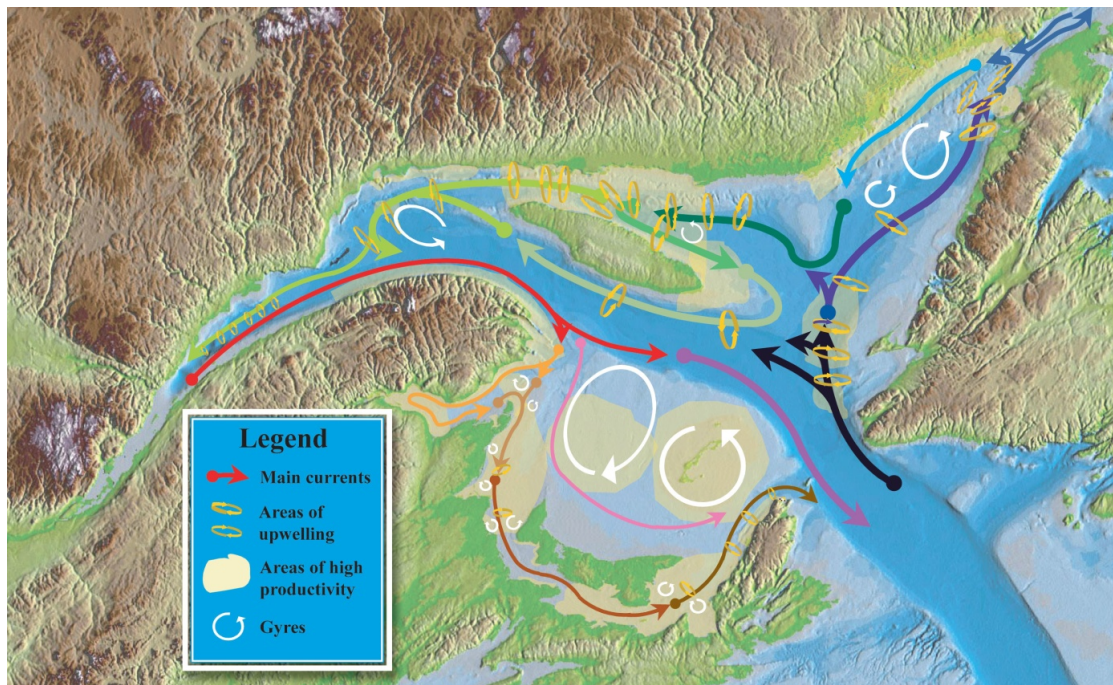


Fig. 49. Major current flow in the Lower Estuary and Gulf of St. Lawrence and associated oceanographic phenomena. Source: 'Atlas of the Marine Environment and Seabed Geology of the Gulf of St. Lawrence' Geological compilation by Heiner Josenhans, digital compilation by Liisa Peitso and Robin Harvey. Geological Survey of Canada report 2004 (www.glf.dfo-mpo.gc.ca/e0006095).

Table 5. Biological-oceanographic zonation of the Lower Estuary and Gulf of St. Lawrence including dominant hydrographic features and plankton characteristics. The zonation is adapted from de Lafontaine et al. (1991). Additional sources: Ardisson & Bourget 1992, Benoit et al. 1985, Descroix et al. 2005, Dufour & Ouellet 2007, El-Sabh 1976, El-Sabh et al. 1982, Grégoire et al. 2006, Harvey et al. 2004, Koutitionsky & Bugden 1991, Le Fouest et al. 2005, Legendre & Watt 1970, Locke 2002, Ouellet & Lefavre 1994, Ouellet et al. 1990, Petrie & Drinkwater 1978, Petrie et al. 1988, Saucier et al. 2003, El-Sabh & Silverberg 1990, White & Johns 1997.

	Lower Estuary	Northwestern Gulf	Gaspé Current	Southern Gulf	Northeastern Gulf
Water depth & Bathymetry	mostly deep, bottom variable	deep in southwest, shallow in northeast, highly variable bottom	mostly deep, bottom mostly uniform	mostly shallow, bottom uniform	mostly deep, highly variable bottom
Sea surface salinity	up to 29psu	ca. 28 to 31psu	ca. 27 to 29psu	ca. 27 to 31psu	ca. 30 to 31psu
Stratification	high	moderate	Moderate	moderate	moderate
Hydrographic features	upwelling near Saguenay Fjord, intense tidal mixing reduces stratification, river plume, large gyres, oceanic influence, large surface & internal tides	large Anticosti Gyre, horizontal front with Gaspé Current, coastal upwellings	strong current, mixing & entrainment of nutrient rich water	continuous gradients in salinity & temperature in top 30 to 50m, small & large gyres, tidal mixing reduces stratification near Magdalen Islands	coastal upwellings, gyres & eddies, intrusion of cold Labrador waters via Strait of Belle Isle, tidal mixing reduces stratification there and in Jacques Cartier Passage, intense mixing at heads of Channels
Phytoplankton Productivity	high in summer	very high in spring, nutrient-limited in summer	very high, continuous from April to October	lower in spring, may be nutrient-limited	high along Québec North Shore, lower along west coast of Newfoundland
Zooplankton Productivity	high	high	high	lower	high
Number of species	low	low	low	high	low
Dominant species	large copepods, ostracod, euphausiids	mysid, large copepods, euphausiids, chatognaths, shrimp	large copepods, euphausiids	small copepods, jellyfish, ctenophores, immature stages of larger organisms	large & small copepods, shrimp
Ichthyoplankton Spawning	low	moderate	moderate	high	low?
Abundance	moderate	moderate	high	high	low?
Dominant species (late June)	Capelin, Atlantic Herring, shanny, Winter Flounder, snailfish	Capelin, sand lance, redfish	Capelin	Atlantic Mackerel	Capelin, Atlantic Herring, redfish

Data on seabird abundance

Data on seabird abundance were collected during two research cruises in June 2008 and 2009 onboard the CCGS 'Teleost', lasting 16 and 17 days respectively. The cruises were conducted in the Lower Estuary and Gulf of St. Lawrence as part of the Atlantic Zone Monitoring Programme (AZMP) of the Department of Fisheries and Oceans (DFO) following a fixed grid of stations where different oceanographic variables were measured. The seabird counts were conducted in cooperation with the Canadian Wildlife Service (CWS) in Sainte-Foy (Québec) and DFO scientists from the Maurice Lamontagne Institute (MLI) in Mont-Joli (Québec). Seabirds were counted from outdoors beside and in front of the bridge by a single observer using a standardized protocol (Tasker et al. 1984, Garthe et al. 2002; Camphuysen et al. 2004). The protocol accounts for observational conditions (sea state) and behavioural aspects of animals (see Camphuysen & Garthe 2004) and uses the distance sampling technique (Buckland et al. 2001). The analyses regarding habitat choice were conducted at seabird species level.

We calculated birds per km as an abundance value for each oceanographic station possible to investigate the influence of different environmental variables on seabird distribution. Therefore, the number of birds per km counted around each oceanographic station within a radius of five nautical miles was calculated separately for both cruises. This simultaneous approach was the standard situation. In a few rare occasions a maximum of two days lay between oceanographic measurements and bird counts. We assigned the bird data to the different radii with ArcView GIS 3.2 software. If these overlapped, we reduced the radius to 2.5 miles. A few radii still overlapped and some stations had to be excluded to guarantee a minimum seabird survey effort of three kilometers around a station. Only survey conditions below sea state 6 were regarded acceptable. This generated a total of 96 stations – 46 in 2008 and 50 in 2009 – where seabird abundance values and simultaneous oceanographic measurements were available (Fig. 50). The majority of stations were located in the Southern Gulf.

As minimum threshold a bird species had to be present at five stations in both years, which relates to a presence of >10% to be included in subsequent statistic models. The following nine seabird species fulfilled this requirement: Common Loon (*Gavia immer*), Northern Fulmar (*Fulmarus glacialis*), Wilson's Storm-Petrel (*Oceanites oceanicus*), Northern Gannet, Black-legged Kittiwake (*Rissa tridactyla*), Herring Gull (*Larus argentatus* belonging to the American subspecies *L. a. smithsonianus*), Great Black-backed Gull (*Larus marinus*), Common Murre (*Uria aalge*) and Razorbill (*Alca torda*).

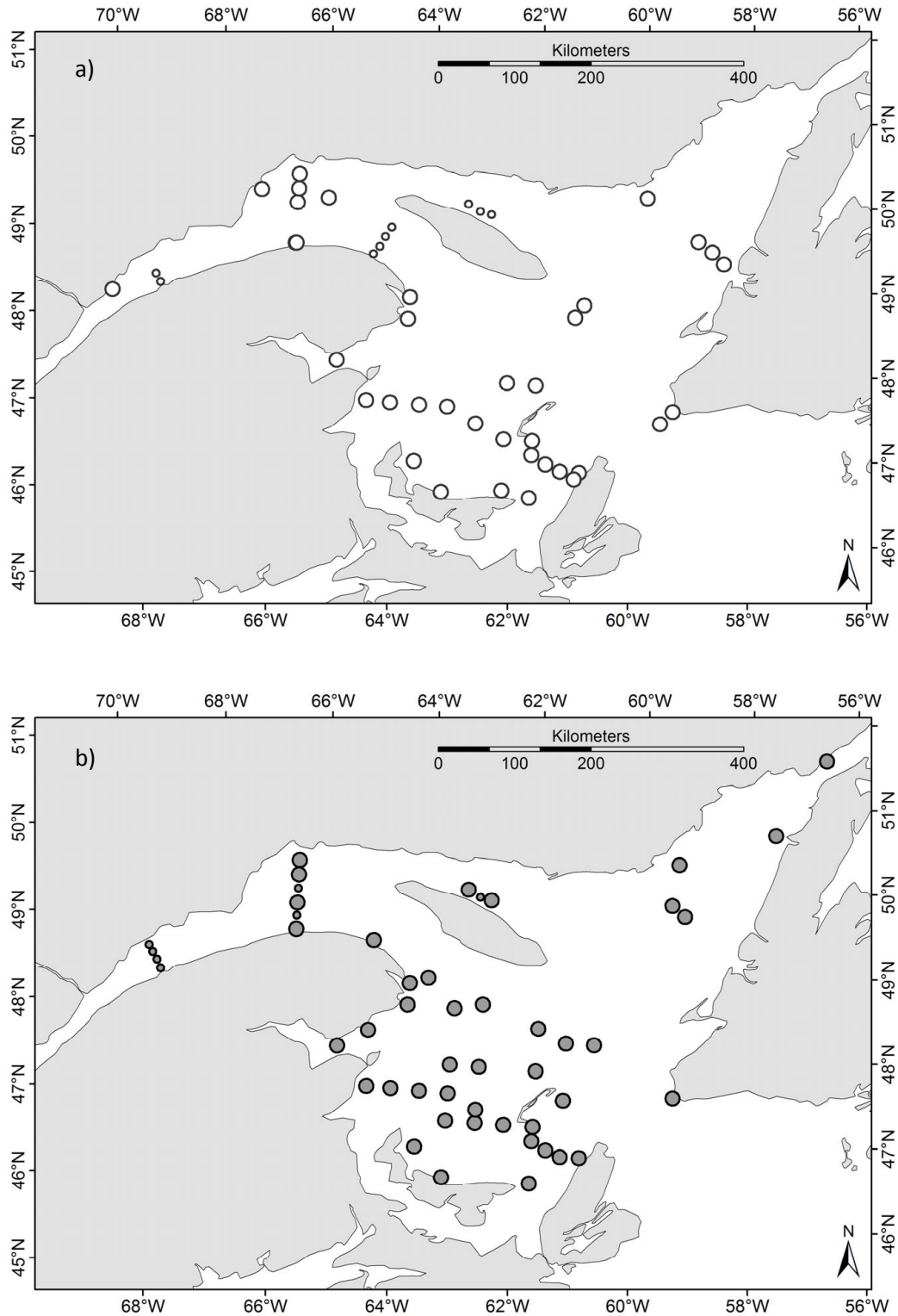


Fig. 50. Distribution of oceanographic stations used for seabird habitat models in the Gulf of St. Lawrence in June (a) 2008 and (b) 2009. The size of the (a) white and (b) grey circles shows the different radii of 2.5 or 5 nautical miles around a station to which seabird census data were assigned to (for details see text).

Data on environmental variables

At each survey station a set of different oceanographic variables (e.g. nutrients, chlorophyll, salinity etc.) was measured. Based on literature and ecological reasoning, we selected six of these variables and two additional environmental variables to be considered as predictors for our habitat models. We used fluorescence (FLUO) as a proxy for chlorophyll a which relates to primary productivity (Scott et al. 2010). To measure if the water column was stratified we used the difference in temperature (ΔT) and salinity (ΔS) between sea surface and bottom (Markones 2007). The maximum water depth, which was treated as bottom value, was fixed at 100 meters for cases when a station exhibited larger water depth. This depth was still considered relevant because Common Murres regularly dive to 60 meters depth and can reach up to 100 meters and deeper (Piatt & Nettleship 1985, Burger & Simpson 1986). As measures of water masses we used sea surface temperature (SST) and salinity (SSS) (Markones 2007), as well as 'sigma_t' as a measure for water density. The first available average (data were rounded at 1m increments) of these variables at 1 to 3 meters depth was used as surface value. Quality of the measurements of these variables was checked by scientists at the IML before being incorporated into the Oceanographic Data Management System (ODMS). We downloaded the summarized data from the ODMS website (Fisheries and Oceans, Canada, Québec Region, Oceanographic Data Management System, Maurice Lamontagne Institute, Mont-Joli (Québec), Canada, www.osl.gc.ca/sgdo; consulted on 2nd July 2010). Only values which were classified as not doubtful or erroneous by the ODMS (qualityflag=1) were used. For FLUO no qualityflags were available.

Additionally, we calculated the distance to the nearest seabird colony (COLONY) or nearest land mass (LAND). As the requirements of reproduction are often demanding for seabirds it was previously shown that the location of colonies often has a pronounced effect of the distribution patterns at sea (e.g. Garthe 1997). The data on colonies for the bordering provinces Québec, Newfoundland and Labrador, Nova Scotia, New Brunswick and Prince Edward Island stemmed from Environment Canada ('Seabird and Waterbird database of Québec', status 13th July 2010 and 'Atlantic Waterbird Colony Database', status 10th July 2010). Both databases included the updates for 2009. For one 'hypercolony' (i.e. a very large colony consisting of many small subcolonies) in the western part of Parc de Mingan (Québec) central coordinates were calculated and incorporated in the analysis. From all mixed colony categories only 'Murre spp.' was used as potentially active colonies for Common Murres. Data on colonies were very heterogenous. When the most recent census (1978 to 2009) supplied 0 values, the colony was treated as abandoned. Some colonies had not been surveyed for several decades. All colonies that were at least considered to be possible breeding sites (minimum criterion) since 1978 (as most recent information) were assumed to be potentially active colonies. All of these colonies were included in the analysis. COLONY was the only variable that changed between bird species. For the Common Loon information on breeding sites was not available and LAND was used instead. Less than a quarter of all Loons were identified as adults in breeding plumage. It was therefore concluded that mostly non-breeders were sampled. The variable LAND was also used for Wilson's Storm-Petrel, as this species breeds in the southern hemisphere. COLONY

therefore did not play a role. COLONY did not seem to be important for the Northern Fulmar in the Gulf either. The abundance at sea was much larger than the breeding population in the vicinity. Inside the Gulf, Fulmars breed only in the Northwestern Gulf on Corossol Island (1 pair in 1996). The next colony on Funk Island is located 350km flight distance away from the northeastern rim of the study area. Although this Fulmar colony is the largest in the area, it is with its 56 pairs breeding in 1996 (CWS unpubl. data) still very small. We checked correlations between all eight variables with Pearson’s correlation coefficient and set the threshold at a conservative value of 0.5 to avoid overfitted model outputs in subsequent analyses. Only five variables remained to analyze the habitat choice of the different seabird species (Table 6). The variables ‘sigma_t’, SST and ΔS were excluded. The maximum correlation coefficient of the remaining variables of -0.46 occurred between factors SSS and FLUO.

Table 6. Final set of environmental variables, their units and relevance for the analysis of habitat choice of seabirds in the Gulf of St. Lawrence with GAMs.

Predictor variable	Unit	Explanation
COLONY	km	Linear distance from an oceanographic station to the nearest colony of a species as indicator of foraging range
LAND	km	Linear distance from an oceanographic station to the nearest land mass including islands as indicator of terrestrial linkage
ΔT	°C	Difference in temperature between sea surface and bottom to a maximum water depth of 100m as indicator of stratification vs. mixing
SSS	psu	Indicator of water mass as estuarine vs. marine
FLUO	mg/m ³	Proxy for chlorophyll a that relates to phytoplankton biomass as indicator of biological activity

Statistical approach

To analyse the habitat choice of seabirds we modelled their distribution based on environmental variables using the free statistical software R, version 2.15.0 (R Development Core Team 2012). Our data were characterized by an over dispersion, which is typical for counts of animals that show pronounced spatial aggregations like seabirds. The over dispersion is evoked by a high number of zero counts and a few very large counts e.g. at feeding flocks. Based on similar studies (e.g. Schwemmer et al. 2009, Scott et al. 2010, Gilles et al. 2011, Gallus et al. 2012) on the analysis of apex predator distribution, we selected generalized additive models (GAMs, e.g. Wood 2006a, Zuur et al. 2009a). We used a quasi-Poisson distribution, which is able to cope with zero inflated datasets (Zuur et al. 2009b, Gallus et al. 2012) applying the mgcv package 1.7.13 (Wood 2004, 2006a, 2011).

The bird data were only superficially checked for autocorrelation. We checked the variograms of residuals for the Northern Gannet and Wilson's Storm-Petrel. The formula for GAMs using normally distributed data could not be applied successfully. We felt confident in ignoring this statistical problem as a range of studies which analysed similar datasets (e.g. Schwemmer et al. 2009, Gilles et al. 2011, see Chapter 3) found that GAMMs (=generalised additive mixed models; e.g. Wood 2006a, b) that take autocorrelation into account generated very similar results and did not perform better than the much less complex GAMs.

Some of the oceanographic stations used for the analysis were measured in both years. We treated year as a random factor using restricted maximum likelihood estimation (REML) to take the latter into account. We used backward selection of models and aimed for a final version that contained only variables which each showed a significant influence (e.g. Redfern et al. 2006, Gilles et al. 2011, Gallus et al. 2012). An explanatory variable was deleted when it presented a low F value and a nonsignificant p-value. The performance of the new model with the old one was tested using analysis of variance (ANOVA) of the *mgcv* package (Wood 2004, 2006a, 2011). If the new reduced model differed significantly from the old one, the fixed factor was sustained for the model.

Additionally, we checked with separate GAMs which single factor of the final models explained most of the observed deviance. We set the threshold for significance at 0.05 for all analyses.

Model quality and analysis of error

We used both the coefficient of determination R^2 (adjusted) and the explained deviance of the final GAM as a first indication of the goodness of fit of our model. Then we compared the final GAM with the original values using a Normal Q-Q plot that plots the deviance residuals vs. the theoretical quantiles, plotted the response vs. the fitted values. Both plots should indicate the performance of the modelled values compared to the original ones. We plotted the residuals vs. the linear predictor and checked the distribution of residuals with a histogram. The latter shows the distribution of the error which should be a normal distribution in the optimal case. In addition we calculated Pearson's correlation coefficient for the final model and the original values.

Moreover, we inferred the quality of our final model by applying a nonparametric bootstrap routine (Efron 1990) that was iterated 500 times. Bootstrapping is a robust approach to investigate the prediction error as the latter will rather be over than underestimated. Each time 96 stations were randomly chosen with replacement out of the 96 original ones, refitting the model with each iteration. Based on the random sample a prediction was generated for the stations that were not included. The difference between the prediction and the original values supplied the prediction error. By bootstrapping we calculated the median prediction error, generated its distribution and its 95% confidence intervals for each analysed species. We checked if the prediction error was normally distributed and the relation of the median error compared to the average and maximum abundance value of the species at the stations.

From an ecological point of view it is most interesting to take into account in which areas the model shows its best performance or its largest weaknesses. Often it is more relevant if the hotspots and areas of low abundance are reflected than the mere size of the prediction error. Thus, we also selected a visual approach when judging the quality of our models. We visualized the modelled seabird abundance as contour plots in latitude and longitude. Into this plot we added the original values at the sampled stations and included a map of the study area using the `rgdal` package 0.7.8 (Keitt et al. 2012) in R (R Development Core Team 2012). Finally, we modelled the distribution of the absolute error between the modelled and original seabird abundance values as contour plots in latitude and longitude using the `vis.gam` functions of the `mgcv` package 1.7.13 (Wood 2004, (Wood 2006a), 2011) in R (R Development Core Team 2012).

Results

Observed and modeled distribution

We compared the observed distribution and abundance of species with that predicted by the habitat models. Furthermore, we inferred their compliance by modeling the absolute error between both.

Common Murre

For Common Murres the observed hot spot off the Gaspé Peninsula around Bonaventure Island, where the largest colony is located, was predicted well by the model (Fig. 51) and also areas of low or zero abundance in the Southern Gulf were well reflected. The absolute error between prediction and observation was low, reaching highest values in the area of maximum abundance off the Gaspé Peninsula (Fig. 51).

Herring Gull

For Herring Gulls the predicted abundance and distribution corresponded well with the observed one (Fig. 52). The hotspots in the Lower Estuary and Chaleur Bay, which are close to major concentrations of colonies, were well reflected as were the predicted areas of low abundance further offshore in the central part of the Gulf. The absolute error between prediction and observation was also low and highest in the areas of maximum abundance (Fig. 52).

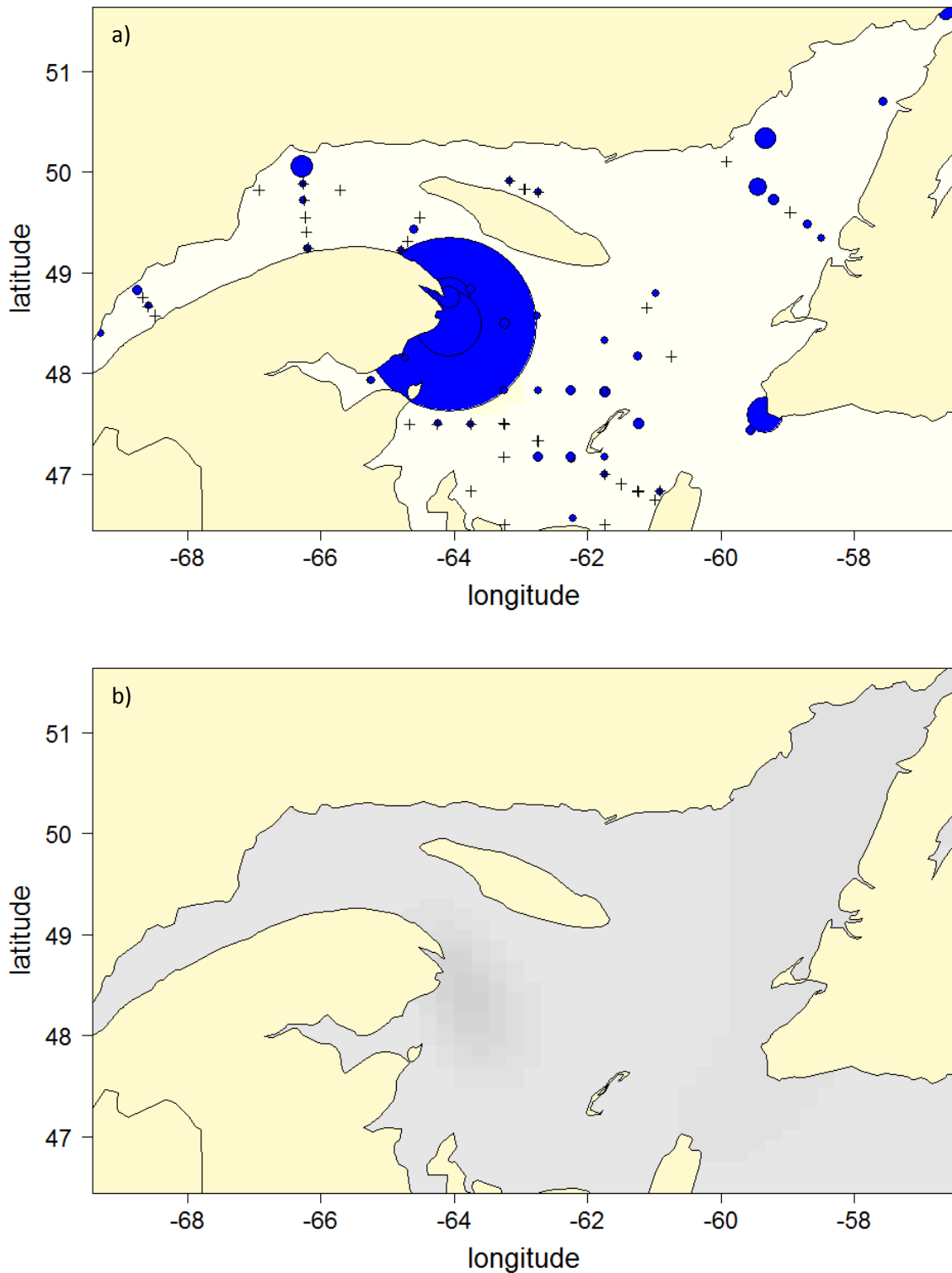


Fig. 51. Distribution of Common Murres (*Uria aalge*) in the Gulf of St. Lawrence in June 2008 and 2009: (a) the observed abundance at each station is depicted as blue circles (size proportionate to abundance) or black crosses (= 0 abundance); the underlying predicted abundance is modeled based on habitat variables applying a GAM (for applied variables see Table 7) and depicted as contour lines which are isolines of abundance (ind./km; Note: not visible here as highest observed abundance (largest blue circle) overlaps area of highest modeled abundance); (b) spatial distribution of the absolute error between observed and predicted abundance using a GAM, the error in is depicted as contour lines which are isolines of abundance (ind./km; Note: not visible here due to low differences between observed and modeled abundance), the colors correlate with the error (light to dark grey: low to high error).

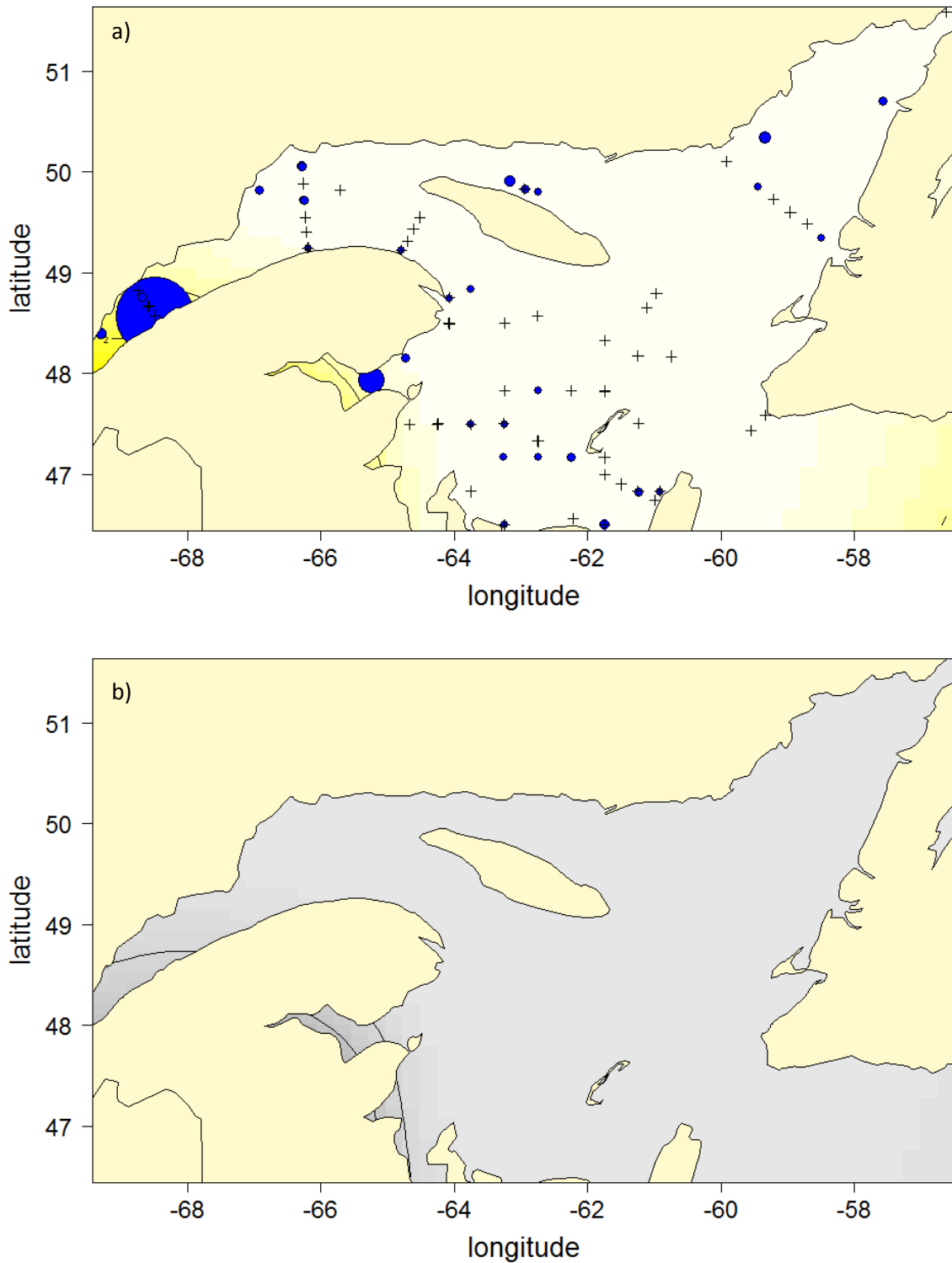


Fig. 52. Distribution of Herring Gulls (*Larus argentatus*) in the Gulf of St. Lawrence in June 2008 and 2009: (a) the observed abundance at each station is depicted as blue circles (size proportionate to abundance) or black crosses (= 0 abundance); the underlying predicted abundance is modeled based on habitat variables applying a GAM (for applied variables see Table 7) and depicted as contour lines which are isolines of abundance (ind./km), the colors correlate with the contour lines (white to orange: low to high abundance); (b) spatial distribution of the absolute error between observed and predicted abundance using a GAM, the error is depicted as contour lines which are isolines of abundance (ind./km), the colors correlate with the contour lines (light to dark grey: low to high error).

