

Aus dem Forschungs- und Technologiezentrum Westküste

**Identification of foraging behaviour and feeding
areas of three seabird species breeding
sympatrically in a highly productive regime, the
northern Gulf of Alaska**

Dissertation

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Jana Kotzerka

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Referent: PD Dr. Stefan Garthe

Co-Referent: Prof. Dr. Dieter Piepenburg

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Der Dekan

„Manche Dinge sehen wir nur, wenn wir das Meer überqueren und nehmen sie nicht zur Kenntnis, wenn wir sie stets vor Augen haben.“

(Aus: Plinius, Epistulae 8.20,1)

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Summary

The Gulf of Alaska, situated at the northeastern boundary of the North Pacific Ocean, is a highly productive regime. Although it undergoes regularly intense regime shifts, it is supporting several millions of seabirds. But populations fluctuate sharply and reasons for that are not completely understood. However, understanding of how seabirds react to their marine environment is essential in order to assess naturally or human induced changes of their abundances and distributions. This thesis focuses on the at-sea distribution, foraging ecology and diving behaviour of three seabird species breeding sympatrically on Middleton Island in the northern Gulf of Alaska. Pelagic Cormorants (*Phalacrocorax pelagicus*), Black-legged Kittiwakes (*Rissa tridactyla*) and Tufted Puffins (*Fratercula cirrhata*) were studied during three consecutive years using novel data logger technologies like GPS data loggers or time-depth-recorders (TDR's). With these selected species it was possible to investigate different marine habitats used by seabirds. Aim of this study was to investigate the species-specific foraging behaviour and feeding areas, with special emphasis on the influence of extrinsic factor on these, and how these species cope with intra- and interspecific competition for prey species and foraging areas.

During the course of this thesis, several new aspects of the foraging ecology of the selected seabird species could be examined. Prior to this thesis, (nearly) no data of the diving behaviour of free-ranging Pelagic Cormorants and Tufted Puffins were available. Further, the foraging trip behaviour and feeding areas used could be described in detail for the first time for all of the three studied species using novel data logger technologies. For breeding Black-legged Kittiwakes it could be shown that this species regularly forages near the colony but frequently undertakes far-ranging foraging trips to distant areas, reaching up to 100 km from their breeding site. The foraging strategies of this species differed significantly between the pre-breeding and breeding season, at least in some years. During the pre-breeding season, when returning from their wintering sites and before starting to build their nests, kittiwakes performed mainly nocturnal foraging trips to deep pelagic waters. Later during the breeding season they foraged only over the continental shelf area in water depths not deeper than 200 m. Those foraging trips were mainly during daytime. The foraging behaviour of Black-legged Kittiwakes was not directly linked to ocean productivity. It probably rather showed the time lag of the

secondary productivity and the availability of varying prey species during different breeding stages.

Pelagic Cormorants showed surprisingly strong foraging-site fidelity throughout all three study years on both individual and population levels. During all study years the sub-colony sampled foraged in a very restricted feeding area in northeastern direction of their breeding site. Individual birds returned to the same foraging site in consecutive foraging trips as well as on successive days. Furthermore, nearly 50 % of the birds that could be equipped repeatedly in different study years with GPS data loggers and time-depth-recorders showed individually specialized diving behaviour and consistency in their foraging trip parameters. Such specialization and reliance on a narrow foraging area might be advantageous for foraging efficiency, especially with regard to intra- and interspecific competition, but could also have severe negative effects on survival and reproduction if environmental conditions change profoundly.

Additional results of this thesis are the first successful deployments and recaptures of two Tufted Puffins equipped with a time-depth recorder and GPS logger, respectively. With that it was possible to determine the foraging area and diving behaviour of free-ranging Tufted Puffins during the chick-rearing period. Those results showed high diving activities throughout the day and the foraging trips obtained by the GPS logger might portend to a dual foraging strategy with short and long distant foraging trips.

The present study improves our knowledge on the distribution and foraging ecology of three widely distributed seabird species of the North Pacific substantially. It provides several completely new aspects of the ecology of these species and indicates how these different seabird species use the marine environment successfully.

Zusammenfassung

Der Golf von Alaska, an der nordöstlichen Grenze des Nordpazifiks gelegen, ist ein hoch produktives Regime. Obwohl er regelmäßig starken Regimeveränderungen unterliegt, bildet der Golf die Nahrungsgrundlage für Millionen von Seevögeln. Aber ihre Populationen schwanken stark und die dem zugrunde liegenden Mechanismen sind noch nicht vollständig erklärbar. Jedoch ist das Verständnis darüber, wie Seevögel auf die marine Umwelt reagieren, unerlässlich, um natürliche oder von Menschen verursachte Änderungen ihrer Abundanzen und Verbreitungen abschätzen und beurteilen zu können. Die vorliegende Doktorarbeit beschäftigt sich mit der Verbreitung auf See, der Nahrungssuchökologie und dem Tauchverhalten von drei Seevogelarten, die sympatrisch auf Middleton Island im nördlichen Golf von Alaska brüten. In drei aufeinander folgenden Untersuchungsjahren wurden Pelagische Kormorane (*Phalacrocorax pelagicus*), Dreizehenmöwen (*Rissa tridactyla*) und Gelbschopflunde (*Fratercula cirrhata*) mit Hilfe von neuesten Datenloggertechnologien wie GPS-Loggern und Tauchtiefenrekordern untersucht. Mit diesen gewählten Arten war es möglich, unterschiedliche, von Seevögeln genutzte Habitate zu untersuchen. Ziel dieser Studie war es, das artspezifische Nahrungssuchverhalten und die Nahrungssuchgebiete, unter spezieller Berücksichtigung des Einflusses von äußeren Faktoren, zu untersuchen und herauszufinden, wie diese Arten mit innerartlicher und zwischenartlicher Konkurrenz um Beutearten und Nahrungssuchgebiete umgehen.

Im Zuge dieser Doktorarbeit konnten wichtige neue Aspekte zur Nahrungssuchökologie dieser ausgewählten Arten herausgefunden werden. Vor diesen Untersuchungen gab es (nahezu) keine Daten zum Tauchverhalten von frei lebenden Pelagischen Kormoranen und Gelbschopflunden. Des Weiteren konnten erstmals das Verhalten während der Nahrungssuchflüge und die Nahrungssuchgebiete für diese drei Arten mit Hilfe von neuesten Datenloggertechnologien detailliert beschrieben werden.

Für die Dreizehenmöwe konnte gezeigt werden, dass diese Art regelmäßig in Kolonienähe auf Nahrungssuche geht, aber auch häufig Nahrungssuchflüge in weiter entfernte Gebiete unternimmt, die bis zu 100 km von ihren Brutplätzen entfernt liegen können. Die Nahrungssuchstrategien dieser Seevogelart unterscheiden sich, zumindest in einigen Jahren, signifikant zwischen der Vorbrutzeit und der Brutzeit. Während der

Vorbrutzeit, wenn die Vögel aus ihren Überwinterungsgebieten zurückkehren und bevor sie mit dem Nestbau beginnen, suchten Dreizehenmöwen hauptsächlich nachts über dem tiefen pelagischen Ozean nach Nahrung. Später während der Brutzeit gingen sie überwiegend über dem Kontinentalschelf, mit Wassertiefen unter 200 m, auf Nahrungssuche. Diese Nahrungssuchflüge fanden vorwiegend tagsüber statt. Das Nahrungssuchverhalten von Dreizehenmöwen konnte nicht direkt mit der Produktivität des Ozeans in Verbindung gebracht werden. Vielmehr spiegelte es wahrscheinlich die zeitliche Verzögerung der Sekundärproduktion und die Verfügbarkeit unterschiedlicher Beutearten während der einzelnen Brutphasen wider.

Die Pelagischen Kormorane zeigten in allen drei Untersuchungsjahren eine überraschend starke Treue zu ihren Nahrungssuchgebiet, sowohl auf Einzeltier- als auch auf Populationsniveau. In allen Untersuchungsjahren ging diese Art in einem relativ abgegrenzten Gebiet in nordöstlicher Richtung von Ihrer Brutkolonie auf Nahrungssuche. Die einzelnen Tiere kehrten sowohl bei aufeinander folgenden Nahrungssuchflügen als auch an aufeinander folgenden Tagen in dasselbe Nahrungssuchgebiet zurück. Weiterhin zeigten fast 50 % der Tiere, die wiederholt in aufeinander folgenden Jahren mit GPS-Loggern und Tauchtiefenrekordern ausgerüstet werden konnten, ein individuell spezialisiertes Tauchverhalten und Konsistenz in den Parametern ihrer Nahrungssuchflüge. So eine Spezialisierung und das Festhalten an einem eng begrenzten Nahrungssuchgebiet mögen vorteilhaft für die Nahrungssucheffizienz sein, speziell im Hinblick auf innerartliche und zwischenartliche Konkurrenz. Es kann aber auch ernste negative Folgen für das Überleben und die Reproduktion haben, falls sich die Umweltbedingungen grundlegend ändern.

Ein weiteres Ergebnis dieser Doktorarbeit war das erste erfolgreiche Ausrüsten und Wiederfangen von zwei Gelbschopflunden mit jeweils einem Tauchtiefenrekorder und einem GPS-Logger. Damit war es erstmals möglich, das Nahrungssuchgebiet und das Tauchverhalten eines frei lebenden Gelbschopflundes während der Brutzeit zu ermitteln. Diese Ergebnisse zeigten eine hohe tägliche Tauchaktivität, und die mit dem GPS-Logger aufgezeichneten Nahrungssuchflüge könnten auf eine duale Nahrungssuchstrategie mit kurzen und weiter entfernten Nahrungssuchflügen hinweisen.

Die vorliegenden Untersuchungen verbessern unsere Kenntnisse über die Verbreitung und die Nahrungssuchökologie von drei weit verbreiteten Seevogelarten des Nordpazifiks maßgeblich. Sie liefern einige komplett neue Aspekte über die Ökologie

dieser Arten und geben Anhaltspunkte darüber, wie diese verschiedenen Seevogelarten die marine Umwelt erfolgreich nutzen.

General Introduction



Seabirds in their marine environment

Marine birds are upper trophic level organisms, and thus top predators of the marine food web. Seabirds spend most time of their life on the ocean. Their distribution at sea, but also of their colonies, is determined by several distinct predictors (Fig. GI-1). These are, for example, the distribution of food organisms (Hunt 1991; Russel et al. 1999; Schneider and Piatt 1986), oceanographic (Garthe 1997; Huettmann and Diamond 2001; Piatt et al. 1991) and climatic parameters (Jones et al. 2002; Springer 1991) as well as human activities such as fishery (Furness and Monaghan 1987; Gandini and Frere 1998; Oro et al. 1995) or even oil and gas exploration (e. g. Wiese et al. 2001).

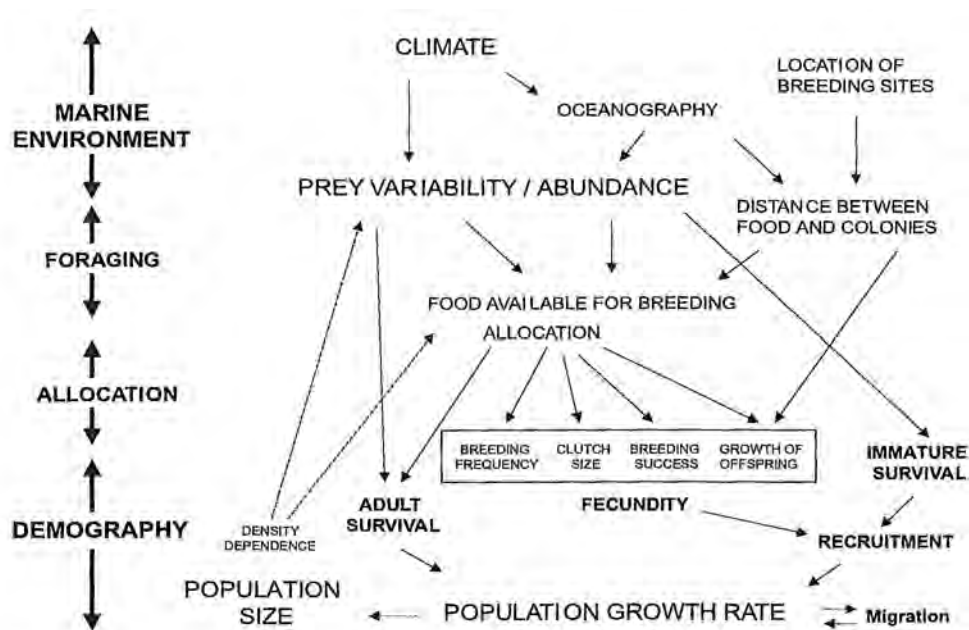


Figure GI-1. Schematic representation of the relationships between demographic traits and seabirds (from: Schreiber and Burger 2002).

One of the most important issues in animal ecology is assessing which habitat seabirds prefer for foraging and feeding and how they react to changes in this chosen environment (Evans and Hammond 2004), especially as seabirds respond to changes in their marine environment in different spatial and temporal scales. Their breeding biology may indicate short- and long term trends in the oceanographic conditions over much

larger areas than only of their direct feeding grounds around the colonies (Hunt and Schneider 1987; Kitaysky and Golubova 2000). During the breeding season the birds have to make short-term decisions on areas where to feed, and which prey species to search for, and have to balance their activities over hundreds of square kilometres at sea (e. g. feeding, courtship behaviour) with those on land (e.g. courtship behaviour, finding a nesting site, egg and chick guarding). During chick-rearing lasting several weeks to a few months, the birds are strongly dependent on local prey availability and weather conditions. At the end of the breeding season their breeding success integrates the results of the decisions made by the birds in response to changing demands and opportunities (Diamond and Delvin 2003). Beyond the breeding season many species migrate to wintering areas that are sometimes located at distances of thousands of kilometres from their colonies.

The marine environment is continually changing. This has a profound effect on marine ecosystems and their trophic levels due to the changing ocean currents, primary productivity, distribution of prey, and thus finally also affects survival rate and productivity of marine birds. Additional changes of the marine environment occur by coastal habitat loss due to industrial, urban, and recreational development, eradication or displacement of species or due to the accumulation of contaminants from industry or agriculture. Species that are not able to adapt to these changes could become rare or even extinct (Dickson and Gilchrist 2002).

Due to their mobility and longevity seabirds are especially well qualified to measure such environmental changes over long periods and in areas that are usually only difficult to access (Burger and Gochfeld 2001). Their survival directly depends on how seabirds react to those changes and how they can adapt. Therefore, seabirds can act as indicator species to monitor changing environmental and climatic conditions.

New approaches - logger technologies, Remote Sensing and GIS

To investigate the behaviour of seabirds at sea, until recently mainly ship- and aircraft-based direct observations were carried out. Due to the remoteness of many areas, and many logistic problems closely connected with that, but particularly because of the exceeding additional knowledge, data loggers and different kinds of transmitters

(compass, light, satellite- and radio telemetry) have increasingly been used in the last years. These tools can provide the positions of the birds at sea as well as different environmental parameters, e. g. temperature, pressure (Harris et al. 2010; Paiva et al. 2010a; Raymond et al. 2010; Wilson et al. 2002) concurrently, without any observer visiting the area and/or the birds at their feeding grounds.

Latest technological developments even make it possible to use miniature GPS-loggers which can additionally be equipped with different sensors. These data loggers have, for example, very precise and rapid-response temperature and pressure sensors and allow a very accurate GPS positioning as well and were already used successfully (Freeman et al. 2010; Grémillet et al. 2004b; Masello et al. 2010).

Further, remote sensing can be used to monitor the environment efficiently (e. g. Lillesand et al. 2004). The need for monitoring terrestrial and oceanic systems that observe, document, quantify and map the changing environments, its natural resources and track interactions within the biosphere, atmosphere, hydrosphere and geosphere has become a global concern (Short 2011).

These new technological developments are able to connect investigations for seabird distributions and foraging strategies with environmental data, which are measured at the same time and the same location. This allows us now to investigate and quantify advanced biological questions to strengthen our knowledge about seabirds further and then to apply them on a large scale and in a general form, e.g., with the help of Geographical Information Systems (GIS), spatial statistics and qualitatively spatial prediction models. Specifically the use of GIS provides exceptional means for integrating timely remote sensing data with other spatial types of data (Wilson et al. 2002). The GIS approach stores, integrates and analyses information that has a practical value in many fields concerned with decision-making in resource management, environmental control, site development, research and conservation (Short 2011). With these new techniques seabirds and their habitat can be appropriately linked with remote sensing information. In that way, along with GIS, marine animals can measure and monitor the physical properties of the ocean in which they live and forage.

Aims of the study

These new methods offer specifically valuable possibilities to better understand the ecosystem requirements of seabirds in remote areas. Due to the seclusion, direct observations are much more difficult in such areas. But such remote areas (e. g. North Atlantic, North Pacific, Southern Oceans) are often important for the functioning of the marine ecosystem and changes of those systems, whether they are naturally or human induced, can have profound and far-reaching effects. Therefore, even for remote regions, the understanding of principle ecological relationships of seabirds and the marine environment is essential.

The North Pacific is a highly productive region supporting a very rich and varied ecosystem with vast populations of birds, mammals, fish and shellfish. Eastern North Pacific seabird populations along the American coast have been well studied in recent times (Ainley et al. 2009; Konyukhov et al. 1998). Other studies focus on the feeding ecology and pelagic distribution in relation to oceanographic features in the Bering Sea or the Aleutians (Hunt et al. 1981; Piatt et al. 1991; Piatt et al. 1992; Russel et al. 1999; Schauer 1991). But less studies concentrate on seabirds in the Gulf of Alaska (Hunt et al. 2005), although the gulf regularly undergoes ecological changes (regime shifts) caused by oceanographic or atmospheric forcing that have fundamental effects on all trophic levels (Mundy 2005; Spies 2007). Fluctuations and changes of seabird populations in the Gulf of Alaska are not well understood. They might be coupled to such regime shifts but could also have other reasons.

The aim of this study is to investigate the foraging areas and diving behaviour of selected but representative seabird species in the Gulf of Alaska, as part of the North Pacific marine ecosystems. Different seabird species were chosen in order to investigate a wide range of possible used foraging habitats, the species-specific foraging behaviour, how these species cope with inter- and intraspecific competition for food and foraging sites and whether and how their foraging strategies are driven by extrinsic factors. Middleton Island in the northern Gulf of Alaska was well suited for this study approach as five seabird species are breeding there. Further, the island hosts a biological research station and is accessible by airplane. Thus, logistical obstacles were minimized.

For this study approach three different groups of seabirds, cormorants (Pelagic Cormorant *Phalacrocorax pelagicus*), gulls (Black-legged Kittiwake *Rissa tridactyla*) and

auks (Tufted Puffin *Fratercula cirrhata*) were selected and their foraging behaviour at sea during the pre-breeding and/or breeding seasons was examined with progressive methods. For this region, their dependence on typical oceanographic and bathymetric parameters was studied with the help of GIS and habitat data. These seabird species include planktivorous and piscivorous species which forage for prey inshore and offshore, but also overlap to some extent in their choice of prey species. By using these different seabird species it is possible to observe a large spectrum of different habitats used by seabirds. The description of the habitat requirements of these birds can therefore be essential for ecosystem-based management and conservation issues.

The following questions should be answered:

1. How are the foraging areas of the selected seabird species distributed in the study area?
2. Which detailed foraging strategies are they exhibiting?
3. How do the individual seabird species cope with interspecific competition for prey?
4. How are the distribution and the foraging strategies driven by the oceanographic and bathymetric parameters?

Those questions were answered while applying novel data logger technologies on these birds. There is little evidence in the literature that any type of these data loggers were already used to determine seabird-habitat-relationships in the North Pacific region. However, some research was undertaken to determine seabird movements in the North Pacific (Block et al. 2003; Irons 1998). Except for a small-scale coastal application (Manly et al. 2002) and few studies using radio telemetry in Prince William Sound (Ainley et al. 2003; Ford et al. 2007) none was used to model spatial and large-scale habitat relationships of seabirds. Though, recently more and more studies have started to use these new developments for seabird research and associated modelling (Ito et al. 2010; Kokubun et al. 2010).

Study Area

The Gulf of Alaska

The Gulf of Alaska is a semi-enclosed basin at the northeastern end of the North Pacific Ocean. It is surrounded by extensive mountain ranges in most of its coastline, except for the southern part, and encompasses a total area of about $3.4 \times 10^6 \text{ km}^2$ (4% of the North Pacific).

The gulf consists of a deep continental shelf region with bays and fjords (often with depths of 200 m within even a few kilometres of the coast), a steep continental slope (that rapidly shoals from 2500 m to 250 m) and a huge abyssal zone that underlies 75% of the gulf area and that reaches depths of 4000 m (Fig. GI-2).



Figure GI-2. Map of the North Pacific Ocean with the study site Middleton Island.

The climate of the Gulf of Alaska cycles between warm and cold regimes on annual or multi-decadal time scales. The last climate regime shift occurred in 1976/77 (and there are indications for another one in 1989 and possible a further one in 1998; Francis et al. 1998; McGowan et al. 1998) and resulted in marked changes in fish abundances. Groundfish (e. g. pleuronectidae and gadidae) and Pacific Salmon fisheries (*Oncorhynchus spec.*) increased sharply whereas some forage fish populations (e. g. capelin *Mallotus villosus* and herring *Clupea pallasii*), shrimps (e. g. northern shrimp *Pandalus borealis*) and crabs (e. g. red King crab *Paralithodes camtschaticus*) collapsed. Possible subsequent changes were the decline of Steller Sea Lion and seabird populations, although a direct link to that regime shift is difficult to verify (Anderson and Piatt 1999; Benson and Trites 2002; Fritz and Hinckley 2005; Piatt and Anderson 1996).

Major circulations in the Gulf of Alaska are counterclockwise flows. In the Gulf of Alaska basin the Alaska Gyre is the dominant current, which is part of the much greater subarctic gyre of the North Pacific. It is driven by large-scale atmospheric flow. In the eastern and northeastern Gulf carries the Alaska Current warm water into the Gulf. The swift Alaska Coastal Current along the continental slope flows on the inner shelf in the northern Gulf and transforms into the Alaskan Stream (northwestern Gulf) (Figure GI-3; Spies 2007; Stabeno et al. 2004).

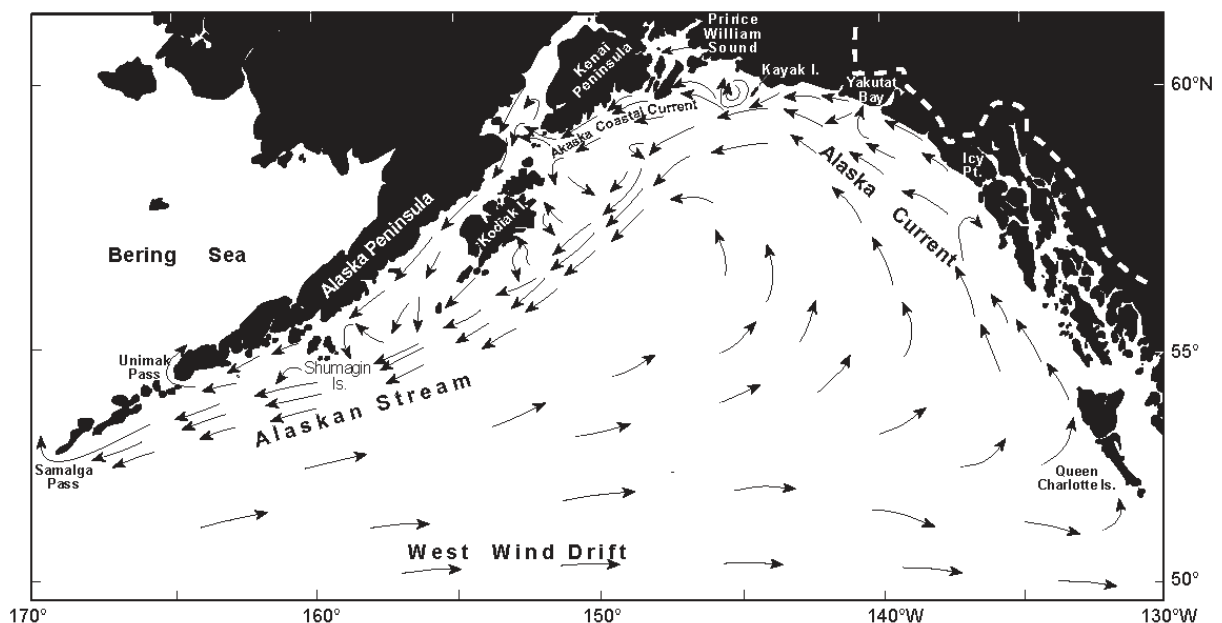


Figure GI-3. Currents of the Gulf of Alaska. The Alaska gyre is indicated with counterclockwise arrows (taken from: Stabeno et al. 2004).

In spring iron-rich but nutrient-poor fresh water that originates from melting snow and ice in the mountains and glaciers runs off into the coastal shelf waters and is floating as a layer over the saltier shelf water. Upwelling, as it occurs in the southern part of the Gulf of Alaska, does not occur in the northern Gulf because the dominant winds produce downwelling at the coast. These environmental characteristics seem to predict an unproductive biological regime, yet the Gulf of Alaska is a paradoxon as the gulf is biologically very productive (Spies 2007). Mechanisms that explain this paradoxon are not yet fully understood. To some extent eddies at the boundary of iron-rich but nutrient-poor coastal waters and waters of the central Gulf of Alaska, that are rich in macronutrients but depleted in iron, cause an exchange of these both water masses (Rovegno et al. 2009; Schwing et al. 2010). Another mechanism that could bring nutrients to the euphotic surface layers might be a deepening of mixed layers (Sarkar 2007).

In fact, the gulf is a highly productive biological regime (Fig. GI-4) in the Pacific with annually more than 300 g C/m² (PICES 2004; Stephensen and Irons 2003). By providing zooplankton as the driving engine for the entire food chain this sea provides the food base for millions of seabirds that either breed there or pass through from northern Asia and the southern hemisphere (e. g. Sooty Shearwater, Short-tailed Shearwater) (Shuntov 2000). The area of the Gulf of Alaska supports alone more than 7.2 million of breeding seabirds (Stephensen and Irons 2003), without counting migrating seabirds.

As one of the tectonically most active zones on earth the geomorphology of the Gulf of Alaska is continuously changing. One of the last big changes in the gulf's geomorphology was the Great Alaska Earthquake of 1964, when parts of the shelf were uplifted by much as 15 m (Plafker 1965). This uplift had also a great impact on parts of the coastline, and thus also on the habitat for breeding seabirds.

Middleton Island

Middleton Island (59.4° N, 146.3° W; Fig. GI-2) is placed in the northern Gulf of Alaska, lying about 80 km south of the entrance to Prince William Sound. It measures about 8 km long by 1.6 km wide, and has a maximum elevation of 47.6 m. The island is situated

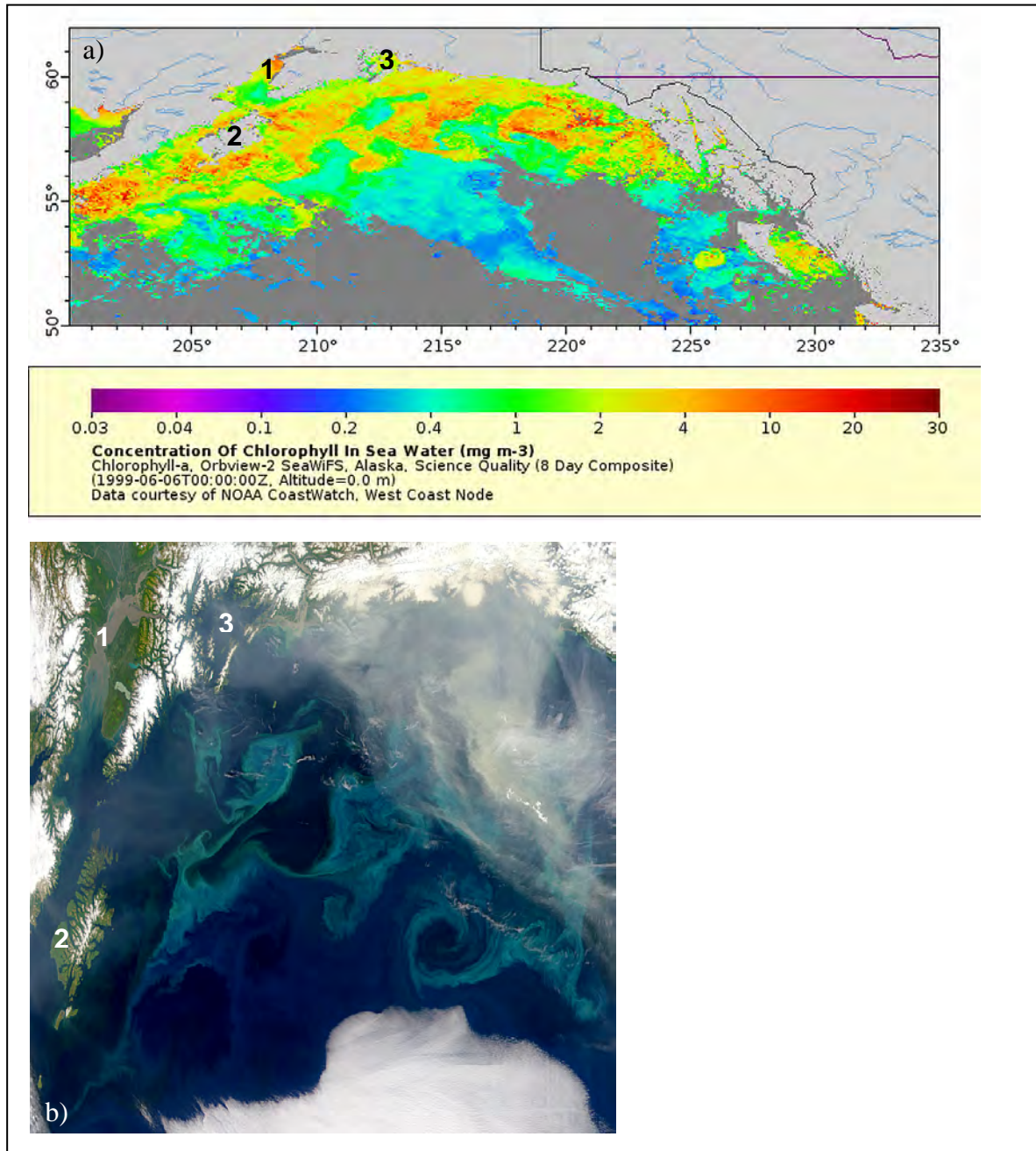


Figure GI-4. a) Chlorophyll concentration in the Gulf of Alaska on 06th June 1999 as measured by SeaWiFS (source: <http://coastwatch.pfel.noaa.gov/erddap/info/index.html>) and b) phytoplankton bloom in the Gulf of Alaska on 5th June 1999 (source: <http://visibleearth.nasa.gov>). 1 = Cook Inlet, 2 = Kodiak Island, 3= Prince William Sound.

at the edge of the continental shelf, where the North American plate is being underthrust and deformed by the Pacific plate along the Aleutian trench (Prescott and Lisowski 1977). Middleton Island is a relatively young island with an age of only about 4,300 years. The parent material consists of marine glacial sediments that have raised out of the

ocean during several episodes of rapid deformation and uplifts. Six marine terraces associated with those intervals give subtle definition to the island's upland area and that strike an initial flat impression of the island to the visitor. The youngest terrace emerged abruptly during the Alaska earthquake of 1964, when an elevational change variously estimated at 2.7 to 3.5 m created large areas of previously submerged land below pre-existing sea cliffs (Plafker 1970). The Great Alaska Earthquake triggered successional changes in physiography, vegetation, animal habitats, and populations that are still proceeding more than 30 years after the event.

Middleton Island supports breeding by seven species of seabirds, including Black-legged Kittiwakes, Pelagic Cormorants, Common Murres (*Uria aalge*), Thick-billed Murres (*U. lomvia*), Tufted Puffins, Rhinoceros Auklets (*Cerorhinca monocerata*) and Glaucous-winged Gulls (*Larus glaucescens*). Furthermore, you can find a wide diversity and abundance of nesting, migrating, or wintering shorebirds, waterfowl, raptors, and passerines. In total, more than 220 bird species were recorded on this small island (S. A. Hatch, unpubl. data).

Seabird populations on Middleton Island are more dynamic than possibly anywhere else in Alaska, but reasons for that are still only partially understood, even though, the island has been an active site for seabird research and monitoring by the U.S. Fish and Wildlife Service, National Biological Service, and U.S. Geological Survey since the mid 1970s.

Some species decline dramatically (currently Black-legged Kittiwakes and Murres), whereas others have increased significantly (currently Glaucous-winged Gulls, Rhinoceros Auklets, American Oystercatchers). Pelagic Cormorants are fluctuating widely and Tufted Puffins are believed to increase presently, though precise data are not available for the latter species. In contrast, before 1970 kittiwake and murre populations both increased at least tenfold between 1956 and 1974 (S. A. Hatch, unpublished data). Pelagic Cormorants also increased during that time, but Rhinoceros Auklets were probably not present in the 1950s and 1960s as well as Glaucous-winged Gulls ((Rausch 1958).

In recent time major research takes place on seabirds (Black-legged Kittiwakes and Pelagic Cormorants) that nest (among other parts at the island) on a U.S. Air Force radar tower, decommissioned and derelict since the 1960s, to which artificial nest sites have been added for research. The birds nest on wooden ledges viewable from inside the

building through sliding panes of one-way mirror glass (Fig. GI-5; Gill and Hatch 2002). Additional investigations are carried out on Rhinoceros Auklet, Tufted Puffins, Glaucous-winged Gulls and shorebirds (e. g. Black Oystercatchers) in their natural habitats.



Figure GI-5. a) The abandoned U.S. Air Force radar tower provides artificial nest sites for Black-legged Kittiwakes and Pelagic Cormorants. b) View from outside the tower on artificial nest sides with wooden ledges on which kittiwakes and cormorants breed. c) View from inside the tower with nest sides backed by one-way mirror glass that enable close observations and better capture possibilities of the birds.

Study species

In order to investigate a wide variety of foraging habitats and feeding grounds I chose three seabird species breeding on Middleton Island. These species enclose three different groups of seabirds as gulls, cormorants and auks.

Black-legged Kittiwake

The Black-legged Kittiwake (hereafter 'Kittiwake') is a small gull species with a real pelagic mode of life. It is widely distributed on the northern hemisphere from the temperate zone up to the arctic and is the most abundant gull species in the world. Kittiwakes usually nest on offshore islands and along coasts on steep cliffs with narrow ledges. During the breeding season it stays closer to the coast and mainly feeds within 50 km from the colony. It is often found along upwelling or ocean fronts. During the non-breeding season kittiwakes forage far offshore over the shelf break and deep ocean areas (del Hoyo et al. 1996; Hatch et al. 2009). For the Pacific region the total population is estimated with 2.4 million Black-legged Kittiwakes breeding in 512 colonies (Fig. GI-6). The Alaskan population is encompassing about half of that number with 1.3 million birds in 356 breeding sites with a substantial proportion of that found in the Gulf of Alaska with about 466,000 birds (USFWS 2008). But census data of Alaska are mostly of the 1970's and 1980's and thus the quality and quantity of many populations probably does not reflect the actual status of the colonies and an updating of the data is urgently required (Hatch et al. 2009). There is no clear evidence of an overall change of kittiwake numbers in Alaska, but most colonies in Alaska are declining, some of them dramatically (e. g. Middleton Island, Chisik Island and Cape Peirce; Hatch et al. 2009). Although, trends are mixed and there are also some colonies that increased over the last years.

Kittiwakes are mainly piscivorous, feeding on small schooling fish like capelin, sandlance (*Ammodytes spec.*) or herring (*Clupea spec.*) during the breeding season. But invertebrates are also found in diets in moderate numbers, probably in years of reduced fish availability. They capture their prey by dipping or surface plunging. Because they are bound to the sea surface for feeding, kittiwakes are vulnerable to changes in the abundance and vertical distribution of their principle prey species (Furness and Tasker 2000; Hatch et al. 1993b).

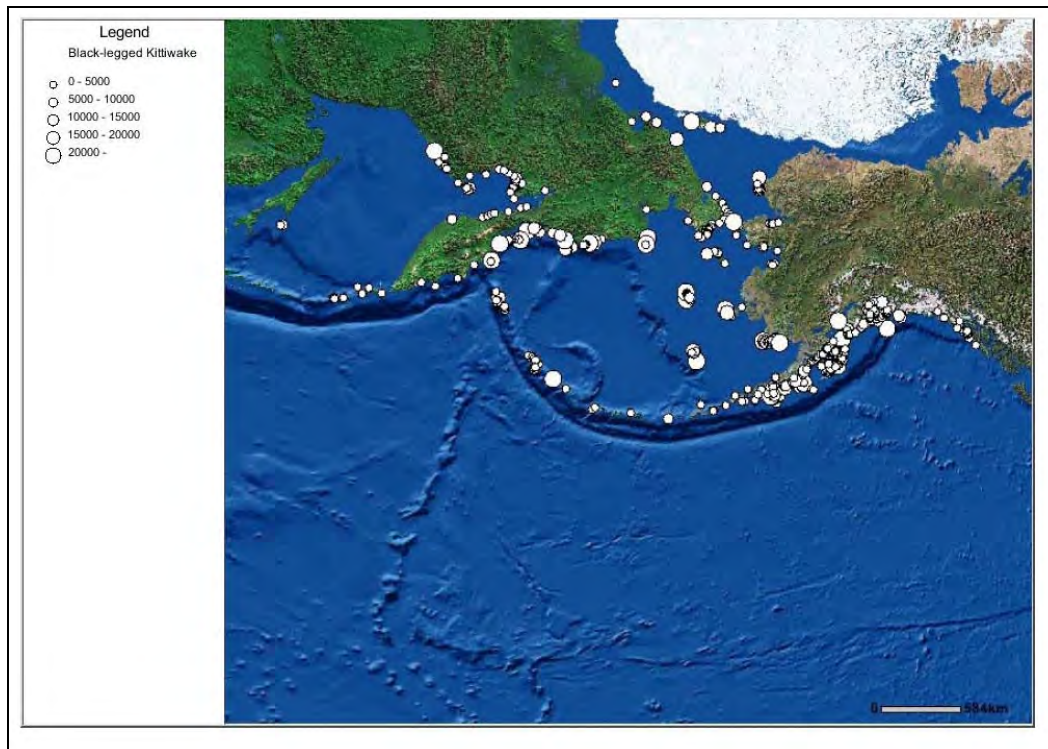


Figure GI-6. Known colonies and numbers of breeding birds of Black-legged Kittiwakes in the North Pacific. Data from the North Pacific Seabird Colony Database (<http://alaska.fws.gov/mbsp/mbm/northpacificseabirds/colonies/default.htm>).

Pelagic Cormorants

Pelagic Cormorants are the smallest and most widely distributed cormorants in the North Pacific (Fig. GI-7). This cormorant species has a huge breeding range from the Arctic to temperate waters. Colonies are found from the Bering Sea south to Baja California and from the Chukchi Sea to the coast of southern China. Despite that broad distribution, little is known about their biology. This is mainly due to their mode of life. Pelagic Cormorants are less gregarious than other cormorant species. Their colonies are typically small and dispersed and situated on steep rocky cliffs and exposed shorelines and are thus difficult to observe. Colonies size is usually not more than 50 birds and reaches rarely more than 500 individuals (del Hoyo et al. 1996; Hobson 1997; Nelson 2005). The total population number is only crudely known, but estimates are about 400,000 birds with about 75,000 pairs breeding in Alaska (Hobson 1997; Nelson 2005). The

largest known Alaskan colony is on Middleton Island with currently approximately 1500 breeding pairs in 2009 (S. A. Hatch, unpubl. data,).

Pelagic Cormorants are feeding exclusively marine, but despite its name it is usually found in inshore waters. This cormorant species is usually feeding on non-schooling, bottom-dwelling medium-sized fish by pursuit-diving, at rocky substrates or kelp beds. Prey species are diverse and include sandlance, sculpins (*Cottidae*), rockfish (*Sebastes spec.*) and *Pholidae*, but also invertebrates like crustaceans and worms (del Hoyo et al. 1996; Hobson 1997; Nelson 2005). Because robust population numbers are not present, especially for the Asian population, it is difficult to analyse trends. Overall status seems to be stable but individual populations are fluctuating.

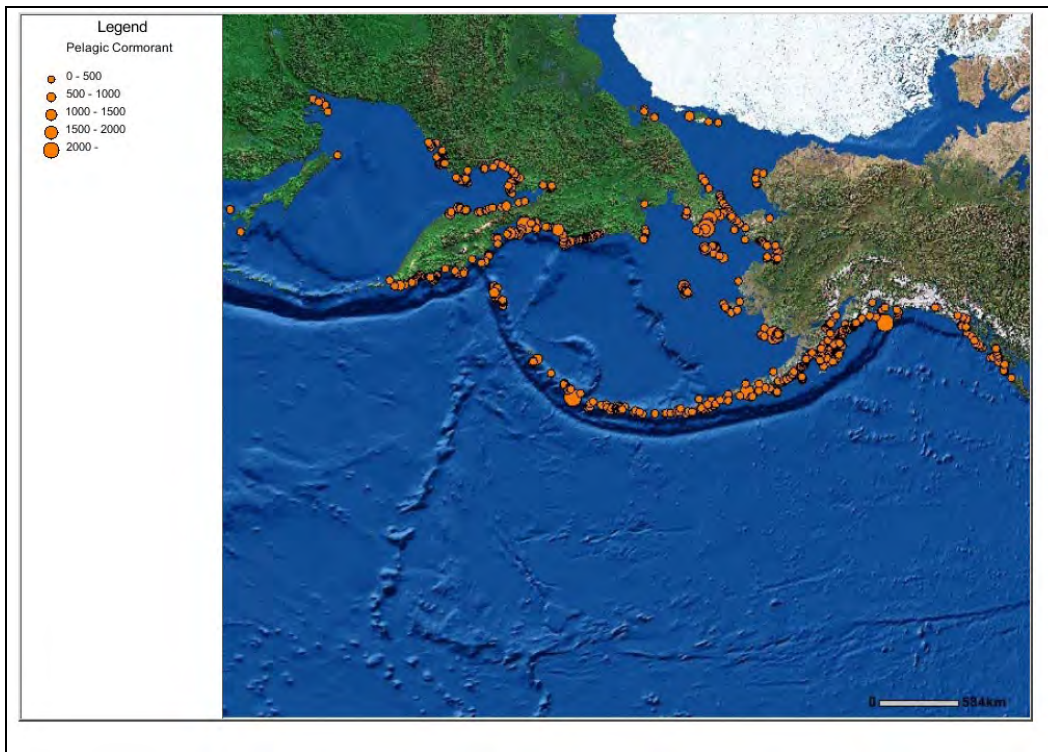


Figure GI-7. Known colonies and numbers of breeding birds of Pelagic Cormorants in the North Pacific. Data from the North Pacific Seabird Colony Database (<http://alaska.fws.gov/mbsp/mbm/northpacificseabirds/colonies/default.htm>).

Tufted Puffin

Tufted Puffins belong to the alcid family and are the largest member of the 'Puffin'-group. They breed over a vast geographic range and extreme of climate zones from the coastal Alaskan Arctic down to southern California and from Hokkaido (Japan) north to the Chukchi Peninsula (Davis et al. 2009; Piatt and Kitaysky 2002). This species is distributed along offshore islands and rocky coasts in the boreal North Pacific. It usually breeds on marine grassy slopes and island tops and rarely on rocky cliffs. The majority of the world population of Tufted Puffins breeds in North America (82 %) with 96% of that found in Alaska (Fig. GI-8). Most colonies are small with a median size of only 140 birds. Only about 50 colonies encompass more than 10,000 individuals. But population counts for this seabird species are quite difficult due to the burrow-nesting habitat. That's why also population trend are difficult to calculate. But results suggest an increasing number of Tufted Puffins in the Gulf of Alaska and westward and declining populations southward from southeastern Alaska to California. The same north-south-pattern is found in the western North Pacific. Populations in Russia seem to increase whereas numbers in Japan dramatically declined (Piatt and Kitaysky 2002).

The Tufted Puffin is the most pelagic alcid and winters far offshore off the continental shelf in oceanic waters in low densities. During the breeding season it is found closer to the colony, though it forages still further from the colony than the other puffin species (del Hoyo et al. 1996; Gaston and Jones 1998; Piatt and Kitaysky 2002). Tufted Puffins capture their prey underwater by wing-propelled diving. They are adapted to capture and carry more than 20 small fishes at a time when delivering prey to their chicks.

Tufted Puffins seem to have a bimodal foraging behaviour. Their offspring is usually fed with fish like Pacific Sandlance *Ammodytes hexapterus*, Pacific Herring *Clupea pallasii*, Capelin *Mallotus villosus* and juvenile Pollock *Theragra chalcogramma* or Rockfish *Sebastes spp.* Adults themselves feed more on different and diverse prey (e. g. invertebrates, like squid and euphausiids and fish) (Gjerdrum 2004; Golubova 2002; Hatch and Sanger 1992; Hobson et al. 1994). These bimodal foraging forces them to exploit a wide range of ocean habitat. Nevertheless, due to their highly pelagic mode of life and extreme sensitivity to human disturbance detailed knowledge about their foraging behaviour at sea is limited.

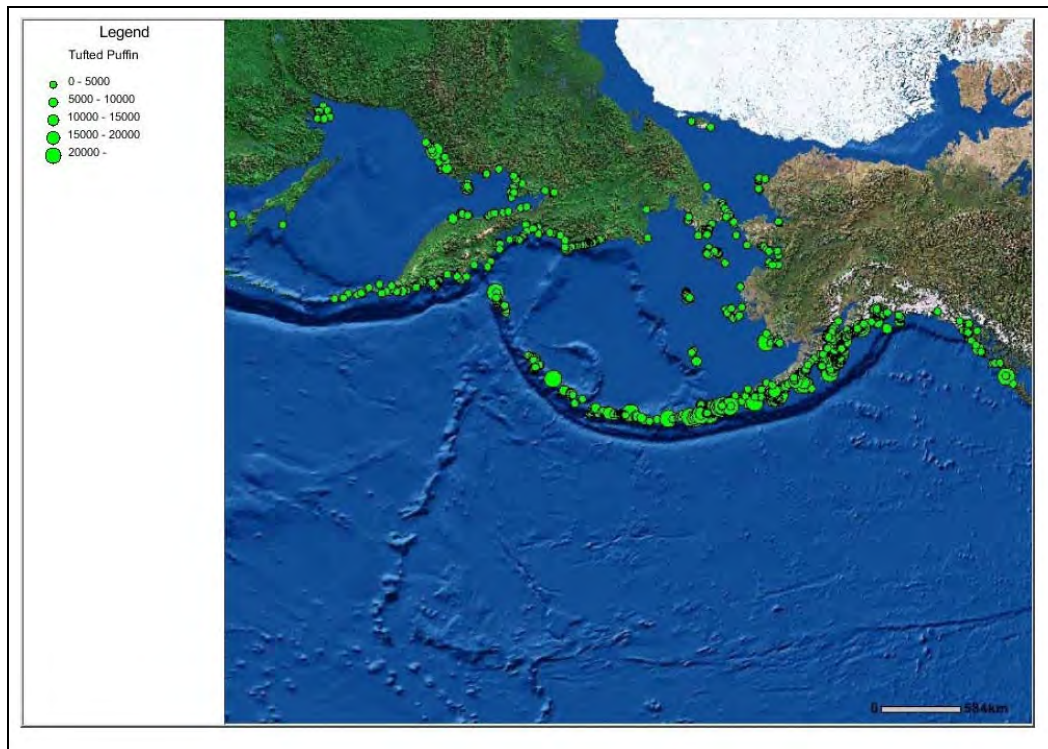


Figure GI-8. Known colonies and numbers of breeding birds of Tufted Puffins in the North Pacific. Data from the North Pacific Seabird Colony Database (<http://alaska.fws.gov/mbsp/mbm/northpacificseabirds/colonies/default.htm>).

Data loggers

1. GPS-TDlog

The GPS-data loggers are three-channelled receivers. The GPS-protocol delivers position (latitude, longitude), speed, DOP (dilution of precision), date and time. The two other channels record pressure and temperature. The size is 100 mm x 48 mm x 24 mm (L x W x H) and it weighs 70 g. The memory is 2 MB. The pressure sensor allows to determine the diving depth of the birds with a resolution of < 0.025 % FS. The rapid-response temperature sensor has a resolution of < 0.005 K at 0 – 20°C and a rapid response time of $T_{0.9} < 2$ s and enables us to distinguish between flight and swim phases. Positional accuracy was usually with 65 % of all positions were within a circle of 10 m around the actual position and 90 % were within 19 m.

2. MiniGPSlog

The MiniGPSlog is a single-channelled receiver. The GPS-protocol delivers position (latitude, longitude), speed, DOP (dilution of precision), date and time. The MiniGPSlog has a dimension of 46.5 mm x 32 mm x 18.5 mm (L x W x H) and weighs 29 g. The memory is 4 MB. Positional accuracy was usually with 65 % of all positions were within a circle of 10 m around the actual position and 90 % were within 19 m.

3. PreciTD

The PreciTD data loggers are two channelled data loggers. They record the pressure and temperature at selected intervals with a resolution of 5 mbar (approx. 5 cm water column) and 0.005 K at 0 – 20°C, respectively. These loggers have a diameter of 19 mm and a length of 75 mm with a mass of 17 g. The memory is 2 MB.

4. GiPSy

The GiPSy data loggers are very small and lightweight GPS receivers. GPS data stored in the device memory contain date, time, latitude, longitude, altitude, geoid-ellipsoid-separation relative to the position (GES), speed and angular deviation with respect to north. The size is 50 mm x 22 mm x 10 mm (L x W x H) with a weight of 8 g. The data storage capacity is 500 000 data points.