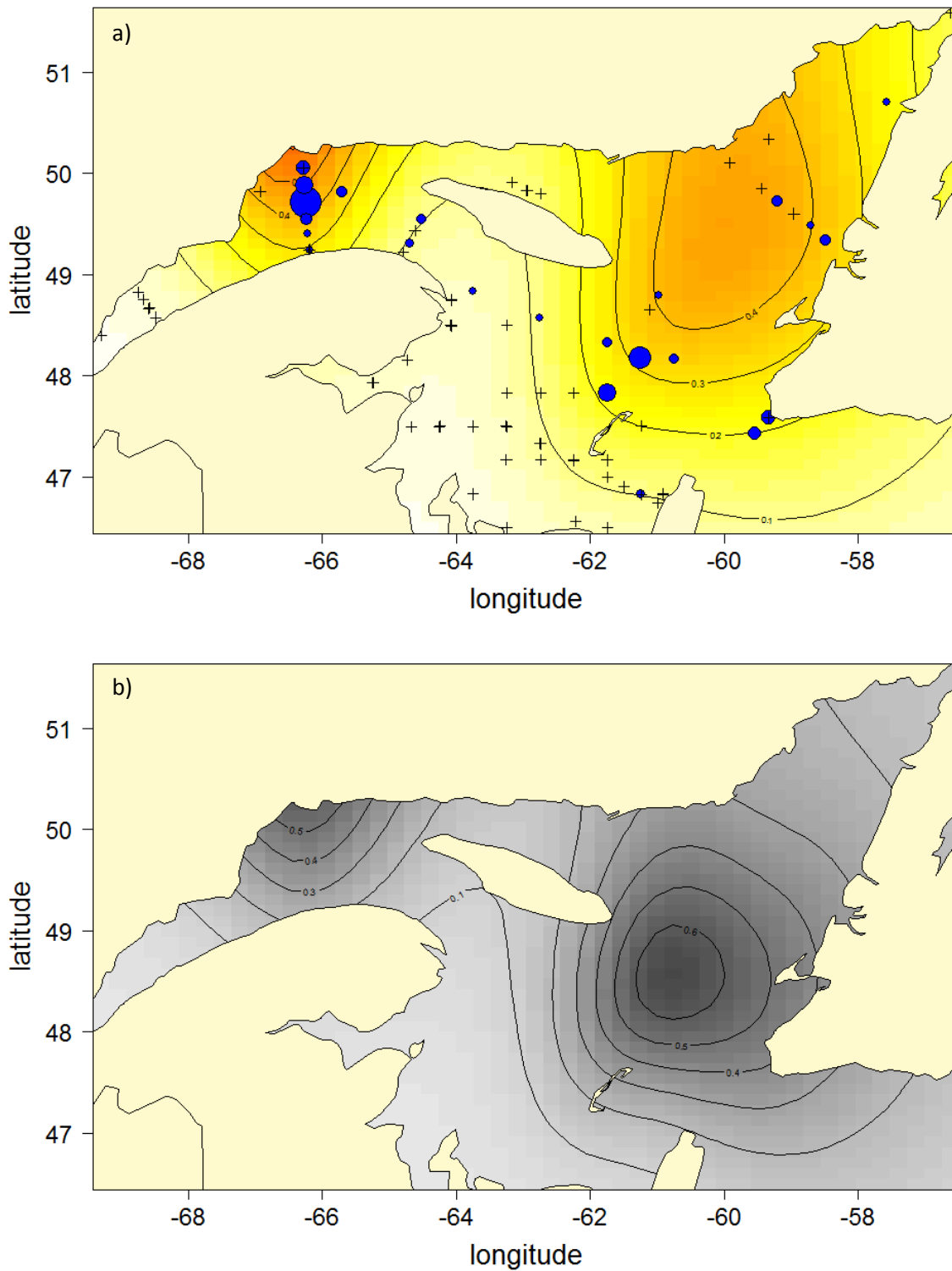


Fig. 53. Distribution of Northern Fulmars (*Fulmarus glacialis*) in the Gulf of St. Lawrence in June 2008 and 2009: (a) the observed abundance at each station is depicted as blue circles (size proportionate to abundance) or black crosses (= 0 abundance); the underlying predicted abundance is modeled based on habitat variables applying a GAM (for applied variables see Table 7) and depicted as contour lines which are isolines of abundance (ind./km), the colors correlate with the contour lines (white to orange: low to high abundance); (b) spatial distribution of the absolute error between observed and predicted abundance using a GAM, the error is depicted as contour lines which are isolines of abundance (ind./km), the colors correlate with the contour lines (light to dark grey: low to high error).

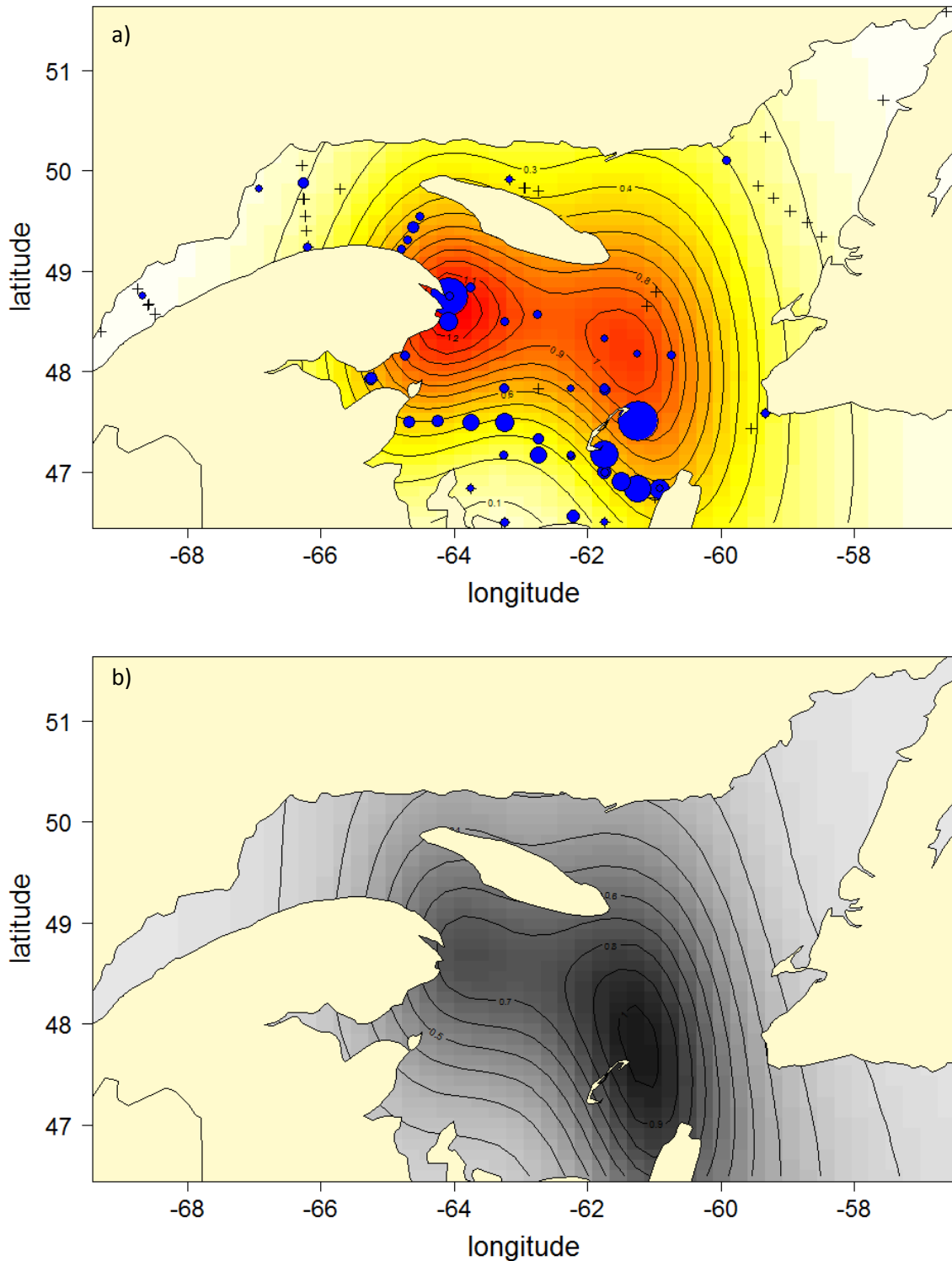


Fig. 54. Distribution of Northern Gannets (*Morus bassanus*) in the Gulf of St. Lawrence in June 2008 and 2009: (a) the observed abundance at each station is depicted as blue circles (size proportionate to abundance) or black crosses (= 0 abundance); the underlying predicted abundance is modeled based on habitat variables applying a GAM (for applied variables see Table 7) and depicted as contour lines which are isolines of abundance (ind./km), the colors correlate with the contour lines (white to orange: low to high abundance); (b) spatial distribution of the absolute error between observed and predicted abundance using a GAM, the error is depicted as contour lines which are isolines of abundance (ind./km), the colors correlate with the contour lines (light to dark grey: low to high error).

Northern Fulmar

Regarding Fulmars, their largest observed hot spot in the Northwestern Gulf is well accounted for by the model, as well as the areas of low or zero abundance in the Southern Gulf (Fig. 53). In the Northeastern Gulf however, another hot spot is predicted that does not entirely match with the observations. Instead, higher abundance could be found on the eastern and southwestern rim of the predicted hot spot particularly north of the Magdalen Islands near the southern rim of the Laurentian Channel. Consequently, the absolute error between model and observation was highest in this area and in the Northwestern Gulf, where the highest abundance occurred (Fig. 53).

Northern Gannet

Regarding the compliance between observed and modeled abundance of Northern Gannets, the hotspot off the Gaspé Peninsula near the Bonaventure Island colony is well accounted for (Fig. 54). Another hotspot is predicted northeast of the Magdalen Islands between the Bird Rocks colony and the colony on the eastern tip of Anticosti Island. However, a certain mismatch can be observed in that area as the census data found the largest concentrations of Gannets east to southeast of the Magdalen Islands. Consequently, the largest error between predicted and observed abundance occurs in this area (Fig. 54).

Other seabird species

Qualitatively similar results as for Fulmars or Gannets regarding a substantial but not full compliance of the predicted with the observed abundance could be seen for a range of species. For Kittiwakes higher abundance could be observed mostly in proximity to colonies in the Lower Estuary, the Northwestern Gulf, around the Magdalen Islands and particularly around the Gaspé Peninsula towards the western tip of Anticosti Island. The latter area of concentration was underestimated by the model and associated with the largest error between observation and prediction. Great Black-backed Gulls could mainly be observed in the Lower Estuary, in the Northwestern Gulf at the tip of the Gaspé Peninsula and in Chaleur Bay, as well as on the western coast of Newfoundland. The largest error between observed and predicted abundance could be found in the Lower Estuary. Razorbills could also be found in different locations near colonies in the Estuary and Gulf. The highest abundance was observed and modeled for the Northeastern Gulf particularly towards the Strait of Belle Isle, which was also the area of the highest error. Wilson's Storm-Petrel showed highest abundance in the central part of the Gulf, as well as southeast of the Magdalen Islands. The observed main concentrations in the central part were spatially well reflected by the model but were also the area of highest error. Most Common Loons could be observed south of the Magdalen Islands, north of Anticosti and particularly in the Northwestern Gulf. The latter concentration was not reflected by the model and the highest error occurred. The highest abundance was predicted for the Estuary where only few Loons were observed.

Environmental variables and seabird habitat models

At first we briefly present some general results of all models for the different species. Thereafter we evaluate single variables and species in more detail. The effect of the selected environmental variables on the distribution patterns differed between seabird species. This was demonstrated both by the number of variables that were significant, as well as by the relevance of a variable for the individual species. For Common Murres and Razorbills for example, all four predictors showed a significant influence, whereas in Northern Gannets and Wilson's Storm-Petrels only a single factor did. Only for Common Loons none of the predictors was significant, but FLUO showed a trend. The habitat models for Common Murres, Herring Gulls and Northern Fulmars performed best explaining 75, 60 and 44% of the observed deviance (Table 7).

In general, the terrestrial factors COLONY or LAND and the oceanographic factor SSS proved to be the most relevant predictors for the majority of species (Table 7 and Table 8). These predictors explained most of the deviance and exhibited the highest F-values. If analyzed solely, COLONY would explain up to 59% of the observed deviance in the distribution of Common Murres and 33% in the case of Northern Gannets (Table 8). SSS had the strongest effect on the distribution of Herring Gulls, Northern Fulmars and Great Black-backed Gulls, explaining 52, 31 and 25% of the observed deviance if the model would be based on this variable alone (Table 8). FLUO showed to be a particularly important factor for Black-legged Kittiwakes, Razorbills and Common Murres (Table 7). ΔT proved to have a pronounced influence, particularly on Northern Fulmars and Razorbills.

Table 7. Effect sizes (F) and levels of significance (p-values) for all environmental variables of final GAMs. The threshold for significance was set at 0.05. The levels of significance were: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'n.s.' 1. The explained deviance (%) measures the variation of residuals of the GAM and corresponds to the sum of squares used in linear regression. The coefficient of determination R² (adjusted) supplies the proportion of variation of the original data that can be explained by the final model. Additional codes: edf = estimated degrees of freedom; for predicting variables see Table 6; 'x' = factor not tested for a species; '-' = factor not significant for final model; Numbers in italics = factor itself not significant but final model performs significantly better (ANOVA) when factor is retained.

Taxon	COLONY			LAND			Δ T			SSS			FLUO			R ² (adj.)	Deviance explained (%)
	edf	F	p-value	edf	F	p-value	edf	F	p-value	edf	F	p-value	edf	F	p-value		
<i>Gavia immer</i>	x	x	x	-	-	<i>n.s.</i>	-	-	<i>n.s.</i>	-	-	<i>n.s.</i>	1.81	3.00	.	0.02	5.6
<i>Fulmarus glacialis</i>	x	x	x	1.88	6.38	**	1.00	8.03	**	1.00	6.82	*	-	-	<i>n.s.</i>	0.38	44.2
<i>Oceanites oceanicus</i>	x	x	x	1.00	12.92	***	1.86	2.67	.	-	-	<i>n.s.</i>	-	-	<i>n.s.</i>	0.10	19.4
<i>Morus bassanus</i>	1.00	36.40	***	x	x	x	-	-	<i>n.s.</i>	-	-	<i>n.s.</i>	-	-	<i>n.s.</i>	0.21	33.0
<i>Rissa tridactyla</i>	1.48	5.75	**	x	x	x	1.82	2.12	<i>n.s.</i>	-	-	<i>n.s.</i>	1.07	9.03	**	0.38	35.2
<i>Larus argentatus</i>	1.00	7.65	**	x	x	x	-	-	<i>n.s.</i>	1.94	44.41	***	1.67	3.45	*	0.68	60.4
<i>Larus marinus</i>	1.23	2.08	<i>n.s.</i>	x	x	x	-	-	<i>n.s.</i>	1.92	24.88	***	1.00	3.60	.	0.38	36.6
<i>Uria aalge</i>	1.99	41.57	***	x	x	x	1.00	6.71	*	1.00	8.07	**	1.89	18.52	***	0.70	75.4
<i>Alca torda</i>	1.00	6.70	*	x	x	x	1.14	13.87	***	1.00	5.34	*	1.00	14.40	***	0.23	36.3

Table 8. Effect sizes (F) and levels of significance (p-values) for the single most important variables of the final GAMs. The threshold for significance was set at 0.05. The levels of significance were: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'n.s.' 1. The explained deviance (%) measures the variation of residuals of the GAM and corresponds to the sum of squares used in linear regression. The coefficient of determination R^2 (adjusted) supplies the proportion of variation of the original data that can be explained by the final model. Additional codes: edf = estimated degrees of freedom; for predicting variables see Table 6; Factor and numbers in italics = factor showed a trend.

Taxon	Main factor	edf	F	p-value	R ² (adj.)	Deviance explained (%)
<i>Gavia immer</i>	<i>FLUO</i>	1.81	3.00	.	0.02	5.6
<i>Fulmarus glacialis</i>	SSS	1.00	23.65	***	0.18	30.6
<i>Oceanites oceanicus</i>	LAND	1.00	14.54	***	0.06	13.1
<i>Morus bassanus</i>	COLONY	1.00	36.40	***	0.21	33.0
<i>Rissa tridactyla</i>	COLONY	1.68	10.46	***	0.20	23.7
<i>Larus argentatus</i>	SSS	1.94	58.80	***	0.53	51.9
<i>Larus marinus</i>	SSS	1.92	21.37	***	0.33	25.1
<i>Uria aalge</i>	COLONY	1.98	38.10	***	0.37	59.4
<i>Alca torda</i>	Δ T	1.00	19.15	***	0.07	20.1

Distance to colony

The distribution of Common Murres in the Gulf of St. Lawrence showed a clear link to COLONY (Fig. 55a). Common Murre abundance was higher than the mean until ca. 38km from a colony. Abundance declined with growing distance, showing the lowest abundance values around 72km and increasing thereafter. Common Murre abundance was again above average and kept increasing with distance from ca. 108km from a colony onwards. For the other species this relationship was simpler with highest seabird abundance closest to a colony declining with growing distance. The distance where the abundance values reached the average and switched from positive to negative deviation differed between species. It ranged from ca. 38km in Herring Gulls (Fig. 55b), increased slightly to ca. 48km in Kittiwakes (Fig. 55c) and ca. 58km in Razorbills. It reached the highest value in Northern Gannets with ca. 150km (Fig. 55d) from the next colony.

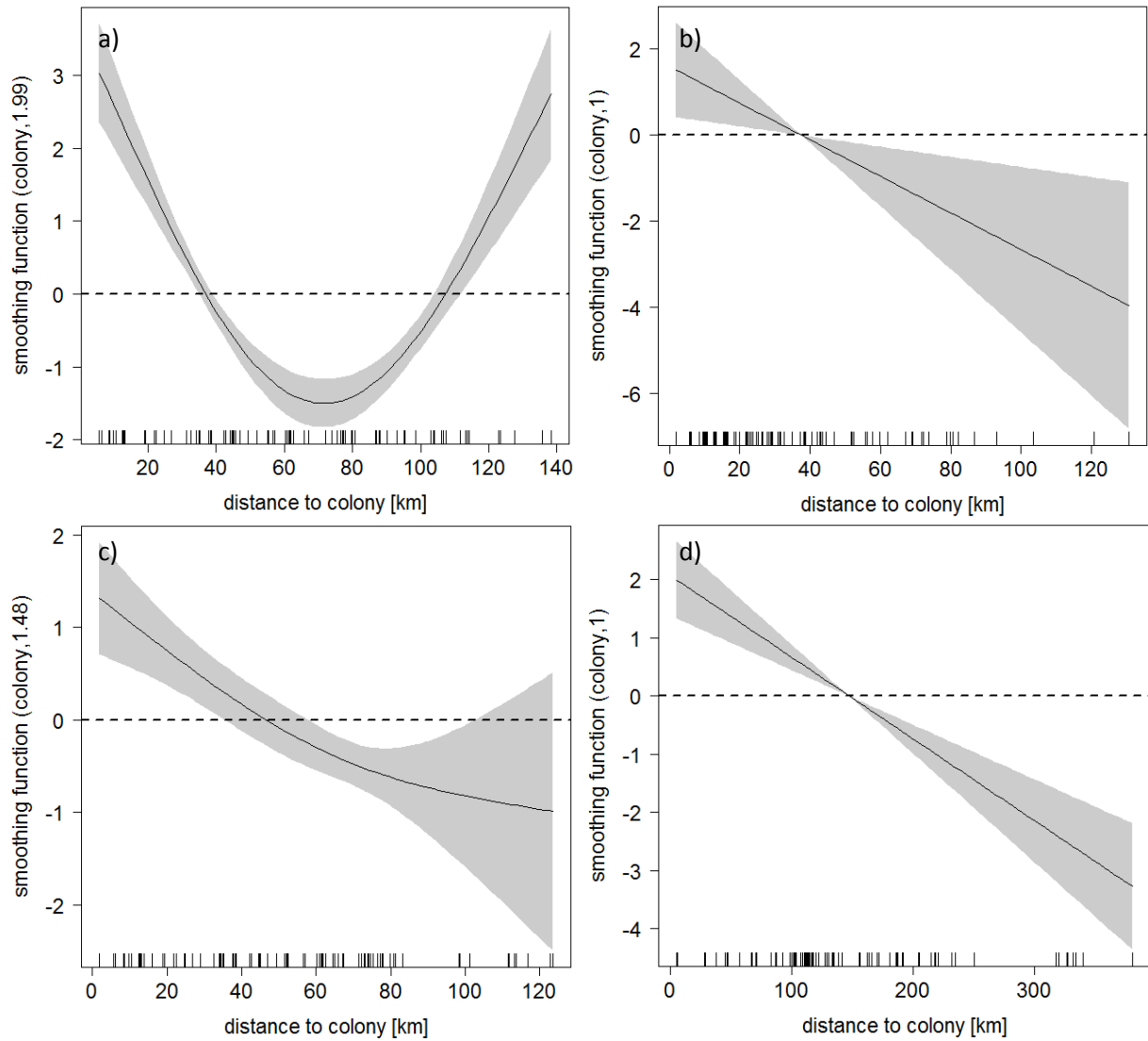


Fig. 55. Smoothing curve of GAM fitted to partial effects of explanatory variables on abundance of (a) Common Murres (*Uria aalge*), (b) Herring Gulls (*Larus argentatus*), (c) Black-legged Kittiwakes (*Rissa tridactyla*) and (d) Northern Gannets (*Morus bassanus*) in the Gulf of St. Lawrence in June 2008 and 2009. Abundance is represented as a function of the predictor variable distance to colony. Grey shade shows the 95% confidence intervals around the main effects. The dashed line shows the mean abundance.

Distance to land

The distribution and abundance of Northern Fulmars and Wilson’s Storm-Petrels were significantly negatively linked with LAND (Fig. 56). Both species showed an increasing abundance with growing distance to the nearest land mass. At distances from land of ca. 20km in Northern Fulmars (Fig. 56a) and 30km in Wilson’s Storm-Petrels (Fig. 56b) the respective average abundance value is reached. Shorter distances to LAND were associated with lower abundance values in both species, and longer distances with higher abundance values.

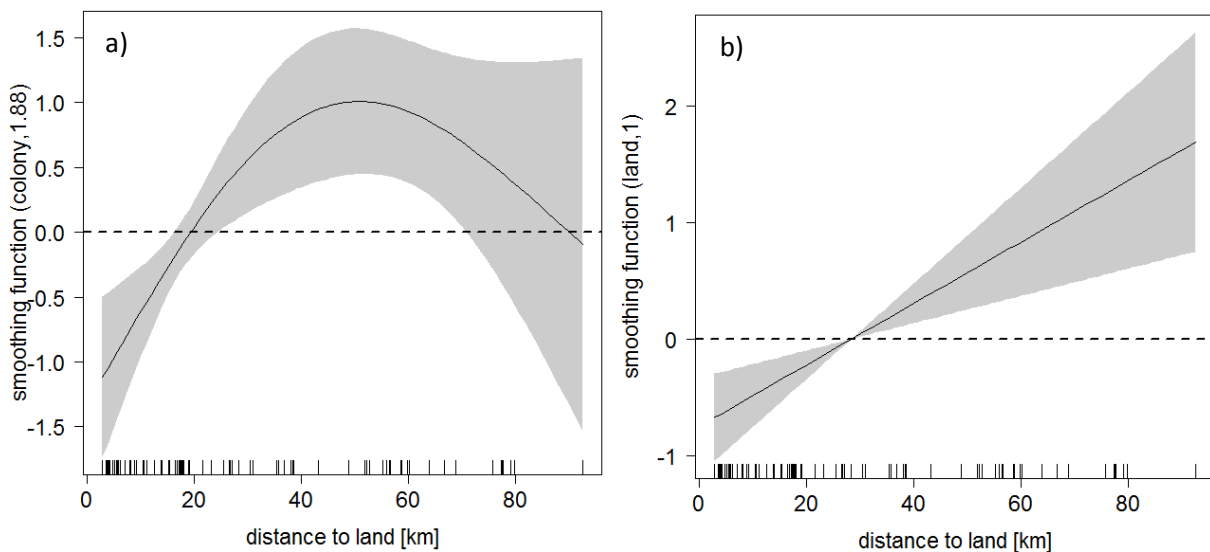


Fig. 56. Smoothing curve of GAM fitted to partial effects of explanatory variables on abundance of (a) Northern Fulmars (*Fulmarus glacialis*) (b) and Wilson’s Storm-Petrels (*Oceanites oceanicus*) in the Gulf of St. Lawrence in June 2008 and 2009. Abundance is represented as a function of the predictor variable distance to land. Grey shade shows the 95% confidence intervals around the main effects. The dashed line shows the mean abundance.

Sea surface salinity

The abundance of Northern Fulmars (Fig. 57a), Common Murres (Fig. 57b) and Razorbills showed a significantly positive relationship with SSS. The abundance of Herring Gulls (Fig. 57c) and Great Black-backed Gulls (Fig. 57d) was negatively linked. SSS values above ca. 29psu led to abundance values above average in Northern Fulmars, Common Murres and Razorbills. In Herring Gulls and Great-Black backed Gulls abundance decreased with increasing SSS. From ca. 27.3psu their abundance values were below average, reaching a minimum around 29psu.

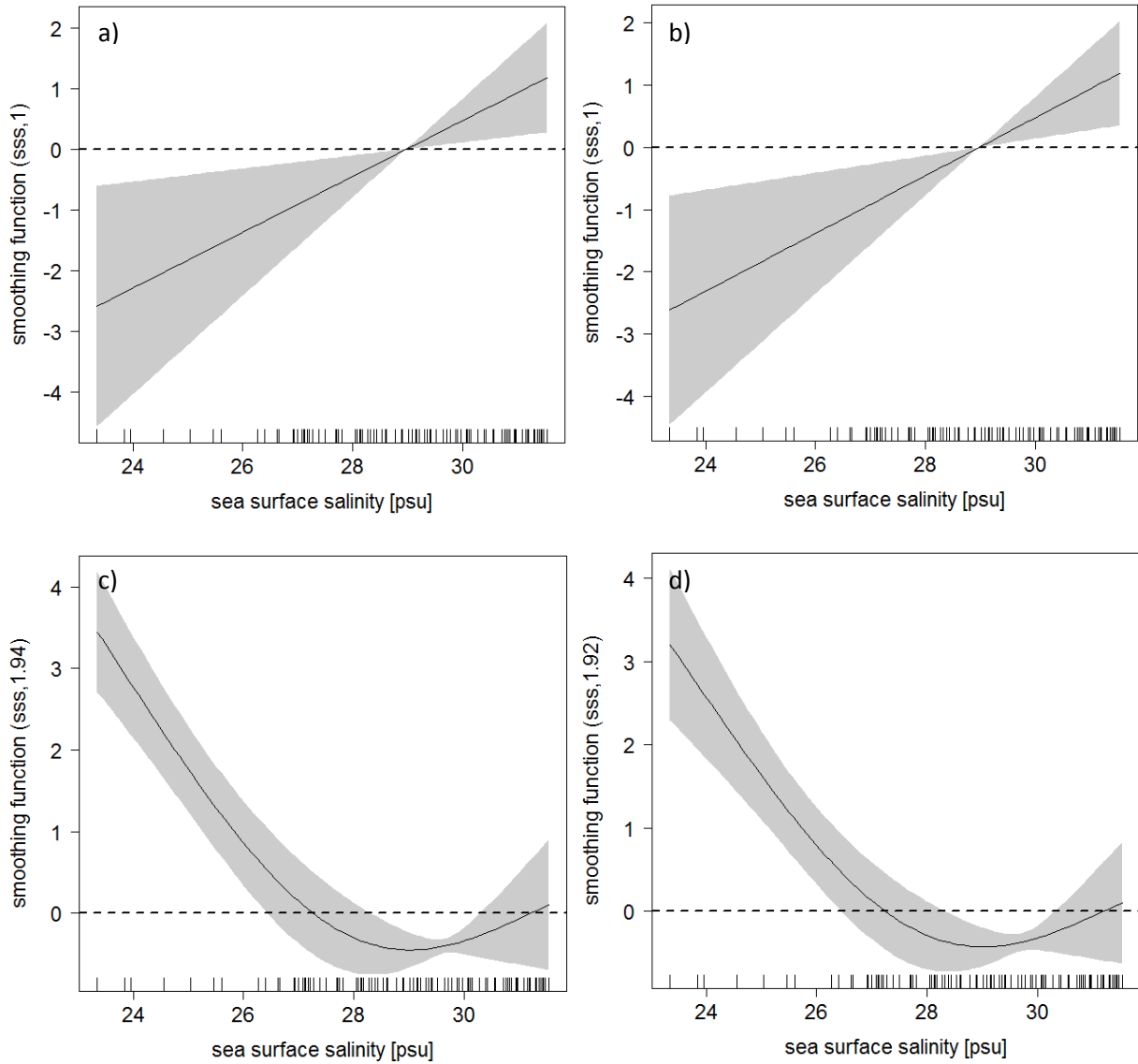


Fig. 57. Smoothing curve of GAM fitted to partial effects of explanatory variables on abundance of (a) Northern Fulmars (*Fulmarus glacialis*), (b) Common Murres (*Uria aalge*), (c) Herring Gulls (*Larus argentatus*) and (d) Great Black-backed Gulls (*Larus marinus*) in the Gulf of St. Lawrence in June 2008 and 2009. Abundance is represented as a function of the predictor variable sea surface salinity. Grey shade shows the 95% confidence intervals around the main effects. The dashed line shows the mean abundance.