The size and weight of the birds determined which type of data loggers was used for the individual bird species. The puffins were equipped with the smaller and lighter MiniGPS loggers or with PreciTD loggers, male cormorants with the bigger and heavier GPS loggers and female cormorants with MiniGPSlog's and PreciTD's. Black-legged Kittiwakes were equipped with GiPSy loggers. The loggers were attached with waterproof tape reversible on the feathers of the birds. After completion of their foraging trips the data loggers were removed and the data could be downloaded to a computer.

Chapter outline

This thesis comprises five chapters characterising and identifying the foraging areas and the foraging behaviour of three seabird species breeding on Middleton Island in the northern Gulf of Alaska. For the both species that are diving to search for their prey, their diving behaviour is additionally analysed.

Chapter I and II

These two chapters describe the foraging areas and the foraging strategies of the Black-legged Kittiwake during two consecutive seasons and during two breeding stages.

Chapter I “**GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes**” investigates the foraging behaviour of the Black-legged Kittiwake in general using, for the first time on this species, small GPS data loggers. It provides comprehensive information on basic foraging behaviour parameters and shows the foraging areas in detail used during the chick-rearing period.

Chapter II “**Contrasting foraging strategies of Black-legged Kittiwakes between pre-breeding and breeding and their relationship to environmental factors**” shows further results of the investigation of different foraging areas of Black-legged Kittiwakes during the pre-breeding and the breeding period and reveals associations to abiotic factors such as water depths and remotely sensed data like sea surface temperatures or chlorophyll a.

Chapter III and IV

The foraging and diving behaviour of Pelagic Cormorants is described in more detail in the chapters III und IV. It was the first time that this species could be equipped with GPS- and data loggers to investigate their foraging behaviour directly.

Chapter III “**Evidence for foraging-site fidelity and individual foraging behaviour of Pelagic Cormorants rearing chicks in the Gulf of Alaska**” describes the foraging area used by Pelagic Cormorants and gives general information about the foraging and diving behaviour of this widespread species. Further, this chapter gives an indication of strong foraging-site fidelity of these birds to a small area northeast of the colony.

Chapter IV “**Individual specialization in the diving behaviour of a widespread North Pacific marine predator**” compares the foraging and diving strategies of nine Pelagic Cormorants sampled during two or three consecutive years, respectively. It answers the question whether individual birds develop individual diving behaviour and whether they use this repeatedly to cope with inter- or intraspecific competition.

Chapter V

The fifth chapter “**First Insights into the Diving and Foraging Behavior of chick-rearing Tufted Puffins (*Fratercula cirrhata*)**” investigates the results of two Tufted Puffins that were equipped with a MiniGPS-logger and a time depth recorder, respectively. It was the first time that this species could successfully be fitted with one of these devices and the data obtained show their foraging areas and the diving behaviour of a free-ranging individual during the chick-rearing period.

Statistical methods used

In this thesis modern statistical approaches were used to analyse the data of the foraging and diving behaviour of three common seabird species breeding in the North Pacific. To analyze the data Generalized Linear Models (GLM's), Linear Mixed Effect Models (LME's), Generalized Linear Mixed Models (GLMM's) and Generalized Additive Models (GAM's) were applied. These methods are widely used in ecological studies. Since they were also used in all chapters of this thesis, an overview of them is provided here.

The GLM is a model for linear and non-linear effects of continuous and categorical predictor variables on a discrete or continuous but not necessarily normally distributed dependent (outcome) variable (Crawley 2007; McCullagh and Nelder 1989). It was used in this thesis for the comparison of the breeding success of equipped and non-equipped birds (chapter I and II) and for the analysis of a correlation between dive depth and dive duration (chapter V).

The LME's and GLMM's use specified mixtures of fixed effects and random effects and allow for the specification of correlation structure amongst the explanatory variables and autocorrelation of the response variable. In addition, GLMM's allow for non-normal errors and non-constant variance (Crawley 2007; Faraway 2006) and take into account the variance between repeated measurements of the same individual. For most of the analyses in chapters II, III and IV I used GLMM's as well as the LME for the analysis of the comparison of the trip duration of nocturnal flights between the pre-breeding and breeding season (chapter II).

The GAM blends the properties of GLM's with additive models (Hastie and Tibshirani 1990; Wood 2006). It is the sum of different submodels of which each submodel analyses the relationship between the predictive and the random variable.

In this thesis GAM's were used to relate foraging areas with environmental factors like water depth, chlorophyll a or sea surface temperature (chapter II) and to analyze dive depth distribution during the daily cycle (chapter III).

Chapter I



***GPS tracking devices reveal foraging strategies of Black-legged
Kittiwakes***

GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes

Abstract

The Black-legged Kittiwake *Rissa tridactyla* is the most abundant gull species in the world, but some populations have declined in recent years, apparently due to food shortage. Kittiwakes are surface feeders and thus can compensate for low food availability only by increasing their foraging range and/or devoting more time to foraging. The species is widely studied in many respects, but long-distance foraging and the limitations of conventional radio telemetry have kept its foraging behaviour largely out of view. The development of Global Positioning System (GPS) loggers is advancing rapidly. With devices as small as 8 g now available, it is possible to use this technology for tracking relatively small species of oceanic birds like kittiwakes. Here we present the first results of GPS telemetry applied to Black-legged Kittiwakes in 2007 in the North Pacific. All but one individual foraged in the neritic zone north of the island. Three birds performed foraging trips only close to the colony (within 13 km), while six birds had foraging ranges averaging about 40 km. The maximum foraging range was 59 km, and the maximum distance traveled was 165 km. Maximum trip duration was 17 h (mean 8 h). An apparently bimodal distribution of foraging ranges affords new insight on the variable foraging behaviour of Black-legged Kittiwakes. Our successful deployment of GPS loggers on kittiwakes holds much promise for telemetry studies on many other bird species of similar size and provides an incentive for applying this new approach for further studies.

Keywords: Black-legged Kittiwake, foraging, Gulf of Alaska, *Rissa tridactyla*, telemetry

Introduction

Seabirds spend most of their time at sea and are difficult to observe when not attending nests during breeding. Research is therefore biased toward land-based observations, with the at-sea biology of smaller species generally limited to counts of travelling and foraging birds from research vessels. Such studies are time- or area-restricted and unable to provide detailed insights into the foraging behaviour of individuals (Weimerskirch et al. 2005). However, knowledge of foraging behaviour is essential to an understanding of both the ecological roles of seabirds and the constraints acting upon them in marine ecosystems (Monaghan 1996; Wilson et al. 2002). The most productive and cost-effective way to study the flight and foraging behaviour of birds at sea makes use of electronic devices attached to individuals (Daunt et al. 2003; Garthe et al. 2007; Grémillet et al. 2004b; Wilson et al. 2002). A variety of loggers and techniques have been developed in the last 40 years (Grémillet et al. 2000; Hamer et al. 2007; Weimerskirch and Wilson 2000). The newest tracking devices to come on line are Global Positioning System (GPS) receivers, which are unlimited in range and capable of much higher resolution and accuracy than satellite transmitters or conventional radio telemetry (Hulbert and French 2001; Hünerbein et al. 2000). As with most new technologies, the first GPS data loggers were too heavy to deploy on all but very large-bodied seabirds such as albatrosses (Diomedidae; (Waugh et al. 2005; Weimerskirch et al. 2002) and gannets (Sulidae; (Grémillet et al. 2004b). The latest equipment, with package sizes in the range of 8 – 12 g, bring small and medium-sized seabirds (approx. ≥ 300 g) into the scope of possible applications.

Black-legged Kittiwakes (*Rissa tridactyla*), widely distributed in north temperate to arctic regions of the northern hemisphere, are the most abundant and one of the most thoroughly studied gull species in the world (Hatch et al. 2009). Detailed knowledge of foraging ecology is still lacking, however, as the species is highly pelagic, especially in winter, and foraging activity is difficult to observe. Kittiwakes stay closer to the coast while breeding, returning frequently to their nests to change incubation duties or deliver food to their chicks (Daunt et al. 2002; Hatch et al. 2009; Suryan et al. 2000), but even then their foraging trips often take them out of range of telemetry techniques that rely on fixed receiving equipment (Camphuysen 2005; Wanless et al. 1992b). Kittiwake body mass averages about 430 g (Pacific) or 390 g (Atlantic) (Hatch et al. 2009), thus telemetry

devices exceeding 20 g (approx. 5% of their body weight) are not recommended (Caccamise and Hedin 1985; Calvo and Furness 1992; Phillips et al. 2003).

Kittiwakes are regarded as useful indicators of marine environmental change in the North Atlantic and North Pacific oceans (Frederiksen et al. 2007; Gill et al. 2002; Wanless et al. 2007). Many colonies have declined in numbers and productivity during the last 20 – 30 years (Daunt et al. 2002; Hatch et al. 2009), probably because of reduced availability of their principal food — small, schooling fish such as sand lance *Ammodytes* spp., capelin *Mallotus villosus*, and juvenile cods (Gadidae) (Frederiksen et al. 2008; Harris and Wanless 1990; Hatch et al. 1993b; Suryan et al. 2006), which they capture by dipping or surface plunging (del Hoyo et al. 1996; Hatch et al. 2009). As obligate surface feeders, kittiwakes are affected by changes in both the abundance and vertical distribution of their food (Furness and Tasker 2000; Hatch et al. 1993b). Breeding kittiwakes may compensate for food shortage by spending more time foraging and/or ranging farther from the colony, although this behaviour could have disadvantages, such as a higher vulnerability to nest site competition and increased predation on eggs or chicks.

Here we report on the first use of miniature GPS data loggers to characterize the foraging behaviour of Black-legged Kittiwakes. The work was conducted during the breeding season of 2007 on Middleton Island in the north-central Gulf of Alaska, where population monitoring and studies of breeding ecology, behaviour, and physiology have been carried out since the mid 1970s (Gill et al. 2002; Hatch et al. 1993a; Hatch et al. 1993b; Roberts and Hatch 1993). Data on foraging trip durations from this colony are available from one prior study (Roberts and Hatch 1993) that employed direct observations of nest attendance in 1988, when the colony was much larger than it is at present. There is concern about the status and viability of this colony, which has declined by more than 90% — from 83,000 pairs to 6,200 pairs — over the last 26 years (Hatch et al. 2009). Understanding the decline will require a thorough understanding of the birds' foraging habits, both during and outside the breeding season. In turn, knowledge of their foraging habits could reveal possible food shortness caused, for example, by competition with other seabird species, oceanographic anomalies and/or fishing activities.

Methods

Middleton Island (59.4° N, 146.3° W) is close to the steep submarine terrain of the continental slope (about 10 – 15 km south) and faces a broad expanse of unsheltered continental shelf to the north (Fig. 1.1). Thus, both neritic and deep ocean habitats are readily available to breeding kittiwakes.

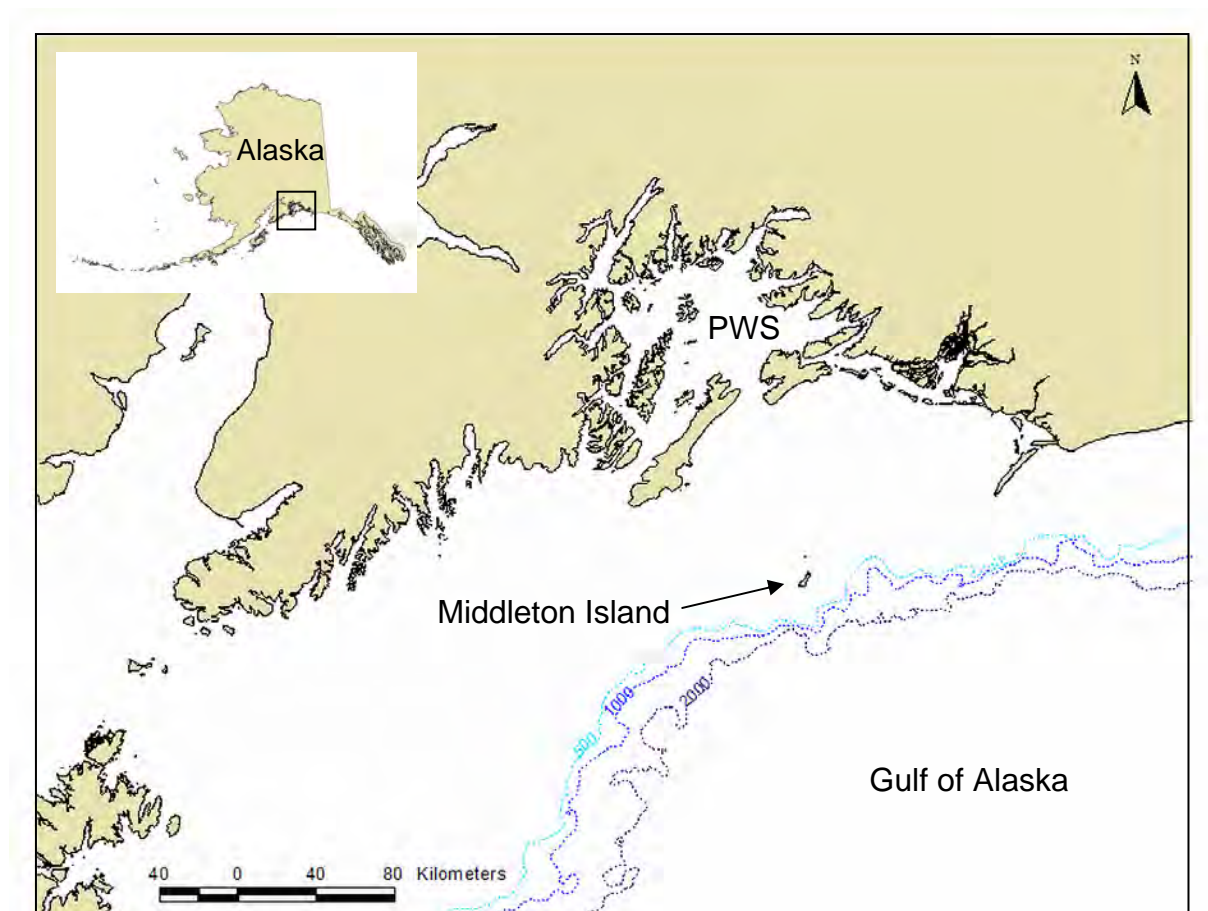


Figure 1.1. Study area in the Gulf of Alaska showing the locations of Middleton Island and Prince William Sound (PWS). Middleton lies about 80 km south of the Alaska mainland. Depth contours indicate the position of the continental slope.

Kittiwakes sampled in the study nested on a U.S. Air Force radar tower, decommissioned and derelict since the 1960s, on which artificial nest sites have been constructed for research purposes. The tower supported 910 nesting pairs in 2007, most using wooden ledges viewable from inside the building through sliding panes of one-way

mirror glass (Gill and Hatch 2002). Birds were snared around the leg with a wire hook passed through a slot in the wall beneath each window. Individuals chosen for logger deployment were actively incubating or rearing chicks. Chick-rearing birds had one or two chicks aged 1 – 40 days. All birds in the study were marked with a unique combination of steel and plastic colour bands for individual recognition. Every nest was checked each morning for egg or chick status and for the presence of adult birds.

Tracking devices were deployed between 1 July and 11 August 2007. We captured 14 adult kittiwakes and deployed GiPSy[®] data loggers (11 g; L 50 x W 22 x H 10 mm) manufactured by TechnoSmart (Rome, Italy). The loggers were programmed to use a 5-min sampling interval. The GPS data stored in the device memory and used for the analysis included date, time, latitude, longitude and speed. The devices were attached to feathers in the middle of the back with TESA[®] tape (Wilson et al. 1997). Before deployment, each bird was weighed to the nearest 5 g using a spring balance. The loggers were 2 – 3 % of mean body mass (397 g, range 345 – 500 g). Mass was the only measurement taken upon first capture to minimize handling time, and additional measurements (bill length, head-bill length, wing length) and banding were taken upon recapture if data were not already available from previous studies. The measurements were used to determine the sex of the birds (Jodice et al. 2000). Handling time (capture to release) was approximately 10 min for deployment and 3 – 15 min for logger removal, banding and measurements as needed. In 28 captures and recaptures, 15 birds returned to their nest within 15 min (five of them immediately), four birds within 31 min, and three birds more than 1 h after capture. The return time for six birds was undetermined due to a lack of nest observations. We deployed 12 of the 14 loggers in the late afternoon or evening, which allowed us to potentially capture information on nighttime foraging. A total of 106 unmanipulated nests on the tower were used as a control group to compare breeding success between equipped and non-equipped birds.

Flight paths were plotted in ArcView[®] 3.2 (ESRI, Redlands, CA) from the positional data obtained. Maximum foraging range was defined as the most distant position in a straight line from the colony. Distance travelled refers to the summed distances between positions from start to end locations of each foraging trip. The elapsed time from start to end of a trip is trip duration. Start and end of a trip were defined using GPS data. Trips started when a positional fix was 300 m away from the colony and subsequent positions were progressively farther away. In calculating mean velocity

(ground speed), we used only flight speeds greater than $10 \text{ km}\cdot\text{h}^{-1}$, excluding one outlier of $119 \text{ km}\cdot\text{h}^{-1}$. Speeds $< 10 \text{ km}\cdot\text{h}^{-1}$ were probably associated with swimming or feeding (Weimerskirch et al. 2006).

Loggers were switched on at deployment — no delayed start was possible — and due to battery depletion or occasional large gaps in data collection, not all foraging trips were well documented from start to finish. In calculating the mean maximum range, mean distance to colony and mean trip duration, we included only complete trips, but estimated values are also reported for individual trips that were incomplete. The missing portion of a track line was extrapolated directly back to the colony, which underestimates the distance travelled by an unknown, but probably by a modest amount. Extrapolated track lines were then used to correct the trip duration of incomplete trips using a mean flight speed of $33 \text{ km}\cdot\text{h}^{-1}$ (as measured in this study; see below). Statistical analyses were carried out in R 2.8.0. (Foundation for Statistical Computing, Vienna, Austria) and SPSS ver. 11.5 (SPSS, Chicago, IL).

Results

All 14 instrumented birds were recaptured after 1 – 7 days. Two birds had shed the logger by pulling out the feathers to which it was attached, although we did not observe the birds pecking at or trying to remove the logger. Two loggers failed to record data for unknown reasons. Among the remaining sample of ten kittiwakes, one bird incubated for nearly 2 days, thus depleting its logger battery before leaving the nest. We therefore used data from nine successful deployments (five females, four males) for our analysis of foraging patterns.

We obtained data for 16 foraging trips, seven of which were complete (Table 1.1). Four birds made one foraging trip, three made two trips and two birds made three foraging trips during the working period of the logger. Loggers recorded between 24 and 626 positional fixes within a foraging trip (mean 123, standard deviation (SD) 144).

The main foraging area was north of the colony, encompassing the continental shelf area between Middleton Island and Prince William Sound (Fig. 1.2). Birds stayed mostly over waters $< 200 \text{ m}$ deep. One bird made repeated visits to the shelf slope south and east of the island but did not access the abyssal zone beyond (Fig. 1.2a, 1.2c). One

bird visited the nearshore area of Hinchinbrook Island at the entrance to Prince William Sound, 92 km from Middleton (Fig. 1.2a, 1.2b).

On nine of the 16 foraging trips, which we categorize as “short” trips, kittiwakes stayed within 13 km of the breeding site (see examples in Fig. 1.2c); this is in contrast to the remaining 7 trips, which were categorized as “long” trips (see examples in Fig. 1.2b) that exceeded 35 km from the colony (Fig. 1.3). Among the completed trips, the maximum range from the colony was 59 km, with a mean foraging range of 25.5 km (SD 22.2 km). However, one incomplete trip had a maximum range from the colony of at least 91.8 km (Table. 1.2). The maximum total distance travelled by a kittiwake on a completed trip was 164.7 km (mean 72.5 km, SD 58.4 km). When incomplete trips are taken into account the total maximum distance travelled per trip was at least 306.3 km.

Table 1.1. Summary of deployments of GPS data loggers attached to Black-legged Kittiwakes on Middleton Island, Alaska during the breeding season in 2007.

Bird no.	Nest	Sex	Brood stage	Date		No. of trips	
				Deployment	Recapture	Complete	Incomplete
1	D-15	Female	Incubating	02 July	04 July	Battery empty before bird left the nest	
2	B-10	Male	Incubating	05 July	10 July	0	1
3	B-6	Male	Incubating	08 July	10 July	0	2
4	D-15	Male	Incubating/chick rearing	11 July	14 July	No data recorded	
5	B-14	Female	Chick rearing	11 July	14 July	No data recorded	
6	D-17	Female	Chick rearing	14 July	16 July	1	2
7	B-16	Female	Chick rearing	14 July	17 July	Logger lost	
8	D-4	Male	Chick rearing	17 July	18 July	1	0
9	D-13	Male	Chick rearing	19 July	20 July	1	0
10	B-4	Female	Chick rearing	21 July	23 July	1	1
11	D-3	Female	Chick rearing	25 July	27 July	1	1
12	D-2	Female	Chick rearing	27 July	28 July	0	1
13	B-4	Male	Chick rearing	29 July	05 August	Logger lost	
14	C-1	Female	Chick rearing	08 August	11 August	2	1

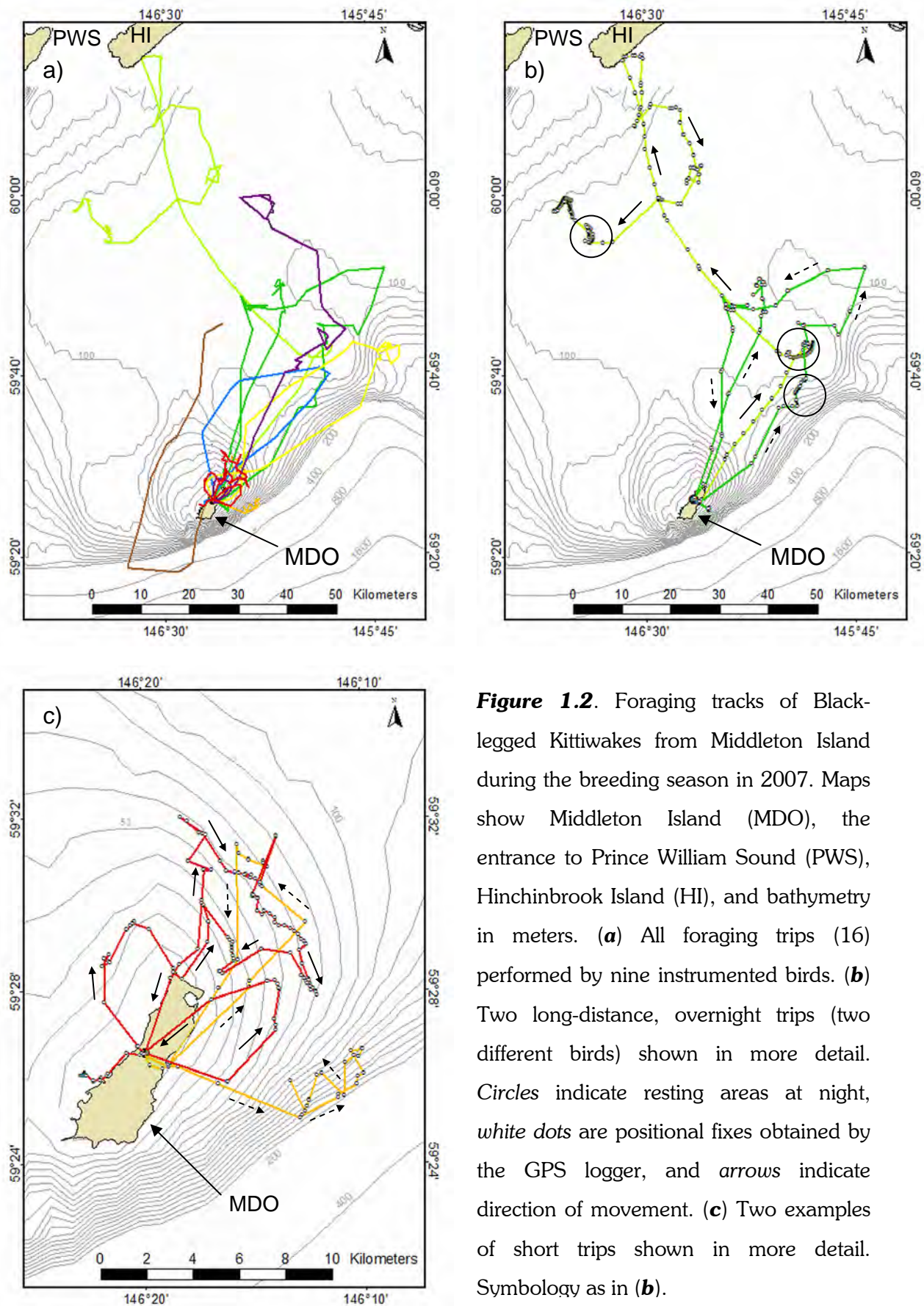


Figure 1.2. Foraging tracks of Black-legged Kittiwakes from Middleton Island during the breeding season in 2007. Maps show Middleton Island (MDO), the entrance to Prince William Sound (PWS), Hinchinbrook Island (HI), and bathymetry in meters. **(a)** All foraging trips (16) performed by nine instrumented birds. **(b)** Two long-distance, overnight trips (two different birds) shown in more detail. Circles indicate resting areas at night, white dots are positional fixes obtained by the GPS logger, and arrows indicate direction of movement. **(c)** Two examples of short trips shown in more detail. Symbolry as in **(b)**.

Trip duration varied from 1.5 h to 16.8 h (mean 7.9 h, SD 5.8 h) for complete trips, whereas one incomplete trip exceeded 33 h. We found a positive relationship between trip duration and total distance travelled per foraging trip for complete trips (Spearman's $r_s = 0.835$, $P < 0.01$) but found no significant relationship between foraging trip duration and maximum distance to colony. Because of the small sample size of complete foraging trips, statistical tests between males and females were not applicable.

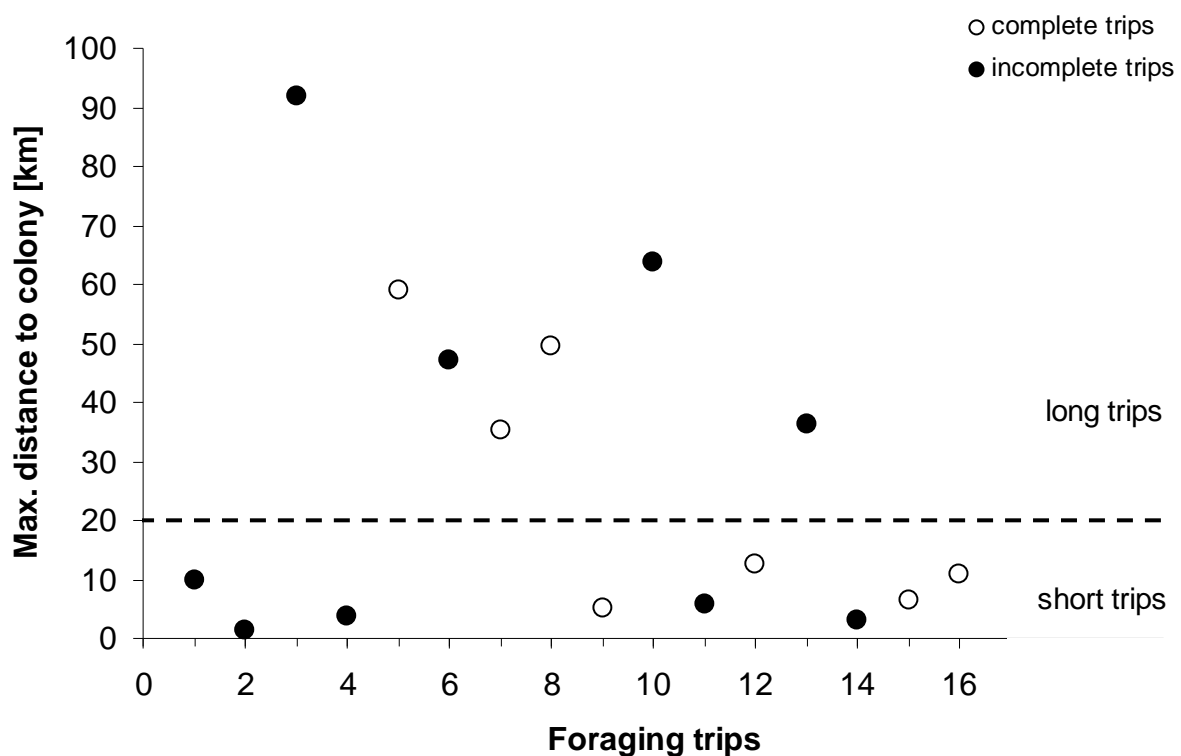


Figure 1.3. Maximum foraging distances (km) for all recorded foraging trips from Middleton Island in 2007, sorted chronologically.

Most trips occurred solely during daylight, but overnight trips were conducted by one female and two males. In one instance, the bird appeared to spend the night in or near another portion of the colony on Middleton, whereas two overnight trips likely entailed foraging, as the birds travelled far from the colony (Table 1.2). Nonetheless, the birds were mostly inactive at night, as indicated by rates of movement $< 10 \text{ km}\cdot\text{h}^{-1}$ (Fig. 1.2b).

Table 1.2. Foraging behaviour of Black-legged Kittiwakes from Middleton Island, Alaska during the breeding season in 2007.

Bird no.	Sex	Brood stage	Trip duration (h)	Range ^a (km)	Total distance travelled ^b (km)	Complete/incomplete ^c	Diel period of trip ^d
2	male	incubating	6.5	9.8	51.2	Incomplete	d
3	male	incubating	2.1	1.4	3.9	Incomplete	d
			33.0	91.8	306.3	Incomplete	n
6	female	chick rearing	2.5	3.8	9.7	Incomplete	d
			12.8	59.0	164.7	Complete	n
			4.6	47.2	100.5	Incomplete	d
8	male	chick rearing	16.8	35.2	92.5	Complete	n
9	male	chick rearing	7.2	49.5	129.7	Complete	d
10	female	chick rearing	2.1	4.9	14.7	Complete	d
			8.8	63.6	179.0	Incomplete	d
11	female	chick rearing	3.8	5.6	18.7	Incomplete	d
			4.2	12.5	35.0	Complete	d
12	female	chick rearing	6.9	36.1	121.4	Incomplete	d
14	female	chick rearing	4.1	3.0	6.7	Incomplete	d
			1.5	6.4	15.5	Complete	d
			10.4	10.9	55.4	Complete	d

^a Range indicates maximum straight-line distance from the colony

^b Total distance travelled is distance covered during one foraging trip

^c Complete/incomplete indicates whether the whole trip was recorded from nest-leaving through to return to the colony

^d Diel period distinguishes overnight only trips (n) and day only trips (d)

Mean flight speed during foraging trips was $33 \text{ km}\cdot\text{h}^{-1}$ (maximum $87 \text{ km}\cdot\text{h}^{-1}$, SD $13 \text{ km}\cdot\text{h}^{-1}$) (Fig. 1.4). Kittiwakes spent only about a third (35%) of their foraging trips engaged in sustained directional flight. The remaining 65% of the time budget consisted of periods of inactivity or other behaviours not characterized by directional flight (speeds $< 10 \text{ km}\cdot\text{h}^{-1}$).

We found no evidence that GPS loggers influenced breeding performance of the subjects. Breeding success (number of chicks fledged/number of eggs laid) of instrumented birds (0.5) was similar to that of controls (0.44) and there were no differences in mean chick mass between groups at three stages of development: newly hatched chicks, mid-chick stage or chicks near fledging (Table 1.3).

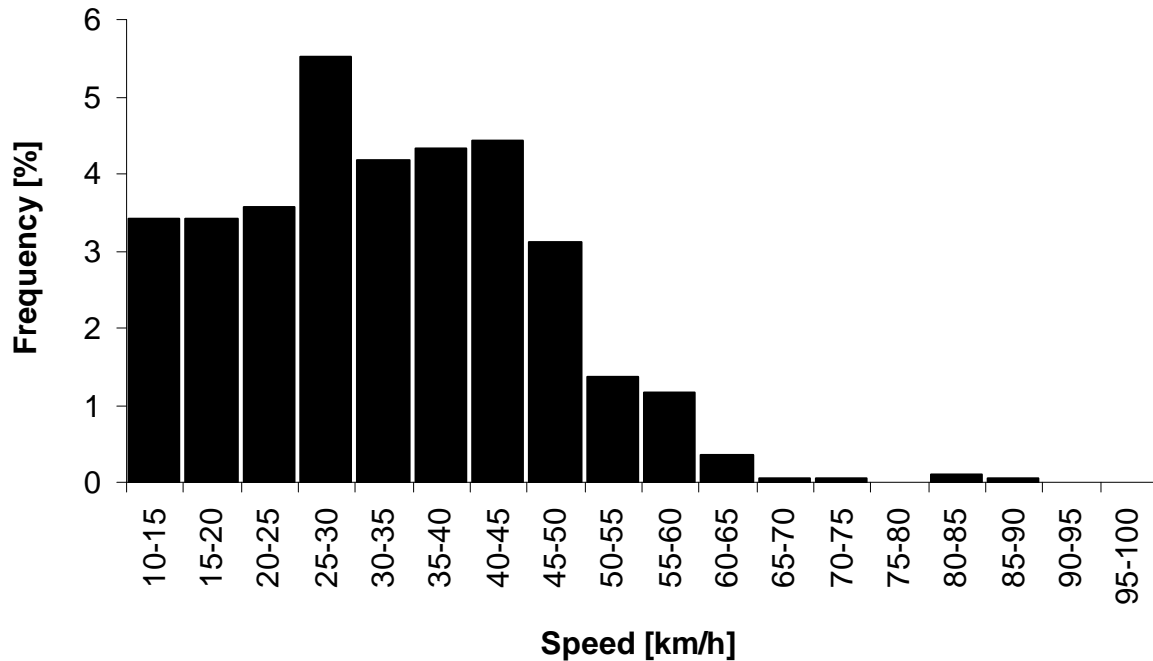


Figure 1.4. Flight speeds of Black-legged Kittiwakes from Middleton Island recorded by GPS data loggers during the breeding season in 2007. Flight speeds $\leq 10 \text{ km}\cdot\text{h}^{-1}$ are not depicted for reasons explained in the text.

Table 1.3. Comparison of breeding success (number of chicks/number of eggs laid) and chick growth at three stages of development between logger-equipped Black-legged Kittiwakes and non-equipped birds in 2007 on Middleton Island, Alaska.

	Logger birds	Non-equipped birds	Statistics (GLM)
No. chicks / no. eggs laid	0.5 (n=13)	0.4 (n=95)	t = 0.617, P = 0.538
Mean chick mass, g (0 days)	36.5 (n=16)	35.7 (n=85)	t = 0.664, P = 0.508
Mean chick mass, g (20 days)	300.3 (n=12)	319.3 (n=75)	t = 1.107, P = 0.271
Mean chick mass, g (35 days)	413.9 (n=8)	422.0 (n=69)	t = -0.538, P = 0.592

Numbers in parentheses are sample sizes

Discussion

Foraging patterns were highly variable among Black-legged Kittiwakes sampled on Middleton Island in 2007, with a tendency towards bimodality in the distances travelled on foraging trips. The longest and most far-ranging excursions were overnight trips, but even day trips tended to range either < 10 km or > 40 km from the island. It may be that shorter trips were used for chick-provisioning, while the longer trips were important for self-feeding by adults, as has been suggested for chick-rearing Procellariiformes (Congdon et al. 2005; Weimerskirch et al. 2001). Further study is needed to confirm this possibility in kittiwakes. The disjunct distribution of foraging distances could also reflect prey distribution, as the main prey of kittiwakes during chick rearing on Middleton, capelin and sand lance (Gill and Hatch 2002), may be available at different distances from the island.

Foraging trips that included a night at sea generally lasted much longer than the trips performed only during daylight (Coulson and Johnson 1993; Hamer et al. 1993; Roberts and Hatch 1993). The importance of nighttime foraging was noted on Middleton in 1988, when 62% of overnight trips resulted in chick feeding upon return of the adult, while 35% of daytime absences resulted in chick-feeding (Roberts and Hatch 1993). Overnight trips may in general access distant foraging areas. Two of three overnight trips recorded in 2007 were among the three most distant trips. Among birds tracked at night, the recorded flight speeds < 10 km·h⁻¹ indicated that hours of darkness were often spent in relative inactivity, probably drifting on the surface, as was also observed by (Hamer et al. 1993) in Shetland. However, birds “on water” might also engage in feeding by picking up small prey items, such as euphausiids or polychaetes, likely available at the surface at night.

Foraging ranges of breeding kittiwakes are variable from one location to another. Ranges (\pm SE) of 41 ± 3 km (Shoup Bay), 26 ± 5 km (Icy Bay), and 21 ± 5 km (Eleanor Island) were reported for three colonies in Prince William Sound (Ainley et al. 2003), with the maximum foraging distance from the Shoup Bay colony was 120 km (Suryan et al. 2000). Values reported here for Middleton Island (mean range of all trips 26 km, maximum 59 km) are intermediate compared to those for Prince William Sound, whereas a study using radio telemetry in the UK (Sumburgh Head, Shetland) in 1990 found that kittiwakes usually travelled more than 40 km from the colony, beyond the

range of the receiving equipment (Wanless et al. 1992b). In the following year, more than 95% of foraging trips stayed within 5 km of the Sumburgh Head colony, a reversal attributed to improved food availability (Hamer et al. 1993). Elsewhere in the UK, maximum ranges of 73 ± 9 km from the Isle of May and 55.5 km from the Farne Islands were estimated from flight duration and speed (Daunt et al. 2002; Pearson 1968). Kittiwakes breeding at Helgoland in the German Bight were observed at a distance of 10 – 35 km from the colony (aerial and ship based transect counts), with only single birds observed at distances up to 70 – 80 km (Dierschke et al. 2004). Those relatively short foraging distances may be explained by low competition for prey — good feeding conditions around the island, small size of the colony, and the isolation of the colony from others of the same species.

Our mean trip duration (7.9 h) was longer than that observed by Roberts and Hatch (1993) on Middleton Island in 1988 (mean 4.1 h for daytime trips that culminated in chick-feeding). Shorter trips have also been reported from other colonies in Alaska and in the UK. Mean trip durations of 3.4 – 6 h were found among kittiwakes in Prince William Sound (Ainley et al. 2003; Suryan et al. 2000), kittiwakes from the Isle of May spent 6.1 h (Humphreys et al. 2006) and 5.5 h (Daunt et al. 2002) at sea, and foraging trips were shorter still in two other Scottish colonies — 3.4 h (Hamer et al. 1993) and 2.8 h (Coulson and Johnson 1993). However, trip durations averaged > 6 h during a year of reduced prey availability (Hamer et al. 1993; Wanless et al. 1992b). Our mean trip duration of nearly 8 h therefore suggests poor food availability near Middleton Island in 2007. Flexible time budgets, as a means of coping with low food availability, are also known from other colonies of kittiwakes and murre (*Uria lomvia* and *U. aalge*) in Alaska (Harding et al. 2007; Kitaysky et al. 2000).

With one exception, kittiwakes foraged only in a northerly direction from the colony, over the continental shelf and within the 200 m depth contour. We expected the shelf edge, a potentially rich feeding habitat close to the island, to be a greater attraction than it was. However, upwelling along the shelf edge is not as strong in summer as in winter (Weingartner et al. 2005), which may explain the absence of kittiwakes in that area during July and August. Observations on the composition of the diet suggest a different situation in April, prior to egg-laying. Prey regurgitated by kittiwakes in the first several weeks after returning to Middleton Island in the spring consist mostly of lanternfishes (Myctophidae) and small squids (S. A. Hatch, unpubl. data). The birds

presumably obtain this prey from the deep ocean habitat of the continental slope and abyssal ocean south of the island. Myctophids and squids are important components of the mesopelagic community that migrate vertically to the ocean surface at night (Beamish et al. 1999; Sinclair and Stabeno 2002). Myctophids, in particular, are high-energy prey (Van Pelt et al. 1997) whose availability to kittiwakes before and during early breeding stages on Middleton is thought to influence breeding success (Gill and Hatch 2002). Such prey are seen also during the incubation period in some years (Gill and Hatch 2002). In this study, we sampled two birds late in the incubation period, one of which went to the shelf edge east of Middleton while the other made the most distant foraging trip observed, on a northwesterly heading to Hinchinbrook Island. More sampling is needed to clarify the relative importance and seasonality of deep ocean versus neritic foraging by kittiwakes from Middleton.

Pennycuik (1987; 1997) and Götmark (1980) observed air speeds for kittiwakes of about 47 and 54 km·h⁻¹, respectively. Our observed mean flight speed of 33 km·h⁻¹ was therefore lower than those speeds and matches better with the minimum power speed of Pennycuik (1987; 1997). However, flight speeds varied greatly during foraging trips. Speed of flight to and from foraging areas ranged from about 20 – 60 km·h⁻¹, while birds searching for food had flight speeds up to 20 km·h⁻¹. It seems that birds changed between minimum power and maximum range speeds (Pennycuik 1987, 1997) while flying to and coming back from foraging areas. Whether this behaviour was weather dependent should be investigated.

In conclusion, we affirm the utility of GPS data loggers in elucidating the movements and marine habitat use of seabirds previously excluded from such investigations because of their small body size. Kittiwakes exhibited flexible foraging behaviour — short and long foraging trips that appeared to change in relative frequencies over the course of chick rearing. Although our sample was limited to 16 foraging trips, only seven of which complete, we gained much insight into the foraging behaviour of Black-legged Kittiwakes from Middleton Island. Nearly all foraging trips were over the continental shelf, in northerly direction of the colony. Thus, we believe the sample typifies the behaviour of most birds in this colony, but further investigations are desirable. Interannual and within-season variation have yet to be fully investigated.

Future applications of this powerful new technology promise many valuable insights on the foraging strategies of kittiwakes and other oceanic birds of similar size.

GPS data loggers are able to track seabirds at distances from the colony that are out of range of conventional radio telemetry. In addition, they are unaffected by weather conditions, an important constraint on ship or aerial transect counts.

Zusammenfassung

GPS-Logger offenbaren Nahrungssuchstrategien der Dreizehenmöwen

Die Dreizehenmöwe (*Rissa tridactyla*) ist die weltweit häufigste Möwenart, aber viele Populationen haben in den letzten Jahren abgenommen, was vermutlich auf Nahrungsverknappung zurückzuführen ist. Dreizehenmöwen suchen ihre Nahrung an der Wasseroberfläche und können deshalb geringe Nahrungsverfügbarkeit nur durch ein Ausweiten ihres Nahrungssuchgebietes und/oder einen erhöhten Zeitaufwand kompensieren. Diese Möwenart ist schon in vielen Aspekten ihrer Biologie untersucht worden, aber durch ihre weiten Nahrungssuchflüge und die Einschränkungen durch die konventionelle Radiotelemetrie konnten diesen Aktivitäten bisher nur wenig untersucht werden. Die Entwicklung von GPS-Loggern schreitet schnell voran. Mit neuen Geräten, die nur noch 8 g wiegen, ist es jetzt auch möglich relativ kleine Seevogelarten, wie die Dreizehenmöwe, mit dieser Technologie auszustatten und zu untersuchen. Hier präsentieren wir erste Ergebnisse der GPS-Loggereinsätze auf Dreizehenmöwen aus dem Jahr 2007 aus dem Nordpazifik. Mit Ausnahme von einem Tier sind alle Vögel in der neritischen Zone nördlich der Insel auf Nahrungssuche gegangen. Drei Vögel suchten nur in unmittelbarer Nähe zur Kolonie (< 13 km) nach Nahrung, während sechs weitere Tiere eine durchschnittliche Entfernung von 40 km zeigten. Die maximale Entfernung zur Kolonie betrug 59 km und die maximale zurückgelegte Distanz während eines Nahrungssuchfluges betrug 165 km. Der längste Nahrungssuchflug dauerte 17 h (Mittelwert: 8 h). Die maximalen Distanzen zur Kolonie der Nahrungssuchflüge machen eine bimodale Verteilung sichtbar, was neue Einsichten in das variable Nahrungssuchverhalten von Dreizehenmöwen liefert. Die erfolgreiche Ausstattung von Dreizehenmöwen mit GPS-Loggern verspricht auch Erfolg mit Telemetriestudien bei vielen anderen Arten ähnlicher Größe und gibt neue Ansätze für weitere Untersuchungen

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Chapter II



Contrasting foraging strategies of Black-legged Kittiwakes between pre-breeding and breeding and their relationship to oceanography

Contrasting foraging strategies of Black-legged Kittiwakes between pre-breeding and breeding and their relationship to oceanography

Abstract

The spatial distribution of seabirds is determined by different environmental and ecological factors. Regions with high primary productivity usually support high abundances of higher trophic levels like fishes, seabirds or marine mammals. The North Pacific is a highly productive regime, along the eastern Bering Sea and the Gulf of Alaska support more than 27 million breeding seabirds. Despite the high productivity of these regions, the breeding success of Black-legged Kittiwakes (*Rissa tridactyla*) in the North Pacific is very low and many populations have declined dramatically in recent years. Therefore, detailed knowledge of their foraging strategies and feeding areas is urgently needed. During pre-breeding (April) and breeding (May – August) in 2008 miniaturised GPS-data loggers were deployed to adult Black-legged Kittiwakes on Middleton Island in the Gulf of Alaska to investigate their foraging behaviour. The results were set in relation to external remote sensing data in order to analyse the results regarding abiotic factors like sea surface temperatures or chlorophyll-a values. In early pre-breeding stage, when returning from their wintering areas in central Pacific, kittiwakes performed almost exclusively nocturnal foraging flights (95 %) in nearly always south-easterly direction of their colony to pelagic deep sea waters. Later during the breeding season they foraged only over continental shelf areas not deeper than 200 m, mainly during daytime. Nocturnal flights occurred only in 24 % of the trips. Nocturnal foraging trips during pre-breeding stage lasted longer than during breeding stage and all overnight trips lasted significantly longer than foraging trips during daytime. Foraging trip duration was significantly longer during the pre-breeding season than during the breeding season and kittiwakes travelled significantly farther from their colony site in April than later from May – August. There was no difference in total distance travelled per foraging trip between both breeding stages. Our results show that Black-legged Kittiwakes of the same colony performed very different foraging strategies during the different breeding stages. They probably alter, to some extent, their foraging behaviour with changing prey availability,

preying on fish species which are easier available. Additionally, foraging areas were not related to areas of high primary production that were identified by remote sensing measurements and which are often used to predict seabird distributions.

Therefore, understanding seabirds foraging ecology in detail is mandatory to study their foraging behaviour not only during the breeding season but also during the rest of the year as constraints acting upon them can occur in very large and distinct areas. Furthermore, predictions about relationships of seabird foraging areas with areas of high primary production should be established carefully since positive correlations do not necessarily exist.

Keywords: breeding season, Black-legged Kittiwake, foraging, Gulf of Alaska, pre-breeding season, remote sensing, *Rissa tridactyla*, GPS logger

Introduction

Spatial distribution patterns of seabirds are formed by different environmental and ecological factors. Many seabirds are highly mobile and forage on small schooling fish or zooplankton and thus should seek out foraging areas with high prey density (Fauchald 2009). Seabird prey is regulated by the availability of resources including nutrients, primary and secondary production. These, in turn, are driven by physical and oceanographic processes like currents, upwelling, fronts and associated vertical mixing and stratification. Consequently, seabirds should be found in areas with oceanographical conditions that favour high prey abundances (Becker and Beissinger 2003; Hunt 1991; Skov and Durinck 2000). However, only few studies could show strong positive correlations with prey species. In many cases only weak or even negative relationships between seabirds and prey species were found (see review in Fauchald 2009; e. g. Logerwell and Hargreaves 1996; Mehlum et al. 1996; Skov et al. 2000; Swartzman and Hunt 2000).

In studies of biological oceanography, marine phytoplankton is increasingly assumed to control higher trophic levels like seabirds, marine mammals and predatory fish, recognized as bottom-up control (Frank et al. 2007; Frederiksen et al. 2006; Stenseth et al. 2006). Nowadays, an increasing number of studies use remote sensing

data of sea surface temperatures and chlorophyll-*a* concentrations to estimate primary productivity. With the easy accessibility of these satellite data to the public community through the world wide web increasing numbers of seabird studies try to link seabird foraging areas to such primary productivity patterns obtained and estimated by satellite data of the marine environment (Catry et al. 2009; Freeman et al. 2010; Grémillet et al. 2008; Shaffer et al. 2009). Only few studies reveal the limitations of using remote sensing data to predict seabird foraging areas (Grémillet et al. 2008).

The identification of factors influencing reproductive success and population dynamics of a given species requires a thorough understanding of the species biology and ecology, including its foraging behaviour. In seabirds, most studies of the foraging behaviour with high spatial and temporal resolution focus on the foraging activities during the breeding season (Ito et al. 2010; Kappes et al. 2010; Kotzerka et al. 2010; Paiva et al. 2010b; Raymond et al. 2010). This is due to the inaccessibility of most seabird species during the non-breeding season, as seabirds typically spend most of this time at sea, mostly with extended periods far from land. Data on the foraging behaviour outside of the breeding season are limited and mainly of low spatial and temporal resolution due to the type of method, like ship based surveys (Holm and Burger 2002; Woodby 1984) and stable isotope analysis (Bond et al. 2010; Phillips et al. 2009), the type of logging devices, like satellite transmitters (Clarke et al. 2003; Hamer et al. 2007) or geolocation loggers (González-Solís et al. 2007; Harris et al. 2010), or due to low sampling frequencies in order to enable long periods (several months) of battery power.

Here we present, to our knowledge for the first time, detailed data about the foraging behaviour of a highly pelagic seabird species, the Black-legged Kittiwake (*Rissa tridactyla*), during the pre-breeding season using miniaturized GPS loggers with high spatial and temporal resolution. We compare these data with data of the following breeding season and analyze both seasons regarding remote sensing data of sea surface temperatures and chlorophyll-*a* contents.