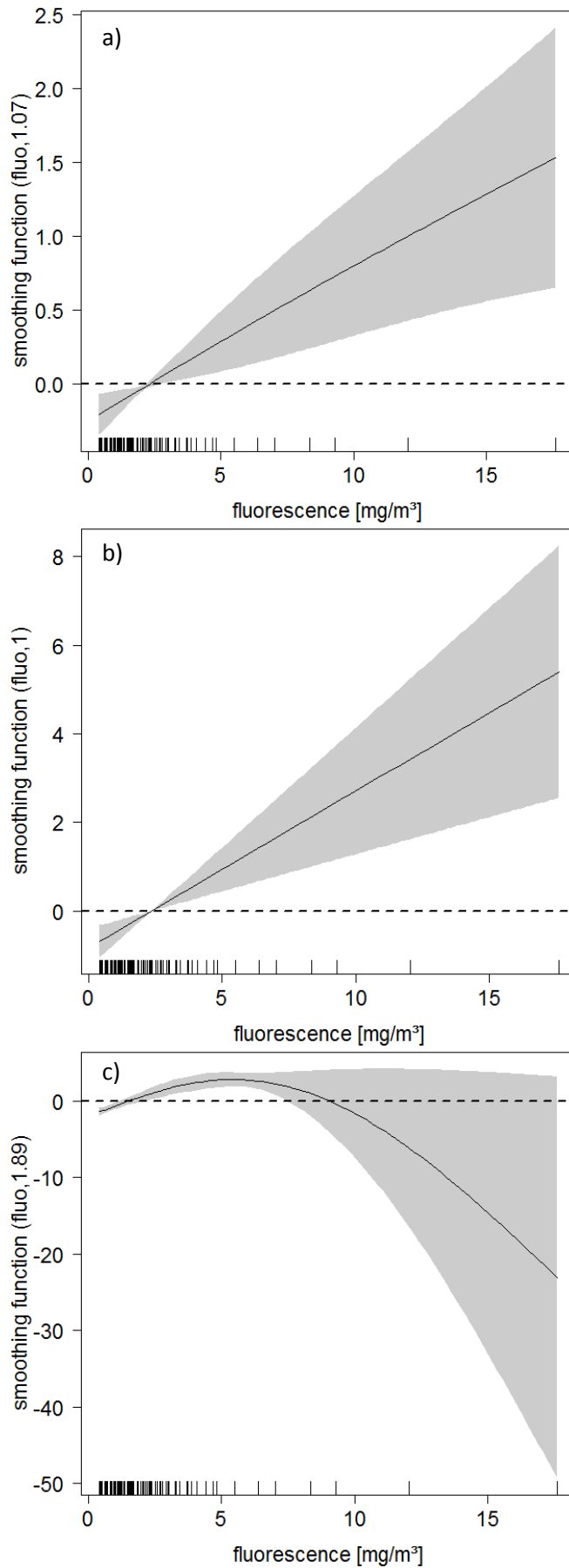


Fig. 58. Smoothing curve of GAM fitted to partial effects of explanatory variables on abundance of (a) Black-legged Kittiwakes (*Rissa tridactyla*), (b) Razorbills (*Alca torda*) and (c) Common Murres (*Uria aalge*) in the Gulf of St. Lawrence in June 2008 and 2009. Abundance is represented as a function of the predictor variable fluorescence. Grey shade shows the 95% confidence intervals around the main effects. The dashed line shows the mean abundance.

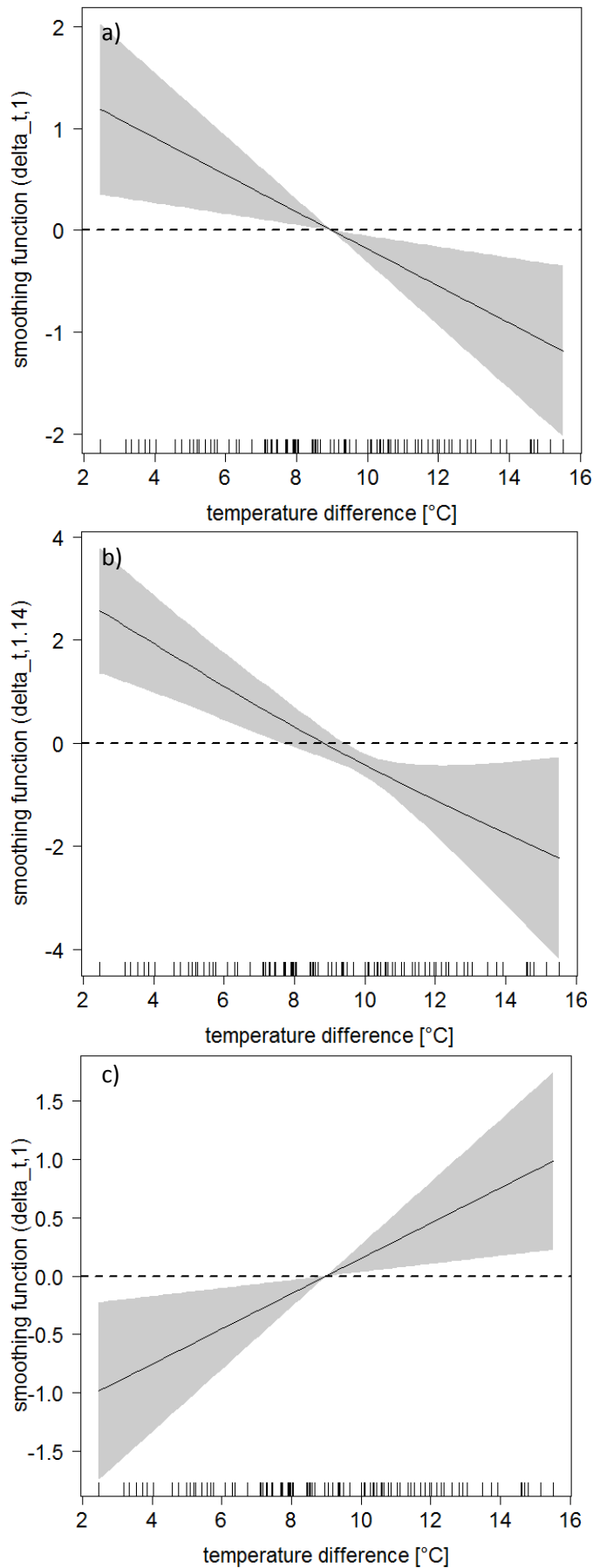


Fig. 59. Smoothing curve of GAM fitted to partial effects of explanatory variables on abundance of (a) Northern Fulmars (*Fulmarus glacialis*), (b) Razorbills (*Alca torda*) and (c) Common Murres (*Uria aalge*) in the Gulf of St. Lawrence in June 2008 and 2009. Abundance is represented as a function of the predictor variable water temperature difference. Grey shade shows the 95% confidence intervals around the main effects. The dashed line shows the mean abundance.

Fluorescence

FLUO had a significantly positive influence on the abundance of Black-legged Kittiwakes (Fig. 58a), Razorbills (Fig. 58b), Common Murres (Fig. 58c) and Herring Gulls. An inverse trend was observed in Common Loons and Great-black backed Gulls. Values above ca. $2\text{mg}/\text{m}^3$ in Kittiwakes and Razorbills and ca. $1.5\text{mg}/\text{m}^3$ in Common Murres and Herring Gulls were associated with abundance values above average. Single high values ($>10\text{mg}/\text{m}^3$) of FLUO associated with low abundance of Common Murres and Herring Gulls are probably outliers evoking an optimum shaped curve.

Water temperature difference

ΔT had a significant effect on the abundance of Northern Fulmars, Razorbills and Common Murres (Fig. 59, Table 7). For Wilson's Storm-Petrels a trend was observed (Table 7). For Northern Fulmars (Fig. 59a) and Razorbills (Fig. 59b) this relationship was negative. Increasing values of ΔT were related to decreasing abundance of these species. At a ΔT around ca. 9°C abundance values changed from above average to below average. For Common Murres ΔT of ca. 9°C was also associated with average abundance, but the relationship was exactly opposite (Fig. 59c).

Model quality and validation

Based on the coefficient of determination R^2 (adjusted) and the explained deviance, the habitat models for Common Murres and Herring Gulls showed the highest values in both categories (Table 7). Comparable habitat models for abundance and distribution were also generated for Northern Fulmars, Black-legged Kittiwakes and Great Black-backed Gulls (Table 7). For Northern Gannets and Razorbills a substantial part of their variation in distribution and abundance was explained, however the associated values for R^2 of these models were lower (Table 7). For Wilson's Storm-Petrels and Common Loons in particular, the habitat models did not seem to cover the main variables that determine their distributional patterns in the Gulf (Table 7).

This overall pattern was also supported when exploring the associated error of the habitat models. The final GAM of each species was compared with the original values using four diagnostic plots (Normal Q-Q, residuals vs. linear predictor, histogram of residuals and response vs. fitted values). The model for Common Murres and Herring Gulls again performed best followed by the other seabird species.

Pearson's correlation coefficient between the final model and the original values paralleled the pattern found for R^2 (adjusted). It was highest in Common Murres (0.87) and Herring Gulls (0.86), followed by Great Black-backed Gulls (0.65), Northern Fulmars (0.64), Black-legged Kittiwakes (0.64),

Chapter 2 – Habitat selection of seabirds

Razorbills (0.53), Northern Gannets (0.46) and Wilson’s Storm-Petrels (0.35). It was again lowest in Common Loons (0.20).

Regarding the stability of our models and the associated error of prediction, the results of the bootstrap were most relevant. The habitat model for Common Murres showed to be stable. This species showed the highest mean abundance (Table 9) and the associated median error of prediction was very small (5%). The prediction error showed a normal distribution and the 95% confidence intervals were relatively narrow compared to the extreme range in abundance from 0 to 22.8 individuals per km at the different stations. The prediction error was also normally distributed in Northern Fulmars, Northern Gannets and Wilson’s Storm-Petrels. In Black-legged Kittiwakes, Herring and Great Black-backed Gulls we found similar results, but a few medium outliers occurred. For Razorbills and Common Loons most errors also occurred close to zero. However, single extreme outliers indicated that the habitat models were less stable than for the other species. In relation to average abundance, the median error of prediction was also small in Razorbills (10%), Herring Gulls (13%) and Northern Fulmars (14%, Table 9). It was medium in Northern Gannets (25%), Kittiwakes (27%), Great Black-backed Gulls (30%) and Wilson’s Storm-Petrel (41%, Table 9). The error of prediction was large in Common Loons (80%) compared with their mean abundance (Table 9).

Table 9. Overview of seabird occurrence, abundance and habitat models (GAMs) errors for the Gulf of St. Lawrence, Canada. Occurrence is depicted as % presence of a species at 96 oceanographic stations. Abundance values and GAM errors are given as birds/km. The median error values and 95% confidence intervals (CI) result from a bootstrap, which was conducted 500 times.

Taxon	Occurrence	Abundance		Error	
	in %	Mean	Maximum	Median	95% CI
<i>Gavia immer</i>	14.6	0.02	0.385	-0.016	-0.045-0.228
<i>Fulmarus glacialis</i>	27.1	0.173	3.346	-0.024	-0.815-1.478
<i>Oceanites oceanicus</i>	21.9	0.121	2.525	-0.05	-0.539-1.081
<i>Morus bassanus</i>	60.4	0.424	4.490	-0.104	-1.044-2.363
<i>Rissa tridactyla</i>	39.6	0.129	1.541	-0.035	-0.398-1.025
<i>Larus argentatus</i>	36.5	0.199	9.759	-0.025	-0.858-0.599
<i>Larus marinus</i>	20.8	0.044	1.337	-0.013	-0.196-0.333
<i>Uria aalge</i>	54.2	0.613	22.798	-0.031	-3.603-2.913
<i>Alca torda</i>	14.6	0.049	1.938	-0.005	-0.428-0.503

Discussion

Quality of habitat models and limitations

Our results confirm that seabird distribution and abundance can be successfully analyzed with habitat models using oceanographic and other environmental variables. A substantial part of the observed deviance in abundance in the Lower Estuary and Gulf of St. Lawrence during summer was explained for the majority of the common seabird species (Table 7). However, some abundant species such as Black Guillemots (*Cephus grylle*) could not be included, as these showed to be restricted to comparatively shallow waters closer to the coast that did not overlap sufficiently with the oceanographic sampling used in our study. Most of the models showed to be stable and the observed prediction error was often relatively low compared to the average abundance (Table 9). For all but one species at least one of the predicting variables proved a significant influence on the abundance patterns (Table 7). The models for Common Murres and Herring Gulls performed best, explaining most of the observed deviance. Further, there was a strong spatial overlap between predicted and observed abundance patterns (Fig. 51 & Fig. 52). A substantial part of the abundance patterns of Fulmars, Gannets, Kittiwakes, Great Black-backed Gulls and Razorbills (Table 7) were explained by their habitat models. A large part of the observed deviance of all species however, could not be explained. Thus, additional variables and mechanisms seem to influence seabird abundance that were not taken into account here. For Loons no convincing habitat model could be generated. We assume this to be at least partly due to the circumstance that some of the main concentration areas of this species, as e.g. along the coast of New Brunswick and Prince Edward Island (see Chapter 1), did not overlap with oceanographic sampling.

Another factor that may be important to at least some species, such as Northern Gannets, is the occurrence of marine mammals as cues to profitable feeding opportunities (e.g. Davoren et al. 2010, Camphuysen 2011). However, because marine mammals were only present at a minority of the 96 analysed stations we had to address this factor separately by applying a different approach (see Chapter 3).

Several studies have emphasized the influence of fishing activity on seabird occurrence (e.g. Garthe & Hüppop 1994, Camphuysen et al. 1995, Arcos et al. 2001), but Markones et al. (2008) showed that the influence of this variable is complex and does strongly interact with other factors. Regarding the Gulf of St. Lawrence, we did not include this factor into our habitat models as the fishing activity was comparatively low in the whole study area, resulting in comparatively low rates of seabirds attracted to fishing vessels, even in *Larus* gulls (N Guse unpubl. data). Elevated fishing activity was mainly observed in some coastal areas around Prince Edward Island. In line with these observations the overall fishing scheme in the Gulf has changed markedly since the mid 1990s due to the collapse of groundfish stocks (Savenkoff et al. 2007a, b). Moreover, discarding is now prohibited (Benoit pers. comm.). The reduced availability of this anthropogenic food source has been regarded as one of the factors responsible for the decline of Herring Gull populations along the North Shore of the Gulf

(Chapdelaine & Rail 1997). Water transparency has also shown to be an important factor relating to water masses and hence, seabird distribution patterns (e.g. Haney 1986, Haney & Stone 1988). Thus, we attempted to use the extinction rates of the photosynthetic active radiation (PAR) sensor as a proxy for the extinction of the visible light spectrum. Due to missing or erroneous data at several stations, this was not possible and transparency could not be taken into account. Moreover, as samples sizes of oceanographic stations and seabird occurrence were limited we could not test all potentially important predictors or their interactions. Thus, we had to preselect a range of the ecologically most promising variables (Garthe et al. 2009) that proved their significance for the majority of species analyzed here.

Spatial constraints and habitat selection

Our study investigated the habitat selection of six common seabird species that were assumed to be spatially constrained and three species that were assumed to select their habitat freely. We hypothesized that spatial constraint would be exerted on the distribution of breeding birds via COLONY (Table 7, COLONY vs. LAND). The necessity to regularly return to a certain site due to parental duties influences the foraging pattern of seabirds regarding feeding locations or foraging ranges, hence their distribution in space and time (e.g. Ashmole 1971, Lewis et al. 2001, Davoren & Montevecchi 2003, Hamer et al. 2007).

Based on the low proportion of immature birds for the majority of these six species (N Guse unpubl. data), we assumed that we mostly dealt with breeding birds. This scheme did not fully apply for Herring and Great Black-backed Gulls, as the proportion of immatures observed during the survey accounted for 48 and 23%, respectively. Thus, it may not be surprising that COLONY did not show such a strong influence on these two gull species. For Great Black-backed Gulls COLONY did not play a significant role (Table 7). For Herring Gulls COLONY proved significance, but SSS showed to have a much stronger effect on their abundance patterns (Table 7 & Table 8). It is therefore possible that immature gulls might forage in slightly different areas than adults, which may have masked or reduced the influence of COLONY.

Nonetheless, COLONY showed a significant influence on the abundance for five out of six species and was one of the most relevant factors overall (Table 7 & Table 8). The abundance for all species, except for Murres, showed a simple negative relationship with growing distance to the nearest colony (Fig. 55). Accordingly, the waters where most of the large colonies are located were also the areas that hosted the largest seabird concentrations. These occurred particularly off the Gaspé Peninsula, around the Magdalen Islands, in the Northwestern Gulf and in the Northeastern Gulf along the Québec North Shore.

The effect of COLONY was very much in line with the different foraging ranges described for the respective species in other studies. Kittiwakes breeding in the Gulf of Alaska for example, regularly exhibited foraging ranges of 40km and more (Kotzerka et al. 2010). This parallels our results of abundance above average up to 48km from the next colony (Fig. 55). Another striking match was found for Gannets. Breeding birds from Bonaventure Island showed an average foraging range of 138km (Garthe et al. 2007a), which is very similar to the 150km range we found with our ship-based approach. As Gannets exhibit a large flexibility in foraging trip length, as well as size and composition of their fish prey (e.g. Garthe et al. 2007a, Hamer et al. 2007), it may not be surprising that this species was not specifically linked to the other oceanographic variables investigated here. The foraging ranges described for Herring Gulls (e.g. Camphuysen 1995) were also similar to our results. Regarding Razorbills we modeled an average range of 58km from the next colony. This is somewhat further than the average of 18km described by (Thaxter et al. 2010). However, a considerable proportion of birds dived at 40 to 50km from shore (Thaxter et al. 2010). Moreover, Razorbills and Common Murres were observed to exhibit much larger maximum foraging ranges (Gaston & Jones 1998). In our study, we found an elevated abundance of Common Murres up to 38km from the nearest colony, which is similar to foraging ranges described elsewhere (e.g. Dierschke et al. 2004, Thaxter et al. 2010). This underlines the significant influence of COLONY on Murre distribution (e.g. Ainley et al. 2005). Highest concentrations were indeed found close to major colonies off the Gaspé Peninsula in the Northwestern and Northeastern Gulf (Fig. 51).

Surprisingly, Murre abundance increased again with growing distance (Fig. 55). Particularly along the west and southwest coast of Newfoundland, medium to high abundance was observed 90 to 150km away from the nearest colony. Even though Common Murres were observed carrying fish at distances of >150km away from breeding sites (Gaston und Jones 1998), it seems more likely that these birds were non-breeders evoking the pattern of increased abundance at higher distances from a colony. Based on estimates for the majority of common seabird species in the Canadian North Atlantic, the proportion of non-breeders might indeed be substantial and lie in the order of 45-65% of the population (Diamond et al. 1986). In our study, Murre abundance was below average between 38 and 108km from a colony. This might suggest a spatial separation of breeders and non-breeders. The latter could be driven by two mechanisms. Firstly, breeding Murres were not able to forage at remote but profitable feeding grounds visited by non-breeders due to the spatial constraints imposed by COLONY. Or secondly, as intraspecific competition for food near colonies can be intense (e.g. Ashmole 1963, Lewis et al. 2001), non-breeders might have been forced to switch to alternative sites.

Overall, most of the analyzed species experienced spatial constraints due to breeding. As breeding seabirds show increased levels of activity and allocate more time to foraging strong habitat bonds can be expected during this period (e.g. Markones et al. 2010). (Shealer 2002) even suggested that habitat relationships are only pronounced during times of spatial constraints. However, the patterns seem to be more complex as seabirds showed strong habitat bonds both during times of spatial

constraints (e.g. Davoren et al. 2002), as well as during periods when seabirds could select their habitat freely (e.g. Markones 2007). Accordingly, we found significant relationships with oceanographic and environmental variables both for spatially restricted species, as well as for species that were not.

Influence of oceanography and distance to land

Environmental variables, such as primary productivity or stratification, have an important influence on top predator distribution at large (e.g. Yen et al. 2004, Worm et al. 2005, Ballance et al. 2006), meso (e.g. Garthe 1997, Ainley et al. 2005, 2009) and small spatio-temporal scales (e.g. Scott et al. 2010, Cox et al. 2012, Embling et al. 2012). We selected a coarse to meso-scale approach and used water mass indicators, as well as primary productivity, as proxies for suitable foraging habitats. We expect these to relate to prey abundance such as fish or zooplankton. However, the interactions of oceanographic factors are complex and thus, their effects are seldom related with seabird abundance in a straightforward manner (Ballance et al. 2006, Garthe et al. 2009). Prey organisms are influenced by the environmental variables themselves and have to trade off foraging against predator avoidance (Fauchald 2009). Hence, a match and mismatch between seabirds and prey regularly occurs. This might further depend on the spatio-temporal scale at which these patterns are investigated (e.g. Hunt & Schneider 1987, Fauchald et al. 2000, Fauchald 2009). For the Benguela upwelling system for example, a match between primary production at the sea surface and seabirds was shown simultaneously with a mismatch between primary production, zooplankton and fish (Grémillet et al. 2008). Thus, a high primary production *per se* does not always mean profitable feeding grounds for seabirds. Additionally, there is increasing evidence that sub-surface chlorophyll maxima can also be very relevant for seabirds and their prey (Grémillet et al. 2008, Scott et al. 2010, Embling et al. 2012). These maxima might create hotspots at very small scales defining critical marine habitat for top predators (Scott et al. 2010, Cox et al. 2012, Embling et al. 2012).

In a study in the Californian Current, the influence of mesoscale physical features on the occurrence of different seabird species proved to be stronger in years when prey was abundant compared to poorer conditions when seabirds were closer linked to prey patches themselves at a smaller spatial scale (Ainley et al. 2009). In our study, alternative information on the abundance of prey such as zooplankton or fish at the investigated stations was scarce or lacking. Thus, we solely relied on the investigated oceanographic and environmental variables to identify important links between seabirds and their habitat at a coarse to medium scale.

In our study, SSS had a significant effect on the abundance of a range of species (Table 7 & Table 8). In accordance with other studies (e.g. Camphuysen 1995, Garthe 1997), Herring Gulls were clearly linked to lower saline water masses and coastal areas (Fig. 52 & Fig. 57). This link explains their main occurrence in the Lower Estuary and western part of the Southern Gulf and reflects their inshore

foraging mode during the breeding period (e.g. Camphuysen 1995, Kubetzki & Garthe 2003). The same pattern held true for Great Black-backed Gulls. Murres, Razorbills and Fulmars on the other hand were clearly linked to higher saline waters as already described in previous studies (e.g. Garthe 1997, Markones 2007, Ainley et al. 2009).

Common Murres were also associated with highly stratified waters in the Gulf (Fig. 59) in accordance with other studies (e.g. Garthe 1997, Daunt et al. 2003, Ainley et al. 2009). Fulmars on the contrary, as well as Razorbills, were associated with less stratified waters. Regarding Razorbills this resembles results from the northeast Pacific (Ladd et al. 2005). Interestingly, a ΔT of 9°C marked the turning point associated with average abundance for all three species. As stratification and pycnoclines can concentrate prey vertically (e.g. Hunt et al. 1990, Haney 1991, Hunt et al. 1999), stratified waters may indicate profitable feeding grounds both for diving and surface-feeding bird species (e.g. Skov & Durinck 2000). Fulmars have shown to be significantly more abundant in upwelling areas with a shallow pycnocline and a flow gradient (Skov & Durinck 2000). As data on pycnocline depth was not available we cannot conclude if this variable was relevant for Fulmars in our study area. Nonetheless, one major concentration area of Fulmars in the Northwestern Gulf (Fig. 53) may be attributed to similar oceanographic mechanisms. In this area, coastal upwelling regularly appears, reducing stratification (Fig. 49, Table 5). In addition a strong flow gradient and horizontal front between the Anticosti Gyre and Gaspé Current occurs. Particularly fronts and convergences as areas of elevated prey availability have proven their influence on the distribution and concentration of top predators in a range of studies (e.g. Schneider 1982, Follestad 1990, Decker & Hunt 1996, Ladd et al. 2005, Doniol-Valcroze et al. 2007). In the Northwestern Gulf oceanographic features create a habitat rich in large zooplankton. This comprises for example mysids, euphausiids and shrimp, as well as small forage fish species such as Capelin and sand lance. The high abundance of suitable prey together with physical processes enhancing its availability, might explain the high abundance of surface-feeders such as Fulmars and Kittiwakes (Fig. 53, Chapter 1). This was also shown in Ladd et al. (2005). Planktivorous Wilson's Storm-Petrels were also found in these waters. They showed largest concentrations in the central deep offshore waters of the Northeastern Gulf, as well as southeast of the Magdalen Islands. Together with Fulmars they significantly avoided coastal waters reflecting their pelagic mode of life.

The different distribution observed in Murres and Razorbills (Chapter 3) in June can be related to the location of their respective colonies, as well as to their opposed response to stratification. For Razorbills the Québec North Shore and adjacent southern Labrador host the main breeding colonies in North America (Nettleship & Evans 1985, Chapdelaine et al. 2001). Major Murre colonies are more widespread in the study area and also located in the Southern Gulf. Accordingly, Murres showed the highest concentrations in the stratified waters of the Gaspé Current and western part of the Southern Gulf. This preference for stratified waters confirms earlier findings (e.g. Daunt et al. 2003, Markones 2007). Razorbills on the contrary were particularly abundant in the Northeastern Gulf and Strait of Belle Isle where coastal upwelling and tidal mixing reduce stratification (Table 5). These differences in distribution and water mass features are probably related to differences in the

preferred prey of the two species. The latter has been linked to interspecific differences regarding wing-load, which influences pursuit diving and flight patterns (Thaxter et al. 2010). In addition, both species differ with regard to transport constraints of prey (Thaxter et al. 2009). For Razorbills and Murres breeding at the St. Mary's Islands on the Québec North Shore the diet delivered to chicks also differed (Chapdelaine & Brousseau 1996, CWS Québec unpubl. data). For both species Capelin was the dominant prey with respect to biomass. But for Razorbills, sand lance was dominant with respect to numerical abundance. It also substantially accounted to biomass consumed (31-46%, Chapdelaine & Brousseau 1996, CWS Québec unpubl. data).

Both these pursuit-diving piscivores showed a significantly positive link with primary productivity in our study. This relationship was paralleled by surface-feeding Herring Gulls and Kittiwakes. We assume that mechanistic links, such as described by Embling et al. (2012), are responsible for these patterns. These authors indicated that primary productivity in combination with stratification and tidal currents lead to surface concentrations of prey which are exploited by Kittiwakes on a small spatio-temporal scale (Embling et al. 2012).

Conclusions

For the majority of analyzed seabird species we could successfully identify significant links with their marine habitat. For the breeding species the spatial constraints were clearly reflected by the different foraging ranges. Moreover, our investigation identified important habitats for seabirds in the Lower Estuary and Gulf of St. Lawrence during summer. Areas off the Gaspé Peninsula, around the Magdalen Islands, in the Northwestern Gulf and along the Québec north shore proved to be particularly important. We showed that the adjacent marine habitats relevant for the birds, in addition to the locations of major colonies, are of a significant size. Identified foraging areas ranged from several tens of km in the majority of the birds to several hundred km in the case of Gannets. At-sea distributions provided in our study should therefore be taken into account when MPAs are designed or related management plans are implemented for these species.

Outlook

Regarding future research on the habitat choice of seabirds it would be most promising to select a combined approach of ship-based surveys of seabirds, sampling of oceanography and prey, in addition to attaching data loggers on breeding birds (Montevecchi et al. 2006). The ship-based

surveys would enable sampling of a substantial part of the local seabird population and account for their behaviour and interactions at sea (e.g. Markones 2007, Camphuysen 2011). Additionally, it would be possible to receive very detailed information on several individuals of known context (i.e. breeding status, colony location etc., see Daunt et al. 2006) by applying data loggers. The latter would enable the investigation of behavioural decisions concerning foraging and reproduction. We recommend continuing seabird censuses during oceanographic surveys such as the Atlantic Zone Monitoring Program (AZMP), as well as during fisheries research surveys. This would be particularly useful in the Northeastern Gulf where research information is traditionally scarce (Dufour & Ouellet 2007), but which proved to be important to many apex predators such as seabirds, seals and cetaceans (White & Johns 1997, Dufour & Ouellet 2007, this study). If the research vessels were equipped with thermosalinographs or ferryboxes, the data basis on key oceanographic variables such as sea surface temperature, salinity, fronts and primary production could be highly increased. Further analyses on the habitat selection of seabirds would also benefit from such approach. Accordingly, additional surveys conducted in important subareas such as in the Gaspé Current and western part of the Southern Gulf, as well as in the Northwestern and Northeastern Gulf, would provide further insight into processes and mechanistic links at a smaller spatio-temporal scale (Stevick et al. 2008, Scott et al. 2010, Embling et al. 2012) and their temporal stability.

Acknowledgements

We are particularly grateful to Alain Gagné, Tom Hurlbut, François Grégoire, Charline Lévesque and their colleagues for the opportunity to join their research cruises. François Bolduc gave invaluable logistic support and enabled the participation onboard. We acknowledge the kind support of the Crews of the ‘Teleost’ and other vessels we worked on. We would like to thank Laure Devine very much for her kind support regarding the download of oceanographic data. We are also very grateful to Jean-François Rail and Carina Gjerdrum for providing data on seabird colonies as well as Esther Rickert for entering census data.

Chapter 3: The influence of marine mammals on the distribution of Northern Gannets in the Lower Estuary and Gulf of St. Lawrence during summer



Chapter 3: The influence of marine mammals on the distribution of Northern Gannets in the Lower Estuary and Gulf of St. Lawrence during summer

Nils Guse (1), Nele Markones (1), Sven Adler (2), Stefan Garthe (1)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Department of Forest Resource Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

Abstract

Marine predators have to rely on behavioural techniques to effectively locate and access their patchily distributed prey. Local enhancement is an important mechanism for foraging avian generalist predators, particularly during reproduction when energetic demands are high and foraging ranges limited. We studied the foraging behaviour of Northern Gannets in the Lower Estuary and Gulf of St. Lawrence (NW Atlantic) during the breeding period with ship-based surveys. At least 21.6% (n=3,452 ind.) of all Gannets were associated with natural phenomena. A majority of these birds (15.8% of all, n=2,525 ind.) occurred in groups associated with natural feeding associations. These were dominated by multi-species feeding associations and/or associations with marine mammals (15% of all). Cetaceans (58% occurrence) and particularly dolphins (33% occurrence) such as the Atlantic White-sided Dolphin were dominant producers in natural feeding associations. Northern Gannets were hardly associated with fishing vessels (0.4% of all, n=66 ind.). Spatial analysis revealed a significant and close spatial association between Gannets and cetaceans. 25% of Gannets occurred within 0.3km, 50% within 2.9km (=median distance, n=8766, 20km radius) to the nearest cetacean. Cetacean abundance proved the largest effect (F=138.81) of all significant predictors when modeling Gannet abundance with a generalized additive model. The strong link between Gannets and cetaceans emphasizes the role of local enhancement for foraging of Northern Gannets. The high abundance of foraging cetaceans which drive and keep suitable prey, such as pelagic fish, in water depths exploitable by Northern Gannets are likely a key mechanism for the latter. This relationship is likely to support the outstanding numbers of breeding Gannets found in these waters.