The Black-legged Kittiwake is the most abundant gull species in the northern hemisphere, but many populations have declined dramatically during the last four decades (Daunt et al. 2002; Hatch et al. 2009). Especially breeding success in Alaskan colonies is very low and resulted in some seasons with complete failures (Hatch et al. 1993b). The main reason is considered to be food shortage. As breeding failures of kittiwakes occur at different stages during the breeding season – failures of nest building,

egg production and egg hatching, or chick losses (S. A. Hatch and V. A. Gill unpubl. data, Irons 1996; White et al. 2010) – it is crucial to understand the foraging behaviour at different breeding stages. On Middleton Island most failures occurred prior to chick rearing (Gill and Hatch 2002). Identifying factors that influence reproductive success and survival rates of a given species require an understanding of how factors (e. g. diet quality and quantity, winter/summer habitat condition) carry over and interact between different seasons (Gill et al. 2001; Gill and Hatch 2002; Norris 2005; Webster et al. 2002). Therefore, we investigated the foraging behaviour of Black-legged Kittiwakes during different breeding stages (pre-breeding and breeding) using GPS loggers and tried to link the results to abiotic factors. The results should allow for a better understanding of their foraging ecology in general and for pointing out factors that may influence their breeding success.

Methods

Study site. This study was conducted on Middleton Island in the Gulf of Alaska (59.4 N, 146.3 W). The island is close to the steep submarine terrain of the continental slope (about 10–15 km south) and a broad continental shelf area in northern direction of the island (Fig. 2.1). Thus, kittiwakes were potentially able to forage both over neritic and deep ocean waters.

During our study period from April – August 2008 we deployed a total number of 50 GPS-loggers to Black-legged Kittiwakes attempting to breed or breeding at the island. We defined pre-breeding as the time between the birds' return from their wintering areas in central Pacific and their start of nest building (April), and breeding as the time after beginning of nest building through to chick-rearing (May – August). Kittiwakes were caught at artificial nest sites on an abandoned U.S. Air Force radar tower. Wooden ledges are constructed to the upper level of the tower and are fitted with sliding panes of one-way mirror glass (Gill and Hatch 2002).

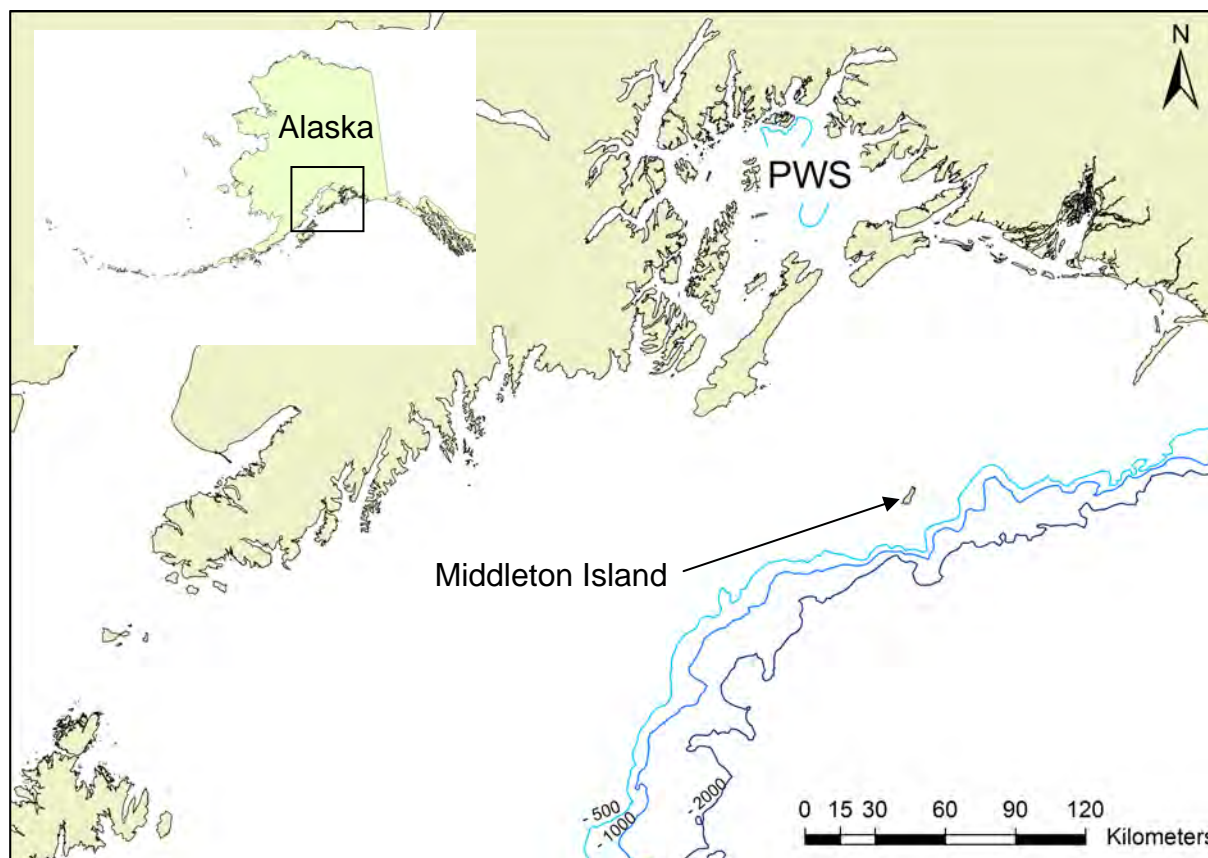


Figure 2.1. Study area in the Gulf of Alaska showing the locations of Middleton Island and Prince William Sound (PWS). Middleton Island is located about 80 km south of the Alaska mainland. Depth contours indicate the position of the continental slope.

Logger deployment. We deployed GiPSy[®] data loggers (11 g; L 50 x W 22 x H 10 mm) manufactured by TechnoSmart (Rome, Italy) to adult Black-legged Kittiwakes. The loggers were 2 – 3 % of the mean body mass (430 g, range 350 – 530 g) and thus should not have had deleterious effects on the birds (Phillips et al. 2003). The loggers were programmed for a 10-min sampling interval during the pre-breeding season and a 5-min sampling interval during the breeding season, respectively. The GPS data stored in the device memory and used for the analysis included date, time, latitude, longitude and speed. Devices were attached to the four central tail feathers using two cable ties.

Upon capture and recapture, each bird was weighed to the nearest 5 g using a spring balance. In order to minimize handling time and to reduce stress body mass was the only measurement taken upon first capture. If the chosen birds were already banded during previous studies, no further measurements were taken. Otherwise, additional measurements (bill length, head-bill length, wing length) and banding were performed

upon recapture. Sex of the equipped birds was determined by using body measurements (Jodice et al. 2000). Logger deployment (capture to release) took on average 5 min (range 3 – 15 min). Birds were recaptured after 1 – 17 days. As devices can have negative effects on the birds' breeding performance (Paredes et al. 2005; Phillips et al. 2003; Whidden et al. 2007) we compared breeding success between equipped and non-equipped birds. We used 108 unmanipulated nests of the tower as a control group.

Environmental data. Remote sensing data as sea surface temperature (hereafter SST, in °C) and chlorophyll-*a* concentration (hereafter chl-*a*, in mg m⁻³) as well as bathymetric data (hereafter depth, in m) were used to characterize the environment around the Black-legged Kittiwake colony on Middleton Island. We downloaded SST and chl-*a* values as ASCII files from <http://reason.gsfc.nasa.gov/Giovanni/> for time (date) intervals corresponding to deployment dates for a grid between 57.5° – 61° N and 146° – 150° W. Sea surface temperatures were chosen from Aqua MODIS and chlorophyll-*a* concentrations were chosen from SeaWiFS or Aqua MODIS (depending on availability of data, with priority of SeaWiFS due to higher temporal resolution). Data were downloaded at the smallest temporal resolution available, with either 8-day (SeaWiFS, chl-*a*) or monthly (Aqua MODIS, chl-*a* and SST) temporal resolution. If one 8-day data set was insufficient in covering the chosen grid area, two 8-day data sets were pooled to assure adequate coverage of the grid. Both SST and chl-*a* data had a spatial resolution of 0,1° (appr. 9 km). Grid cells with invalid data (e.g. due to cloud cover) were removed for both SST and chl-*a* data sets (values = 65535.0).

For further analyses we converted SST, chl-*a* and bathymetric files to raster data of 0.1° by interpolation using the X-Tools Pro® extension 6.2.1 (Data East, Russia) in ArcGIS® 9.2 (ESRI, Redlands, CA). From these raster data we used a sub sample with a radius of 200 km (based on the maximum foraging range of 159 km as measured in this study) around the breeding colony to relate these data to the foraging behaviour of Black-legged Kittiwakes.

Data analysis. Positional data from GPS-loggers were used to plot foraging tracks in ArcGIS® 9.2. Start and end of a trip were defined using the GPS data. To compare the foraging behaviour between the pre-breeding and breeding season we calculated descriptive statistics as maximum foraging range, total distance travelled per foraging trip

and foraging trip duration. Maximum foraging range was defined as the most distant position in a straight line from the colony. Total distance travelled corresponds to the summed linear distances between successive positions from the start to the end of each foraging trip. The elapsed time between the last location in the colony before departure and the first location at arrival is defined as trip duration.

Due to early battery depletion of some loggers or occasional large gaps in GPS data collection, 38 % of all tracks (including non-foraging trips) were incompletely recorded from start to end. Thus, we included only complete trips to calculate the mean total distance travelled per trip and mean trip duration. We excluded trips, which were only to the adjacent beach or tidal lagoons from the analysis. These places are known to be used for roosting, preening or socializing by personal observations and are thus probably not used for foraging. In Hatch et al. (2009) loafing near the colony is described as the third highest focal activity encompassing 17 % of daily activities.

Statistical analyses were carried out using linear mixed-effects models (LME), generalized linear mixed models (GLMM) and generalized additive models (GAM; Wood 2006) in R 2.10.1 (R Development Core Team 2009) using the *mgcv* package (Wood 2000) and the *nlme* package. Mean values are reported \pm SD. Results are regarded as significant with $p < 0.05$.

To analyze the foraging data of the kittiwakes in relation to SST, chl-*a* and bathymetric data we used a multi-step procedure: we only used positional fixes of the foraging trips which were supposed to comprise feeding locations. To extract these feeding locations we used randomly selected foraging trips in the created ArcView/ArcGIS maps. From those we defined feeding areas as areas with higher GPS position densities in contrast to flight paths with constant forward movements. From the GPS positions of these potential feeding areas we plotted a flight speed histogram. According to this histogram we ignored all positions with flight speeds $< 6 \text{ km}\cdot\text{h}^{-1}$ (probably resting or sleeping at the water surface) and $\geq 30 \text{ km}\cdot\text{h}^{-1}$. We finally applied this flight speed selection to all foraging trips to extract all potential feeding locations.

We retrieved all 12 loggers deployed during the pre-breeding season (5 females, 7 males) and 36 out of 38 deployed during breeding, respectively. One GPS logger was lost due to moulting of the central tail feathers and one logger got lost due to unknown reason (probably insufficient attachment). Three of the loggers deployed during breeding failed to sample or download data, thus we retrieved data from 33 kittiwakes with 19

females and 14 males during the breeding season. Six birds did not leave the nest or did not perform any foraging trip during logger deployment. We recorded foraging data continuously of 1 – 2.5 days. Overall, we could record 20 foraging trips during pre-breeding, of which 10 were completely recorded and 81 foraging trips during the breeding season, with 34 complete trips.

Results

All trips obtained of 45 birds during the pre-breeding and breeding season 2008 are shown in Table 2.1. During the early pre-breeding season, when Black-legged Kittiwakes returned from their wintering grounds in the central Pacific, the birds performed nearly exclusively nocturnal flights (95 %) in south-easterly direction of their colony to pelagic deep sea waters. Later during the breeding season, they foraged only over continental shelf areas not deeper than 200 m, mainly during daytime; nocturnal flights occurred in only 24 % of the trips (Fig. 2.2 and 2.3). Nocturnal foraging trips during the pre-breeding stage (mean: 10.7 h \pm 2.6 h) lasted significantly longer (LME, $P < 0.05$, $t = -2.390$, $df = 12$, $n = 20$; Fig. 2.4) than during the breeding stage (mean: 7.5 h \pm 3.4 h) and all overnight trips (mean: 9.1 h \pm 3.4 h) lasted significantly longer (GLMM, $P < 0.001$, $t = -3.252$, $df = 45$, $n = 47$) than foraging trips during daytime (mean: 3.5 h \pm 1.8 h; Fig. 2.5a). Furthermore, kittiwakes travelled significantly farther from their breeding site during overnight trips (mean: 41.3 km \pm 33.7 km) than during daytime trips (mean: 20.7 km \pm 16.1 km; GLMM, $P < 0.001$, $t = -0.713$, $df = 45$, $n = 47$; Fig. 2.5b) and the total distance travelled per trip was also greater in overnight trips (mean: 101.6 km \pm 76.5 km) than in foraging trips during daytime (mean: 47.4 km \pm 34.1 km; GLMM, $P < 0.001$, $t = -0.454$, $df = 45$, $n = 47$; Fig. 2.5c).

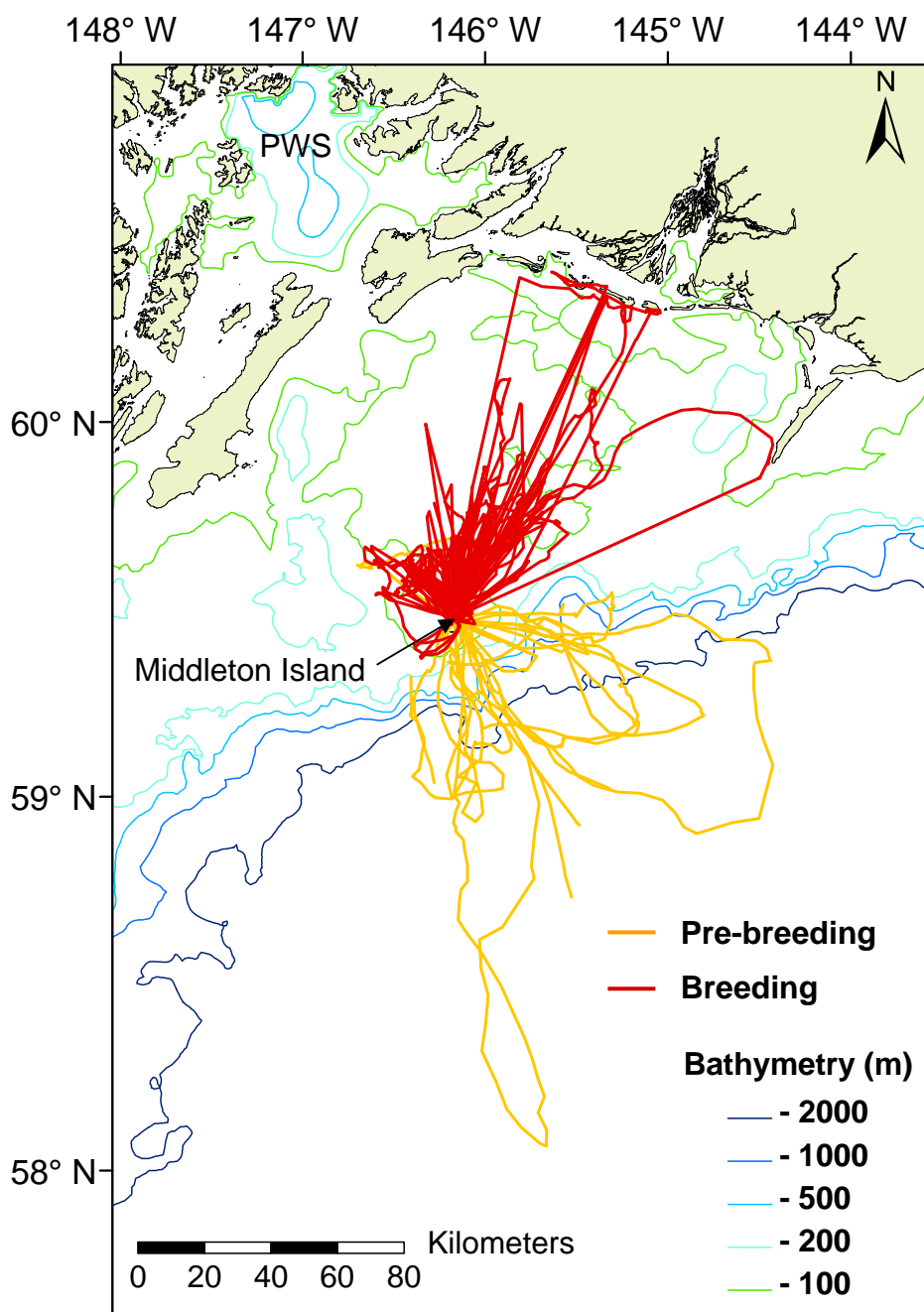


Figure 2.2. Foraging trips of Black-legged Kittiwakes during the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska. PWS indicates the Prince William Sound.

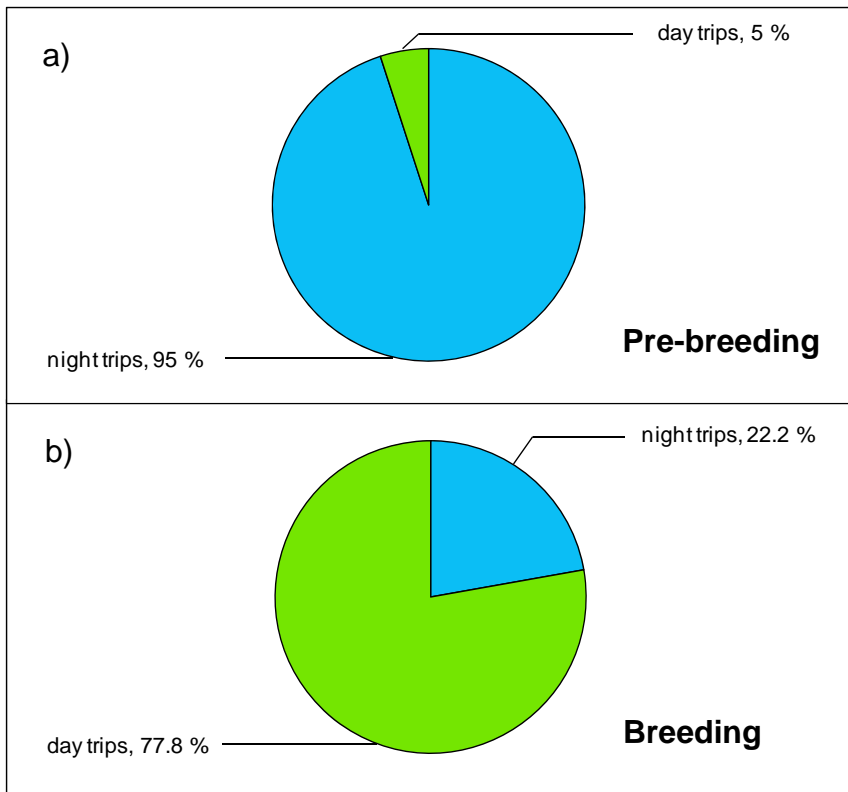


Figure 2.3. Percentage of night and day foraging trips during the pre-breeding season (a) and breeding season (b) 2008 of Black-legged Kittiwakes breeding on Middleton Island, Gulf of Alaska.

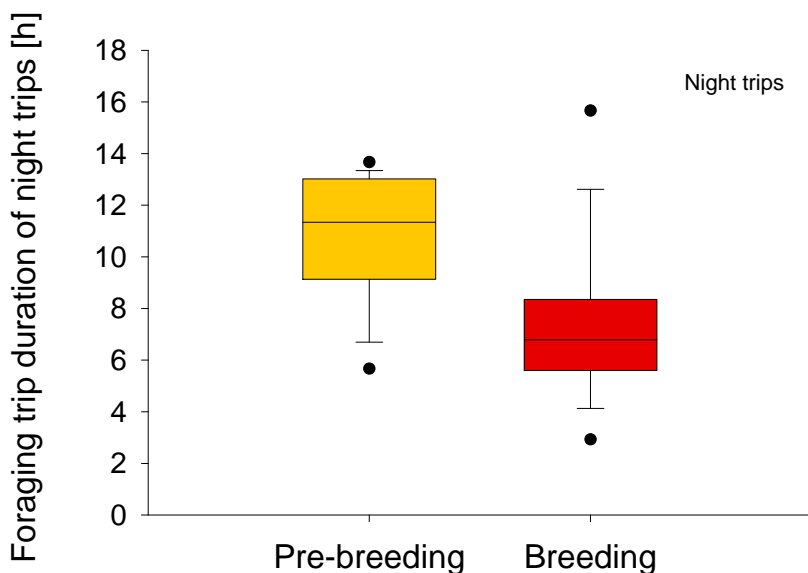


Figure 2.4. Comparison of foraging trip duration [h] of night trips of Black-legged Kittiwakes between the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska. Boxplots show the median, the 5th and 95th percentiles and outliers.

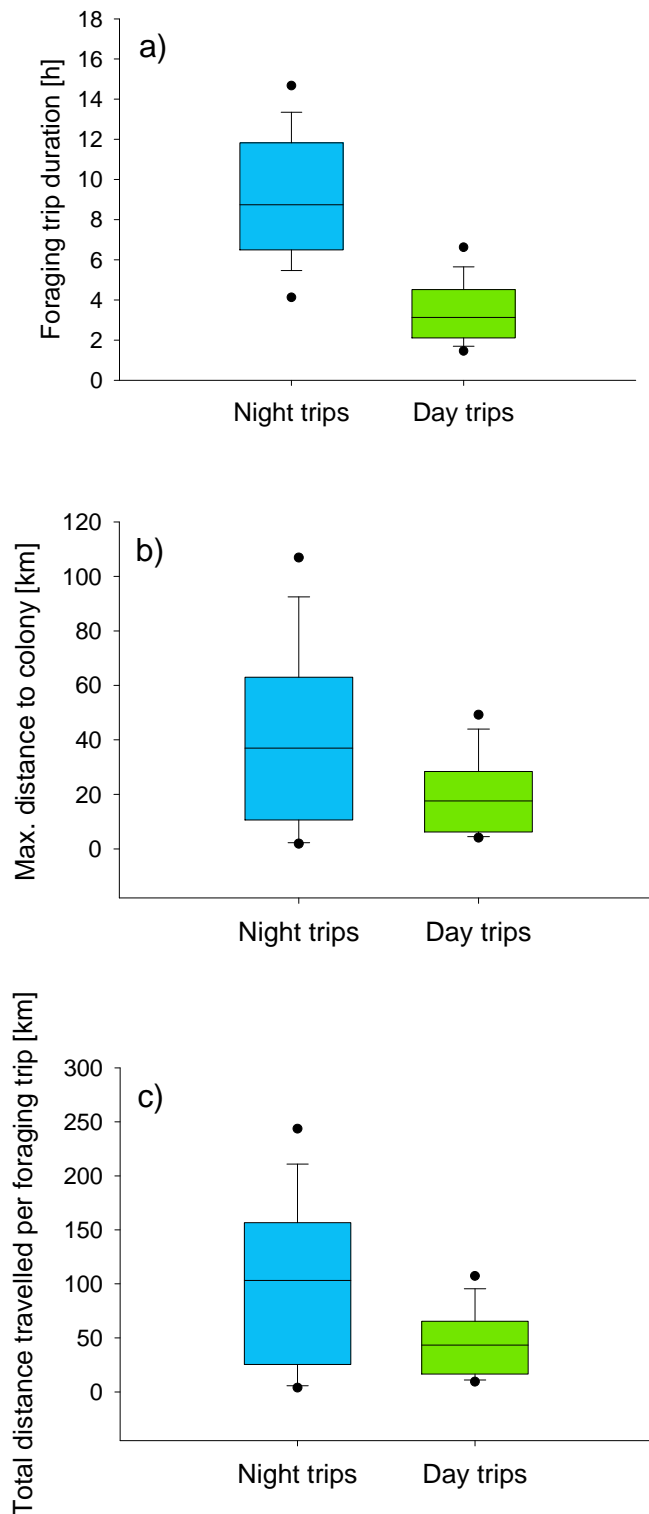


Figure 2.5. Comparison of the foraging behaviour of Black-legged Kittiwakes between day and night trips during the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska. Boxplots show the median, the 5th and 95th percentiles and outliers. a) Foraging trip duration [h], b) Distance to colony [km], c) Total distance travelled per foraging trip [km].

In general, when regarding all foraging trips, foraging trip duration was significantly longer (GLMM, $P < 0.001$, $t = -2.068$, $df = 45$, $n = 47$) during the pre-breeding season (mean: 10.7 h, ± 2.6 h) than during the breeding season (mean: 4.5 h, ± 2.9 h; Fig. 2.6a). There were neither statistically significant differences in the maximum foraging range between trips in April (mean: 41.6 km \pm 24.7 km) and later during trips from May – August (mean: 26.2 km \pm 26.8 km) nor differences in the total distance travelled per foraging trip during pre-breeding (mean: 105.7 km, ± 58.6 km) and breeding (mean: 61.0 km, ± 59.7 km). However, the max. distance to the colony and the total distance travelled per trip tended to be shorter during the breeding season than during the pre-breeding season (Fig. 2.6b, c).

During the early pre-breeding season (April), when the kittiwakes performed mainly flights in south-easterly direction of their colony, we found a significant relationship to bathymetry (GAM, $\chi^2 = 54.111$, $P < 0.001$, R^2 adj. = 0.0166), as the birds foraged only over the deep ocean (Fig. 2.7a). Their foraging trips were neither related to chl-*a* values nor SST's (Fig. 2.8a, 2.9a). Later during the breeding season the significant relation between flight patterns and bathymetry was reverse. During the breeding time kittiwakes foraged only over the shallow continental shelf area, not deeper than 200 m (GAM, $\chi^2 = 46.32$, $P < 0.001$, Fig. 2.7b). Foraging areas were also significantly associated with low chl-*a* values (GAM, $\chi^2 = 46.22$, $P < 0.001$) and intermediate SST's around 10°C (GAM, $\chi^2 = 73.92$, $P < 0.001$; Fig 2.8b, 2.9b). The R^2 value (adj.) for this model was 0.024.

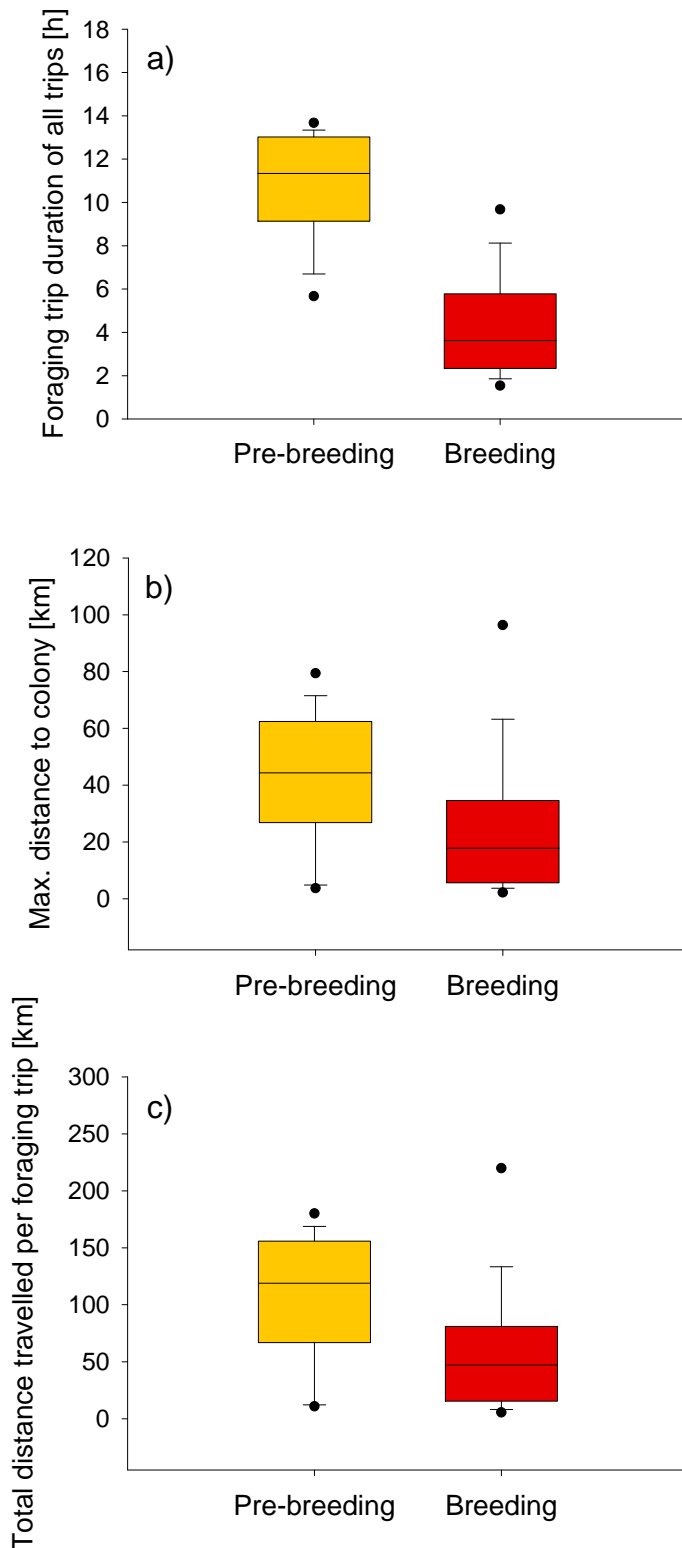
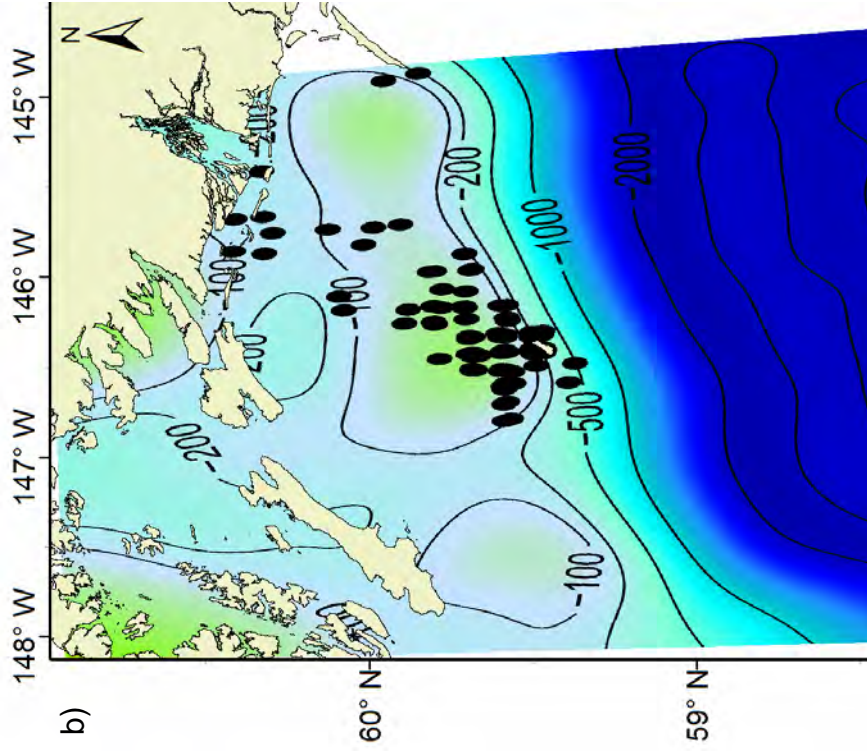


Figure 2.6. Comparison of the foraging behaviour Black-legged Kittiwakes between the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska. Boxplots show the median, the 5th and 95th percentiles and outliers. a) Foraging trip duration [h], b) Distance to colony [km], c) Total distance travelled per foraging trip [km].

Bathymetry - breeding (May - August) 2008



Bathymetry - pre-breeding (April) 2008

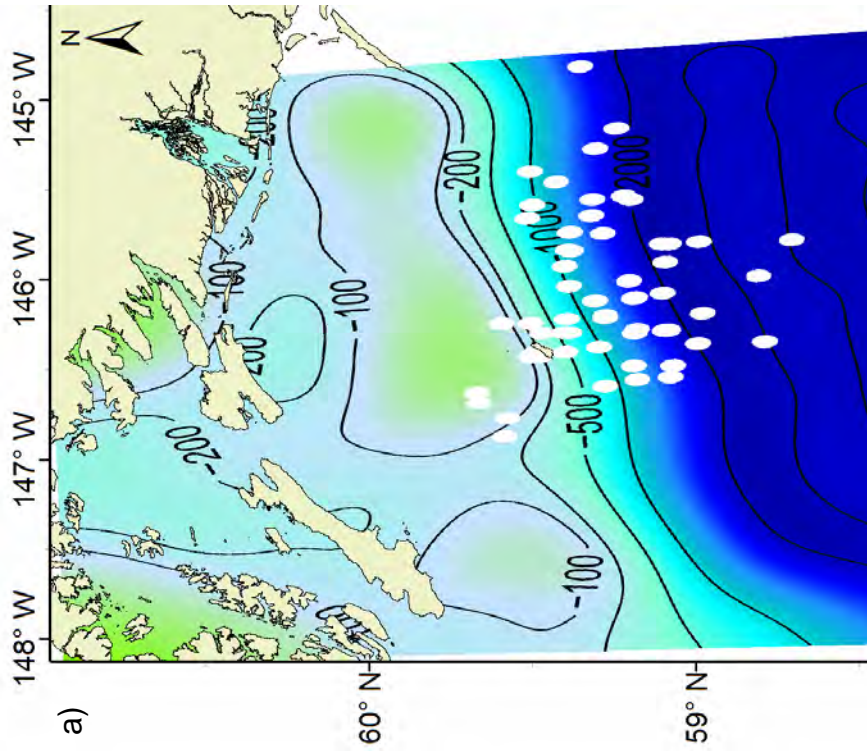


Figure 2.7 . Spatial interpolation of the estimation of the GAM (probability to encounter feeding Black-legged Kittiwakes during the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska, in relation to water depth). Black lines indicate water depth in m and white and black dots indicate proposed feeding locations during pre-breeding and breeding, respectively. a) Kittiwake foraging locations as a function of water depth during the pre-breeding season ($\chi^2 = 54.111$, $P < 0.001$, $R^2 = 0.0166$). b) Kittiwake foraging locations as a function of water depth during the breeding season ($\chi^2 = 46.32$, $P < 0.001$, $R^2 = 0.024$).

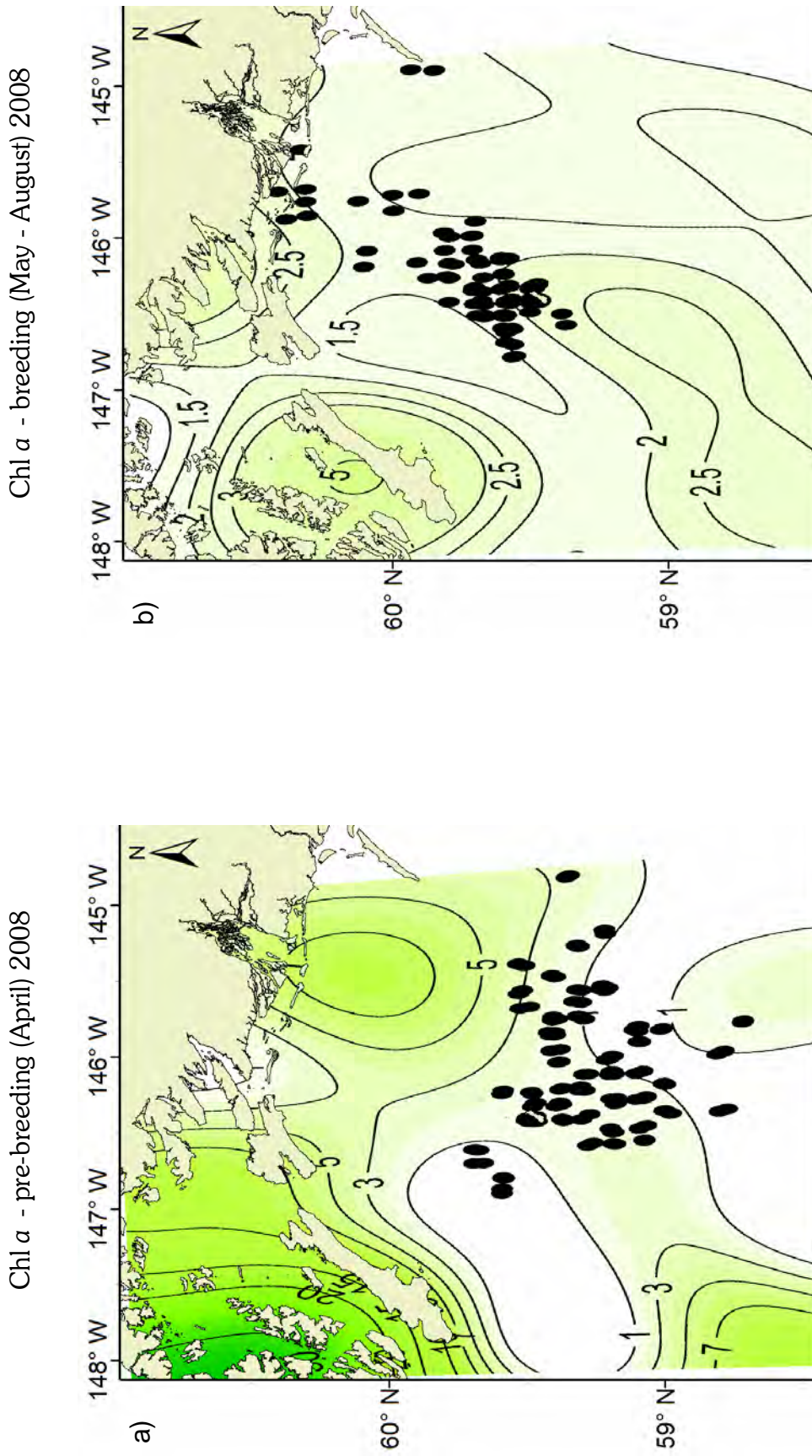
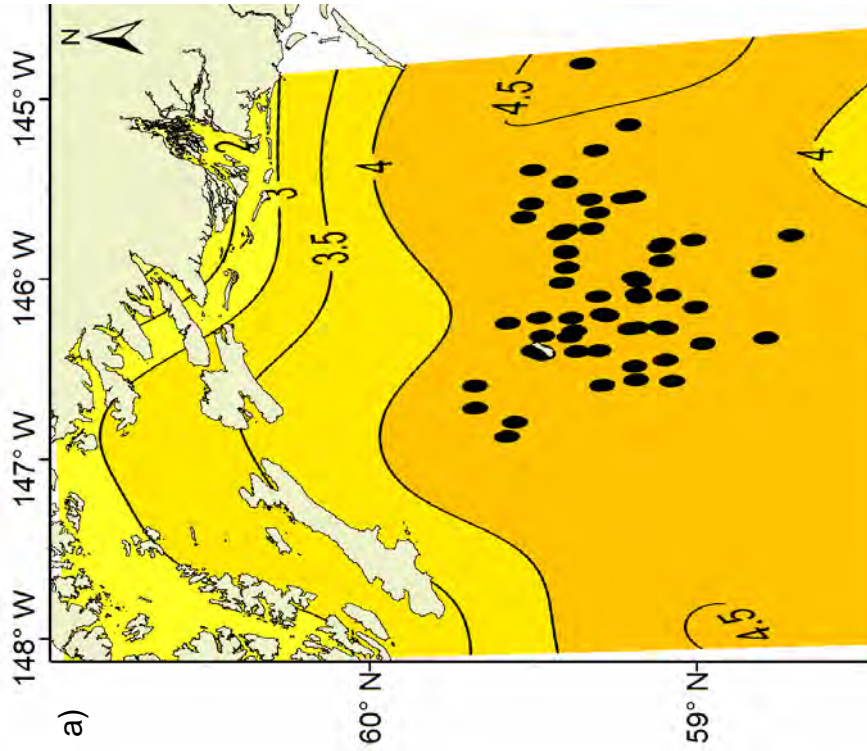


Figure 2.8 . Spatial interpolation of the estimation of the GAM (probability to encounter feeding Black-legged Kittiwakes during the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska, in relation to chlorophyll- a values). Black lines indicate chlorophyll- a concentration in mg/m^3 and black dots indicate proposed feeding locations. a) Kittiwake foraging locations as a function of chl- α during the pre-breeding season ($\chi^2 = 0.147$, $P = 0.938$, $R^2 = 0.0166$). b) Kittiwake foraging locations as a function of chl- α during the breeding season ($\chi^2 = 46.22$, $P < 0.001$, $R^2 = 0.024$).

SST - pre-breeding (April) 2008



SST - breeding (May - August) 2008

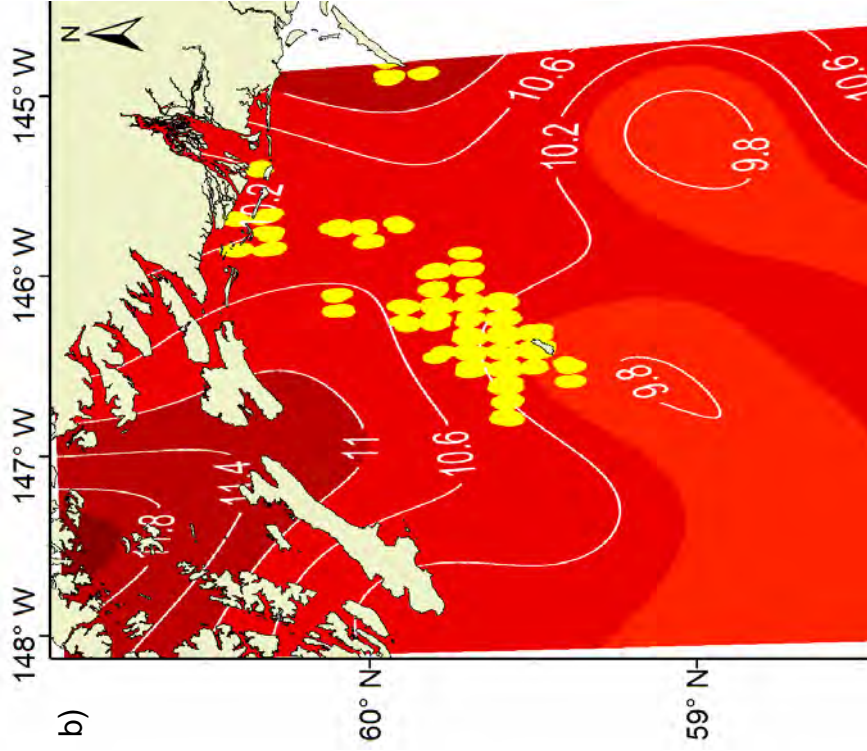


Figure 2.9 . Spatial interpolation of the estimation of the GAM (probability to encounter feeding Black-legged Kittiwakes during the pre-breeding and breeding season 2008 on Middleton Island, Gulf of Alaska, in relation to sea surface temperatures (SST)). Black and white lines indicate sea-surface temperatures in °C and black and yellow dots indicate proposed feeding locations during pre-breeding and breeding, respectively. a) Kittiwake foraging locations as a function of SST during the pre-breeding season ($\chi^2 = 2.810$, $P = 0.434$, $R^2 = 0.0166$). b) Kittiwake foraging locations as a function of SST during the breeding season ($\chi^2 = 73.92$, $P < 0.001$, $R^2 = 0.024$).

Table 2.1. Foraging behaviour of Black-legged Kittiwakes during the pre-breeding and breeding season 2008 at Middleton Island, Gulf of Alaska.

Bird no.	Sex	Breeding status	Max. range (km) ^a	Total distance travelled (km) ^{b,c}	Trip duration (h) ^c	Complete/incomplete ^d	Diel period of trip ^e
1	female	pre-breeding (April)	89.9	(91.1)	(2.4)	Incomplete	N
2	female	pre-breeding (April)	108.2	(255.1)	(15.7)	Incomplete	N
			159.0	(299.6)	(14.8)	Incomplete	N
3	male	pre-breeding (April)	53.4	(68.9)	(10.3)	Incomplete	N
			71.5	(76.8)	(5.5)	Incomplete	N
4	male	pre-breeding (April)	17.4	(20.5)	(2.8)	Incomplete	N
			68.4	(73.7)	(5.2)	Incomplete	N
5	female	pre-breeding (April)	63.6	155.9	11.5	Complete	N
6	male	pre-breeding (April)	41.0	113.9	9.8	Complete	N
			47.6	124.0	13.0	Complete	N
7	female	pre-breeding (April)	26.8	66.8	9.1	Complete	N
8	male	pre-breeding (April)	60.5	(141.6)	(12.5)	Incomplete	N
9	male	pre-breeding (April)	33.0	101.9	11.2	Complete	N
10	female	pre-breeding (April)	52.7	132.4	12.2	Complete	N
			49.0	(54.8)	(2.9)	Incomplete	N
11	male	pre-breeding (April)	3.7	10.8	7.7	Complete	N
12	male	pre-breeding (April)	62.4	157.5	13.7	Complete	N
			79.4	180.1	13.0	Complete	N
			5.9	13.6	5.7	Complete	N
			15.2	(15.4)	(0.7)	Incomplete	D
15	male	with nest	44.7	(57.0)	(2.5)	Incomplete	D
			55.0	(57.8)	(1.9)	Incomplete	D
			106.6	(141.6)	(4.9)	Incomplete	D
17	male	with nest	48.6	104.5	5.3	Complete	N
			16.9	36.3	1.5	Complete	D
			41.2	(53.1)	(1.2)	Incomplete	D
			79.6	180.4	6.42	Complete	N
18	female	with nest	73.2	(92.1)	(11.6)	Incomplete	N
			66.9	140.6	5.5	Complete	D
19	male	with nest	105.4	241.2	15.7	Complete	N

Table 2.1. continued...

Bird no.	Sex	Breeding status	Max. range (km) ^a	Total distance travelled (km) ^{b,c}	Trip duration (h) ^c	Complete/incomplete ^d	Diel period of trip ^e
21	female	with nest	4.4 39.1	11.5 (45.1)	4.67 (3.1)	Complete Incomplete	D N
22	male	with nest	4.2 5.6 105.8	11.1 11.9 (106.3)	2.08 1.65 (0.5)	Complete Complete Incomplete	D D N
25	male	incubation	34.5 31.9	(37.7) (33.7)	(1.8) (1.7)	Incomplete Incomplete	D N
26	female	with nest	110.1	(287.3)	(23.4)	Incomplete	N
27	male	with nest	31.0 9.3	(47.1) (18.7)	(2.2) (0.5)	Incomplete Incomplete	N D
29	female	incubation	28.5 41.3	65.4 (47.1)	9.73 (2.6)	Complete Incomplete	D D
32	female	chick rearing	15.3 19.4 24.5 14.7 15.2 32.8	37.3 47.6 (34.8) 37.5 47.2 (87.9)	2.93 2.3 (1.7) 2.18 2.35 (3.9)	Complete Complete Incomplete Complete Complete Incomplete	N D D D D D
33	female	incubation	9.0	(34.5)	(8.5)	Incomplete	D
34	male	chick rearing	6.7 23.2 8.5	(6.9) (31.6) (8.5)	(0.1) (0.6) only 1 position at sea	Incomplete Incomplete Incomplete	D D D
35	male	chick rearing	53.5 108.4 21.2	(57.1) 245.9 (38.0)	(1.6) 9.57 (2.4)	Incomplete Complete Incomplete	D N D
36	female	chick rearing	17.6 19.2 7.5 20.4 9.1 19.3	42.4 (96.1) (7.5) (27.9) 19.9 43.4	3.33 (2.8) only 1 position at sea (1.2) 2.02 2.7	Complete Incomplete Incomplete Incomplete Complete Complete	D D D D D D

Table 2.1. continued...

Bird no.	Sex	Breeding status	Max. range (km) ^a	Total distance travelled (km) ^{b,c}	Trip duration (h) ^c	Complete/incomplete ^d	Diel period of trip ^e
37	female	chick rearing	46.1	96.1	4.07	Complete	D
			20.2	(29)	(1)	Incomplete	D
39	female	chick rearing	58.6	(61)	(5)	Incomplete	D
			41.3	(46)	(3)	Incomplete	D
40	female	chick rearing	44.4	93.4	5.68	Complete	D
			20.9	(47)	(10)	Incomplete	N
41	male	chick rearing	19.1	(31)	(3)	Incomplete	D
			22.5	79.9	8.35	Complete	N
43	female	chick rearing	23.0	(40)	(3)	Incomplete	D
			5.6	15.2	4.85	Complete	D
44	male	chick rearing	4.1	(5.3)	(0.7)	Incomplete	D
			10.1	23.3	1.85	Complete	D
45	male	chick rearing	24.6	72.0	5.6	Complete	N
			34.2	(42.8)	(2.0)	Incomplete	D
46	female	chick rearing	6.3	(17.4)	(3.2)	Incomplete	D
			3.6	7.6	2.55	Complete	D
47	male	chick rearing	39.6	(72.7)	(8.1)	Incomplete	N
			34.7	(54.0)	(1.3)	Incomplete	D
48	male	chick rearing	42.7	(45.3)	(1.1)	Incomplete	D
			32.8	76.7	3.37	Complete	D
49	male	chick rearing	17.8	47.3	3.13	Complete	D
			4.8	9.8	1.35	Complete	D
50	female	chick rearing	42.3	101.5	4.68	Complete	D
			24.1	(25.8)	(1.2)	Incomplete	D
51	male	chick rearing	32.8	(33.5)	(1.0)	Incomplete	D
			34.9	(39.4)	(2.2)	Incomplete	D
52	male	chick rearing	24.7	57.0	3.05	Complete	D
			28.1	65.5	3.62	Complete	D
53	male	chick rearing	5.5	15.4	1.88	Complete	D
			22.6	48.7	3.25	Complete	D
54	male	chick rearing	16.6	(16.9)	(0.6)	Incomplete	D

Table 2.1. continued...