Introduction

Seabirds as avian predators have evolved a multitude of strategies to locate and capture their prey in the ever-changing marine environment (Nelson 1978). Their prey often consists of pelagic fish and squid (Montevecchi 1993), which may be patchily distributed and predictable only at larger spatial scales. Bathymetric and oceanographic features might concentrate prey, as well as anthropogenic activities such as fishing (e.g. Camphuysen et al. 1995, Garthe 1997). Another important mechanism might be the feeding activity of other pursuit-diving (penguins and auks) or waterborne predators such as large predatory fish and cetaceans increasing the availability of prey near the sea surface (e.g. Camphuysen & Webb 1999, Catry et al. 2009, Davoren et al. 2010, Camphuysen 2011). As many seabird species are visual hunters exploiting the uppermost meters of the water column, the mechanism of local enhancement of prey might be of crucial importance. Particularly feeding whales have been described to initialize feeding associations of seabirds (e.g. Obst & Hunt 1990).

In our study we focus on the foraging habits of Northern Gannets (*Morus bassanus*, hereafter: Gannets) and the factors influencing their abundance. Gannets are capable of covering large areas during their foraging trips (e.g. Garthe et al. 2000, 2003, Hamer et al. 2001, 2007) and may capture their prey by plunge-diving or diving from the surface (Camphuysen 2011), reaching up to 20m water depth. The Gannet is the only sulid that occurs in high latitudes occupying a niche with prey that may be abundant and rich but hard to find and capture as weather conditions can be severe and visibility might be low (Nelson 2002). Despite these challenging conditions, Gannets have expanded and increased throughout the North Atlantic after a period of intense persecution by humans (Nelson 2002).

In several studies around the world the association of Gannets with cetaceans has been described (Evans 1982, Camphuysen & Webb 1999) and it has been demonstrated that Gannets show closer spatial association with cetaceans than with their prey (Davoren et al. 2010). As foraging cetaceans on the one hand may be easily spotted by Gannets over larger distances and on the other hand might hamper the avoidance response of their prey, larger frenzies of Gannets may build up taking advantage of such opportunities (Camphuysen 2011).

In our study area in the Northwest Atlantic, one of the most important breeding sites of Gannets worldwide is found. Their prey mostly comprises fast-swimming large pelagic fish in these waters during summer (Garthe et al. 2000, Garthe et al. 2007a, Chapter 4). We selected a combined approach of behavioural analysis, spatial analysis and spatial modeling to investigate the following main questions:

Firstly, how important are natural phenomena such as multi species feeding associations (hereafter: MSFAs) compared with anthropogenic activities such as fishing for foraging Gannets at sea? Secondly, which species participate in these associations and what is their role? These questions were analyzed based on behavioural data collected at sea.

Thirdly, what is the spatial scale of association between Gannets and cetaceans? This question was addressed by spatial analysis.

Fourthly, how large is the effect of cetacean abundance on Gannet distribution alongside with other environmental predictors? We addressed this question with spatial modeling.

Material & Methods

Study area & data on seabirds and marine mammals

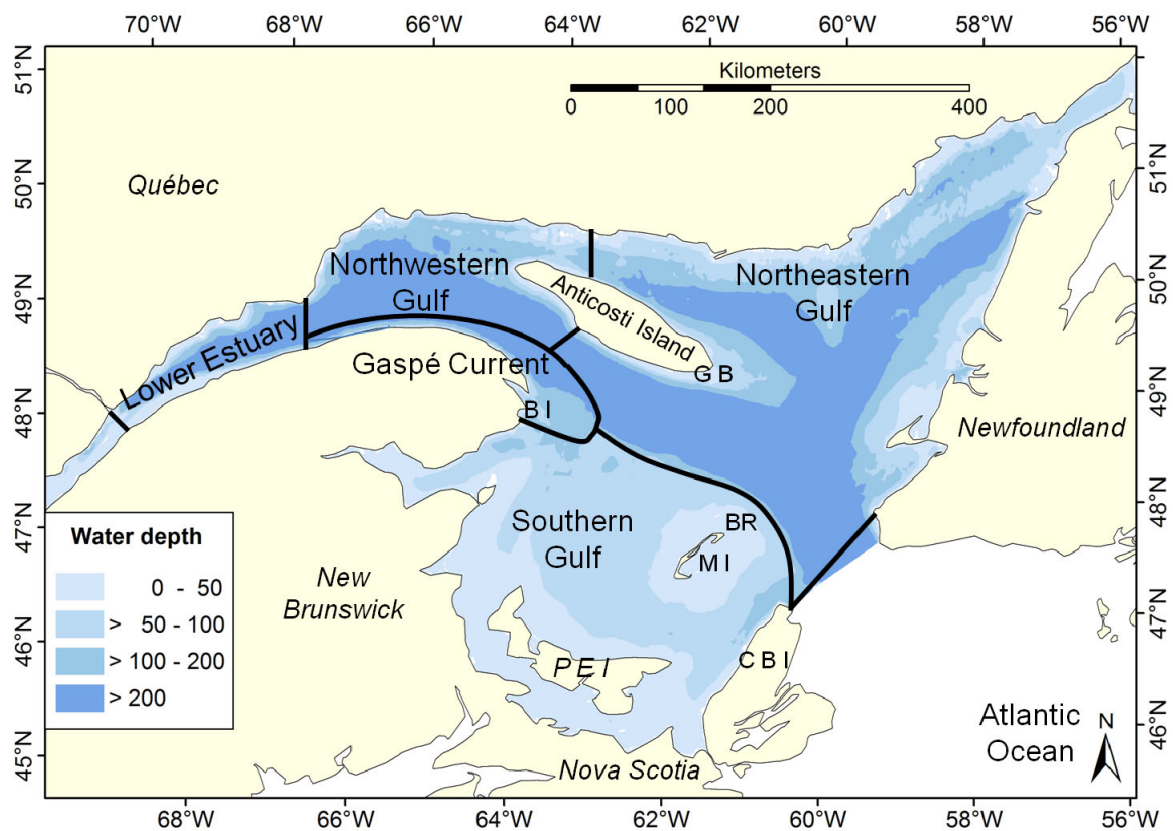


Fig. 60. Study area comprising the Lower Estuary and Gulf of St. Lawrence. Depicted are the five main marine subdivisions (Lower Estuary, Gaspé Current, Northwestern Gulf, Northeastern Gulf and Southern Gulf) modified after de Lafontaine et al. (1991) and Government of Canada (1991), the different provinces (in italics) and other locations mentioned in the text. Abbreviations: BI=Bonaventure Island, BR=Bird Rocks, CBI=Cape Breton Island, GB=Gullcliff Bay, MI=Magdalen Islands, PEI=Prince Edward Island.

The study area (Fig. 60) on the east coast of Canada is a semi-enclosed shelf sea in the Northwest Atlantic Ocean. It is a hotspot for marine mammals and seabirds (White & Johns 1997, Dufour &

Ouellet 2007). With regard to Gannets it probably is the most important breeding area worldwide with ca. 90,000 pairs in 2009 in the two main colonies (JF Rail, Canadian Wildlife Service (CWS) unpubl. data).

We collected at-sea data on seabirds and marine mammals during ship-based research cruises and along ferry routes in the summer months (June to September) of 2007 to 2009 in the Lower Estuary and Gulf of St. Lawrence (Fig. 61). The majority of data were collected during five oceanographic and fisheries research cruises onboard the CCGS 'Teleost'. The complete data set comprised a survey effort of 15,532km of adjusted line-transect counts.

These data were collected in cooperation with the Canadian Wildlife Service (CWS) in Québec, the Maurice Lamontagne Institute (MLI) in Mont-Joli (Québec) and the Gulf Fisheries Center in Moncton (New Brunswick) of the Department of Fisheries and Oceans (DFO). The censuses were carried out by a single observer from outdoors beside and in front of the bridge applying a standardized protocol (for details see Chapter 1, Tasker et al. 1984, Garthe et al. 2002; Camphuysen et al. 2004). This protocol applies the distance sampling technique (Buckland 2001) and takes behavioural aspects of animals (see Camphuysen & Garthe 2004) and observational conditions into account.

Feeding associations with Northern Gannets

To analyze the role of natural phenomena and anthropogenic activities for the foraging of Gannets observed at sea we followed Camphuysen (2011) using the codes of Camphuysen & Garthe (2004). As far as applicable, we assigned behaviour and associations codes (e.g. with fronts, seaweed, fishing vessels, MSFAs etc.) to all Gannets and other marine megafauna observed (e.g. birds, mammals, bony fishes). Furthermore, we recorded whether birds and other marine animals occurred in groups. Behaviour e.g. comprised actively searching, plunge-diving and resting. Only Gannets that lacked specific information on behaviour or association or showed resting behaviour (e.g. sleeping or preening) were excluded from further analysis. The analyses of foraging behaviour comprised several steps (see details below). We calculated the proportion of all Gannets that showed behaviour or association related to:

(1) Foraging activities; **(2)** Foraging activities related to natural phenomena; **(3)** Foraging activities related to fishing vessels; **(4)** Feeding associations in groups; **(5)** Natural feeding associations in groups; **(6)** Fishery-related feeding associations in groups.

(1) Behaviour or association related to foraging activities comprised single Gannets and groups or associations of / involving Gannets that showed active foraging behaviour, e.g. plunge-diving, and also mere presence without perceptible foraging activity in groups or associations within a foraging context (e.g. swimming next to a fishing vessel or a visible oceanographic front). This category was further separated into:

(2) Behaviour or association related to foraging activities connected with natural phenomena comprised all Gannets associated e.g. with feeding conspecifics, MSFAs and/or with specific oceanographic or environmental features. This incorporated all Gannets specified under **(1)**, except for birds clearly associated with anthropogenic activity i.e. **(3)** fishing vessels (see below).

(3) Behaviour or association related to foraging activities connected with fishing vessels comprised all Gannets that were e.g. following or plunge-diving next to a fishing trawler etc.

Finally, we focused in more detail on:

(4) Behaviour or association related to feeding associations in groups. This comprised all Gannets specified under **(1)** that occurred in groups which consisted of at least two individual animals (i.e. only Gannets or at least one Gannet plus at least one other species). These groups were separated into:

(5) Natural feeding associations in groups. This comprised all Gannets in groups associated with natural phenomena (see **(2)**).

(6) Fishery-related feeding associations in groups. This comprised all Gannets in groups associated with fishing vessels (see **(3)**). We identified main functional groups and species of the **(5)** natural feeding associations (e.g. other MSFA-predators), as well as of the **(6)** fishery related feeding associations.

Spatial scale of association

We analyzed the spatial scale at which Gannets were associated with cetaceans. Some transects were covered twice within a day e.g. along ferry routes with an outward journey in the morning and a return journey in the afternoon. Therefore, each census was split into two parts per day (morning and afternoon unit) and analyzed separately. Thus, we addressed the temporal nature of these associations and avoided that overlapping transects would create erroneous results of close spatial associations for Gannets and cetaceans sighted at the same position during different times of the day. We created two separate files on Gannet and cetacean abundance (ind./km) that contained the exact position of each sighting and the associated temporal information.

Davoren et al. (2010) showed that Gannets exhibited maximum association with cetaceans at a scale of 0.6 to 2.8km in adjacent waters. Hence, we considered a search radius of 20km around each Gannet sighting to be sufficiently large. In contrast to the behavioural analysis (see above) we included *all* Gannets and cetaceans in our analysis regardless of behaviour or association. Since the aim was to investigate the underlying effect of cetacean abundance on the overall Gannet distribution. The observed number of Gannet sightings relative to distance to the nearest cetacean sighting was calculated using ArcGIS 10 software (ESRI®ArcMap™10.0). The entire dataset and true

positions (UTM projection) were used with each half-day transect (see above) treated separately by adding an individual ID. First, the distance between each Gannet sighting and each cetacean sighting within the 20km search radius was calculated. Then, shortest distance between each Gannet sighting and each cetacean sighting was selected. Finally, a frequency distribution with number of Gannets relative to distance to nearest cetacean sighting was generated.

As both Gannets and cetaceans were abundant in the Gulf we compared the observed pattern with a dataset that distributed the same number of individual cetaceans and sightings randomly over all positions of the survey. This allowed investigating if the animals were randomly distributed or if the distribution of Gannets depended on the distribution of cetaceans. We used Kolmogorov-Smirnov's test (Conover 1971, Marsaglia et al. 2003) of the free statistical software R, version 2.15.0 (R Development Core Team 2012) to investigate if the abundance patterns of Gannets differed between observed and randomly distributed cetaceans.

Spatial modeling

For spatial modeling, the study area was divided into a grid of 2,311 rectangular cells of 5' latitude * 3' longitude ($\sim 6.2 \times 5.6 \text{ km}$ or $\sim 34.4 \text{ km}^2$). The aim was to investigate the influence of cetacean abundance (ind./km), colony location and distance to land on Gannet distribution and abundance (ind./km). The distance to the nearest colony was selected as it proved to be the only significant factor on Gannet abundance at sea in a study on habitat selection during the breeding season (see Chapter 2). Further, distance to the nearest land was included as it has shown to be a relevant factor for preferred foraging areas of Gannets in the study area and adjacent waters (Garthe et al. 2007a).

All data on Gannet and cetacean abundance were used regardless of behaviour or association to infer how strong the underlying influence of predictors was. This means if the latter proved significance at the level of overall Gannet distribution and abundance (see above). Following similar investigations of top predator distribution (e.g. Schwemmer et al. 2009, Scott et al. 2010, Gilles et al. 2011, Gallus et al. 2012), we selected a generalized additive model (GAM, e.g. Hastie & Tibshirani 1990, Wood 2006a, Zuur et al. 2009a) of the mgcv package 1.7.13 (Wood 2004, 2006a, 2011) in R. We assumed a quasi-Poisson distribution as this is able to cope with zero inflated datasets (Zuur et al. 2009b, Gallus et al. 2012). We included latitude and longitude as additional predictor. Distance to the nearest colony and land were calculated from the grid cell center. The size of cells reflected twice the spatial scale of the median distance between Gannets to the nearest cetacean (see Results) and we set 3km of ship transect as minimum effort for each cell. Each survey across a cell was regarded as a separate measurement of Gannet and cetacean abundance and treated as such. Some grid cells were surveyed repeatedly between different years, months and days. Thus, we included year and month as random effects into the model and used the restricted maximum likelihood estimation (REML; Wood 2011) to analyze the seasonal and interannual influence on Gannet abundance. All

predictors were tested for correlation to avoid overfitting of the model. Correlation between predictors was low ($R < 0.4$). Surveying cells on different days of a month were regarded as repeated measurements. Repetitions within a day were excluded. This was based on effort, i.e. the longer transect within a cell was used, the other discarded. By applying a variogram of residuals, we found that our data were autocorrelated. To account for autocorrelation a generalized additive mixed model (GAMM; Wood 2006a, b) was performed and compared with the results of an ordinary GAM. As both models showed no significant differences (using the ANOVA function in mgcv), we proceeded with the simpler GAM, which performed better, acknowledging that parts of the results might be influenced by autocorrelation. We set the threshold for significance of predictors at 0.05 for all analyses.

We checked the stability of the observed patterns in our model with a nonparametric bootstrap routine (Efron 1990) that applied 25,000 iterations. In each step 2,311 grid cells (=total number of grid cells) were randomly selected out of the original dataset, refitting the model with each iteration. The random sample supplied a prediction for the grid cells that were not selected and the difference between the original values and the prediction generated the error of prediction. We checked the distribution of the error for normality and calculated its median and its 95% confidence intervals and compared it with the average and maximum abundance of Gannets.

Results

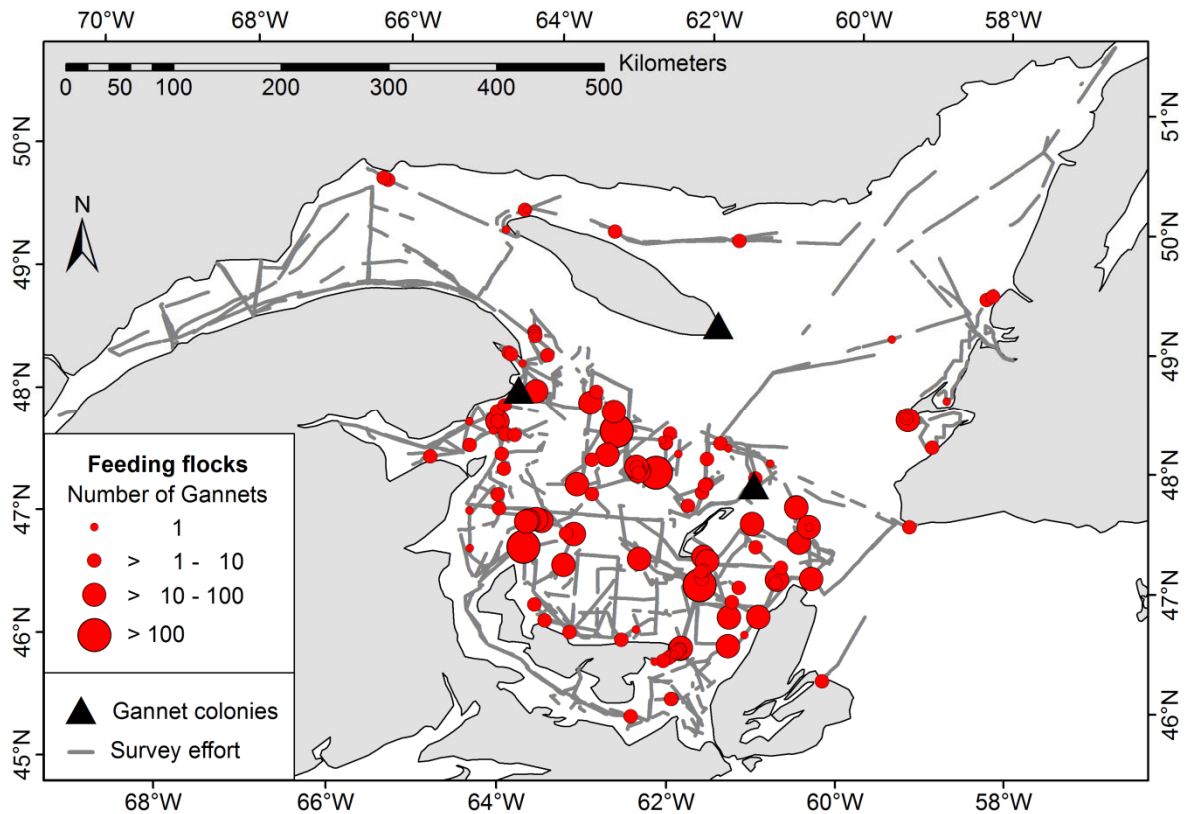


Fig. 61. Location and number of Northern Gannets (*Morus bassanus*) participating in natural single and multi species feeding associations in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Depicted is the survey effort, as well as the location of breeding colonies (top, center: Gullcliff Bay - Falaise aux Goélands, Anticosti Island); middle, left: Bonaventure Island; bottom, right: Bird Rocks – Rochers aux Oiseaux.

Feeding associations with Northern Gannets

All foraging activities

(1) At least 22.0% (n=3,518 ind.) of all 16,004 Gannets observed showed active foraging behaviour or were grouped or associated with specific features (i.e. natural phenomena and anthropogenic activities) within a foraging context (for details see Methods).

Foraging activities related to natural phenomena

(2) A proportion of 21.6% (n=3,452 ind.) of all Gannets was associated with natural phenomena (for details see Methods). This category was dominated by associations with marine mammals and/or MSFAs (15.0% of all Gannets). Only 0.9% of all Gannets, occurring single or in groups, were associated with other environmental or oceanographic features alone (e.g. land, visible

oceanographic front etc.) and 5.7% of all Gannets showed foraging behaviour without any association recorded.

Foraging activities related to fishing vessels

(3) A proportion of 0.4% of all Gannets only, was associated with fishing vessels.

All feeding associations in groups

(4) At least 16.2% of all Gannets (n=2,585 ind.) occurred in feeding associations consisting of groups (for details see Methods). Their composition paralleled the results above.

Natural feeding associations in groups

5) A proportion of 15.8% of all Gannets (n= 2,525 ind.) occurred in groups related to natural feeding associations (Table 10). The latter were dominated by associations with marine mammals or MSFAs accounting for 15.0% of all Gannets (n=2,400 ind.), followed by Gannets without association (0.8%) and those associated with other environmental and oceanographic features (<0.1%). MSFAs involved other bird species, marine mammals and bony fishes (Table 10, Appendix-Table 2). The functional group of MSFA producers was observed in at least 64% of natural feeding associations with Gannets. Marine mammals and cetaceans in particular were dominant producers and accounted for 61% and 58%, respectively (Table 10). Unidentified dolphins, Atlantic White-sided Dolphins and Harbour Porpoises were frequent producers of feeding associations. Pursuit diving seabirds were observed in 6% of the cases. Other surface feeding avian predators occurred in 29% of the associations, most often Herring and Great Black-backed Gulls. These natural feeding associations comprised on average 2.2 taxa, reaching a maximum of 10 different taxa.

Fishery-related feeding associations in groups

(6) Only 0.4% of all Gannets occurred in groups related to fishing vessels (Table 11). The total number of individuals and groups of other taxa associated with fishing vessels was also much smaller than in natural feeding associations (compare Table 10 & Table 11). Large *Larus* gulls, in particular Herring Gulls, were most frequent participants in addition to Gannets in these associations.

Table 10. Composition of (5) natural Northern Gannet (*Morus bassanus*) feeding associations in groups in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Presented are the main participants (at least 5% frequency of occurrence) of single and multi species feeding associations (MSFAs). Included are three groups with five Gannets associated solely with other environmental or oceanographic features (seaweed, line in sea, land; for details see Methods). The total number of Gannets involved (2,525 ind.) accounts for 15.8% of all Gannets observed (see Text). Summarized taxa that include other taxa presented in the table are written in italics and marked with the appendix 'sum'. The mean number of individuals per group is calculated for presence of a taxon only. The table is sorted downwards by % occurrence within the different groups (mammals and birds). For full list of all taxa with scientific names see Appendix.

Taxon	Total (n=ind.)	Total (n=groups)	Occurrence % (n=groups)	Mean (ind./group)	Max. (ind./group)
<i>All animals (sum)</i>	3794	126	100	30	1069
Northern Gannet	2525	126	100	20	584
<i>Marine mammals (sum)</i>	373	77	61	5	35
<i>Cetaceans (sum)</i>	361	73	58	5	35
<i>Dolphins (sum)</i>	246	42	33	6	35
Unidentified dolphin	106	21	17	5	20
Atlantic White-sided Dolphin	94	14	11	7	35
Harbour Porpoise	54	13	10	4	11
Minke Whale	17	9	7	2	6
White-beaked Dolphin	23	6	5	4	10
<i>Large gulls (sum)</i>	580	19	15	31	439
Herring Gull	62	14	11	4	20
Great Black-backed Gull	168	11	9	15	136
Storm-petrels	163	10	8	16	102
Black-legged Kittiwake	30	9	7	3	12
Northern Fulmar	10	6	5	2	5
Common Murre/Razorbills	7	6	5	1	2

Table 11. Composition of **(6)** fishery-related Northern Gannet (*Morus bassanus*) feeding associations in groups in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Presented are all participants of single and multi species fishing associations. The total number of Gannets involved (60 ind.) accounts for 0.4% of all Gannets observed (see Text). Summarized taxa that include other taxa presented in the table are written in italics and marked with the appendix 'sum'. The mean number of individuals per group is calculated for presence of a taxon only. The table is sorted downwards by % occurrence. For full list of all taxa with scientific names see Appendix.

Taxon	Total (n=ind.)	Total (n=groups)	Occurrence % (n=groups)	Mean (ind./group)	Max. (ind./group)
<i>All animals (sum)</i>	287	16	100	18	87
Northern Gannet	60	16	100	4	15
<i>Large gulls (sum)</i>	78	12	75	7	33
Herring Gull	55	11	69	5	21
Northern Fulmar	29	4	25	7	23
Black-legged Kittiwake	52	3	19	17	48
Great Black-backed Gull	18	3	19	6	12
Unidentified gull	63	2	13	32	61
<i>Shearwaters (sum)</i>	5	2	13	3	3
Unidentified large gull	4	2	13	2	2
Sooty Shearwater	3	1	6	3	3
Great Shearwater	2	1	6	2	2
Lesser Black-backed Gull	1	1	6	1	1

Scale of association between Northern Gannets and cetaceans

Gannets showed a high degree of association with cetaceans. They were spatially significantly closer associated with the observed cetaceans compared to randomly distributed ones (Kolmogorov-Smirnov's test: $D = 0.278$, $p < 0.0001$). The number of Gannets was highest in direct proximity to cetaceans and decreased sharply with increasing distance (Fig. 62). 25% of Gannets occurred within 0.3km, 50% within 2.9km (=median distance, $n=8766$, 20km radius) and 75% within 9km distance to the nearest cetacean.

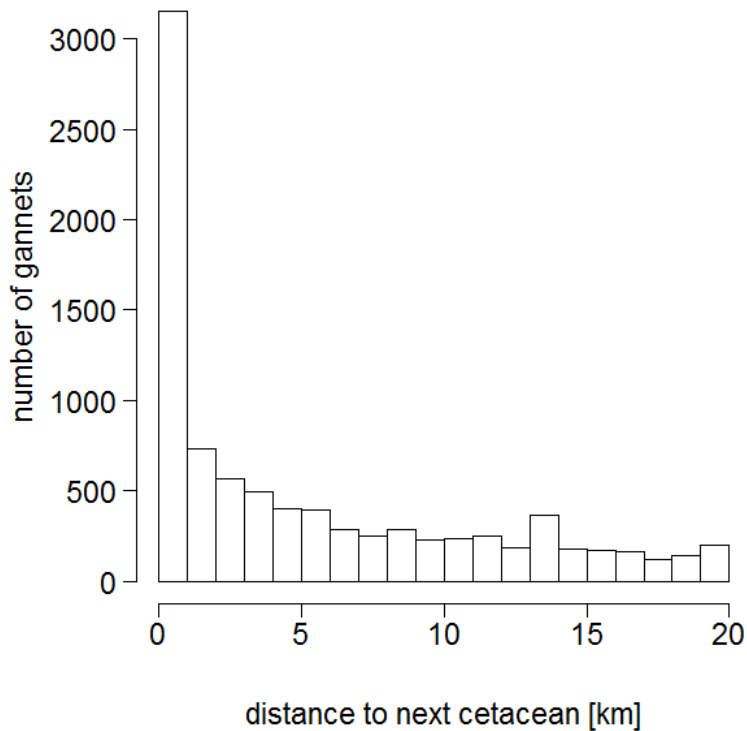


Fig. 62. Spatial association of Northern Gannets (*Morus bassanus*) with cetaceans in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Depicted is the number of Gannets (n=8,766) in relation to the distance to the nearest cetacean (1km classes) within a radius of 20km around each Gannet.

Model on spatial abundance of Northern Gannets

All five predictors of the model on Gannet abundance in the Estuary and Gulf of St. Lawrence were highly significant (Table 12). Cetacean abundance showed the largest effect. The total explained deviance of the residuals of the GAM comprised 51.3% and R^2 (adjusted) was 0.29. The abundance of Gannets increased markedly with the abundance of cetaceans (Fig. 63). This pattern was reverted for areas of highest cetacean abundance. Gannet abundance decreased with increasing distance to the nearest colony and was higher in coastal waters, as well as further from shore compared to intermediate distances from land. The median of Gannet abundance increased both from year to year (2007: 0.18; 2008: 0.23; 2009:0.26), as well as more markedly from month to month (June: 0, July: 0.25, August: 0.32; September: 0.75). Pearson’s correlation coefficient between the GAM and the original values was 0.55. The bootstrap indicated comparable stability of the observed patterns. The prediction error and its 95% confidence intervals reached from -3.01 to 4.13. The median error of prediction was -0.11 compared to a mean abundance of 1.02 Gannets per km. The observed abundance within a grid cell ranged from a minimum of 0 to a maximum of 87.16 birds per km.

Chapter 3 – Marine mammals & Northern Gannet distribution

Table 12. Significant predictors of the model on Northern Gannet (*Morus bassanus*) abundance in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. All predictors of the GAM are depicted with their respective units, estimated degrees of freedom (edf), associated effect sizes (F) and levels of significance (p-values). The threshold for significance was set at 0.05. The levels of significance were: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'n.s.' 1.

Predictor	Unit/sample	edf	F	p-value
Cetacean abundance	individuals/km	1.99	138.81	***
Distance to land	Km	1.97	24.89	***
Distance to colony	Km	1.58	19.82	***
Latitude & longitude (grid)	decimal degrees	41.06	14.26	***
Month (as random effect)	June, July, August, September	2.76	27.05	***
Year (as random effect)	2007, 2008, 2009	1.85	7.60	***

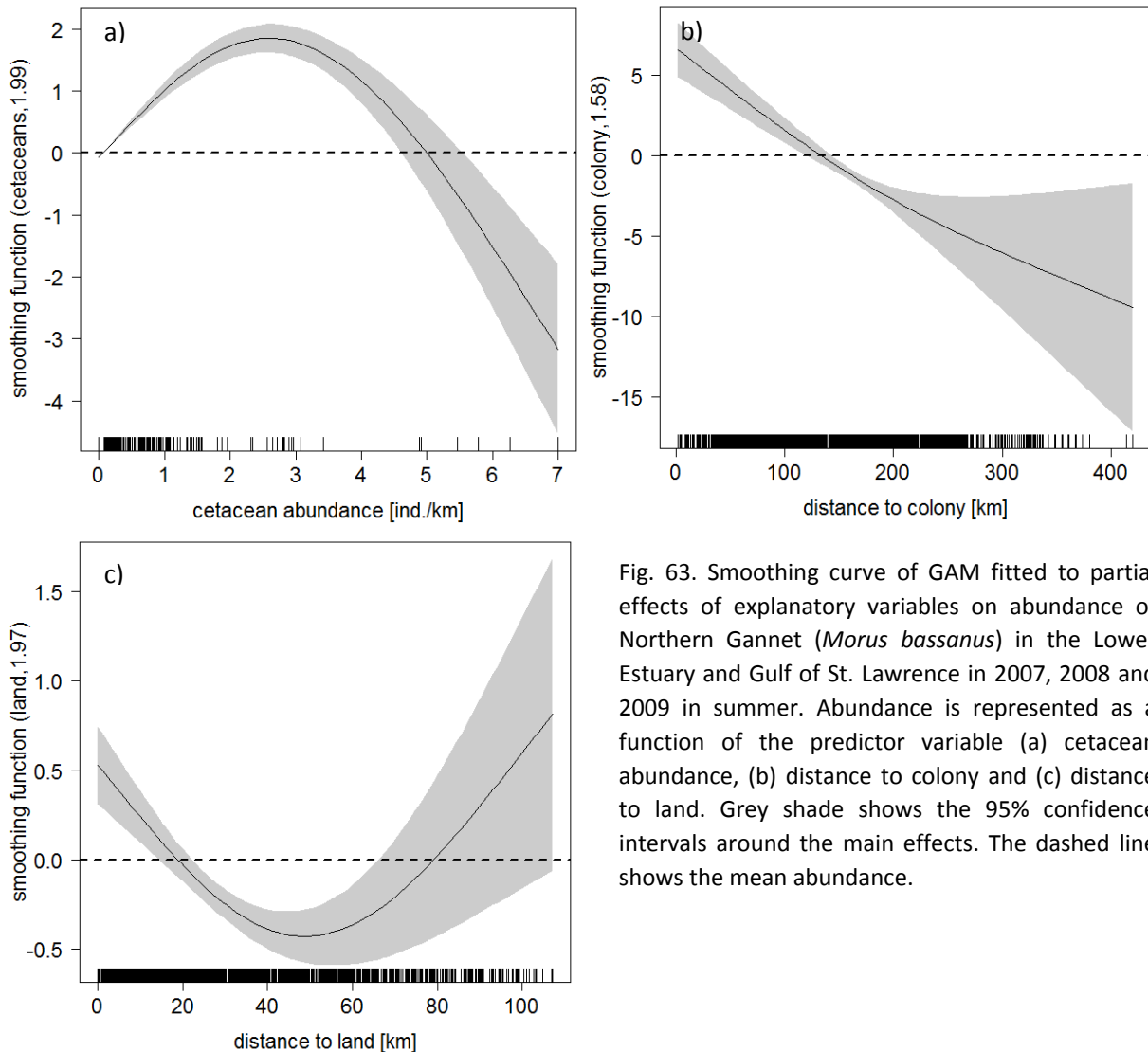


Fig. 63. Smoothing curve of GAM fitted to partial effects of explanatory variables on abundance of Northern Gannet (*Morus bassanus*) in the Lower Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Abundance is represented as a function of the predictor variable (a) cetacean abundance, (b) distance to colony and (c) distance to land. Grey shade shows the 95% confidence intervals around the main effects. The dashed line shows the mean abundance.

Discussion

A substantial proportion of all Gannets observed during the standardized seabird counts showed foraging behaviour and the majority of these birds participated in MSFAs, often including marine mammals. The allocation of behaviour, association and grouping was limited by the distance of animals to the platform and the time available for each observation. Thus, the total number of feeding associations with Gannets in this study represents a minimum number and its proportion is probably considerably higher. The most relevant producers in these natural feeding associations were cetaceans, namely dolphins, such as the oceanic Atlantic White-sided Dolphin. Harbour Porpoises and Minke Whales were also important, which parallels the findings described for Gannet-cetacean interactions in the North Sea (Camphuysen 2011). However, in the North Sea a rather strict spatial separation was found between inshore and offshore MSFAs. Inshore MSFAs were small, short-lived and consisted mostly of seabirds, often with Common Murres and Razorbills, as producers (Camphuysen & Webb 1999). In offshore MSFAs on the contrary, cetaceans played this role (Camphuysen 2011). This spatial separation was not apparent in our study. This may partly be due to an underestimation of other MSFA participants compared to Gannets, as the latter can be identified even at distances of a few kms away from the platform (Camphuysen 2011, pers. observation) and to the fact that less effort occurred in waters below 10m depth and in closest proximity to land. However, we conclude that a considerable proportion of these different patterns can be addressed by the different topography and location of colonies between both study areas. In the Lower Estuary and Gulf of St. Lawrence Gannet colonies rather lie in the center of the studied area and the bathymetry is highly complex and waters of several hundred meters depths can be found in proximity to land (Chapter 2). In contrast to Camphuysen (2011) we found MSFAs with cetaceans in coastal waters e.g. around the western and eastern tip of Prince Edward Island, near Cape Breton and Anticosti Island. Moreover, in contrast to the North Sea, auks were in general only rarely observed in MSFAs, which we would mostly attribute to the different distribution and abundance of Gannets and auks (see Chapter 1). Gannets were much more abundant compared with auks and foraged mainly throughout the Southern Gulf (Magdalen Shallows). Common Murres mostly concentrated around their main colonies along the northern rim of the Southern Gulf, as well as in the Northwestern and Northeastern Gulf (Chapter 1). The pattern was similar in Razorbills and an even higher proportion of birds was found in the Northern Gulf. The latter was much less frequented by Gannets and these differences may be evoked by physiological mechanisms (Cairns et al. 2008). These authors emphasized that water temperature and the mode of capturing exothermic prey influences the distribution of its endothermic predators. Murres and Razorbills, which rely on pursuit diving to capture their prey, would thus be more affected by increased water temperatures and resultant higher swimming speeds of their prey than the plunge-diving Gannets. Plunge-diving is successfully used by other sulids in even much warmer waters such as the tropics (e.g. Le Corre 1997, Lewis et al. 2005, Weimerskirch et al. 2005). Thus, the relatively warmer waters of the Southern Gulf might be a more attractive foraging site for Gannets compared with auks.

Gannets were hardly associated with fishing vessels in our study. This was reflected by the low number of groups associated with fishing activity and the mean and maximum number of participating Gannets compared with the far more important natural feeding associations. Particularly, associations with cetaceans sometimes attracted large number of Gannets. This is in line with the results of Camphuysen (2011) who suggested that larger frenzies may build up when the avoidance response of the prey is hampered by other predators. He also describes the decreasing role of fishery for Gannets in the North Sea but, in contrast to our study, still found the highest mean and maximum Gannet abundance values behind discarding trawlers. We attribute the negligible role of this anthropogenic food source in the Lower Estuary and Gulf of St. Lawrence mostly to the profound changes both in fish stocks and fishery over the last decades (e.g. Savenkoff et al. 2007a, b, Bundy et al. 2009, Morissette et al. 2009). The ecosystem has changed from being dominated by groundfish, particularly large Atlantic Cod (*Gadus morhua*), to a system dominated by pelagic species such as Atlantic Mackerel (*Scomber scombrus*) and small forage species such as Capelin (*Mallotus villosus*) (e.g. Savenkoff et al. 2007a, b). The fishing effort on groundfish, which produced most discards, has been greatly reduced and discarding has been generally forbidden (H. Benoit pers. comm.).

Gannets were spatially closely associated with cetaceans in our study. Moreover, cetacean abundance had the largest effect on Gannet abundance of all predicting variables in our model. Remarkably, these patterns emerged clearly when analyzed for the overall distribution of Gannets and cetaceans regardless of their behaviour or association. This suggests a strong link between both groups and supports the results on the role of natural feeding associations for Northern Gannets. These findings parallel those from adjacent waters off eastern Newfoundland where Gannets preferentially track cetaceans to access their main prey (Davoren et al. 2010). This emphasizes that local enhancement can play an important role for Gannets and other avian predators to find and access their prey effectively (e.g. Catry et al. 2009, Davoren et al. 2010, Camphuysen 2011). Within the study area the Southern Gulf and its boundaries where most intensively used for foraging and many feeding associations could be documented compared to the Northern Gulf. As most survey effort occurred in the Southern Gulf and less in the other areas, these differences might be slightly biased. Nonetheless, not a single feeding association could be documented for the Lower Estuary and further upstream in the Gaspé Current despite the reasonable effort in these waters. This confirms earlier findings of data-logger studies that showed foraging trips from breeding Gannets of Bonaventure to be mainly directed into the Southern Gulf and the downstream part of the Gaspé Current (Garthe et al. 2007a).

The analysis of habitat selection of Gannets in the study area in early summer only revealed distance to the nearest colony as a significant predictor of Gannet abundance (Chapter 3). The striking similarity in the distance of mean Gannet abundance relative to the nearest colony by at-sea surveys to the mean foraging trip range of 138km found by Garthe et al. (2007a) for breeding birds from Bonaventure is remarkable (Chapter 2). This pattern was confirmed by our model, which is based on

a much larger effort at sea both spatially and temporally and comprised a substantial proportion of the entire Gannet population in this area during summer. The main effect of colony location presumably relates to spatial constraints as parental duties e.g. nest building, breeding and provisioning of offspring, require regular returns to a certain site. Moreover, distance to the nearest land also had a significant effect on Gannet abundance. The latter was high up to 20km from land or further than 80km offshore. We thus corroborated the pattern found for foraging trips of breeding birds from Bonaventure, which was assumed to reflect the habitat requirements of the different prey species captured (Garthe et al. 2007a).

Both month and year as random effects showed a significant influence on Gannet abundance. We assume this to be mostly an artifact due to different monthly and spatial effort between the study years. In August and September only the Southern Gulf was censused, which holds the main concentrations of Northern Gannets in the study area (Chapter 1 & 2). This likely biased the median abundance leading to higher values compared with June and July when also the Northern Gulf was surveyed. This is supported by the continuously high estimated totals of Northern Gannets for the Southern Gulf alone during the whole summer period (Chapter 1). However, cetaceans and particularly dolphins, which were dominant producers in MSFAs (Camphuysen 2011, this study), were more abundant in the Southern Gulf later in summer (Chapter 1). Thus, the effect of cetacean abundance on Gannet abundance could have well increased during the progression of summer.

Gannets have shown high foraging site fidelity at coarse spatial scales (e.g. Hamer et al. 2001, Garthe et al. 2007c, Montevecchi et al. 2009) and often higher variability at smaller scales (Garthe et al. 2007a). A large part of the resultant variation in abundance can be attributed to the extreme flexibility of Gannets in adjusting energetic costs when foraging (Davoren et al. 2010), which is seen as an important factor for observed increases in Gannet populations (Montevecchi & Myers 1997). As our study area might hold the largest number of breeding Gannets worldwide (JF Rail, CWS unpubl. data) with resultant large concentrations at sea (Chapter 1) and probably high intraspecific competition, Gannets have to find and access their prey effectively. This may further be affected by the fact that mostly fast swimming large pelagic fish species, such as Mackerel and Atlantic Herring (*Clupea harengus*), constitute the prey of breeding birds at Bonaventure (Chapter 4), which may rather be unpredictable in occurrence (Garthe et al. 2007a). Under these challenging foraging conditions, feeding associations with highly visible and often prey-driving cetaceans might provide the best opportunities to localize and capture prey cost-effectively. Thus, at a finer spatial scale the abundance of cetaceans, which showed the largest effect, seems to be crucial for the abundance patterns of Gannets in the study area, particularly in the Southern Gulf. A presumed high abundance of pelagic fish on the one hand, and local enhancement by cetaceans that facilitate access to this resource on the other hand, supported various feeding frenzies both in coastal and offshore waters. This interaction might be a key mechanism supporting the high number of Gannets foraging and breeding in this area.

Acknowledgements

We would like to thank Alain Gagné, Tom Hurlbut, François Grégoire, Charline Lévesque and their colleagues very much for the opportunity to join their research cruises. François Bolduc enabled the participation onboard and his logistic support was highly appreciated. We thank the Crews of the 'Teleost' and other vessels we worked on for their good cooperation during the surveys. Jean-François Rail kindly provided data on seabird colonies. We are also very grateful to Esther Rickert for entering census data.

Appendix

Appendix-Table 2. Composition of natural Northern Gannet (*Morus bassanus*) feeding associations in the Estuary and Gulf of St. Lawrence in 2007, 2008 and 2009 in summer. Presented are all participants of single and multi species feeding associations (MSFAs). Included are three groups with five Gannets associated solely with other environmental or oceanographic features (seaweed, line in sea, land; for details see Methods). For taxa identified at species level the scientific name is given. The taxon 'All animals' (in italics and marked with the appendix '(sum)') includes all other taxa. The mean number of individuals per group is calculated for presence of a taxon only. The table is sorted downwards by % occurrence.

Taxon/Scientific name	Total (n=ind.)	Total (n=groups)	Occurrence % (n=groups)	Mean (ind./group)	Max. (ind./group)
<i>All animals (sum)</i>	3794	126	100.0	30.1	1069
Northern Gannet (<i>Morus bassanus</i>)	2525	126	100.0	20.0	584
Unidentified dolphin	106	21	16.7	5.0	20
Atlantic White-sided Dolphin (<i>Lagenorhynchus acutus</i>)	94	14	11.1	6.7	35
Herring Gull (<i>Larus argentatus</i>)	62	14	11.1	4.4	20
Harbour Porpoise (<i>Phocoena phocoena</i>)	54	13	10.3	4.2	11
Great Black-backed Gull (<i>Larus marinus</i>)	168	11	8.7	15.3	136
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	30	9	7.1	3.3	12
Minke Whale (<i>Balaenoptera acutorostrata</i>)	17	9	7.1	1.9	6
White-beaked Dolphin (<i>Lagenorhynchus albirostris</i>)	23	6	4.8	3.8	10
Northern Fulmar (<i>Fulmarus glacialis</i>)	10	6	4.8	1.7	5
Unidentified storm-petrel	110	5	4.0	22.0	101
Wilson's Storm-Petrel (<i>Oceanites oceanicus</i>)	47	4	3.2	11.8	38
White-beaked/White-sided Dolphin (<i>Lagenorhynchus albirostris/L. acutus</i>)	23	4	3.2	5.8	12
Long-finned Pilot Whale (<i>Globicephala melas</i>)	20	4	3.2	5.0	8
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	6	4	3.2	1.5	3
Unidentified whale	5	4	3.2	1.3	2
Sooty Shearwater (<i>Puffinus griseus</i>)	49	3	2.4	16.3	45

Chapter 3 – Marine mammals & Northern Gannet distribution

Appendix-Table 2. Continued.

Taxon/Scientific name	Total (n=ind.)	Total (n=groups)	Occurrence % (n=groups)	Mean (ind./group)	Max. (ind./group)
Common Murre (<i>Uria aalge</i>)	4	3	2.4	1.3	2
Unidentified large gull	350	2	1.6	175.0	300
Unidentified marine mammal	9	2	1.6	4.5	5
Unidentified cetacean	5	2	1.6	2.5	3
Great Shearwater (<i>Puffinus gravis</i>)	4	2	1.6	2.0	3
Common Loon (<i>Gavia immer</i>)	3	2	1.6	1.5	2
Razorbill (<i>Alca torda</i>)	2	2	1.6	1.0	1
Unidentified large whale	2	2	1.6	1.0	1
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	35	1	0.8	35.0	35
Fin Whale (<i>Balaenoptera physalus</i>)	6	1	0.8	6.0	6
Unidentified shearwater	4	1	0.8	4.0	4
Unidentified tuna	4	1	0.8	4.0	4
Sperm Whale (<i>Physeter macrocephalus</i>)	4	1	0.8	4.0	4
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	3	1	0.8	3.0	3
Unidentified phalarope	3	1	0.8	3.0	3
Common Tern (<i>Sterna hirundo</i>)	1	1	0.8	1.0	1
Common Murre/Razorbill (<i>Uria aalge/Alca torda</i>)	1	1	0.8	1.0	1
Humpback Whale (<i>Megaptera novaeangliae</i>)	1	1	0.8	1.0	1
Unidentified seal	1	1	0.8	1.0	1
Grey Seal (<i>Halichoerus grypus</i>)	1	1	0.8	1.0	1
Common Seal (<i>Phoca vitulina</i>)	1	1	0.8	1.0	1
Unidentified roqual whale	1	1	0.8	1.0	1

Chapter 4: The Daily Catch: Flight altitude and diving behaviour of Northern Gannets feeding on Atlantic Mackerel



Chapter 4: The Daily Catch: Flight altitude and diving behaviour of Northern Gannets feeding on Atlantic Mackerel

Stefan Garthe (1), Nils Guse (1), William A. Montevecchi (2), Jean-François Rail (3), François Grégoire (4)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Departments of Psychology, Biology and Ocean Science Centre, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

(3) Canadian Wildlife Service, Environment Canada, Ste-Foy, Québec, G1V 4H5, Canada

(4) Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, Québec, G5H 3Z4, Canada

Abstract

Predators utilize a variety of behavioural techniques to capture elusive prey. Behavioural flexibility is essential among generalist predators that pursue a diversity of prey types, and capture efficiency is expected to be intense during the breeding season for parents that engage in self- and offspring-provisioning. We studied the foraging behaviour of parental Northern Gannets in the northwestern Atlantic (Gulf of St. Lawrence) when they were feeding on Atlantic Mackerel almost exclusively. Data-loggers recorded short (mean duration: 6.3s), high speed (inferred vertical speeds of up to 54.0m*s⁻¹, equivalent to 194km*h⁻¹), shallow dives (mean depth: 4.2m; maximum: 9.2m). Dives tended to occur in bouts, varying between 0.3 and 4.6 per hour (mean = 1.6). During foraging, overall flight heights ranged from 0 to 70 m, with no clear preferences for height. Most plunge-dives were initiated at flight altitudes of 11-60m (mean ± SE = 37.1 ± 2.8m; range 3-105m except for 1 of 162 dives that was initiated at the sea surface). Dive depth and flight altitude at plunge-dive initiation were positively and significantly correlated, though it appears that low flight altitudes were sufficient to reach dive depths at which Mackerel were present. Almost all dives were V-shaped indicating that a high acceleration attack is the most effective strategy for Gannets feeding on large rapid-swimming prey such as Mackerel that owing to thermal preferences do not occur below the thermocline and are thus well available and essentially trapped in the water depths exploited by Northern Gannets.

Introduction

To maximize success and efficiency, predators use a variety of foraging and prey capture tactics (Hixon 1982). Predation efficiency is particularly critical for parents provisioning themselves and their offspring (Orians & Pearson 1979). Many seabirds adjust their aerial diving behaviour and underwater pursuit of prey (Elliot et al. 2008a, b). Generalist predators with a broad diet breadth make flexible decisions about the most effective behavioural interactions with prey (Hamer et al., 2007; Harding et al. 2007, Paiva et al. 2010).

Red-footed boobies (*Sula sula*), for example, exhibit a series of very specific flight and aerial adjustments in their pursuit of tropical fishes (Weimerskirch et al. 2005). The closely-related Northern Gannet (*Morus bassanus*) also modifies its aerial and underwater diving behaviour when pursuing different prey (Garthe et al. 2000). (Ropert-Coudert et al. 2009a) demonstrated that the maximum dive depths reached using the plunge-diving technique was 10-11m. Using a biomechanical model they show that little additional depth can be obtained from momentum alone when initiating a plunge from heights higher than 40m. Comparisons of dive angles by Australasian Gannets (*Morus serrator*) similarly showed that dive patterns were adjusted before the bird entered the water (Machovsky Capuska et al. 2011a), confirming that dive depth is determined in the aerial phase of the plunge as suggested by Ropert-Coudert et al. (2009a). Machovsky Capuska et al. (2011a) also showed that Australasian Gannets altered the height of their foraging flights to the depth of fish schools showing that in these circumstances dive profile is associated with prey location, as suggested by Elliot et al. (2008a, b).

Northern Gannets feed on a diverse array of pelagic fishes and squid that range in weights from grams to hundreds of grams and that are returned to chicks in loads consisting of from tens of prey items to single large individual prey (Montevecchi 2007). Of the prey that Northern Gannets consume and deliver to chicks, Atlantic Mackerel (*Scomber scombrus*) have the highest lipid contents and energy density (Montevecchi et al. 1984). Mackerel is one of the largest and fastest swimming pelagic fish consumed by an aerial diving seabird weighing many hundreds of grams and exhibits maximum burst speeds of up to $5\text{m}\cdot\text{s}^{-1}$ (He 1993).

We had hypothesized previously that rapid short duration V-shaped dives were aimed at large pelagic fishes and squids and that extended deep U-shaped dives by Gannets were directed towards schools of small pelagic fishes such as Capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.; Garthe et al. 2000). This was broadly confirmed for Gannets feeding on a mix of pelagic fish prey during another study (Garthe et al. 2011).

Here we report on a study at the largest colony of Northern Gannets in the northwestern Atlantic in the Gulf of St. Lawrence, where Gannets were almost exclusively feeding on Atlantic Mackerel during the 2007 breeding period. We analyze the foraging behaviour of central-place foraging Northern Gannets preying on Atlantic Mackerel, through the application of different data-logging units. We focus on the following questions:

- (1) How deep and long do Gannets dive when preying primarily on Atlantic Mackerel?
- (2) Does a distinct diel rhythm exist?
- (3) How high do Gannets fly when they search for prey, and from which altitudes do they initiate their plunge-dives?
- (4) Is the flight altitude before the start of the plunge-dive related to the dive depth?
- (5) How can the flying and diving behaviour of Northern Gannets observed in this study be explained by the biology of the Atlantic Mackerel as their main prey?

Material & Methods

Study area

This study was carried out between 1 and 11 July 2007 on Bonaventure Island (48°29' N, 64°09' W), a 5km² island located 3km off the Gaspé Peninsula in the boreal waters of the Gulf of St. Lawrence, Québec, Canada. Bonaventure Island is the site of the largest Gannet colony in North America (ca. 59,600 pairs in 2009, JF Rail, CWS unpubl. data).

Diet sampling

Dietary data were collected by approaching Gannets at the periphery of the colony such that some birds regurgitated food loads, and from observations of food scraps and feedings in the colony. Furthermore, some birds regurgitated food while being handled for attachment or removal of GPS devices. Dietary data are presented as the percentage of total prey loads identified. For mixed prey regurgitations the respective proportions of the prey categories were calculated. In addition to samples collected during the above mentioned study period, archived data from the Canadian Wildlife Service were analyzed to provide a broader picture of food consumption by Northern Gannets on Bonaventure Island.

Capture and handling of birds

Adult Gannets incubating eggs or having small chicks (max. two weeks old) were captured and recaptured after 1-7 days with a telescoping noose-pole. To minimize disturbance, nests were chosen on the periphery of the colony. To reduce any potential bias due to unexperienced birds breeding at the periphery of the colony, birds were selected from the third or fourth row from the outer edge. Parental behaviour and egg and chick survival appeared unaffected at nests where we attached data

loggers to one parent. Capturing took usually 2-3min, and attaching devices and marking a bird lasted 5-10min at maximum. All birds were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

Data loggers used

Birds were equipped with either an altimeter or a GPS logger.

Altimeters (15g, 65mm length, 16mm diameter) specifically designed for this study by earth & OCEAN Technologies (Kiel, Germany) consisted of a pressure and a temperature sensor. The range of the pressure sensor was set to include altitudes from 2,000m high through dives to ca. 7m deep; measurements were taken at a 1s interval. Dives deeper than ca. 7m were also recorded but the value remained at the deepest available option (we checked the raw values of the pressure channel for this purpose). The resolution was ca. 2m in air with an estimated accuracy of ca. 8.5m, and 0.0024m in water with an estimated accuracy of 0.1m (information provided by earth & OCEAN Technologies). Data collected were further calibrated; see section on flight altitude analysis below. Nine birds were equipped with these loggers all of which were recaptured, with seven data sets obtained for data analysis.

GPS TD logs (100x48x24 mm, 70g; earth & OCEAN Technologies, Kiel, Germany) were attached to six birds of which five were recaptured with downloadable data. GPS loggers were taped to body feathers on the lower back just above the uropygeal gland with Tesa® tape (Garthe et al. 2011). Devices included temperature/pressure sensors and comprised about 2% of adult body mass. Only data on pressure (i.e. dive depth) were used for this manuscript.

Diving analysis

Dives were analyzed using MultiTrace-Dive (Jensen Software Systems) and were defined as immersions deeper than 0.3m; shallower measurements were attributed to bathing and preening movements. Two different dive types can be distinguished in recordings from Northern Gannets (Garthe et al. 2000): i) V-shaped dives, being usually relatively short and shallow, and with the ascent period following almost immediately the descent period; ii) U-shaped dives, being relatively long and often deep, with time spent at depth between descent and ascent periods. Dives were analyzed differently for the two devices. As dive depth was limited to ca. 7m (varying slightly between the specific devices according to the calibration protocols) in altimeters, dive depth analysis for greater depth was limited to GPS TD loggers. It is important to note however that all dives deeper than ca. 7m were also recorded by the altimeters (see above). Time of day was analyzed by relating each dive to the next full hour (i.e. 05 = 04:30-05:29), following Davoren et al. (2010). Inter-dive times were analyzed per foraging trip and day separately, measuring the time from the offset of one dive to the onset of the next.

Flight altitude analysis

All pressure values from the altimeters were first corrected for changing air pressure values by incorporating hourly measurements at the nearby weather station in Gaspé (data were downloaded from the Environment Canada website: www.climate.weatheroffice.gc.ca/climateData/canada_e.html). This was achieved by adding/subtracting air pressure measurements from the pressure values provided by the altimeter sensor to standardise air pressure in the atmosphere (to e.g. 1,000 hPa). Altimeters were attached atop tail feathers, so that they remained above water when birds were swimming in order to determine 0m altitude. This pressure calibration of the data sets was carried out frequently based on the periods when the birds were swimming. Data from lower pressure values were turned into flying height values (a difference of 1hPa equates to a difference of ca. 8.4m altitude in air).

Flight altitudes were determined separately for travel flight segments (periods of continuous flight after leaving the colony area and before reaching the foraging area; not further analyzed in this manuscript) and foraging bouts (periods with dives that are spaced less than 20min apart). Flight altitudes were classified into 10m classes separately for each individual.

Vertical speeds in the air were derived from differences in altitude between successive measurements (that are available in 1s intervals, see above) after initiating the plunge-dive, resulting in speed values ($m \cdot s^{-1}$).

Results

Diet

Gannets from Bonaventure Island fed mostly on large pelagic fish species during late incubation and the entire chick-rearing periods (Fig. 64). Although varying from year to year, Atlantic Mackerel was always the species consumed most frequently (49-91%), followed by Atlantic Herring (*Clupea harengus*, 6-44%). Other fish species were of minor importance. There was a tendency for Mackerel to slightly decrease from June-July to August-September while Atlantic Herring increased in frequency as Gannet prey.

During the period of logger deployment in 2007 (1-11 July), 94% of the 149 regurgitations contained Mackerel, 3% Capelin, 2% Herring and 3% other species. Seven of the 14 birds retrieved with data loggers regurgitated Mackerel, and none regurgitated any other fish species.

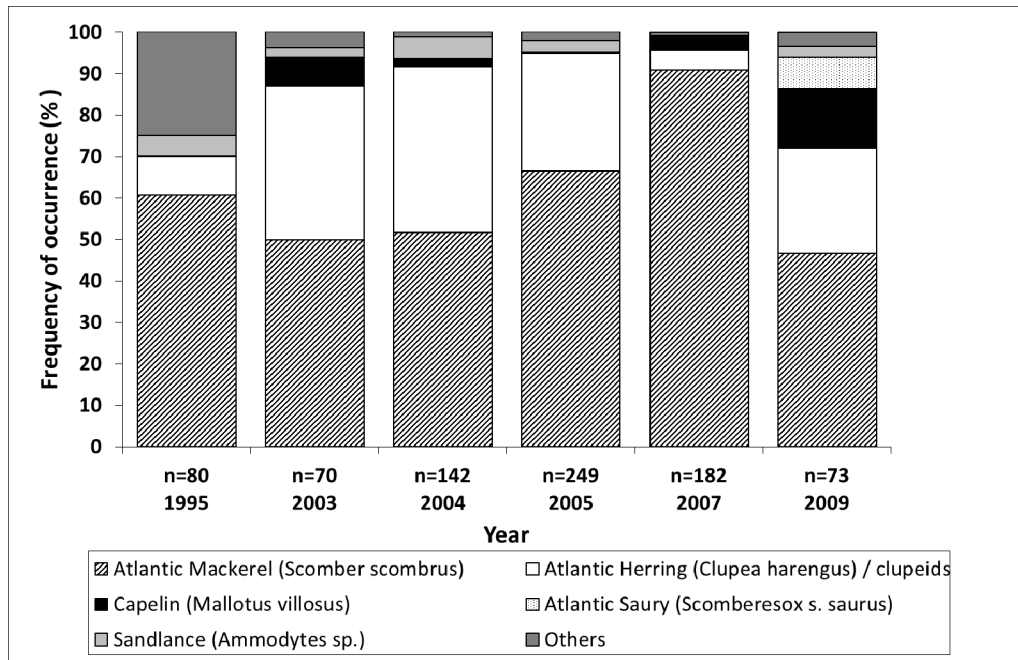


Fig. 64. Diet of Northern Gannets (*Morus bassanus*) from Bonaventure Island from late June to mid-September during six years.

Diving behaviour

Dives occurred between 03:48 and 20:52 local daylight savings time. Diving activity was only slightly elevated in the morning while there was a clear gap around mid-day (Fig. 65a). While some dives occurred during the first light and twilight periods, no dives occurred at night (sunrise: 04:20, sunset: 20:24, respectively).

The number of dives per hour at sea varied between 0.3 and 4.6, with a mean of 1.6 (n=10 birds). Dives tended to occur in sequences of several dives rather than spread out equally over the foraging trips. In 33% of all dives another dive followed within 2min, and in 73% of all dives another dive followed within 20min (Fig. 65b). Only 17% of all dives were spaced by more than 1h from the next dive. When dives occurred in bouts with little time in between, dives depths mostly remained at similar depths. In few cases, dive depths decreased and increased, respectively.

Most of the plunge-dives were initiated at flight altitudes of 11-60m (Fig. 65c). Only 1 out of the 162 dives investigated was initiated at the sea surface (= 0m); all others were initiated at heights ranging from 3 to 105m. Mean flight heights before diving ranged from 28.9 to 45.6 per individual, with an overall mean \pm SE of 37.1 ± 2.8 m (n=7 individuals).

Dives were usually shallow, with 91% of them less than 7m deep with no clear evidence of any depth class preference (Fig. 65d). Mean dive depth was 4.2m (GPS TD loggers only; n=288), and the deepest dive was 9.2m. Dives were mostly briefer than 11s, with a mean of 6.3s and a maximum of 23s (n=731). The proportion of U-shaped dives (dives that showed an extended horizontal phase after descent and before ascent) was 6%.