Bird no.	Sex	Breeding status	Max. range (km) ^a	Total distance travelled (km) ^{b,c}	Trip duration (h) ^c	Complete/incomplete ^d	Diel period of trip ^e
48	female	chick rearing	39.9 18.6 20.7	84.5 (19.4) (20.7)	3.87 (0.5) only 1 position at sea	Complete Incomplete Incomplete	D D D
49	female	chick rearing	1.8 8.1 2.5 2.0	4.7 23.1 6.9 3.2	7 6.07 6.57 7.22	Complete Complete Complete Complete	N D N N
50	male	chick rearing	5.1 37.1	(14.5) (54.1)	(1.9) (4.2)	Incomplete Incomplete	D D

^a Maximum range indicates maximum straight-line distance from the colony.

^b Total distance travelled is distance covered during one foraging trip.

^c Total distance travelled and trip duration are shown in parentheses for incomplete trips.

^d Complete/incomplete indicates whether the whole trip was recorded from nest-leaving through return to the colony.

^e Diel period distinguishes overnight and day trips.

Discussion

GPS-loggers did not seem to influence the birds substantially as their behaviour and number of eggs laid/nest were similar in logger birds (1.8 ± 0.8) and control birds (1.8 ± 0.5). Furthermore, the breeding success (number of chicks fledged/number of eggs hatched) did not differ significantly between equipped (0.7 ± 0.4) and non-equipped birds (0.6 ± 0.4).

Kittiwake foraging strategies during the pre-breeding and breeding season 2008 differed fundamentally. During the pre-breeding season birds exclusively foraged over deep pelagic waters in south-easterly direction of the colony. Foraging trips were mainly conducted during night. In contrast, foraging trips during the breeding season were only targeted to the continental shelf area in northerly direction of the colony. During the breeding season birds performed foraging trips mainly during day time. These findings of the foraging behaviour during the breeding season coincide well with the results found in 2007 in the same colony (Kotzerka et al. 2010). In the previous breeding season in 2007 the birds showed the same foraging behaviour with conducting their foraging trips only over the continental shelf area in northerly direction of the colony. The total distance travelled per trip as well as the max. distance to the colony were similar in both years, though foraging trip duration was nearly twice as high in 2007 (Kotzerka et al. 2010). It might be possible that feeding conditions in 2007 were less favourable than in 2008, so that birds had to search longer to find enough food to provide to their offspring. With longer foraging trips they were able to compensate for the possible food shortage as the breeding success in both years was similar.

During the pre-breeding season, after returning from the wintering grounds, birds usually left the colony in the late afternoon or evening for long-ranging foraging trips in south-easterly direction to pelagic deep sea waters and returned only the next morning. A similar behaviour is described in Glutz von Blotzheim and Bauer (1982) for kittiwakes in Britain. Harrison (1982) observed during aerial survey in the western Gulf of Alaska, that kittiwakes were most numerous over the continental slope (180 – 1000 m) in March and April. However, in May and June he observed them only over the shelf (< 180 m). The foraging areas southeast of the breeding colony on Middleton Island concur with overwintering areas of Black-legged Kittiwakes from Prince William Sound colonies. During the breeding season 2006 breeding Kittiwakes of the Prince William Sound were

fitted with geolocation loggers and results indicated their wintering areas in the northern central Pacific (D. B. Irons and Aly McKnight, unpubl. data).

These contrasting foraging areas between pre-breeding and breeding probably reflect prey abundance in the Gulf of Alaska at different temporal scales. During the early pre-breeding season, when the kittiwakes forage over deep pelagic waters, they probably feed to a high proportion on lampfishes (Myctophidae). Gill and Hatch (2002) found in some years that 50 % of all sampled prey species of kittiwake regurgitations consisted of lampfishes. Myctophidae have the highest energy content measured in studies of energy densities of North Pacific forage fishes (Anthony et al. 2000; Van Pelt et al. 1997). It is a fish species that usually lives beyond the continental shelf in depths of several hundred meters during daytime (Nelson 1994; Sinclair and Stabeno 2002). Thus, it is unavailable to seabirds during that time of the day. It only becomes available to foraging seabirds during its vertical migrations conducted at night, when it follows its principle prey, the zooplankton, to the water surface (Beamish et al. 1999; Westheide and Rieger 2004). The energy demand of Black-legged Kittiwakes, as of seabirds in general, during the pre-breeding season is very high in order to restore the body energy reserves after the winter months and to provide enough energy for the following breeding period (egg production). During the pre-breeding season in April myctophids seem to be an easily accessible prey species, since they usually occurs in high biomasses (Westheide and Rieger 2004). Other prey species like capelin (*Mallotus villosus*) are probably not yet available in high densities (Brown 2002). Many nearshore fish species leave the cold upper water layers in fall to spend the winter time in warmer depths (Rogers et al. 1987 in Spies 2007). Pacific sand lance (*Ammodytes hexapterus*) is only available in high larvae densities, that just hatched from overwintering eggs and that are of low energy density (Doyle et al. 2009; Van Pelt et al. 1997). At this time of the year (April) the phytoplankton-bloom in the Gulf of Alaska have just started and zooplankton-blooms are not yet grown (Spies 2007). Hence, the food base for forage fish species like capelin or Pacific sand lance is not yet established.

Later, during the breeding season from May – August, capelin and sand lance become available for kittiwakes and other seabirds over the continental shelf area as found by net samplings. Aerial surveys conducted along the coasts of the Prince William sound and adjacent fjords and bays also revealed capelin schools in high abundances (Brown 2002). Otherwise, Myctophids were less abundant in samples during surveys

conducted from May – June (Doyle et al. 2002). During the breeding season at least five of our sampled kittiwakes went to islands bordering the Prince William Sound in the south, where they probably fed on nearshore spawning capelin. But since many foraging flights of the kittiwakes could only be sampled incompletely, we assume that the actual amount of kittiwakes feeding on nearshore spawning capelin is higher, as many of these incomplete foraging trips started with flight directions towards the coast of Prince William Sound.

These considerations are supported by our findings of the relationships of kittiwakes foraging in areas during the pre-breeding and breeding season with remotely sensed SST and chl-*a* values in the surrounding ocean. We did not find a relationship of kittiwake foraging areas during the pre-breeding season with SST or chl-*a* content of the Gulf of Alaska. We only found a positive relationship of kittiwake foraging areas with the pelagic deep ocean. Concurrent with the absence of a relationship of kittiwake foraging areas with chl-*a* values during pre-breeding we did not find a relationship with SST's. Sea surface temperatures in the surrounding ocean are more or less homogeneous during that time of the year, only narrow coastal areas show colder SST's as a result of melting ice and snow. This snow melt also carries nutrients into the sea that in turn supports the phytoplankton bloom. In April, the highest chl-*a* values measured by satellites were found in Prince William Sound and along the northern coast of the Gulf of Alaska but foraging trips of kittiwakes were to areas southeast of the colony with lower chl-*a* values. The high chl-*a* values in Prince William Sound and along the coast show the spring phytoplankton-bloom that just developed after the cold winter months and that is not yet fed down by the following grazing zooplankton-bloom appearing one to two months later (Spies 2007). Thus, it can not yet support high fish abundances for foraging seabirds. An exception is the Pacific herring (*Clupea pallasii*). Although this prey species is already spawning in high densities in southern Prince William Sound in mid-April (Spies 2007), this species or its eggs and milt does not seem to be used as a major prey species for kittiwakes from Middleton Island during the pre-breeding season. Reasons for the disregard of this easily available prey species are unknown, though Spies (2007) writes that generally “the annual herring spawning draws large numbers of seabirds, other fishes and mammals (..) in a nearshore feeding frenzy”. One explanation for not using spawning herring as prey during the pre-breeding season might be that herring abundances and their size classes are not predictable and highly variable among different

years (Link et al. 2009; Paul and Paul 1999). It is likely that kittiwakes from Middleton Island switch between main prey species during pre-breeding according to the availability of fish species (Springer et al. 1996; Springer 2005). Gill and Hatch (2002) found relatively low amounts of herring in kittiwake regurgitations during the pre-breeding season in years with high lampfish (Myctophidae) frequencies. In years with low or no lampfish frequencies the amount of Pacific herring in regurgitations was higher.

Later during the breeding season, the kittiwakes were associated with low chl-*a* values, intermediate SST's and shallow water depths. These associations reflect well the foraging areas over the shallow continental shelf area (not deeper than 200 m) and probably also show the depletion of the phytoplankton-bloom by grazing zooplankton, that in turn supports high prey fish abundances (e. g. capelin, Pacific sand lance, Pacific herring) in this area during the summer months.

Another reason for the abrupt switch of foraging strategies of kittiwakes between the pre-breeding and breeding season might be, that feeding during daylight over the continental shelf, in shorter distances to the colony and with shorter foraging trip durations is advantageous in terms of nest site and brood defence during the breeding stage. Birds can spend more time together at the nest site and prevent nest takeover and egg or chick losses by fighting with intruding birds.

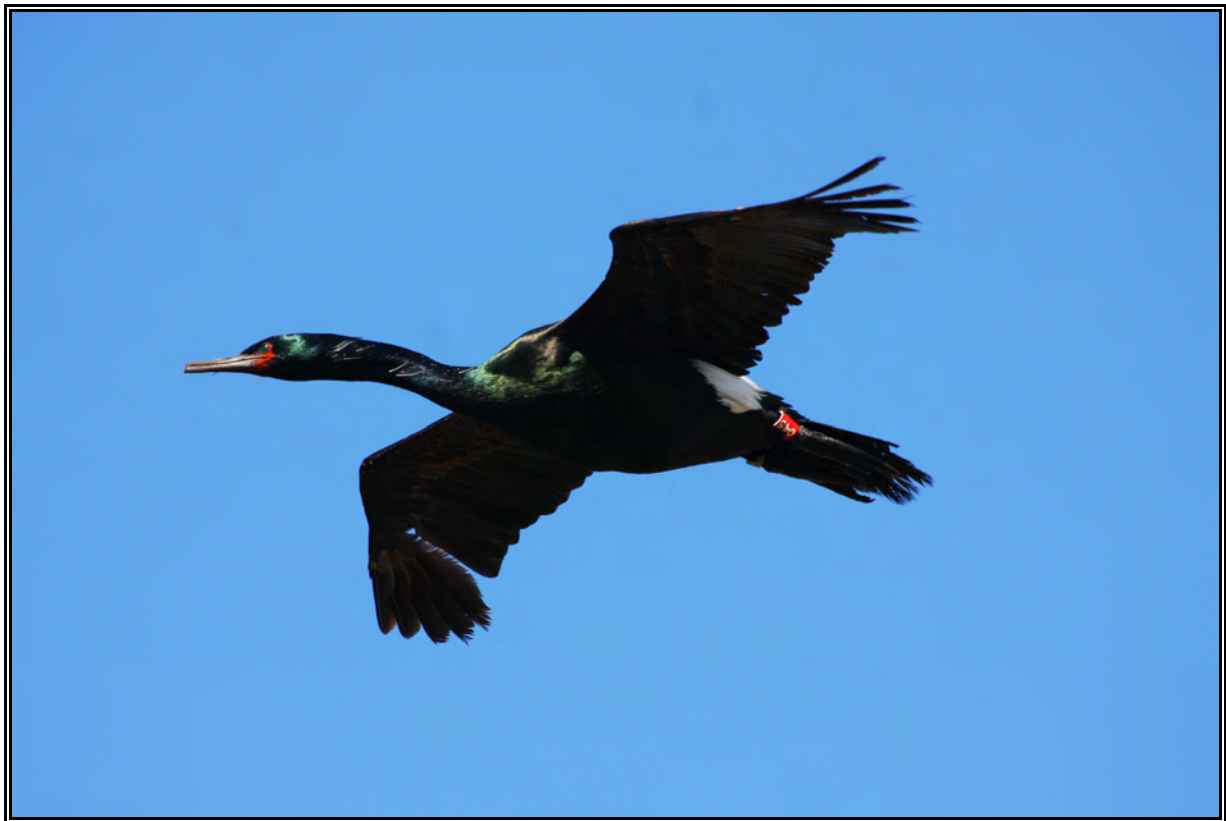
In conclusion, our results show that kittiwakes on Middleton Island perform very distinct foraging strategies during the pre-breeding and breeding season and that these strategies likely reflect different prey availabilities at these stages. To some extent they are able to adjust their foraging behaviour according to prey availability. But as they are not able to dive they can only exploit prey near the water surface. Since their prey species can be variable in densities and size among different years, nutrient and lipid rich species are not always available and kittiwakes have to switch to less favourable prey species, what probably results in lower breeding success. Remote sensing data of SST's and chl-*a* values indicating areas with high primary production are not necessarily related to seabird foraging areas, as there is a temporal delay in secondary production and following higher trophic levels. Thus, remote sensing data are not mandatory useful to predict seabird feeding grounds. Those predictions have to be made carefully according to particular regional, environmental and seasonal conditions. Using additional factors that can influence prey abundances (e. g. currents, upwelling, season) may improve the predictability. But our data of the foraging behaviour of Black-legged Kittiwakes during

the pre-breeding season only reflect the foraging behaviour of one season and two seasons during the breeding season, respectively. More research is necessary to reveal foraging strategies of kittiwakes in different years with different environmental conditions and concurrently with diet sampling. It is essential to understand the foraging ecology in detail for a declining seabird species like the Black-legged Kittiwakes. This is especially important for an area like the Gulf of Alaska which is highly productive, but however, has a very low breeding success of Black-legged Kittiwakes. Results can then be used to establish potential management and conservation plans.

Acknowledgements

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Chapter III



***Evidence for foraging-site fidelity and individual foraging behaviour
of Pelagic Cormorants rearing chicks in the Gulf of Alaska***

Evidence for foraging-site fidelity and individual foraging behaviour of Pelagic Cormorants rearing chicks in the Gulf of Alaska

Abstract

The Pelagic Cormorant (*Phalacrocorax pelagicus*) is the most widespread cormorant in the North Pacific, but little is known about its foraging and diving behaviour. However, knowledge of seabirds' foraging behaviour is important to understanding their function in the marine environment. In 2006, using GPS data loggers, we studied the foraging behaviour of 14 male Pelagic Cormorants rearing chicks on Middleton Island, Alaska. For foraging, the birds had high fidelity to a small area 8 km north of the colony. Within that area, the cormorants' diving activity was of two distinct kinds — near-surface dives (1 – 6 m) and benthic dives (28 – 33 m). Individuals were consistent in the depths of their dives, either mostly shallow or mostly deep. Few showed no depth preference. Dive duration, time at maximum depth, and pauses at the water surface between consecutive dives were shorter for shallow dives than for deep dives. The cormorants made dives of both types throughout the day, but the frequency of deep dives increased toward evening. Maximum foraging range was 9 km; maximum total distance travelled per trip was 43.4 km. Trip durations ranged from 0.3 and 7.7 hr. Maximum depth of a dive was 42.2 m, and duration of dives ranged from 4 to 120 sec. We found that Pelagic Cormorants on Middleton Island were faithful to one particular foraging area and individuals dived in distinct patterns. Distinct, specialized foraging behaviour may be advantageous in reducing intra- and interspecific competition but may also render the species vulnerable to changing environmental conditions.

Keywords: Alaska, diving activity, foraging behaviour, GPS data loggers, Pelagic Cormorant, *Phalacrocorax pelagicus*, site fidelity

Introduction

Seabirds' distribution at sea is strongly influenced by the patchy distribution of their prey, which is often caused by oceanographic and hydrographic features (Ainley et al. 2009; Bost et al. 2009; Hunt 1991). Therefore, seabirds' foraging behaviour vary through time and space (Schneider and Duffy 1985). Intra- and interspecific competition within or between colonies may deplete prey around colonies (Forero et al. 2002; Grémillet et al. 2004b; Lewis et al. 2001). Hence, the search for unevenly distributed prey in the surrounding ocean plays a major role in seabird's daily activities (Santora et al. 2009). Especially during the breeding season, when the demand for energy for self-maintenance and raising chicks is high, seabirds have to make the right decisions on where to forage successfully in an appropriate time span.

Learning and remembering how and where to forage could increase birds' foraging efficiency and individual fitness (Hamer et al. 2001; Weimerskirch 2007), but also depend on the distribution and predictability of their prey. The degree of faithfulness to a foraging site should depend on the degree of the prey's predictability and depletion (Irons 1998). In addition, individual specialization may increase foraging success and reduce intraspecific competition (Bolnick et al. 2003; Mehlum et al. 2001; Ropert-Coudert et al. 2003).

For the relationships between predators and prey to be better understood, it is crucial that predators' foraging behaviour be studied and that their feeding and home ranges as well as movement patterns and diving activities be determined. Such information is important in explaining how seabirds use various marine areas and how they interact with the marine environment. Foraging ranges and feeding areas can help to define the ecological roles of seabirds and constraints acting upon them in marine ecosystems (Monaghan 1996; Wilson et al. 2002).

The Pelagic Cormorant (*Phalacrocorax pelagicus*) is the most widely distributed and abundant cormorant in the North Pacific. In the eastern part of the basin, its distribution extends from arctic North America (Chukchi Sea) to Baja California, and in the west it stretches from Siberia to southern China (Hobson 1997; Nelson 2005). Despite that broad distribution, information on many aspects of the species' biology is very limited. Current knowledge of its foraging and diving behaviour amounts to a few

observations of surface activity and duration of dives (Cooper 1986; Hobson and Sealy 1985).

Less gregarious than other cormorants (Hobson 1997), the Pelagic Cormorant generally breeds in small, loosely aggregated colonies on steep, rocky cliffs. These habits contribute to the difficulty of investigating the species. Middleton Island, in the north-central Gulf of Alaska, has one of the largest known colonies (~1500 pairs in 2009; S.A. Hatch, unpubl. data), but the population is declining substantially (Dragoo et al. 2009). Part of the population uses artificial nest sites at which access to the birds is much easier than in any natural breeding habitat. We studied the foraging movements and diving activity of Pelagic Cormorants during the breeding season of 2006 to identify important foraging areas and to obtain detailed information on the species' diving behaviour. These findings will allow us to characterize the marine ecology of this widespread but poorly known species more fully and may indicate reasons for the decline.

Methods

Middleton Island (59.4° N, 146.3° W) is situated at the edge of the continental shelf in the northern Gulf of Alaska (Fig. 3.1). In 2006, about 150 Pelagic Cormorants nested on a U.S. Air Force radar tower, decommissioned and derelict since the 1960s, to which artificial nest sites have been added for research. The birds nested on wooden ledges viewable from inside the building through sliding panes of one-way mirror glass (Gill and Hatch 2002).

Between 19 June and 5 August 2006, we caught 14 males that were rearing chicks. We identified them as males by their bands applied in previous studies or by bill size (Hobson 1997). We used males for attaching logger because of their larger body size and more favourable ratio of body mass to device's mass. All birds in the study were marked with a steel band and a laminated plastic band numbered for individual identification. Nests were checked each morning for the status of the eggs or chicks and the presence of the adults.

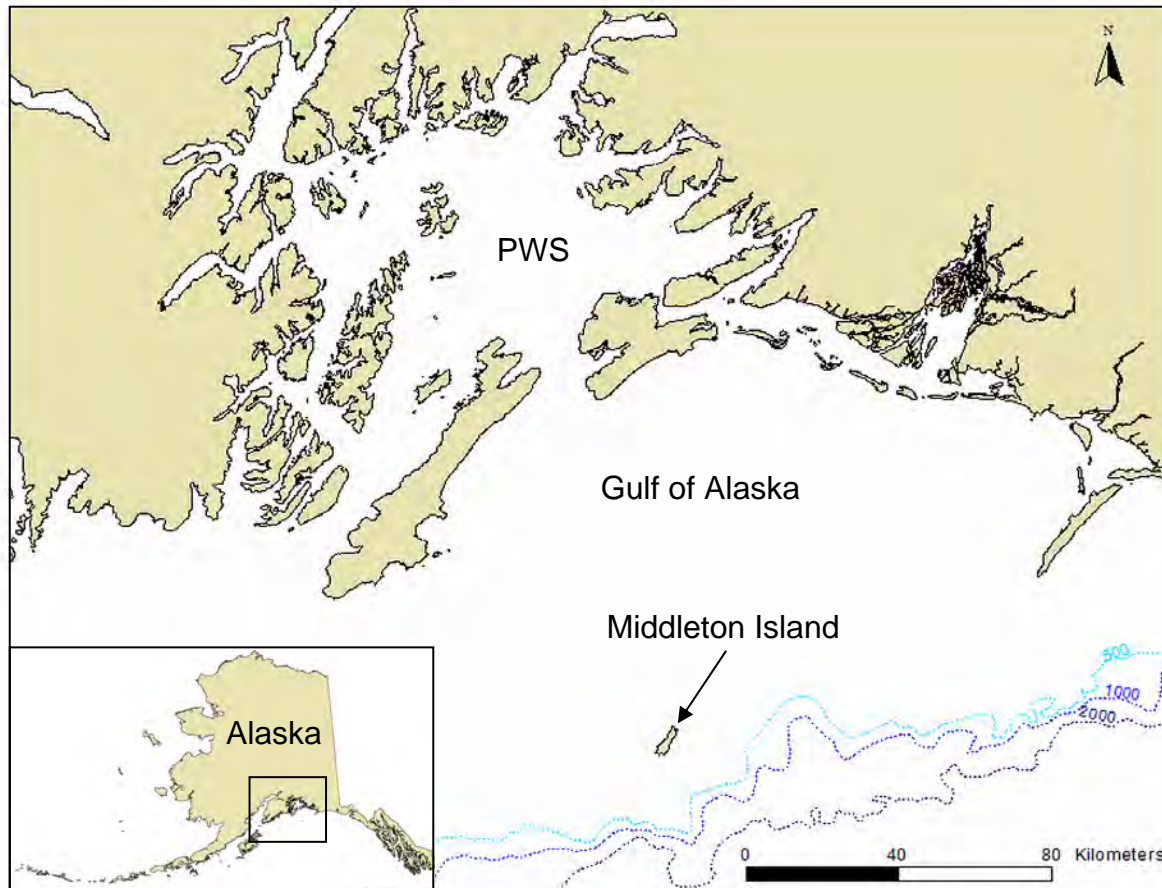


Figure 3.1. Study area in the Gulf of Alaska showing the locations of Middleton Island and Prince William Sound (PWS). Middleton lies about 80 km south of the Alaska mainland. Depth contours indicate the position of the continental slope.

We attached GPS data loggers (70 g, dimensions 100 x 48 x 24 mm) with integrated pressure and temperature sensors (earth & Ocean Technologies, Kiel, Germany) temporarily to the feathers of the lower back with waterproof TESA® tape (Wilson *et al.* 1997). In field testing, 65% of the positional fixes were within 10 m of the actual location, and 90% were within 19 m. Data stored in the device's memory and used for this analysis included date, time, latitude, longitude, speed, pressure, and temperature. The logger was set to sample date, time, latitude, longitude, and speed at intervals of 1, 2, or 3 min (different birds were sampled at different intervals). The pressure and temperature sensor (with corresponding date and time) was set to record every 1 or 2 sec (different birds were sampled at different intervals). Before attaching the logger, we weighed each bird to the nearest 20 g with a spring balance. The loggers represented 3 – 4% of mean body mass (1.8 kg, range 1.64 – 1.97 kg). Each bird was

caught only twice, for attachment and retrieval of the logger. We used birds from 79 unmanipulated nests on the tower as a control group to compare the breeding success of birds with and without a logger.

From the positional data obtained, we plotted flight paths in ArcView[®] 3.2 (ESRI, Redlands, CA). We defined the maximum foraging range as the bird's most distant position in a straight line from the colony. Distance travelled refers to the summed distances between start and end locations of each foraging trip. Elapsed time from start to end of a trip is trip duration. We defined the start and end of a trip with GPS data. Trips started when a positional fix was at least 300 m from the colony and subsequent positions were progressively farther. To analyze data on dives we used the software MultiTrace-Dive (Jensen Software Systems, Laboe, Germany) and an individually written Matlab script by T. Mattern. We considered a vertical immersion a dive if it was deeper than 1 m. Statistical analyses were carried out in R 2.8.0 (R Development Core Team 2008). Mean values are reported \pm SD; median values are reported with the 95% confidence interval (CI₉₅).

Results

We recorded location data from all 14 male Pelagic Cormorants equipped in the study, all of which were actively engaged in chick rearing. We obtained usable dive data from 13 of the tagged cormorants. Loggers recorded foraging data continuously for periods of 1 to 3.5 days. We recorded 100 foraging trips, for 65 of which GPS coverage was complete. An obstructed view of the sky limited signal reception at the nest site, and depletion of the batteries occasionally resulted in data for a trip being incomplete. For the analysis of distance to colony, total distance travelled, and associated statistical tests we used data for complete trips only.