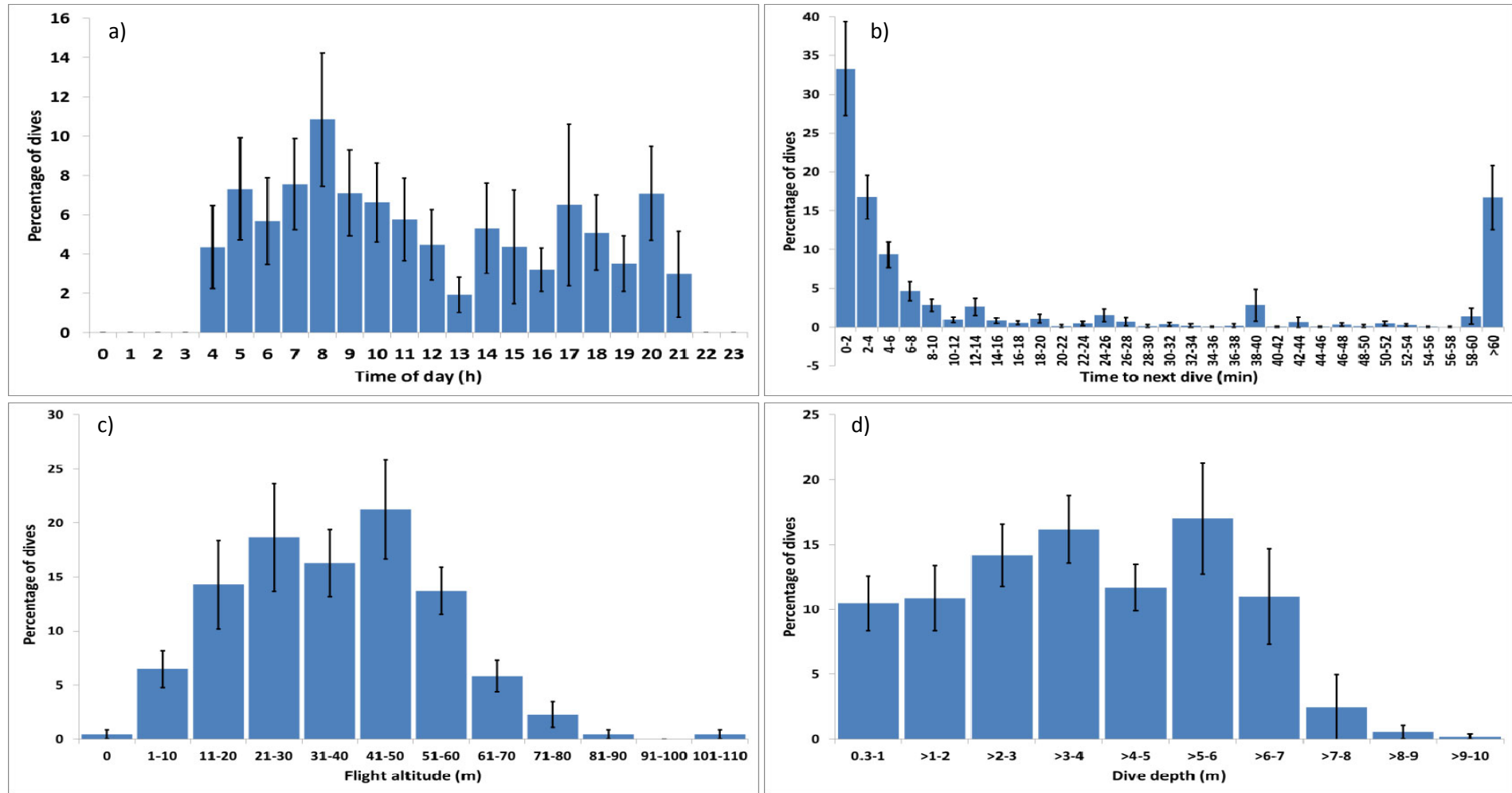


Fig. 65. Diving behaviour of Northern Gannets (*Morus bassanus*) from Bonaventure Island in July 2007.

a) Diel rhythm of dives; n=731 dives from 14 individuals. Vertical lines indicate standard errors. For details see text.

b) Time from the offset of one dive to the onset of the next dive; n=699 inter-dive times from 14 individuals. Vertical lines indicate standard errors.

c) Flight altitudes before plunge-diving; n=162 measurements from seven individuals. For details see text. Vertical lines indicate standard errors.

d) Dive depths from 731 dives from 14 individuals; both altimeters and GPS loggers. Vertical lines indicate standard errors.

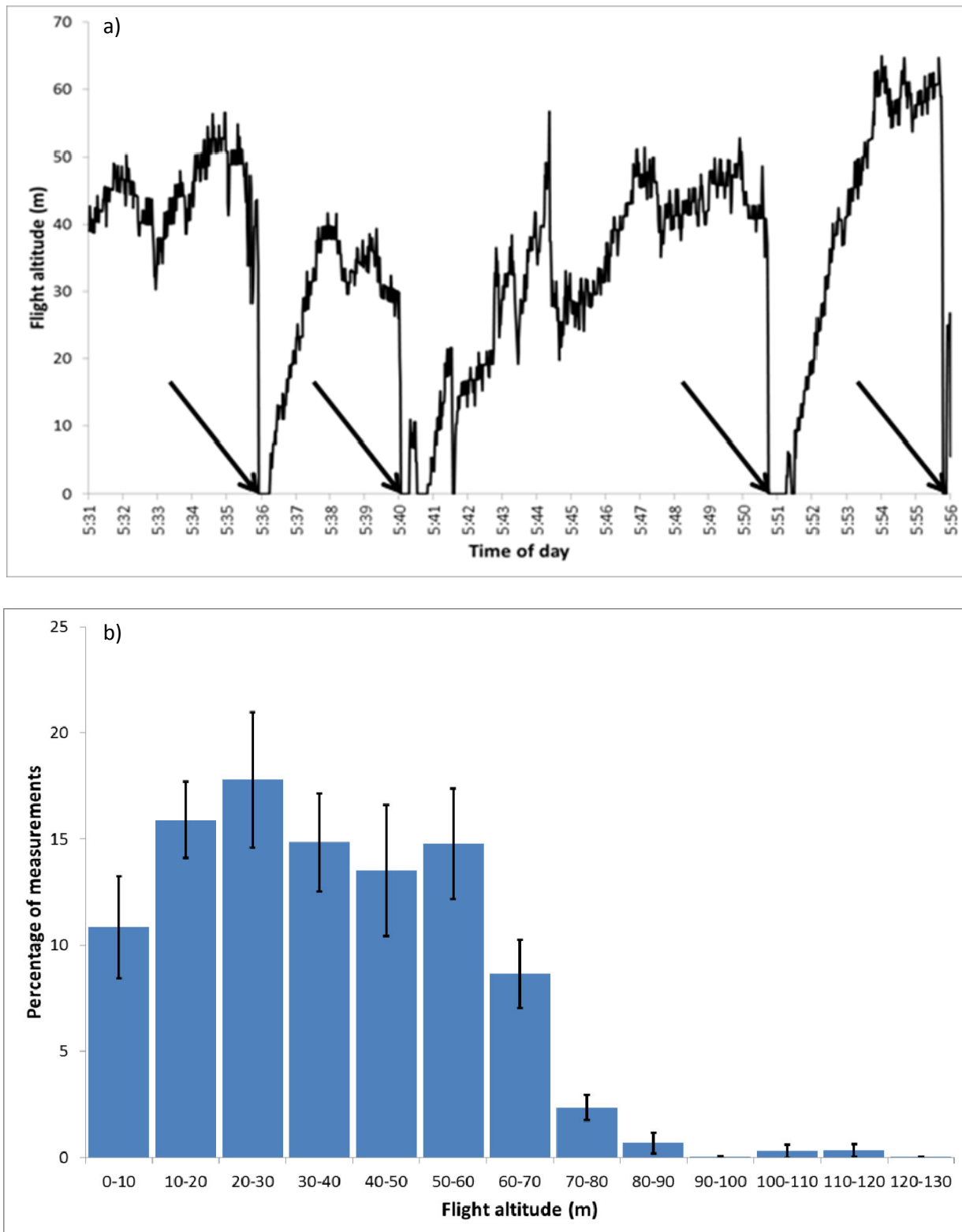


Fig. 66. Flying behaviour of Northern Gannets (*Morus bassanus*) from Bonaventure Island in July 2007.
 a) Flight altitude examples (25min) for one individual. Dives are indicated by arrows; other approaches to (almost) 0m were not related to dives.
 b) Flight altitudes during foraging; n=36,389 measurements from seven individuals. Vertical lines indicate standard errors.

Flying behaviour

Northern Gannets used a wide range of altitudes when foraging. They often altered their flying heights, mainly because of plunge-dives (see examples in Fig. 66a) or attempts to plunge-dives, both of them involving an almost free fall and subsequent climbs. Most flights during foraging were conducted at altitudes of 0-70, with no clear preferences for heights of 10-60m (Fig. 66b).

There was a positive significant relationship between dive depth and the flight altitude at which the plunge-dive was initiated ($t=7.69$, $p<0.001$, Linear Model) with higher onset altitudes generally resulting in deeper dives. There was, however, substantial variation in the data: dives of about 1m depth were initiated at altitudes of 3-35m, whereas those of about 5m depth at altitudes of 16-85m (Fig. 67). Similar to dive depth, there was a positive significant relationship between dive duration and the flight altitude at which the plunge-dive was initiated ($t=7.04$, $p<0.001$, Linear Model). We derived the speed of free-falling Gannets from the vertical measurements. Differences in pressure from one measurement to the next (1s interval) suggest vertical speeds of up to $54.0\text{m}\cdot\text{s}^{-1}$, equivalent to $194\text{km}\cdot\text{h}^{-1}$. Finer resolution of the pressure sensor would probably even better capture the fastest part of the vertical movement and may thus reveal even higher speeds.

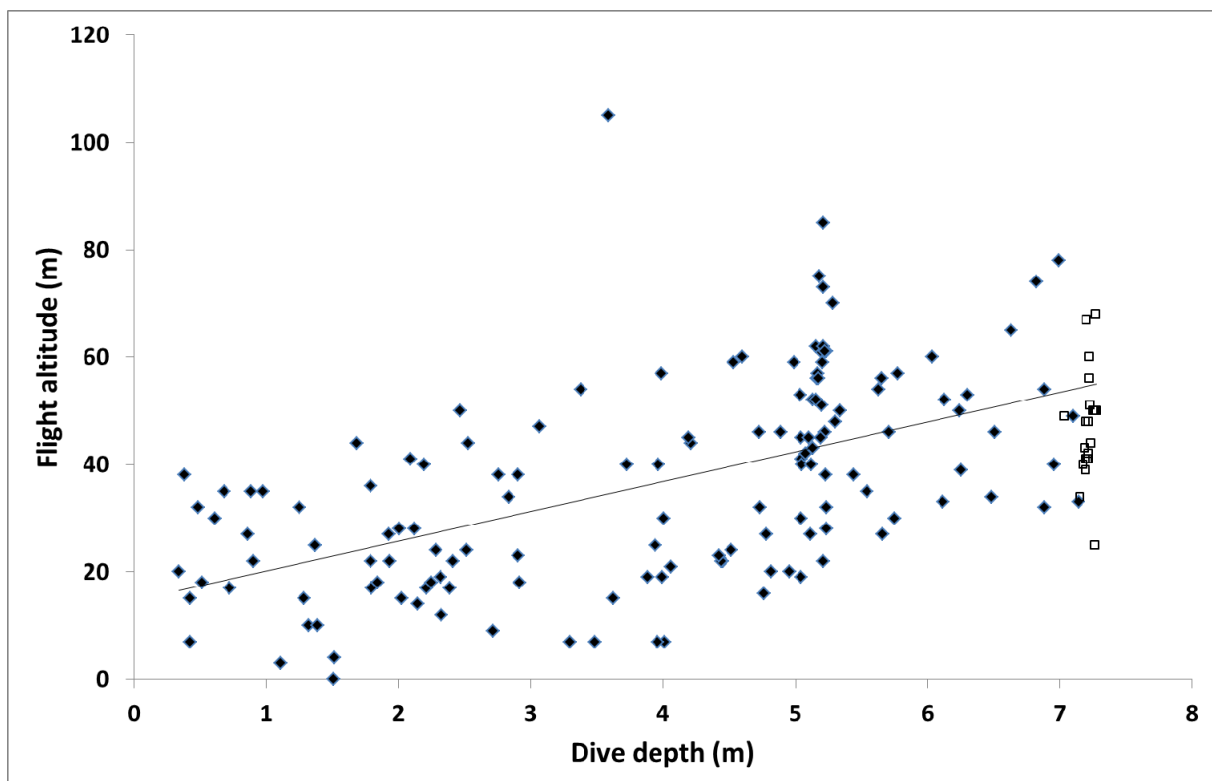


Fig. 67. Flight altitudes of Northern Gannets (*Morus bassanus*) just before plunge-diving as a function of dive depth. Data originate from Bonaventure Island in July 2007; $n=162$ measurements from seven individuals; altimeters only. Open squares indicate measurements when the maximum values of the pressure sensor of the altimeters were reached; in these cases the effective dive depth remains unknown (for details see Methods); these data were not used for the regression line. Equation: $y = 5.545x + 14.631$; $r^2=0.29$.

Discussion

Mackerel as Gannet prey in the Gulf of St Lawrence

Atlantic Mackerel has the highest energy density of any prey of Northern Gannets (Montevecchi et al. 1984) and has been the principal prey of Northern Gannets in the Gulf of St. Lawrence (Nelson 1978), seemingly a preferred choice. Other studies have also revealed Atlantic Mackerel to be an important part of the diet of Gannets, e.g. off Newfoundland (Montevecchi & Myers 1997, Montevecchi 2007), in the Celtic Sea (Votier et al. 2010) and in the North Sea (Hamer et al. 2007), with substantial variation between sites, years and season. Flight patterns, activity and diving behaviour differed often remarkably as a consequence of the different prey choices (Hamer et al. 2007, Garthe et al. 2011).

The Southern Gulf of St. Lawrence is the most important spawning ground for Atlantic Mackerel on the east coast of Canada (e.g. Sette 1943, Arnold 1970, Mackay 1979). The large mature fish begin their spring migration earliest entering the Gulf followed by the juveniles (Sette 1950, Mackay 1967). Owing to varying swimming speeds, Mackerel aggregate in size-associated schools (Sette 1950). At 25 cm total length, 50% of this stock is mature (Grégoire et al. 2009). The slight decrease of Mackerel in the Gannets' diet in late summer can be well explained by their partial redistribution in the Gulf of St Lawrence, with individuals leaving for the Estuary as well as northern and eastern areas (F Grégoire unpubl. data).

Atlantic Herring are also abundant and have important spawning grounds in the Southern Gulf of St. Lawrence in proximity to Bonaventure Island (LeBlanc et al. 2010). Both species are key prey for Gannets with high energy density (10.3kJ/g wet weight for Mackerel and 9.2kJ/g for Herring; much higher than those for Capelin (4.2kJ/g wet weight, Montevecchi et al. 1984).

The thriving of the Gannet population on Bonaventure Island is associated with good availability of high quality prey species such as Mackerel and Herring. The year-class strength of Mackerel fluctuates profoundly, and a single strong year-class dominates (1999) the commercial catches for several years (Grégoire et al. 2009). Moreover, the Mackerel's migration and distribution patterns as well as spawning grounds are undergoing profound changes (Grégoire et al. 2009). Recently, there has been a marked increase in fisheries landings of Mackerel on the east coast of Newfoundland which has been accompanied by a drop in the catches in the Southern Gulf of St. Lawrence (Grégoire et al. 2009). Thus, the availability and hence the importance of Mackerel for Northern Gannets breeding on Bonaventure might alter in the future.

Foraging behaviour in relation to Mackerel as principal prey

We were fortunate to work in the colony on Bonaventure during a period when the Gannets were almost exclusively preying on Mackerel so that we can relate flight and dive patterns to this type of fish. GPS data were too few to make conclusive inferences, but the data from the five birds were

within the spatial pattern described by Garthe et al. (2007a) for the same colony during summer 2003.

The flight altitude of Northern Gannets that forage on Mackerel could be influenced by both the required acceleration for a sufficiently deep plunge dive and the search for a suitable prey school. We suggest that the latter factor may be more relevant as the relationship between flight altitude and dive depth is weak (Fig. 67) and low flight altitudes are obviously sufficient to reach dive depths at which Mackerel were present and to provide the power and impact to stun and capture these large pelagic fishes. Time intervals between successive dives are short, in fact shorter than those previously reported for Northern Gannets (Garthe et al. 2011). This observation supports other findings which indicate that locating a suitable prey school is a key component for Gannets when preying on Mackerel and other pelagic shoaling fish species. Though viewed from a different perspective, Lewis et al. (2001) argued that density-dependent fish disturbance by Gannets is sufficient to significantly reduce the profitability of fish shoals close to colonies, thereby generating suitable conditions for intra-specific competition. However, when preying predominantly on Capelin in waters off northeast Newfoundland, Gannets keyed in on spatially and temporally predictable prey shoals (Davoren et al. 2006) and concentrated foraging efforts in these areas (Garthe et al. 2007c, Montevecchi et al. 2009). In such circumstances involving intense diving activity, Gannets also risk injury from plunging conspecifics (Machovsky Capuska et al. 2011b).

Once a suitable prey school has been located, frequent diving may enable rapid prey consumption. Unfortunately, success rates for dives could not be investigated in this study. Simultaneous and successive attacks by a predator presumably disrupt the attacked prey school (Camphuysen 2011). Thus, we expected that Mackerel would try to escape to deeper waters when attacked by plunge diving Gannets. Hence, successive dives by an individual Gannet should result in increasing dive depths. In a few cases we could observe this scenario but in many more cases the dive depth of successive dives remained the same or was even lower. We assume that this tendency towards shallower dives by the Gannets was due to the Mackerels' escape burst speeds which could only be maintained in the warmest surface water (i.e. that the Mackerel tried to stay in the uppermost water level because of the water temperature), or because the fish were also being attacked from below, impeding escape to deeper water. During ship-based seabird surveys in the Gulf of St. Lawrence from 2007 to 2009, we observed that a high proportion of foraging Northern Gannets were indeed associated with marine mammals, particularly dolphins, such as the Atlantic White-sided Dolphin (*Lagenorhynchus acutus*, Chapter 3). Off Newfoundland, Davoren et al. (2010) found a closer spatial association between Northern Gannets and foraging marine mammals than with their primary prey (Capelin).

Apart from the general abundance and the energy density of prey, its availability is a crucial feature for the predator. Mackerel is mostly distributed in the upper 10-15 meters of the water column during summer in the Southern Gulf of St. Lawrence as its thermal preferences do not allow it to go below the thermocline (Sette 1950; Grégoire 2006). In contrast, Herring is associated with colder and deeper water. Thus, Mackerel might be particularly available in the water depths which are exploited

by plunge-diving Northern Gannets. Darbyson et al. (2003) sampled Mackerel and Herring with mid-water trawling in water depths of 3 to 24m in the Southern Gulf of St. Lawrence in June and found high catch rates for both Herring and Mackerel. Thus, Herring is probably similarly available in water depths used by diving Gannets, which is supported by its high level of importance in the diet of the breeding Gannets from the Bonaventure colony over the years (Fig. 64). Yet Herring schools may well have better escape options than Mackerel by being able to move to depths below the thermocline. The thermocline may be an important foraging habitat for diving seabirds by concentrating prey at a specific depth (Ropert-Coudert et al. 2009b, Kokubun et al. 2010).

Besides its vertical distribution, prey swimming speed also influences availability for the predator. Mackerel and Herring possess similar swimming capabilities (He & Wardle 1988) being considerably faster than most other marine fish species. The probability of a successful attack is highly influenced by the burst speed of the prey. Atlantic Mackerel has the highest recorded burst speed (Videler & Wardle 1991) and reaches up to 5.50m or 18 body lengths per second (Wardle & He 1988, He 1993). The high acceleration and powerful impact of the dives of the Northern Gannet likely enable it to exploit this large and powerful pelagic fish. Thus, Mackerel represents a prototype of fast swimming and schooling pelagic prey. The foraging and particularly the diving behaviour of Gannets clearly respond to the characteristics of such a prey. In our study, we could show that the average dive depth was rather shallow and did not seem to require high flight altitudes to perform a successful dive. Strikingly, almost all recorded dives were V-shaped suggesting that a high acceleration attack at relatively low water depth is the most effective strategy for Gannets preying on Mackerel. If failure occurs, it seems to be more profitable for the Gannets to invest in a new plunge dive compared to pursuing their prey underwater, despite the elevated cost associated with the take off following a plunge (Weimerskirch et al. 2000). This conclusion is also supported by the fact that the intervals between dives are short. The underwater pursuit of prey would result in U-shaped dives, which have proven to be a successful strategy applied by Gannets when feeding on smaller and slower forage fish species, such as Capelin (Garthe et al. 2000). It is also likely that at times Gannets capture multiple similarly sized Mackerel during a rapid succession of dives, as indicated in food loads sampled at the colony (WA Montevicchi unpubl. data).

Conclusions

Atlantic Mackerel is both an attractive but also elusive target, to which its predator, the Northern Gannet shapes its foraging behaviour. This comprises adjustments regarding flight altitude as well as depth, frequency and specific shape of the dive. Mackerel is mostly distributed in the uppermost water column and thus in water depths that can be exploited by plunge-diving Northern Gannets. The high acceleration during the plunges and the apparent surprise attack from the air likely enables the Gannets to capture this fast-swimming and large pelagic fish. (High) Flight altitudes are apparently mostly relevant for prey searching as low flight altitudes are obviously sufficient to reach dive depths at which Mackerel were present. Dives often occurred frequently at short time intervals.

These facts corroborate the idea that locating a suitable prey school is a key component for Gannets when preying on Mackerel and other pelagic shoaling fish species.

Acknowledgements

This research is a joint German–Canadian collaboration with support from the Natural Sciences and Engineering Research Council of Canada (NSERC), Canadian Wildlife Service, Memorial University of Newfoundland, and the Research and Technology Centre (FTZ) at Kiel University. We thank R. Plourdes and his crew from the Bonaventure Island Provincial Park for logistical support and assistance, and P. Bertrand for assisting with field work. G. Peters from earth & Ocean Technologies (Kiel, Germany) provided very valuable technical support. The experiments performed comply with the current laws in Canada, permission was given by the Environment Canada scientific permit number SC-1586.

General Discussion & Conclusions

The aim of this study was to investigate habitat relationships of the most abundant seabirds in the Lower Estuary and Gulf of St. Lawrence during summer. Despite the increasing number of studies and new insights on the links between seabirds and their marine habitats, important gaps remain. Substantial information is available on the foraging ecology of Northern Gannets, Common Murres and Black-legged Kittiwakes from North Atlantic and North Pacific waters. Gannets and several other species were previously investigated in the study area with respect to their foraging ecology and diet. However, general information on the marine ecology of most of the species is still very limited. In addition, current information on the at-sea distribution of seabirds during the breeding season was almost completely lacking. In order to fill some of these gaps, I chose to census the Lower Estuary and Gulf of St. Lawrence with standardized ship-based seabird surveys. These surveys supplied abundance values (ind./km²) for all commonly encountered seabird species as well as (ind./km) for the less frequently observed seabirds and cetaceans (Chapter 1). Total numbers at sea were estimated for 13 species for the Southern Gulf. The results emphasized the significance of the study area for several species in a regional and international context (Chapter 1). The census additionally formed the foundation for the analysis of habitat selection (Chapter 2). Therefore, I selected nine frequent and representative species of the at-sea avifauna during midsummer. These species differed substantially regarding their diet (piscivores, omnivores and planktivores), their feeding technique (dipping, surface pecking, shallow and deep plunge-diving and pursuit diving) and spatial distribution (inshore, intermediate and offshore). The differences between species and a widespread oceanographic sampling ensured a comprehensive consideration of various marine habitats. In addition, the species selection comprised species that were spatially constrained due to breeding, as well as species that were not restricted. Detailed information on the links between seabirds and oceanography on a coarse to meso-scale were gained by spatial modeling (Chapter 2). To analyze these results in more detail, I selected the Northern Gannet as a focal species, as it has one of its main concentration areas in these waters worldwide (Chapter 1 & 2). In addition, important aspects of its foraging ecology were already investigated in the study area and elsewhere. The importance of cetaceans for the foraging ecology of Northern Gannets was documented in adjacent waters and in the Northeast Atlantic (Davoren et al. 2010). I assessed the influence of cetaceans on the foraging ecology of Gannets by selecting a combined approach of behavioural analysis and spatial modeling (Chapter 3). To my knowledge, the influence of cetaceans on the general spatial distribution of Gannets was investigated for the first time together with spatial constraints and other variables. It has been shown that the link between seabirds and oceanography or other predators respectively, is their prey. Thus, we studied the diet alongside with flight and diving behaviour of breeding Gannets with altimeters. These newly applied devices enabled conclusions on how seabirds shape their foraging behaviour in relation to the behaviour and distribution of a certain type of prey (Chapter 4). Overall, I focused on the following four questions that were the motivation for my work:

- 1) How are common seabird species and cetaceans distributed in the study area during summer and what is the significance of this site?
- 2) How are seabirds with and without spatial constraint linked with oceanographic variables?
- 3) How important is local enhancement for the spatial distribution of a generalist avian predator?
- 4) How do avian predators adjust their diving behaviour in response to a certain type of prey?

Summer distribution of seabirds in the Lower Estuary and Gulf of St. Lawrence and its regional and international importance

Our study supplied new information on the current distribution patterns of a wide range of common seabirds and cetaceans in the study area. We applied a standardized ship-based survey protocol (e.g. Tasker et al. 1984, Garthe et al. 2002) that is widely used and enables the calculation of seabird abundance by applying the distance sampling technique (Buckland et al. 2001). The latter allowed compensation of imperfect detection probability of birds at sea. We were able to compare our new results with past patterns based on the PIROP framework (Brown 1986) and results from adjacent waters (Fifield et al. 2009), which were gained with a compatible protocol (Gjerdrum et al. 2012). This latter point is important, as the increasing anthropogenic use of marine habitats is more frequently located in offshore waters that are subject to jurisdictions of different countries (Fifield et al. 2009). Aerial surveys (e.g. Diederichs et al. 2002, Camphuysen et al. 2004) including digital methods (Buckland et al. 2012) are other census techniques which are increasingly used, particularly in the context of Ecological Impact Assessments (EIAs). Dependent on the goal of census and the studied species, either aerial or ship-based surveys are most adequate (Camphuysen et al. 2004, 2012, Markones & Garthe 2012). We chose ship-based surveys, as these supplied a high level of identification of animals, allowing to simultaneously collect *in situ* data on oceanographic variables at the spatial and temporal scale we focused on in our analysis of habitat selection (Chapter 2). In addition, we collected detailed behavioural information of seabirds (Camphuysen & Garthe 2004) during our surveys. This allowed a further in depth analysis of the role of cetacean abundance for Northern Gannets (Chapter 3). All census methods are snapshots of seabird distribution. Consequently, considerable spatial and temporal variation in distribution can be expected, but the variability in patterns is far from random. In contrast to the methodological differences, some species such as Northern Gannets, Northern Fulmars, Leach's Storm-Petrels and Great Black-backed Gulls, showed similar distributions as in the past (see Brown 1986). Wilson's Storm-Petrels on the opposite proved to be far more abundant during our surveys. Particularly Gannets, Kittiwakes, Common Murres, Razorbills and Black Guillemots are known to have important colonies in the study area (Cairns et al. 1991, Fifield et al. 2009). Together with Wilson's Storm-Petrels, Northern Fulmars, Herring, Great Black-backed Gulls and Common Loons, these species formed the dominant at-sea avifauna during summer. With our surveys many hotspots were identified in the study area. However, some gaps in the central and Northeastern Gulf and in waters shallower than 10m depth,

General Discussion & Conclusions

remain. Thus, the habitat of seabirds, such as the Common Eider, was not quantitatively sampled. Increased survey effort, including coastal waters, could further improve the validity of our results and increase our knowledge on Black Guillemots, Razorbills and Common Loons.

Many of the observed seabird hotspots have already been recognized in the past and emphasized the relative stability of such sites, which are believed to be linked to bathymetric and oceanographic anomalies. Each subdivision of the study area held substantial concentrations of seabirds (Chapter 1). The locations of main concentrations differed between species. Despite the limited coverage of the Northern and particularly Northeastern Gulf, high concentrations of Common Murres and Razorbills were found along the Québec North Shore. Black Guillemots showed particularly high concentrations along the west coast of Newfoundland. Several other multispecies hotspots were identified, among others, along the northern rim of the Lower Estuary, in the Northwestern Gulf, in Cabot Strait, around Cape Breton and the Magdalen Islands and east of Prince-Edward-Island (Chapter 1 & 2).

The Southern Gulf was most intensively surveyed. It was the only area with census data available for the late summer period. Several species showed contrasting use of these waters with higher abundance values occurring either in mid or in late summer (Chapter 1). The multispecies hotspot around the eastern part of the Gaspé Peninsula was clearly identified in this area. Bonaventure Island and other main colonies are located in these waters. For Gannets, Kittiwakes, alcids and large *Larus* gulls, this area was very important throughout the whole summer. This was paralleled by the high abundance of other top predators such as Atlantic White-sided Dolphins, Fin and Blue Whales.

The good data basis for the Southern Gulf enabled furthermore the calculation of 'population' estimates for 13 common species. These waters proved to be highly important for several species when comparing at-sea numbers with numbers of the Canadian breeding population or biogeographic population. For Northern Gannets, this site is one of the most important during summer worldwide and Gannet numbers at sea relate to the vast majority of the breeding population. At-sea numbers of Razorbills and Kittiwakes also made up a significant part of their Canadian breeding population. Estimated totals of Herring and Great Black-backed Gulls, as well as Common Loons in the Southern Gulf were also internationally significant.

Our study underlined that ship-based seabird surveys represent a powerful tool to recognize single and multispecies hotspots and assess the significance of whole marine regions on a regional and international scale. This enables further studies of habitat relationships (see Chapter 2). Moreover, seabird abundance values and estimated totals are also vital for the designation of Marine Protected Areas (MPAs) and other marine spatial planning applications such as risk assessments and EIAs. We demonstrated the regional and international significance of these waters during summer for a range of seabird species and the outstanding importance for Northern Gannets.

Habitat selection of seabirds with and without spatial constraint and their links with oceanography

We selected a coarse to meso-scale approach to model seabird distribution based on oceanographic variables measured during the Atlantic Zone Monitoring Program (AZMP) in addition to distance to the nearest colony or land. Our analyses identified significant links with the marine habitat for eight out of nine common seabird species in the Lower Estuary and Gulf of St. Lawrence during the breeding season. The study site hosts unique oceanographic properties, is highly productive in plankton and fish, and a known hotspot for marine mammals. The latter plays an important role in the food web (Morissette et al. 2006, Savenkoff et al. 2007a, b) and showed to be linked to certain hydrographic features such as thermal fronts (Doniol-Valcroze et al. 2007). The high abundance of marine mammals together with known links between marine mammals and their habitat was one of the initial drivers to investigate similar bonds in this study site for other abundant and important top predators – seabirds. For similar studies bird-borne devices such as data loggers and satellite transmitters have increasingly been used in conjunction with chlorophyll *a* from remote sensing as a proxy for primary productivity (e.g. Worm et al. 2005, Catry et al. 2009, Kotzerka 2011). While such studies supply very detailed information on a mostly very small sample size of birds, our ship-based approach enabled the sampling of a substantial proportion of the local seabird population (*sensu* Markones 2007, Camphuysen 2011, Camphuysen et al. 2012).

Our study revealed a significant effect of colony location on five out of six species, which proved to be one of the variables with the largest explanatory power. For Northern Gannets this was the only variable exhibiting a significant effect on observed abundance. Results on the decreasing abundance with increasing colony distance strikingly paralleled the foraging range described for breeding birds from Bonaventure Island that were equipped with GPS loggers (Garthe et al. 2007a). Similar matches between our models and foraging ranges described in the literature were also found for Black-legged Kittiwakes, Common Murres and Herring Gulls (e.g. Camphuysen 1995, Dierschke et al. 2004, Thaxter et al. 2010, Kotzerka et al. 2010). The models for the latter two species performed best regarding the overall explained deviance. Observed and predicted areas of high and low concentrations of Common Murres and Herring Gulls were well reflected. Links with water mass indicators and primary productivity were shown for the majority of species, which were presumably spatially constrained (colony location), as well as for Northern Fulmars, which were not. The latter were positively linked to sea surface salinity (SSS), as were Common Murres and Razorbills. Herring and Great Black-backed Gulls on the opposite were linked to less saline coastal waters. Common Murres were associated with stratified waters, whereas Razorbills and Fulmars were negatively linked to stratification. Primary productivity had a positive effect on the abundance of Kittiwakes, Herring Gulls, Murres and Razorbills. Our analyses not only confirmed hotspots for the different seabird species (Chapter 1), but also showed which oceanographic variables proved to be responsible for these aggregations.

The observed differences between species relate to their differences in diet, foraging ranges, feeding technique and colony location. Consequently, their preferred habitats differed considerably.

Nonetheless, several areas, such as the northwestern part of the Southern Gulf, the waters around the rim of the Anticosti Gyre in the Northwestern Gulf and along the Québec North Shore, as well as around the Magdalen Islands, proved to be significant for several species, which may exploit the same spatial area in very different ways.

Ultimately of course, seabirds are not interested in oceanography, but in finding and catching sufficient prey. Like in other studies which coupled seabird distribution with oceanographic or bathymetric variables, we assumed that by measuring habitat characteristics we indirectly measure the availability of suitable prey. The prey in turn is also influenced by oceanographic processes. In most cases and on a larger scale this approximation via oceanography will often be correct. However, some studies have shown that despite good match of seabirds e.g. with primary productivity pronounced mismatch with their prey can occur (Gremillet et al. 2008). But receiving good data on prey availability directly also has its pitfalls and, most importantly, is often hard to measure. In case of pelagic fishes and squid, which constitute an important part of most seabirds' diet (Montevecchi 1993), this prey often is simultaneously predator of smaller fishes or plankton. Thus, the distribution of the prey of seabirds is also influenced by its own prey, which in turn is influenced by hydrographic features. Moreover, many studies look at prey distribution only from the perspective of the predator but all prey has a vital interest to avoid predation (Fauchald 2009). In addition to the effect of predator avoidance (e.g. Ashmole 1963, Lewis et al. 2001, Camphuysen 2011), the encounters of seabirds with their prey are usually extremely limited in space and time. Seabirds have also shown to need a certain threshold of sufficiently available prey rather than concentrating always in areas of maximum prey biomass (Mehlum et al. 1999, Piatt et al. 2007, Cury et al. 2011). The sum of these features make considerable temporal and spatial mismatch of seabirds with their prey likely. Thus, our indirect approach was the best option to characterize the underlying traits of seabird habitats for the dominant species in the study area during the breeding season. Our study emphasized the strong spatial influence of spatial constraint via the colony location on the abundance of breeding birds at sea. It enabled the identification of general links with oceanography and the comparison with other studies throughout the world. It helped to recognize particularly relevant water mass indicators and biological hotspots for the different species. These results form the basis for further in depth studies in this area incorporating relevant processes such as local enhancement (Chapter 3), foraging behaviour and prey (Chapter 4).

The influence of local enhancement on the distribution of a generalist avian predator

This study shed light on some of the general aspects of the foraging behaviour of Northern Gannets. We focused on this species as it has been shown to be a dominant avian predator in the North Atlantic. Its total population has strongly increased over the last decades, which is attributed to its behavioural flexibility and reduced human persecution (Nelson 2002). Moreover, it has one of its main concentration areas worldwide in our study area during summer (Chapter 1). With only colony

location and none of the oceanographic variables having a significant effect on its distribution, we decided to further investigate the processes and factors important for this predator. Many aspects of its foraging behaviour were already studied with bird-borne devices (e.g. Hamer et al. 2001, Montevecchi et al. 2009) and at-sea surveys (e.g. Camphuysen 2011, Davoren et al. 2010). In addition, due to the application of data loggers and diet analysis during earlier studies, information on the foraging ecology of breeding adults from Bonaventure Island was already available (e.g. Garthe et al. 2000, 2003, 2007a). Based on detailed behavioural observations at sea during ship-based surveys (Camphuysen & Garthe 2004), it was possible to account for the context in which individual birds interact with their marine environment (Markones 2007), while simultaneously sampling a considerable proportion of the Gannet population.

During our ship-based census we were able to show that a significant proportion of all Gannets showed foraging behaviour and often aggregated in groups. These foraging associations sometimes only consisted of Northern Gannets but were more often MSFAs reaching large aggregations. Gannets were only negligibly associated with fishery and aggregations were usually smaller and held few other species. The natural MSFAs mostly contained cetaceans as producers and hardly pursuit-diving seabirds such as alcids. Dolphins, particularly Atlantic White-sided Dolphins, participated most frequently. Most MSFAs occurred in the Southern Gulf where dolphins and Gannets were most abundant (Chapter 1 & 3).

For adjacent waters it has been shown that Gannets were spatially closer associated with cetaceans compared to their prey (Davoren et al. 2010). For our study area we could also show an extremely close spatial association between Gannets and cetaceans. Consequently, when modeling the abundance of all Gannets, the abundance of cetaceans proved to have a significant influence. Cetaceans were thus at least as important for the general distribution of Gannets as the distance to the next colony or nearest land. The process behind this pattern is local enhancement. Dolphins or other cetaceans drive prey such as pelagic fish and thus block their avoidance response (Camphuysen 2011). This increases the prey availability in the upper part of the water column which can be effectively exploited by Gannets. The high abundance of cetaceans in our area might thus also have a positive influence on the large population of Gannets in these waters.

Avian predators adjust their diving behaviour in response to a certain type of prey

In our study we researched the diving behaviour of individual Northern Gannets breeding on Bonaventure Island in the Gulf of St. Lawrence with bird-borne data loggers. With this high resolution approach we supplied important information complementary to the preceding investigations on the distribution (Chapter 1), habitat relationships (Chapter 2) and processes important for the foraging behaviour of Gannets in this area (Chapter 3). This enabled zooming in on a specific part of the foraging technique and warranted some general lessons on predator prey relationships. High

predation efficiency is crucial especially for parental birds as they need to provision offspring in addition to themselves (Orians & Pearson 1979). Gannets have been shown to be highly flexible generalist predators with a large dietary breadth, able to adjust their aerial diving behaviour, as well as their underwater pursuit of prey (Garthe et al. 2000).

Recent studies on a closely related species have shown that the dive depth is determined in the aerial phase of the plunge (Machovsky Capuska et al. 2011a). We focused on flight altitudes and dive depths of Gannets applying newly designed altimeters during a period when the birds almost exclusively preyed on Atlantic Mackerel. This fish species has the highest energy density (Montevecchi et al. 1984) and is among the largest and fastest swimming pelagic fish species (He 1993) captured by an aerial diving seabird. The Southern Gulf used to be the most important spawning ground for this species on the east coast of Canada (e.g. Sette 1943, Arnold 1970, Mackay 1979). Our results suggest that flight altitudes of Gannets were mostly influenced by searching for a suitable prey school, which seems to be a vital element for Gannets that preyed on pelagic fish such as Mackerel. The dive depth was only weakly linked with flight altitude before the plunge, suggesting that diving depths for reaching Mackerel could easily be attained. Due to the low thermocline during summer, Mackerel might be trapped in the upper water column due to its thermal preferences. This would make Mackerel particularly available in waters exploited by Gannets. In addition, Mackerel are also preyed upon by cetaceans and local enhancement might further facilitate access to Gannets (Chapter 3). This was indicated by some of the successive dives being stable in depth or even becoming shallower. This contrasts with an unhampered avoidance response as fish has been observed to escape to deeper waters if successively attacked from above (Camphuysen 2011).

Strikingly, almost all diving profiles were V-shaped. This means a fast descent followed by almost direct ascent without prolonged horizontal diving phase as in U-shaped dives. The latter have been associated with smaller and slower types of prey such as Capelin. Hence, when Gannets dive for Mackerel and fail they seem to invest considerable energy into a new plunge rather than pursuing this fast prey underwater. This was also supported by the short intervals between dives. Thus, Mackerel is an attractive but elusive prey. This study strongly suggests that predators fine-tune their foraging behaviour in response to the requirements of a certain type of prey which can result in only applying one extreme technique.

Synthesis & future perspectives

My study underlined the regional and international significance of the Lower Estuary and Gulf of St. Lawrence for a range of seabird species during summer. By combining ship-based censuses with oceanographic sampling it was possible to fill important gaps regarding their distribution patterns and analyze the oceanographic variables behind the different hotspots with spatial modeling. Thus, we identified important at-sea habitats for the different species and the ranges breeding birds operate in. With detailed behavioural observations, spatial modeling and the equipment of breeding

General Discussion & Conclusions

Northern Gannets with data loggers, we gained substantial new insights into the foraging ecology of this focal species. For Northern Gannets the study area is one of the most important sites in the world with respect to its breeding population and at-sea abundance. Mackerel, which has had an extremely important spawning site in the area, has proven to be a key prey at the largest Gannet colony on Bonaventure Island. In addition, we showed that cetaceans exert a significant influence on the general Gannet distribution. This mechanism most likely acts through local enhancement as prey-driving cetaceans facilitate access of foraging Gannets to this resource. The combination of rich feeding grounds with reduced human persecution most likely has supported the long lasting population increase of Gannets in this area.

However, the study area and adjacent waters have undergone and probably are still undergoing severe changes regarding oceanography and food webs (e.g. Savenkoff et al. 2007a, b, Bundy et al. 2009, Gaston et al. 2009). Northern Gannets have long shown no negative response, but they seem to have passed their climax in these waters. This is best documented for the breeding population at Bonaventure Island, which is decreasing since 2009. However, their breeding success has been steadily declining with a mean of 74% during 1979 to 2004, 68% in 2005, 50% in 2009, 22% in 2011 and finally disastrous 8% in 2012 (WA Montevecchi et al. unpubl. data, JF Rail, CWS unpubl. data). During the catastrophic breeding season of 2012, sea surface temperature was unusually high and other extraordinary events such as the die-off of fish, krill and marine mammals were documented (WA Montevecchi et al. unpubl. data). Some of these events could be explained by red tides (saxitoxin, JF Rail pers. comm.). The exceptionally low breeding success of Gannets was accompanied by birds being observed alive or found dead in areas where they had not been documented before. In addition, breeding success at the Gannetry at Cape St. Mary's on the southeast coast of Newfoundland was also particularly poor in 2012, corresponding only to 39%. This was much lower than the breeding success of 78% in 2009 and 68% in 2011 (WA Montevecchi et al. unpubl. data, C Mooney pers. comm.). As Gannets have been shown to be highly flexible in diet, foraging range and technique, they are able to trade-off energy expenditure in a multitude of ways (Davoren et al. 2010). Hence, it is of ecological significance that this species recently seems to be in severe trouble in one of its strongholds. This might point towards pronounced perturbations in oceanographic processes and food web structure. Indeed, Montevecchi et al. (2013) described the warm water perturbation of August 2012 to be nested in a larger scale anomaly throughout the Northwest Atlantic. Such events are in line with an increasing frequency of extreme weather events as forecasted by climate change models (WA Montevecchi et al. unpubl. data). It can be expected that a range of other seabird species that are more restricted in their foraging range or diving depth, such as Kittiwakes or *Larus* gulls, would have even been more affected. The current observed peculiarities in Gannets have been hypothesized to be related to food shortage within their foraging ranges around the colonies, as the body mass of adults and chicks has been significantly lower than usual (WA Montevecchi et al. unpubl. data, JF Rail, S Garthe pers. comm.). Food shortage was most likely linked to the warm water perturbation of August 2012, which could have temporally driven prey to water depths that could not be exploited by Northern Gannets (WA Montevecchi et al. unpubl. data). However, apart from this immediate perturbation, the abundance of Mackerel, a key prey in the

General Discussion & Conclusions

Southern Gulf (Nelson 1978, Chapter 4), is already longer in decline in these waters, and reproduction has presumably largely failed since 1999 (F Bolduc pers. comm.). In addition, a shift in its distribution from the Southern to the Northern Gulf has been observed (WA Montevecchi et al. unpubl. data).

In order to further test the hypothesis of climate driven changes in the prey basis, we suggest an integrated approach by combining the deployment of GPS data loggers on breeding Gannets on Bonaventure Island together with ship-based seabird and cetacean surveys. The latter should comprise oceanographic measurements and hydro-acoustic surveys of pelagic fish during the breeding season of Northern Gannets. Where possible, surveys should take place in the Southern and Northern Gulf or at least cover the foraging range of breeding birds from Bonaventure. This would allow to test if the foraging ranges of Gannets still sufficiently overlap with the concentrations of pelagic fish species such as Mackerel or Herring. We could also investigate which oceanographic variables (e.g. sea surface temperature) might have changed and triggered this new distribution of Mackerel. In addition, we could gain insights into possible changes in cetacean abundance. Such integrated approaches have proven to be extremely valuable with regard to conclusions on ecosystem change as demonstrated for the east coast of Newfoundland (e.g. Davoren et al. 2003, 2006, 2010). Such a study would have the potential to generate knowledge far beyond seabird ecology. It would supply crucial information on possible ecosystem perturbations and commercially important species such as Mackerel and Herring, which were identified as important components of the marine food web in these waters (Savenkoff et al. 2007 a, b).

References

- Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA (2009) Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Mar Ecol Prog Ser* 389:271–294
- Ainley DG, Spear LB, Tynan CT, Barth JA, Cowles TJ, Pierce SD (2005) Factors affecting occurrence patterns of seabirds in the northern California current, spring and summer 2000. *Deep Sea Res II* 52:123–143
- Arcos JM, Oro D, Sol D (2001) Competition between the Yellow-legged Gull *Larus cachinnans* and Audouin's Gull *Larus audouinii* associated with commercial fishing vessels: the influence of season and fishing fleet. *Mar Biol* 139:807–816
- Ardisson PL, Bourget E (1992) Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna. *Mar Ecol Prog Ser* 83:15–34
- Arnold PW (1970) Spawning and aspects of the early life history of the Atlantic Mackerel (*Scomber scombrus* L.) in the Gulf of St. Lawrence. Bsc thesis, Acadia University, Wolfville
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103b:458–473
- Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS, King JR (eds) *Avian Biology*. Academic Press, London, p 223–286
- Bächler E, Liechti F (2007) On the importance of g (0) for estimating bird population densities with standard distance-sampling: implications from a telemetry study and a literature review. *Ibis* 149:693–700
- Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Prog Oceanogr* 69:360–390
- Bellebaum J, Diederichs A, Kube J, Schulz A, Nehls G (2006) Flucht- und Meidedistanzen überwinternder Seetaucher und Meeresenten gegenüber Schiffen auf See. *Ornithol Rundbr M-V* 45:86–90
- Benoit J, El-Sabh MI, Tang CL (1985) Structure and seasonal characteristics of the Gaspé Current. *J Geophys Res* 90:3225–3236
- Bibby CJ, Burgess ND, Hill DA (1992) *Bird Census Techniques*. BTO & RSPB. Academic Press, London
- Bost CA, Cotte C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- Boyd IL, Wanless S, Camphuysen CJ (2006) *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge University Press, Cambridge
- Brown RG (1986) *Revised atlas of eastern Canadian seabirds*. Canadian Wildlife Service, Ottawa

References

- Brown RG, Nettleship DN, Germain P, Tull CE, Davis T (1975) Atlas of eastern Canadian seabirds. Canadian Wildlife Service, Ottawa
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of wildlife populations. Oxford University Press, Oxford
- Buckland ST, Burt ML, Rexstad EA, Mellor M, Williams AE, Woodward R (2012) Aerial surveys of seabirds: the advent of digital methods. *J Appl Ecol* 49:960–967
- Bundy A, Heymans JJ, Morissette L, Savenkoff C (2009) Seals, Cod and forage fish: a comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. *Prog Oceanogr* 81:188–206
- Burger AE, Simpson M (1986) Diving Depths of Atlantic Puffins and Common Murres. *Auk* 103:828–830
- Busch M, Kannen A, Garthe S, Jessopp M (2012) Consequences of a cumulative perspective on marine environmental impacts: offshore wind farming and seabirds at North Sea scale in context of the EU Marine Strategy Framework Directive. *Ocean Coast Manage* 71:213–224
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biol Oceanogr* 5:261–271
- Cairns DK, Chapdelaine G, Montevicchi WA (1991) Prey exploitation by seabirds in the Gulf of St. Lawrence. In: Therriault J-C (ed) *The Gulf of St. Lawrence: small ocean or big estuary?* *Can Spec Publ Fish Aquat Sci* 113:277–291
- Cairns DK, Gaston AJ, Huettmann F (2008) Endothermy, ectothermy and the global structure of marine vertebrate communities. *Mar Ecol Prog Ser* 356:239–250
- Camphuysen CJ (1995) Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. *Ardea* 83:365–380
- Camphuysen CJ (2011) Northern Gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock. *Brit Birds* 104:60–75
- Camphuysen CJ, Calvo B, Durinck J, Ensor K, Follestad A, Furness RW, Garthe S, Leaper G, Skov H, Tasker M, Winter CJN (1995) Consumption of discards by seabirds in the North Sea. NIOZ-rapport 5, Texel
- Camphuysen CJ, Fox AD, Leopold MF, Petersen IK (2004) Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. COWRIE-Report BAM-02-2002, Texel
- Camphuysen CJ, Garthe S (2004) Recording foraging seabirds at sea: standardised recording and coding of foraging behaviour and multi-species foraging associations. *Atl Seabirds* 6:1–32
- Camphuysen CJ, Shamoun-Baranes J, Bouten W, Garthe S (2012) Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biol Conserv* 156:22–29
- Camphuysen CJ, Webb A (1999) Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea* 87:177–198

References

- Catry T, Ramos JA, Corre M Le, Phillips RA (2009) Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the Wedge-tailed Shearwater in the western Indian Ocean. *Mar Ecol Prog Ser* 391:231–242
- Chapdelaine G, Brousseau P (1996) Diet of Razorbill *Alca torda* chicks and breeding success in the St. Mary's Islands, Gulf of St. Lawrence, Québec, Canada, 1990-1992. In: Montevecchi WA (ed) *Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems.* *Can Wildl Serv Occas Pap* 91: 27–36
- Chapdelaine G, Diamond AW, Elliot RD, Robertson GJ (2001) Status and population trends of the Razorbill in eastern North America. *Can Wildl Serv Occas Pap* 105:1–19
- Chapdelaine G, Rail J-F (1997) Relationship between Cod fishery activities and the population of Herring Gulls on the north shore of the Gulf of St. Lawrence, Québec, Canada. *ICES J Mar Sci* 54:708–713
- Coe JM, Rogers DB (1997) *Marine debris: sources, impacts, and solutions.* Springer, New York
- Conover WJ (1971) *Practical Nonparametric Statistics.* John Wiley & Sons, New York
- Corre M Le (1997) Diving depths of two tropical Pelecaniformes: the Red-tailed Tropicbird and the Red-footed Booby. *Condor* 99:1004–1007
- Cotté C, Simard Y (2005) Formation of dense krill patches under tidal forcing at whale feeding hot spots in the St. Lawrence Estuary. *Mar Ecol Prog Ser* 288:199-210
- Cox S, Scott B, Camphuysen C (2012) Combined spatial and tidal processes identify links between pelagic prey species and seabirds. *Mar Ecol Prog Ser* DOI: 10.3354/meps10176, URL: www.int-res.com/prepress/m10176.html
- Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJ, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M (2011) Global seabird response to forage fish depletion—one-third for the birds. *Science* 334:1703–1706
- Darbyson E, Swain DP, Chabot D, Castonguay M (2003) Diel variation in feeding rate and prey composition of Herring and Mackerel in the Southern Gulf of St. Lawrence. *J Fish Biol* 63:1235–1257
- Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Elston DA, Wanless S (2002) Foraging strategies of the Black-legged Kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245:239–247
- Daunt F, Peters G, Scott B, Grémillet D, Wanless S (2003) Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Mar Ecol Prog Ser* 255:283–288
- Daunt F, Wanless S, Peters G, Benvenuti S, Sharples J, Grémillet D, Scott BE (2006) Impacts of oceanography on the foraging dynamics of seabirds in the North Sea. In: Boyd IL, Wanless S, Camphuysen CJ (eds) *Top predators in marine ecosystems: their role in monitoring and management.* Cambridge University Press, Cambridge, p 177–190
- Davoren GK, Anderson JT, Montevecchi WA (2006) Shoal behaviour and maturity relations of spawning Capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns. *Can J Fish Aquat Sci* 63:268–284

References

- Davoren GK, Garthe S, Montevecchi WA, Benvenuti S (2010) Influence of prey behaviour and other predators on the foraging activities of a marine avian predator in a Low Arctic ecosystem. *Mar Ecol Prog Ser* 404:275–287
- Davoren GK, Montevecchi WA (2003) Consequences of foraging trip duration on provisioning behaviour and fledging condition of Common Murres *Uria aalge*. *J Avian Biol* 34:44–53
- Davoren GK, Montevecchi WA, Anderson JT (2002) Scale-dependent associations of predators and prey: constraints imposed by flightlessness of Common Murres. *Mar Ecol Prog Ser* 245:259–272
- Davoren GK, Montevecchi WA, Anderson JT (2003) Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecol Monogr* 73:463–481
- Decker MB, Hunt GLJ (1996) Foraging by murres (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Mar Ecol Prog Ser* 139:1–10
- Derraik JGB (2002) The pollution of the marine environment by plastic debris: a review. *Mar Poll Bull* 44:842–852
- Descroix A, Harvey M, Roy S, Galbraith PS (2005) Macrozooplankton community patterns driven by water circulation in the St. Lawrence marine system, Canada. *Mar Ecol Prog Ser* 302:103–119
- Diamond AW, Gaston AJ, Brown RG (1986) Converting PIROP counts of seabirds at sea to absolute densities. *Can Wildl Serv Prog Not* 164, Ottawa
- Dickie LM, Trites RW (1983) The Gulf of St. Lawrence. In: Ketchum, BH (ed) *Ecosystems of the World* 26. Estuaries and Enclosed Seas. Elsevier, New York, p 403-425
- Diederichs A, Nehls G, Petersen IK (2002) Flugzeugzählungen zur großflächigen Erfassung von Seevögeln und marinen Säugern als Grundlage für Umweltverträglichkeitsstudien im Offshorebereich. *Seevögel* 23:38–46
- Dierschke V, Garthe S, Markones N (2004) Aktionsradien Helgoländer Dreizehenmöwen *Rissa tridactyla* und Trottellummen *Uria aalge* während der Aufzuchtphase. *Vogelwelt* 125:11–19
- Doniol-Valcroze T, Berteaux D, Larouche P, Sears R (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Mar Ecol Prog Ser* 335:207–216
- Drinkwater KF (1993) Overview of Environmental Conditions in the Northwest Atlantic in 1992. DFO Atl Fish Res Doc 1993/1
- Dufour R, Ouellet P (2007) Estuary and Gulf of St. Lawrence marine ecosystem overview and assessment report. *Can Tech Rep Fish Aquat Sci* 2744E
- Efron B (1979) Bootstrap methods: another look at the jackknife. *Ann Stat* 7:1–26
- Efron B (1990) More efficient bootstrap computations. *J Am Stat Assoc* 85:79–89
- Efron B, Tibshirani R (1993) *An introduction to the Bootstrap*. Chapman & Hall, New York
- Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fish Res* 95:6–13

References

- Elliot KH, Woo K, Gaston AJ, Bevenuti S, Dall'Antonia L, Davoren GK (2008a) Seabird foraging behaviour indicates prey type. *Mar Ecol Prog Ser* 354:289-303
- Elliott KH, Davoren GK, Gaston AJ (2008b) Time allocation by a deep-diving bird reflects prey type and energy gain. *Anim Behav* 75:1301–1310
- El-Sabh MI (1976) Surface circulation pattern in the Gulf of St. Lawrence. *J Fish Res Board Can* 33:124–138
- El-Sabh MI, Lie HJ, Koutitonsky VG (1982) Variability of the near-surface residual current in the Lower St. Lawrence Estuary. *J Geophys Res* 87:9589–9600
- El-Sabh MI, Silverberg N (1990) *Oceanography of a Large-Scale Estuarine System: The St. Lawrence. Coastal and Estuarine Studies* 39. Springer, Berlin
- Embling CB, Illian J, Armstrong E, Kooij J van der, Sharples J, Camphuysen CJ, Scott BE (2012) Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine ecosystems: a functional data analysis approach. *J Appl Ecol* 49:481–492
- Evans PHG (1982) Associations between seabirds and cetaceans: a review. *Mammal Rev* 12:187–206
- Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. *Mar Ecol Prog Ser* 391:139–151
- Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783
- Fifield DA, Lewis KP, Gjerdrum C, Robertson GJ, Wells R (2009) Offshore seabird monitoring program. *Environ Stud Res Funds Rep* 183, St. John's
- Follestad A (1990) The pelagic distribution of Little Auk *Alle alle* in relation to a frontal system off central Norway, March/April 1988. *Polar Res* 8:23–28
- Fouest V Le, Zakardjian B, Saucier FJ, Starr M (2005) Seasonal versus synoptic variability in planktonic production in a high-latitude marginal sea: The Gulf of St. Lawrence (Canada). *J Geophys Res* 110:1-21
- Furness RW, Greenwood JJ (1993) *Birds as monitors of environmental change*. Chapman & Hall, London
- Furness RW, Monaghan P (1987) *Seabird ecology*. Blackie, Glasgow and London
- Gallus A, Dähne M, Verfuß UK, Bräger S, Adler S, Siebert U, Benke H (2012) Use of static passive acoustic monitoring to assess the status of the 'critically endangered' Baltic Harbour Porpoise in German waters. *Endang Spec Res* 18:265–278
- Garthe S (1997) Influence of hydrography, fishing activity, and colony location on summer seabird distribution in the south-eastern North Sea. *ICES J Mar Sci* 54:566–577
- Garthe S, Benvenuti S, Montevecchi WA (2000) Pursuit plunging by Northern Gannets (*Sula bassana*) feeding on Capelin (*Mallotus villosus*). *Proc Biol Sci* 267:1717–1722
- Garthe S, Benvenuti S, Montevecchi WA (2003) Temporal patterns of foraging activities of Northern Gannets *Morus bassanus* in the north-west Atlantic. *Can J Zool* 81:453–461

References

- Garthe S, Camphuysen CJ, Furness RW (1996) Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Mar Ecol Prog Ser* 136:1–11
- Garthe S, Hüppop O (2004) Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *J Appl Ecol* 41:724–734
- Garthe S, Hüppop O, Weichler T (2002) Anleitung zur Erfassung von Seevögeln auf See von Schiffen. *Seevögel* 23:47–55
- Garthe S, Markones N, Hüppop O, Adler S (2009) Effects of hydrographic and meteorological factors on seasonal seabird abundance in the southern North Sea. *Mar Ecol Prog Ser* 391:243–255
- Garthe S, Markones N, Mendel B, Sonntag N, Krause JC (2012) Protected areas for seabirds in German offshore waters: designation, retrospective consideration and current perspectives. *Biol Conserv* 156:126–135
- Garthe S, Montevecchi WA, Chapdelaine G, Rail J-F, Hedd A (2007a) Contrasting foraging tactics by Northern Gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Mar Biol* 151:687–694
- Garthe S, Montevecchi WA, Davoren GK (2007c) Flight destinations and foraging behaviour of Northern Gannets (*Sula bassana*) preying on a small forage fish in a low-arctic ecosystem. *Deep Sea Res II* 54:311–320
- Garthe S, Montevecchi WA, Davoren GK (2011) Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnol Oceanogr* 56:802–812
- Garthe S, Sonntag N, Schwemmer P, Dierschke V (2007b) Estimation of seabird numbers in the German North Sea throughout the annual cycle and their biogeographic importance. *Vogelwelt* 128:163–178
- Gaston AJ, Bertram DF, Boyne AW, Chardine JW, Davoren G, Diamond AW, Hedd A, Montevecchi WA, Hipfner JM, Lemon MJ (2009) Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. *Environ Rev* 17:267–286
- Gaston AJ, Jones IL (1998) *The Auks - Alcidae*. Oxford University Press, Oxford
- Gilles A, Adler S, Kaschner K, Scheidat M, Siebert U (2011) Modelling Harbour Porpoise seasonal density as a function of the German Bight environment: implications for management. *Endang Spec Res* 14:157–169
- Gjerdrum C, Fifield DA, Wilhelm SI (2012) Eastern Canada Seabirds at Sea (ECSAS) standardized protocol for pelagic seabird surveys from moving and stationary platforms. *Can Wildl Serv Tech Rep Ser* 515, Atlantic Region
- Gjerdrum C, Head EJM, Fifield DA (2008) Monitoring seabirds at sea in Eastern Canada. *AZMP Bulletin PMZA* 7:52–58
- Government of Canada (1991) *The State of Canada's Environment*. Minister of Supply and Services, Ottawa
- Gratton Y, Pettigrew B, Pelchat B, Gilbert D, Couture M, Landry J (1994) Overview of the environmental conditions in the Gulf of St. Lawrence in 1993. *DFO Atl Fish Res Doc* 1994/055

References

- Grégoire F (2006) Vertical distribution of the midwater trawl catches of Atlantic Mackerel (*Scomber scombrus* L.) in relation with water temperature. DFO Can Sci Advis Sec Res Doc 2006/097
- Grégoire F, Barry W, Barry J (2006) West coast of Newfoundland Capelin (*Mallotus villosus* M.) and Atlantic Herring (*Clupea harengus harengus* L.) larval survey, part 2: Abundance estimates and marine community analyses of the data collected in partnership with the industry (Barry Group) in July 2004. Can Tech Rep Fish Aquat Sci 2650
- Grégoire F, Lévesque C, Beaulieu J-L, Gendron M-H (2009) Commercial fishery and biology of the Atlantic Mackerel (*Scomber Scombrus* L.) in NAFO Subareas 3 and 4 in 2007. DFO Can Sci Advis Sec Res Doc 2009/025
- Grémillet D, Dell’Omo G, Ryan PG, Peters G, Ropert-Coudert Y, Weeks SJ (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape Gannets from neighbouring colonies. Mar Ecol Prog Ser 268:265–279
- Grémillet D, Lewis S, Drapeau L, Lingen CD v. D, Huggett JA, Coetzee JC, Verheye HM, Daunt F, Wanless S, Ryan PG (2008) Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? J Appl Ecol 45:610–621
- Hamer KC, Humphreys EM, Garthe S, Hennenke J, Peters G, Grémillet D, Phillips RA, Harris MP, Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of Gannets in the North Sea: flexibility, consistence and constraint. Mar Ecol Prog Ser 338:295–305
- Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. Mar Ecol Prog Ser 224:283–290
- Haney JC (1986) Seabird segregation at Gulf Stream frontal eddies. Mar Ecol Prog Ser 28:279–285
- Haney JC (1990) Winter habitat of Common Loons on the continental Shelf of the southeastern United States. Wilson Bull 102:253–263
- Haney JC (1991) Influence of pycnocline topography and water column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, northern Bering Sea, Alaska. Mar Biol 110:419–435
- Haney JC, Stone AE (1988) Seabirds foraging tactics and water clarity: are plunge divers really in the clear? Mar Ecol Prog Ser 49:1–9
- Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Pelt TI van, Kettle AB, Speckman SG (2007) Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). Ecology 88:2024–2033
- Harvey M, St-Pierre J-F, Devine L, Gagné A, Gagnon Y, Beaulieu M-F (2004) Oceanographic conditions in the Estuary and the Gulf of St. Lawrence during 2003: zooplankton. DFO Can Sci Advis Sec Res Doc 2004/080
- Hastie T, Tibshirani R (1990) Generalised Additive Models. Chapman & Hall, London

References

- Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele, JH (ed) *Spatial pattern in plankton communities*. Plenum Press, New York, p 277–327
- He P (1993) Swimming speeds of marine fish in relation to fishing gears. In: ICES Mar Sci Symp 196:183–189
- He P, Wardle CS (1988) Endurance at intermediate swimming speeds of Atlantic Mackerel, *Scomber scombrus* L., Herring, *Clupea harengus* L., and Saithe, *Pollachius virens* L. *J Fish Biol* 33:255–266
- Head EJH, Pepin P (2007) Variations in overwintering depth distributions of *Calanus finmarchicus* in the slope waters of the NW Atlantic continental shelf and the Labrador Sea. *J Northw Atl Fish Sci* 39:49–69
- Heinemann D (1981) A range finder for pelagic bird censusing. *J Wildl Manage* 45:489–493
- Hixon MA (1982) Energy maximizers and time minimizers: theory and reality. *Am Nat* 119:596–599
- Huettmann F, Diamond AW (2001) Seabird colony locations and environmental determination of seabird distribution: a spatially explicit breeding seabird model for the Northwest Atlantic. *Ecol Model* 141:261–298
- Hunt GLJ, Harrison NM, Cooney RT (1990) The influence of hydrographic structure and prey abundance on foraging of Least Auklets. *Stud Avian Biol* 14:7–22
- Hunt GLJ, Mehlum F, Russell RW, Irons D, Decker MB, Becker PH (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams NJ, Slotow RH (eds) *Proc 22th Int Ornithol Congr, Durban*. BirdLife South Africa, Johannesburg, p 2040–2056
- Hunt GLJ, Russell RW, Coyle KO, Weingartner T (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Mar Ecol Prog Ser* 167:241–259
- Hunt GLJ, Schneider DC (1987) Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall JP (ed) *Seabirds - feeding ecology and role in marine ecosystems*. Cambridge University Press, New York, p 7–41
- Hyrenbach KD, Forney KA, Dayton PK (2000) Marine protected areas and ocean basin management. *Aquatic Conserv: Mar Freshw Ecosyst* 10:437–458
- Hyrenbach KD, Henry MF, Morgan KH, Welch DW, Sydeman WJ (2007) Optimizing the width of strip transects for seabird surveys from vessels of opportunity. *Marine Ornithol* 35:29–37
- Keitt TH, Bivand R, Pebesma E, Rowlingson B (2012) rgdal: Bindings for the Geospatial Data Abstraction Library. URL: <http://CRAN.R-project.org/package=rgdal>
- Kokubun N, Takahashi A, Ito M, Matsumoto K, Kitaysky AS, Watanuki Y (2010) Annual variation in the foraging behaviour of Thick-billed Murres in relation to upper-ocean thermal structure around St. George Island, Bering Sea. *Aquat Biol* 8:289–298
- Kotzerka J (2011) Identification of foraging behaviour and feeding areas of three seabird species breeding sympatrically in a highly productive regime, the northern Gulf of Alaska. Doctoral thesis, University of Kiel, Kiel

References

- Kotzerka J, Garthe S, Hatch SA (2010) GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes. *J Ornithol* 151:459–467
- Koutitonsky VG, Bugden GL (1991) The physical oceanography of the Gulf of St. Lawrence: a review with emphasis on the synoptic variability of the motion. In: Therriault J-C (ed) *The Gulf of St. Lawrence: small ocean or big estuary?* *Can Spec Publ Fish Aquat Sci* 113:57–90
- Kubetzki U, Garthe S (2003) Distribution, diet and habitat selection by four sympatrically breeding gull species in the southeastern North Sea. *Mar Biol* 143:199–207
- Ladd C, Jahncke J, Hunt GL, Coyle KO, Stabeno PJ (2005) Hydrographic features and seabird foraging in Aleutian Passes. *Fish Oceanogr* 14:178–195
- Lafontaine Y de, Demers S, Runge J (1991) Pelagic food web interactions and productivity in the Gulf of St. Lawrence: a perspective. In: Therriault J-C (ed) *The Gulf of St. Lawrence: small ocean or big estuary?* *Can Spec Publ Fish Aquat Sci* 113:99–123
- Lascelles BG, Langham GM, Ronconi RA, Reid JB (2012) From hotspots to site protection: identifying marine protected areas for seabirds around the globe. *Biol Conserv* 156:5–14
- LeBlanc CH, Swain DP, Bourque C, MacDougall C (2010) Assessment of the NAFO Division 4T Southern Gulf of St. Lawrence Herring stocks in 2009. *DFO Can Sci Advis Sec Res Doc* 2010/059
- Legendre L, Watt WD (1970) The distribution of primary production relative to a cyclonic gyre in Baie des Chaleurs. *Mar Biol* 7:167–170
- Lewis S, Schreiber EA, Daunt F, Schenk GA, Orr K, Adams A, Wanless S, Hamer KC (2005) Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* 147:408–414
- Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819
- Locke A (2002) The ichthyoplankton and invertebrate zooplankton of the coastal waters of Cape Breton Island: a review. *Can Manuscr Rep Fish Aquat Sci* 2606
- Longhurst AR, Pauly D (1987) *Ecology of tropical oceans*. Academic Press, San Diego
- Machovsky Capuska GE, Gabriel E, Dwyer SL, Alley MR, Stockin KA, Raubenheimer D (2011b) Evidence for fatal collisions and kleptoparasitism while plunge-diving in Gannets. *Ibis* 153:631–635
- Machovsky Capuska GE, Vaughn RL, Würsig B, Katzir G, Raubenheimer D (2011a) Dive strategies and foraging effort in the Australasian Gannet *Morus serrator* revealed by underwater videography. *Mar Ecol Prog Ser* 442:255–261
- Mackay KT (1967) An ecological study of Mackerel *Scomber scombrus* (Linnaeus) in the coastal waters of Canada. *Fish Res Board Can Tech Rep* 31
- Mackay KT (1979) Synopsis of biological data on the northern population of Atlantic Mackerel (*Scomber scombrus* L.). *Fish Mar Serv Tech Rep* 885
- Markones N (2007) Habitat selection of seabirds in a highly dynamic coastal sea: temporal variation and influence of hydrographic features. Doctoral thesis, University of Kiel, Kiel

References

- Markones N, Dierschke V, Garthe S (2010) Seasonal differences in at-sea activity of seabirds underline high energetic demands during the breeding period. *J Ornithol* 151:329–336
- Markones N, Garthe S (2009) Erprobung eines Bund/Länder-Fachvorschlags für das Deutsche Meeresmonitoring von Seevögeln und Schweinswalen als Grundlage für die Erfüllung der Natura 2000-Berichtspflichten mit einem Schwerpunkt in der deutschen AWZ von Nord- und Ostsee (FFH-Berichtsperiode 2007-2012). Teilvorhaben Seevogel Endbericht für das Bundesamt für Naturschutz, Vilm
- Markones N, Garthe S (2011) Monitoring von Seevögeln im Offshore-Bereich der schleswig-holsteinischen Nordsee im Rahmen von NATURA 2000 in den Jahren 2004 bis 2009. *Corax* 22:11–50
- Markones N, Garthe S (2012) Ermittlung von artspezifischen Korrekturfaktoren für flug-gestützte Seevogelerfassungen als Grundlage für Bestandsberechnungen von Seevögeln im Rahmen des Monitorings in der deutschen Ausschließlichen Wirtschaftszone von Nord- und Ostsee. Endbericht für das Bundesamt für Naturschutz, Vilm
- Markones N, Garthe S, Dierschke V, Adler S (2008) Small-scale temporal variability of seabird distribution patterns in the south-eastern North Sea. In: Wollny-Goerke K, Eskildsen K (eds) *Marine mammals and seabirds in front of offshore wind energy*. Teubner, Wiesbaden, p 115–140
- Markones N, Schwemmer H, Garthe S (2012) „Seevogel-Monitoring 2011/2012 in der deutschen Nord- und Ostsee“. Bericht für das Bundesamt für Naturschutz, Vilm
- Marsaglia G, Tsang WW, Wang J (2003) Evaluating Kolmogorov's distribution. *J Statist Softw* 8:1-4
- Mehlum F, Hunt GLJ, Klusek Z, Decker MB (1999) Scale-dependent correlations between the abundance of Brünnich's Guillemots and their prey. *J Anim Ecol* 68:60–72
- Melvin EF, Parrish JK (2001) *Seabird bycatch. Trends, roadblocks and solution*. University of Alaska Sea Grant, Fairbanks, Alaska
- Mendel B (2012) Anthropogene Nutzungen und deren Auswirkungen auf Seevögel in der Deutschen Bucht: Entwicklung methodischer Ansätze und Bewertung der Effekte. Doctoral thesis, University of Kiel, Kiel
- Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJD (eds) *Birds as monitors of environmental change*. Chapman & Hall, London, p 217–266
- Montevecchi WA (2007) Binary dietary responses of Northern Gannets *Sula bassana* indicate changing food web and oceanographic conditions. *Mar Ecol Prog Ser* 352:213–220
- Montevecchi WA, Benvenuti S, Garthe S, Davoren GK, Fifield D (2009) Flexible foraging tactics by a large opportunistic seabird preying on forage and large pelagic fishes. *Mar Ecol Prog Ser* 385:295–306
- Montevecchi WA, Garthe S, Davoren GK (2006) Biophysical influences on seabird trophic assessments. In: Boyd IL, Wanless S, Camphuysen CJ (eds) *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge University Press, Cambridge, p 118–130

References

- Montevecchi WA, Myers RA (1997) Centurial and decadal oceanographic influences on changes in Northern Gannet populations and diets in the Northwest Atlantic: implications for climate change. *ICES J Mar Sci* 54:608–614
- Montevecchi WA, Ricklefs RE, Kirkham IR, Gabaldon D (1984) Growth energetics of nestling Northern Gannets (*Sula bassana*). *Auk* 101:334–341
- Morissette L, Castonguay M, Savenkoff C, Swain DP, Chabot D, Bourdages H, Hammill MO, Hanson JM (2009) Contrasting changes between the Northern and Southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks. *Deep Sea Res II* 56:2117–2131
- Morissette L, Hammill MO, Savenkoff C (2006) The trophic role of marine mammals in the Northern Gulf of St. Lawrence. *Mar Mamm Sci* 22:74–103
- Nelson JB (1978) *The Gannet*. Poyser, Berkhamsted
- Nelson JB (2002) *The Atlantic Gannet*, 2nd edition. Fenix Books, Great Yarmouth
- Nettleship DN, Evans PH (1985) Distribution and status of the Atlantic Alcidae. In: Nettleship DN, Birkhead, TR (eds) *The Atlantic Alcidae*. Academic Press, Orlando, p 53–154
- Obst BS, Hunt GLJ (1990) Marine birds feed at Gray Whale plumes in the Bering Sea. *Auk* 107:678–688
- Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) *Analysis of ecological systems*. Ohio State University Press, Columbus, p 154–177
- Ouellet P, Lefavre D (1994) Vertical Distribution of Northern Shrimp (*Pandalus borealis*) Larvae in the Gulf of St. Lawrence; Implications for Trophic Interactions and Transport. *Can J Fish Aquat Sci* 51:123–132
- Ouellet P, Lefavre D, Koutitonsky V (1990) Distribution of shrimp (*Pandalus borealis*) larvae and hydrographic pattern in the Northern Gulf of St. Lawrence. *Can J Fish Aquat Sci* 47:2068–2078
- Paiva VH, Geraldés P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010) Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Mar Ecol Prog Ser* 398:259–274
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669
- Petrie B, Drinkwater K (1978) Circulation in an open bay. *J Fish Res Board Can* 35:1116–1123
- Petrie B, Toulany B, Garrett C (1988) The transport of water, heat and salt through the Strait of Belle Isle. *Atmos Ocean* 26:234–251
- Piatt JF, Harding AMA, Shultz M, Speckman SG, Pelt TI van, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Mar Ecol Prog Ser* 352:221–234
- Piatt JF, Nettleship DN (1985) Diving depths of four alcids. *Auk* 102:293–297
- R Development Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna

References

- Rail J-F, Chapdelaine G (1998) Food of Double-crested Cormorants, *Phalacrocorax auritus*, in the Gulf and Estuary of the St. Lawrence River, Québec, Canada. *Can J Zool* 76:635–643
- Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good CP, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT (2006) Techniques for cetacean–habitat modeling. *Mar Ecol Prog Ser* 310:271–295
- Ropert-Coudert Y, Daunt F, Kato A, Ryan PG, Lewis S, Kobayashi K, Mori Y, Grémillet D, Wanless S (2009a) Underwater wingbeats extend depth and duration of plunge dives in Northern Gannets *Morus bassanus*. *J Avian Biol* 40:380–387
- Ropert-Coudert Y, Kato A, Chiaradia A (2009b) Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the Little Penguin. *Proc Biol Sci* 276:4105–4109
- Saucier FJ, Roy F, Gilbert D, Pellerin P, Ritchie H (2003) Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada. *J Geophys Res* 108:3269–3289.
- Savenkoff C, Castonguay M, Chabot D, Hammill MO, Bourdages H, Morissette L (2007a) Changes in the Northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? *Est Coast Shelf Sci* 73:711–724
- Savenkoff C, Swain DP, Hanson JM, Castonguay M, Hammill MO, Bourdages H, Morissette L, Chabot D (2007b) Effects of fishing and predation in a heavily exploited ecosystem: comparing periods before and after the collapse of groundfish in the Southern Gulf of St. Lawrence (Canada). *Ecol Model* 204:115–128
- Schneider DC (1982) Fronts and seabird aggregations in the southeastern Bering Sea. *Mar Ecol Prog Ser* 10:101–103
- Schneider DC (1993) Scale-dependent spatial dynamics: marine birds in the Bering Sea. *Biol Rev Camb Philos Soc* 68:579–598
- Schneider D, Harrison NM, Hunt GLJ (1987) Variation in the occurrence of marine birds at fronts in the Bering Sea. *Est Coast Shelf Sci* 25:135–141
- Schreiber EA, Burger J (2002) *Biology of marine birds*. CRC Press, New York
- Schwemmer P, Adler S, Guse N, Markones N, Garthe S (2009) Influence of water flow velocity, water depth and colony distance on distribution and foraging patterns of terns in the Wadden Sea. *Fish Oceanogr* 18:161–172
- Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe S (2011) Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. *Ecol Appl* 21:1851–1860
- Scott BE, Sharples J, Ross ON, Wang J, Pierce GJ, Camphuysen CJ (2010) Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Mar Ecol Prog Ser* 408:207–226
- Sette OE (1943) *Biology of the Atlantic Mackerel (Scomber scombrus) of North America*. Part 1. Early history. *US Fish Wildlife Service Fish Bull* 38:149–237

References

- Sette OE (1950) Biology of the Atlantic Mackerel (*Scomber scombrus*) of North America. Part 2. Migration and habits. US Fish Wildlife Service Fish Bull 49:251–358
- Shealer DA (2002) Foraging behavior and food of seabirds. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, Boca Raton, p 137–177
- Skov H, Durinck J (2000) Seabird distribution in relation to hydrography in the Skagerrak. Cont Shelf Res 20:169–187
- Skov H, Durinck J, Leopold MF, Tasker ML (1995) Important bird areas for seabirds in the North Sea including the Channel and the Kattegat. BirdLife International, Cambridge
- Sonntag N, Mendel B, Garthe S (2006) Die Verbreitung von See- und Wasservögeln in der deutschen Ostsee im Jahresverlauf. Vogelwarte 44:81–112
- Stearns S (1992) The evolution of life histories. Oxford University Press, Oxford
- Stevick PT, Incze LS, Kraus SD, Rosen S, Wolff N, Baukus A (2008) Trophic relationships and oceanography on and around a small offshore bank. Mar Ecol Prog Ser 363:15–28
- Sutcliffe WHJ, Loucks RH, Drinkwater KF (1976) Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J Fish Res Board Can 33:98–115
- Sydeman WJ, Brodeur RD, Grimes CB, Bychkov AS, McKinnell S (2006) Marine habitat “hotspots” and their use by migratory species and top predators in the North Pacific Ocean: Introduction. Deep Sea Res II 53:247–249
- Tasker ML, Hope Jones P, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk 101:567–577
- Thaxter CB, Wanless S, Daunt F, Harris MP, Benvenuti S, Watanuki Y, Grémillet D, Hamer KC (2010) Influence of wing loading on the trade-off between pursuit-diving and flight in Common Guillemots and Razorbills. J Exp Biol 213:1018–1025
- Thaxter CB, Wanless S, Harris MP, Daunt F, Benvenuti S, Watanuki Y, Grémillet D, Greenstreet S, Hamer KC (2009) Flexibility of foraging behaviour in two pursuit-diving seabirds: the importance of prey transport constraints. In: Stienen E et al. (eds) Seabird Group 10th Int Conf Book of Abstracts, Brugge
- Videler JJ, Wardle CS (1991) Fish swimming stride by stride: speed limits and endurance. Rev Fish Biol Fish 1:23–40
- Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. J Appl Ecol 47:487–497
- Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Mar Ecol Prog Ser 391:165–182
- Wardle CS, He P (1988) Burst swimming speeds of Mackerel, *Scomber scombrus* L. J Fish Biol 32:471–478

References

- Weimerskirch H, Corre M Le, Ropert-Coudert Y, Kato A, Marsac F (2005) The three-dimensional flight of Red-footed Boobies: adaptations to foraging in a tropical environment? *Proc Biol Sci* 272:53–61
- Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc Biol Sci* 267:1869–1874
- Wetlands International (2012) Waterbird Population Estimates. Retrieved from wpe.wetlands.org on 4th Dec 2012
- White L, Johns F (1997) Marine environmental assessment of the Estuary and Gulf of St. Lawrence. Fisheries and Oceans Canada, Dartmouth and Mont-Joli
- Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, Schaefer-Neth C, Scolaro JA, Bost CA, Plötz J, Nel D (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Mar Ecol Prog Ser* 228:241–261
- Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J Am Stat Assoc* 99:673–686
- Wood SN (2006a) *Generalized additive models: an introduction with R*. CRC Press, London
- Wood SN (2006b) Low-rank scale-invariant tensor product smooths for generalized additive mixed models. *Biometrics* 62:1025–1036
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B* 73:3–36
- Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. *Science* 309:1365–1369
- Yen PPW, Sydeman WJ, Hyrenbach KD (2004) Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *J Mar Syst* 50:79–99
- Zuur AF, Ieno EN, Meesters E (2009a) *A Beginner's Guide to R*. Springer, New York
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009b) *Mixed effects models and extensions in ecology with R*. Springer, New York

Description of the individual scientific contributions to multiple-author papers

The chapters 1-4 of this thesis were written as manuscripts with multiple authors and are currently under revision (Chapter 4) or intended for submission (Chapters 1-3) to peer-reviewed scientific journals. In the following I will specify my individual scientific contribution to these manuscripts.

Chapter 1: Distribution of seabirds and cetaceans in the Lower Estuary and Gulf of St. Lawrence during summer

Authors: Nils Guse (1), Nele Markones (1), François Bolduc (2), Stefan Garthe (1)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Canadian Wildlife Service, Environment Canada, 801 - 1550, Avenue d'Estimauville, Québec, G1J 0C3, Canada

Stefan Garthe developed the idea for the study. Nils Guse conducted the field work. Nils Guse carried out the analysis with Nele Markones. Nils Guse, Nele Markones and Stefan Garthe discussed the results. Nils Guse wrote the manuscript. Nele Markones, François Bolduc and Stefan Garthe reviewed and approved the manuscript.

Chapter 2: The influence of colony location and oceanography on seabird distribution in the Lower Estuary and Gulf of St. Lawrence during summer

Authors: Nils Guse (1), Nele Markones (1), Sven Adler (2), Stefan Garthe (1)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Department of Forest Resource Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

Stefan Garthe developed the idea for the study. Nils Guse conducted the field work and carried out the analysis with support from Sven Adler on statistics. Nils Guse, Nele Markones and Stefan Garthe discussed the results. Nils Guse wrote the manuscript. Nele Markones, Sven Adler and Stefan Garthe reviewed and approved the manuscript.

Chapter 3: The influence of marine mammals on the distribution of Northern Gannets in the Lower Estuary and Gulf of St. Lawrence during summer

Authors: Nils Guse (1), Nele Markones (1), Sven Adler (2), Stefan Garthe (1)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Department of Forest Resource Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

Nils Guse and Stefan Garthe developed the idea for the study. Nils Guse conducted the field work. Nils Guse and Nele Markones carried out the analysis with support from Sven Adler on statistics. Nils Guse wrote the manuscript. Nele Markones, Sven Adler and Stefan Garthe reviewed and approved the manuscript.

Chapter 4: The Daily Catch: Flight altitude and diving behaviour of Northern Gannets feeding on Atlantic Mackerel

Authors: Stefan Garthe (1), Nils Guse (1), William A. Montevecchi (2), Jean-François Rail (3), François Grégoire (4)

(1) Research and Technology Centre (FTZ), University of Kiel, D-25761 Büsum, Germany

(2) Departments of Psychology, Biology and Ocean Science Centre, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

(3) Canadian Wildlife Service, Environment Canada, Ste-Foy, Québec, G1V 4H5, Canada

(4) Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, Québec, G5H 3Z4, Canada

Stefan Garthe developed the idea for the study. Stefan Garthe, William Montevecchi and Nils Guse conducted the field work. Jean-François Rail supplied data on diet of Gannets. François Grégoire supplied background information on Mackerel biology. Stefan Garthe and Nils Guse carried out the analysis. Stefan Garthe wrote the manuscript with Nils Guse and William Montevecchi. Jean-François Rail and François Grégoire reviewed and approved the manuscript.

Danksagung/Acknowledgements

Ein besonders herzlicher Dank gilt Stefan Garthe vom Forschungs- und Technologiezentrum (FTZ), der die Idee zu dieser Doktorarbeit hatte und mich über die Jahre hervorragend betreut hat. Vielen Dank Stefan, für die Motivation und die zahlreichen Gespräche und Emails, für die du trotz deines Arbeitspensums immer Zeit eingeräumt hast. Danke auch dafür, dass ich selbstständig so vieles ausprobieren durfte. Du hast mir sehr dabei geholfen, die Ideen zu bündeln und mich aufs Wesentliche zu konzentrieren. Besonders dankbar bin ich dir auch dafür, dass ich durch dich eines der vielleicht spannendsten und schönsten Studiengebiete der Welt kennenlernen durfte. Danke auch dafür, dass du mir in der Endphase so viel Freiraum gegeben hast.

Nele Markones (FTZ) hat ebenfalls großen Anteil an dem Gelingen meiner Doktorarbeit. Durch die zahllosen inhaltlichen Diskussionen, konkreten Tipps und der Unterstützung bei den verschiedenen Analysen hast du ganz Entscheidendes beigetragen. Deine Durchsichten und konstruktive Kritik haben mir sehr dabei geholfen, die Texte deutlich zu verbessern.

Very special thanks to François Bolduc from the Canadian Wildlife Service (CWS) in Québec City for his kind support and cooperation and valuable discussions. Due to your efforts François, I was able to join the the research cruises and collect data for my thesis and for the CWS. Your logistic support was highly appreciated.

I am also particularly grateful to Alain Gagné from the Maurice Lamontagne Institute (IML) in Mont-Joli, Tom Hurlbut from the Gulf Fisheries Centre (GFC) in Moncton, François Grégoire (IML), Charline Lévesque (IML) and their colleagues for letting me join their research cruises and for supplying various ecological details on the Gulf. Alain and Tom, you also deserve special credit for taking the trouble to filling out the various forms required for having a foreigner onboard. Charline, merci beaucoup pour l'aide! Thanks a lot to the Crews of the 'Teleost' and other vessels for their support during all cruises. It was a great pleasure to work there with you guys! I also enjoyed discussing with Hughues Benoit (GFC) and learn more on the fish and fishing in the Gulf. Laure Devine (IML) also deserves special thanks for her kind support regarding background information on the oceanographic data. Laure, thanks a lot for giving advice on the download of data. I am also grateful to David Cairns from Department of Fisheries and Oceans (DFO) in Charlottetown for taking time to share his knowledge on seabirds in the Gulf with me.

Sven Adler (ehem. FTZ) von der Swedish University of Agricultural Sciences (SLU) in Umeå danke ich ganz herzlich für die ausführliche Statistikberatung und –hilfe (auch zur Selbsthilfe ;-)) mit R. Sven, tack ska du ha für deine Mühe und die gründlichen Durchsichten der Kapitel.

Esther Rickert vom Helmholtz-Zentrum für Ozeanforschung (GEOMAR) in Kiel möchte ich ganz herzlich für die Eingabe der vielen, vielen SAS-Zählbögen von 116 Seetagen und mehr als 15.000 Schiffskilometern danken.

Danksagung/Acknowledgements

Für die gründliche Durchsicht meiner Arbeit und die sehr guten Verbesserungsvorschläge zur englischen Ausdrucksweise möchte ich mich ebenfalls ganz besonders bei Julia Sommerfeld (FTZ) bedanken.

I am very grateful to Jean-François Rail (CWS Ste-Foy) and Carina Gjerdrum (CWS Dartmouth) for providing data on seabird colonies. Jeff, thanks a lot for your kind support and sharing your detailed knowledge on the seabirds in the Gulf.

Ein großer Dank geht auch an meine aktuellen und ehemaligen Arbeitskollegen in der AG Seevogelökologie am FTZ. Danke an euch für alles Mögliche an großer und kleiner Unterstützung über die Zeit und die vielen netten Gespräche. Danke dafür, dass ihr einfach so ein netter Haufen seid! Ich danke Kai Borkenhagen, Anna-Marie Cormann, Bettina Mendel, Jana Kotzerka, Stefan Weiel, Jette Schwemmer, Philipp Schwemmer, Nicole Sonntag, Katta Ludynia, Sabine Müller, Franziska Güpner, Dagmar Cimiotti, Nele Markones, Henning Volmer, Julia Sommerfeld, Leonie Enners, Ulrike Kubetzki und Stefan Garthe.

I would also like to thank Donna Goodwin and François Bolduc for their great hospitality during my stays in Québec City. You have made me feel welcome and at home. Special thanks also for my lobster premiere and the other extraordinarily yummy food. Québec – je me souviens!

Thanks a lot as well to Tobie Surette (GFC) and his family for their hospitality. It was most enjoyable at your home in Moncton and your kids were particularly cute.

Thanks also to Kevin Pauley from the Bedford Institute of Oceanography (BIO) in Dartmouth simply for his positive attitude. Kevin, I hardly ever met anybody knowing so many great stories and making me laugh so hard.

Vielen lieben Dank an meine Familie Guse und Familie Markones für die tolle Unterstützung und den Rückhalt über die ganzen Jahre. Ein ganz besonderer Dank für Alles und vor allem Liebe geht an meine Eltern Birgit und Dieter! Ohne euch wäre ich nicht hier (im wahrsten Sinne des Wortes ;-)). Herzlichen Dank auch an meine Brüder Jan und Arne, einfach dafür dass sie da sind. Jungs, euch würde ich gerne noch viel öfter sehen. Ein lieben Dank auch an meine Oma Gerda und meinen Opa Helmut, die mich immer wunderbar unterstützt haben.

Meine allerliebste Nele, wie soll ich dir nur danken? Ohne dich, deine Liebe und beispiellose Unterstützung wäre das alles wohl kaum etwas geworden. Was für ein Riesenglück, dass ich dich habe!

Liebe Ida, liebe Jonna, was seid ihr für zwei kleine Wunder! Es ist das größte Geschenk euer Papa sein zu dürfen. Vielen Dank auch dafür, dass ihr nachts ab und zu mal schläft...

Erklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbständig angefertigt habe und dass sie in Form und Inhalt meine eigene Arbeit ist. Es wurden, abgesehen von der Beratung meiner akademischen Betreuer, keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Die Arbeit wurde unter Einhaltung der Regeln zu guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft erstellt.

Dies ist mein erster Promotionsversuch. Ich habe diese Arbeit weder ganz noch zum Teil im Rahmen eines Prüfungsverfahrens schon an einer anderen Stelle vorgelegt.

Für die Prüfung wird die Form einer Disputation gewählt. Der Zulassung von Zuhörerinnen und Zuhörern bei der mündlichen Prüfung wird nicht widersprochen.

Kiel, den