The cormorants foraged primarily in a 6-km² area located about 8 km north of the island (Fig. 3.2a). At least 13 of the 14 studied individuals visited the site – GPS data for one bird were too fragmented for us to determine the location of its foraging. The birds had high fidelity to the primary foraging site. They used it throughout chick-rearing, in consecutive foraging trips, and on consecutive days (Fig. 3.2b, c). Birds flew to the feeding area mostly in direct flights, making no attempt to search for prey in other areas.

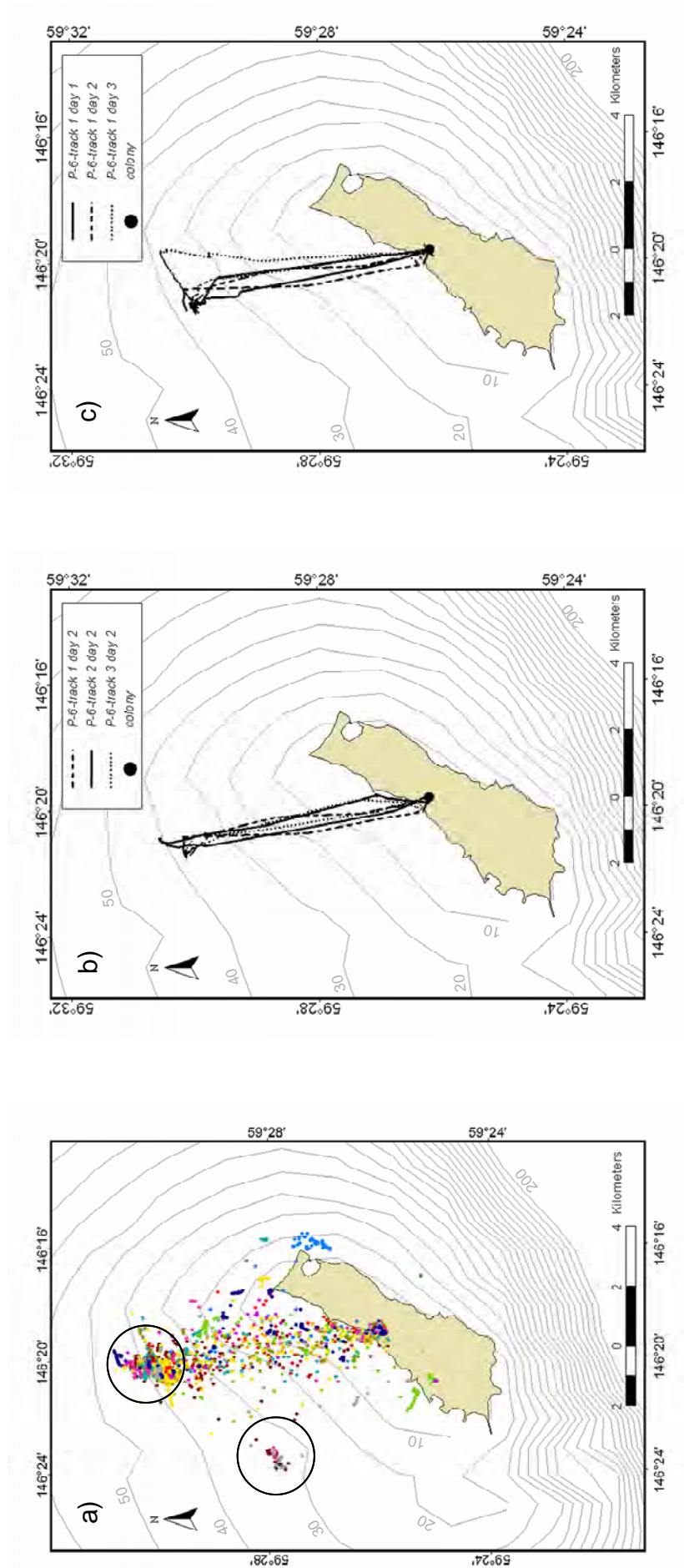


Figure 3.2. GPS positions of 14 Pelagic Cormorants tracked on foraging trips from Middleton Island. Each individual shown in a different color (a). Circles denote the primary and one smaller secondary foraging area identified in 2006. Details of three consecutive foraging trips during the same day (b) and in consecutive days (c) by male P-6, showing high foraging site fidelity and track lines of a typical round trip. Depth contours indicate bathymetric isobars in 10-m intervals.

Another small foraging area northwest of the island was used by three birds. There were no foraging flights to the south of the colony (Fig. 3.2a).

Most birds dived in individually consistent patterns, with three birds (4, 5, 12) executing mainly shallow, near-surface dives, and seven birds (2, 3, 7, 8, 9, 10, 13) performing mainly deep, benthic dives. Three birds (1, 6, 11) showed no preference for specific dive depths (Fig. 3.3).

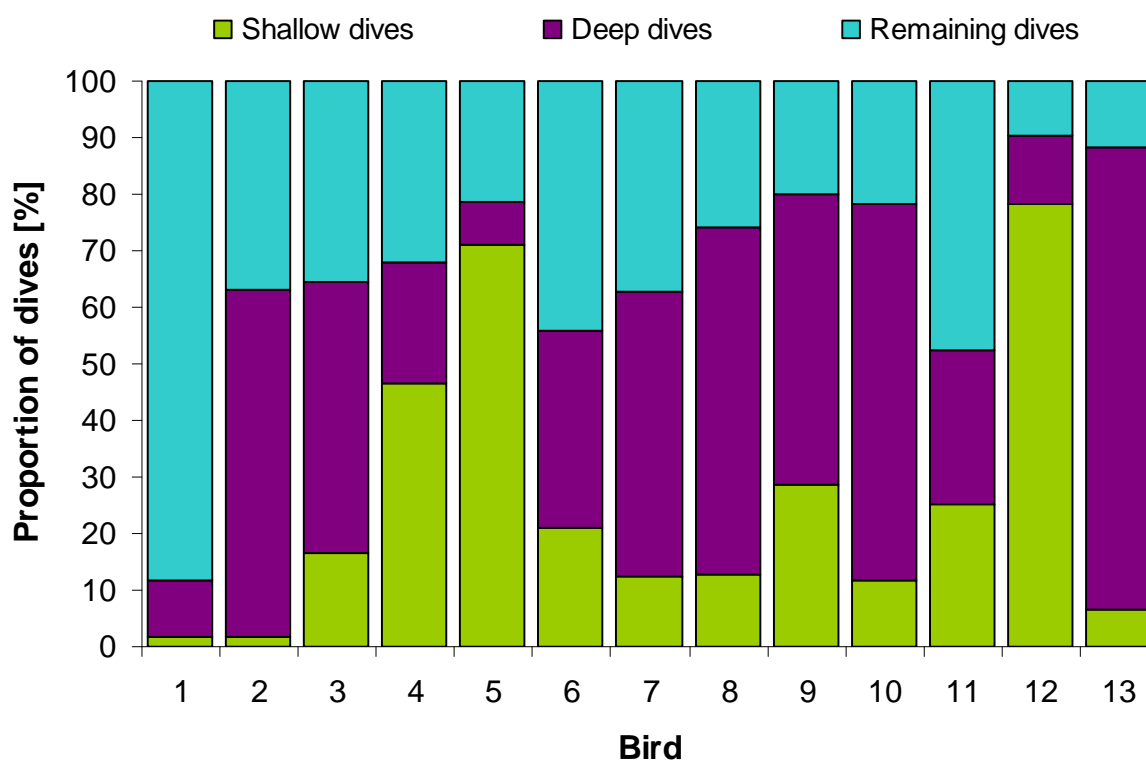


Figure 3.3. Proportions of shallow (near-surface, 1 – 6 m), deep (benthic, >28 m), and remaining (6.1 – 27.9 m) dives of Pelagic Cormorants on Middleton Island in 2006.

These patterns are also reflected in dive durations. On average, birds performing mainly shallow dives made briefer dives than birds that performed mainly deep dives. In general, dive duration ranged from 4 to 120 sec (median 52.0 sec; CI_{95} 10.0 – 94.0 sec) (Table 3.1) and was positively correlated with dive depth ($P < 0.001$, $t = 16.24$, $df = 2110$, $r^2 = 0.65$). The maximum dive depth was 42.2 m (median 17.3 m, CI_{95} 1.2 – 33.4 m).

Table 3.1. Durations and depths of dives by foraging Pelagic Cormorants during the chick-rearing period in 2006 on Middleton Island.

Bird	Dive depth (m)		Dive duration (sec)		<i>n</i>
	Maximum	Median	Maximum	Median	
1	40.1	12.8	107.4	54.0	61
2	34.0	28.9	95.3	75.4	55
3	42.2	28.1	100.5	76.0	50
4	no data		no data		
5	32.1	6.4	87.5	28.0	29
6	35.2	5.2	83.0	32.8	239
7	37.1	14.0	88.9	52.1	267
8	38.7	27.5	100.4	55.3	146
9	36.3	29.6	101.1	64.0	71
10	34.5	28.2	90.0	54.0	270
11	33.7	29.4	94.0	66.0	121
12	34.2	18.1	103.7	60.0	195
13	34.6	2.2	92.0	31.8	339
14	36.5	30.5	120.0	73.5	283
Total (all dives)	42.2	17.3	120.0	52.0	2112

The maximum foraging range recorded was 9 km (mean 7.2 ± 1.6 km), and the maximum total distance travelled per trip was 43.4 km (mean 17.3 ± 5.5 km) (Table 3.2). Trip duration varied between 0.3 and 7.7 hr (mean 1.7 ± 1.4 hr) (Table 3.2). We found a positive correlation between trip duration and total distance travelled per trip ($P < 0.01$, $t = 0.698$, $df = 63$, $r^2 = 0.30$) but no significant relationship between trip duration and maximum distance to the colony.

Among the 100 foraging trips observed, only three were overnight; all others were during daylight only. Moreover, diving was mainly restricted to daylight hours. There were few dives before sunrise or after sunset and none during twilight or nighttime. Diving activity was distributed bimodally through the day, with one peak in the morning between 9:00 and 10:00 and a second peak in the early evening between 17:00 and 18:00, although the frequency of dives in the intermediate hours was also substantial

(Fig. 3.4a). Dive depths were evenly distributed through the day, with no dive depth preferred at any given time (Fig. 3.4b).

Overall, we identified two distinct dive depths in this study. Cormorants most often performed shallow dives to 1 – 6 m (33%) or deep dives to 28 – 33 m (36%). Relatively few dives terminated at intermediate depths (Fig. 3.5). Although the cormorants made both deep and shallow dives throughout the day, the frequency of deep dives increased toward the afternoon (Fig. 3.6a; $P < 0.001$, $F = 6.993$, $edf = 4.116$). The two peaks of overall diving activity in the morning and late afternoon (Fig. 3.4a) correspond to similar peaks in the occurrence of shallow dives during the day (Fig. 3.6b).

Table 3.2. Summary of foraging behaviour of Pelagic Cormorants on Middleton Island, Alaska during the chick-rearing period in 2006.

Bird	Maximum range (km) ^a		Total distance travelled (km) ^b		Trip duration (hr)		n^c
	Maximum	Mean \pm SD	Maximum	Mean \pm SD	Maximum	Mean \pm SD	
1	8.9	6.4 \pm 3.6	22.4	22.2 \pm 0.3	4.0	2.9 \pm 1.6	2
2	7.8	7.7 \pm 0.1	30.4	21.2 \pm 7.9	3.1	1.7 \pm 1.3	3
3	8.4	8.2 \pm 0.2	43.4	26.1 \pm 15.0	3.2	2.3 \pm 0.8	3
4	8.6	6.6 \pm 1.7	19.2	13.6 \pm 4.7	3.4	2.0 \pm 1.0	5
5	7.8	7.5 \pm 0.3	18.1	16.5 \pm 1.6	1.8	1.3 \pm 0.6	3
6	2.6	2.2 \pm 0.4	5.3	4.6 \pm 0.8	16.4	8.8 \pm 6.8	3
7	9.0	7.1 \pm 1.9	22.1	15.1 \pm 5.1	3.6	1.8 \pm 1.2	15
8	8.2	8.0 \pm 0.2	24.9	17.1 \pm 3.7	5.1	2.2 \pm 1.5	8
9	8.7	7.7 \pm 0.4	17.4	15.3 \pm 1.5	12.8	2.9 \pm 3.9	9
10	8.2	7.0 \pm 2.0	25.0	16.5 \pm 5.8	2.4	1.5 \pm 0.5	10
11	8.2	7.0 \pm 1.9	17.9	15.0 \pm 3.9	5.7	1.8 \pm 1.4	10
12	8.1	6.6 \pm 1.8	19.6	15.4 \pm 3.3	7.7	3.0 \pm 1.8	10
13	8.5	6.7 \pm 1.8	29.1	16.0 \pm 6.0	7.2	3.6 \pm 2.3	8
14	8.5	8.0 \pm 0.2	23.3	18.7 \pm 2.2	2.5	1.7 \pm 0.4	11
Total (complete trips)	9.0	7.2 \pm 1.6	43.4	17.3 \pm 5.5	7.7	1.7 \pm 1.4	65

^a Maximum straight-line distance from the colony.

^b Distance travelled in a single foraging trip.

^c Foraging trips per bird.

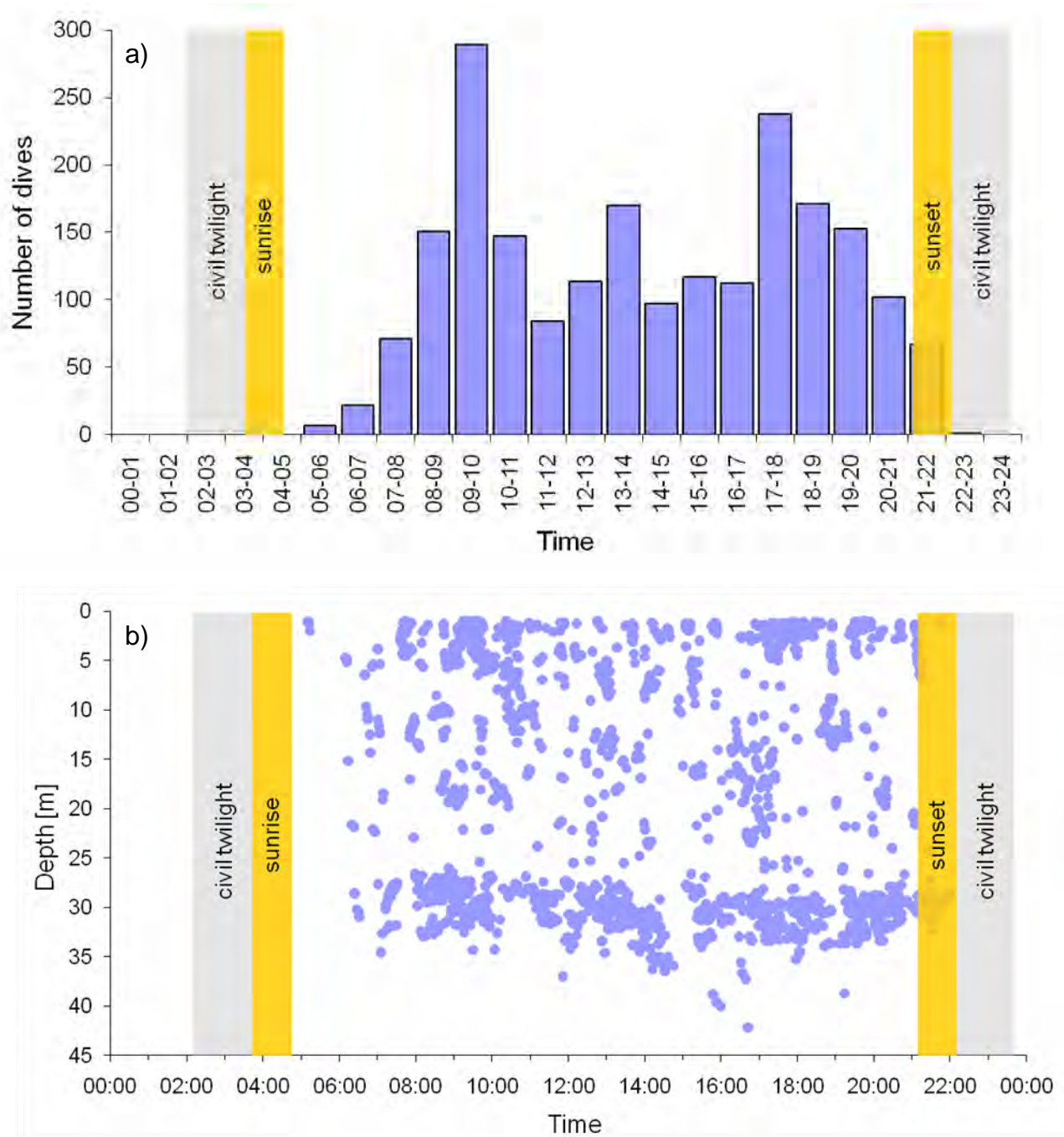


Figure 3.4. Dives of Pelagic Cormorants on Middleton Island from June – August 2006 in relation to time and daylight. (a) Frequency of dives. (b) Maximum dive depths.

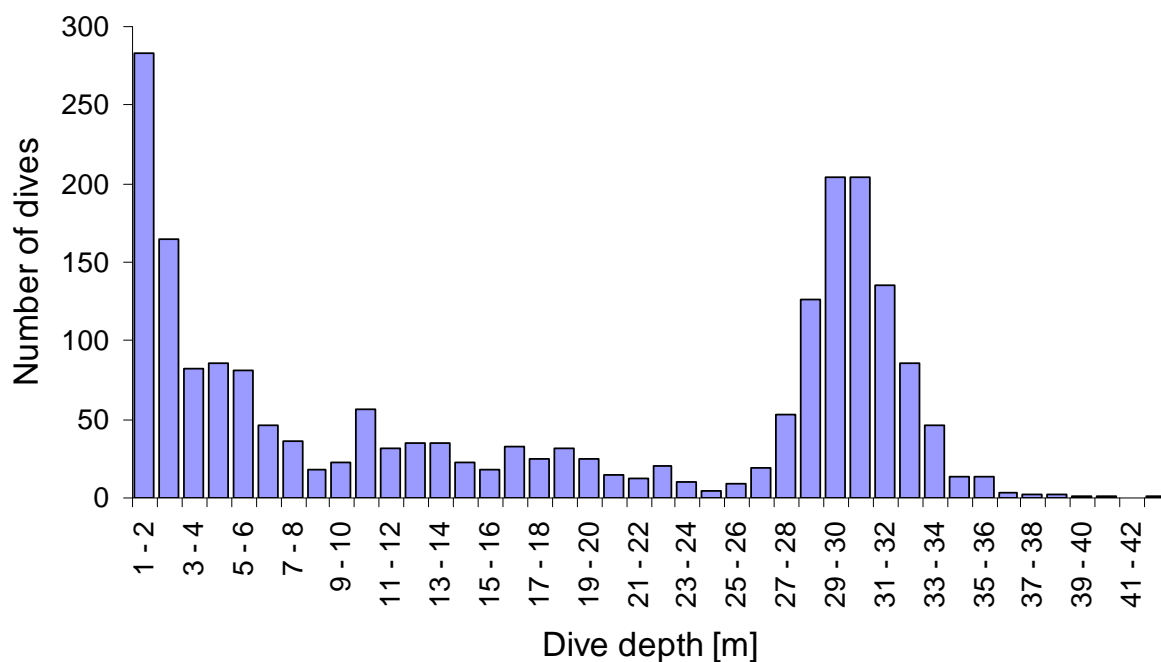


Figure 3.5. Frequency distribution of maximum dive depths by 13 Pelagic Cormorants on Middleton Island in 2006.

Shallow and deep dives had distinctly different profiles (Fig. 3.7a, b). Shallow dives included in their bottom phase depth changes of up to 2.4 m (Fig. 3.7a), consistent with foraging in the water column. Such dives (“near-surface” dives) did not reach the ocean floor. In contrast, the bottom phase of deep dives was nearly flat (Fig. 3.7b), consistent with foraging along the ocean floor (i.e., “benthic” dives). The duration of shallow dives was shorter (median 25.5 sec, CI_{95} 6.9 – 41.9 sec) than deep dives (median 70.4 sec, CI_{95} 48.8 – 100.0 sec), and the time spent at maximum depth followed the same pattern (shallow dives: median 14.0 sec, CI_{95} 0.0 – 32.0 sec; deep dives: median 26.0 sec, CI_{95} 6.0 – 55.0 sec) ($t = 10.04$ and 4.781 , respectively, $P < 0.001$, $df = 1458$, $n = 13$ birds). Pauses at the water surface between consecutive shallow dives were also shorter (median 10.0 sec, CI_{95} 0.0 – 189.6 sec) than between consecutive deep dives (median 92.0 sec, CI_{95} 38.0 – 243.6 sec) ($P < 0.001$, $t = 0.923$, $df = 1380$, $n = 13$ birds).

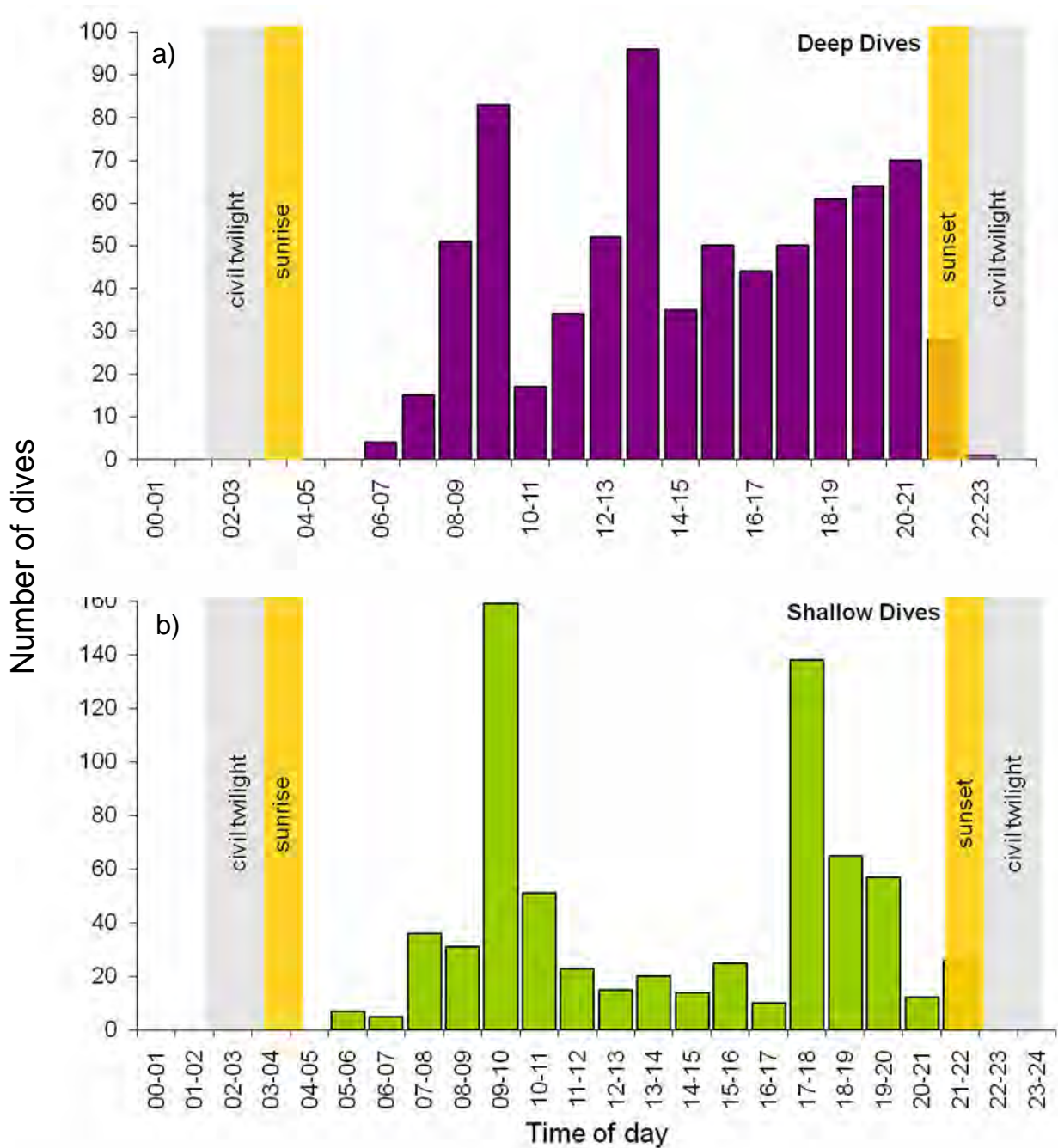


Figure 3.6. Frequency distributions of a) deep dives (28 – 33 m), and b) shallow dives (1 – 6 m) by 13 Pelagic Cormorants on Middleton Island in 2006.

The attachment of the data loggers seemed not to have influenced the behaviour of cormorants. There was no evidence that instrumented birds changed their behaviour after we attached the loggers, and the breeding success (chicks fledged/chicks hatched) of equipped (0.6 ± 0.39) and non-equipped birds (0.71 ± 0.36) did not differ significantly.

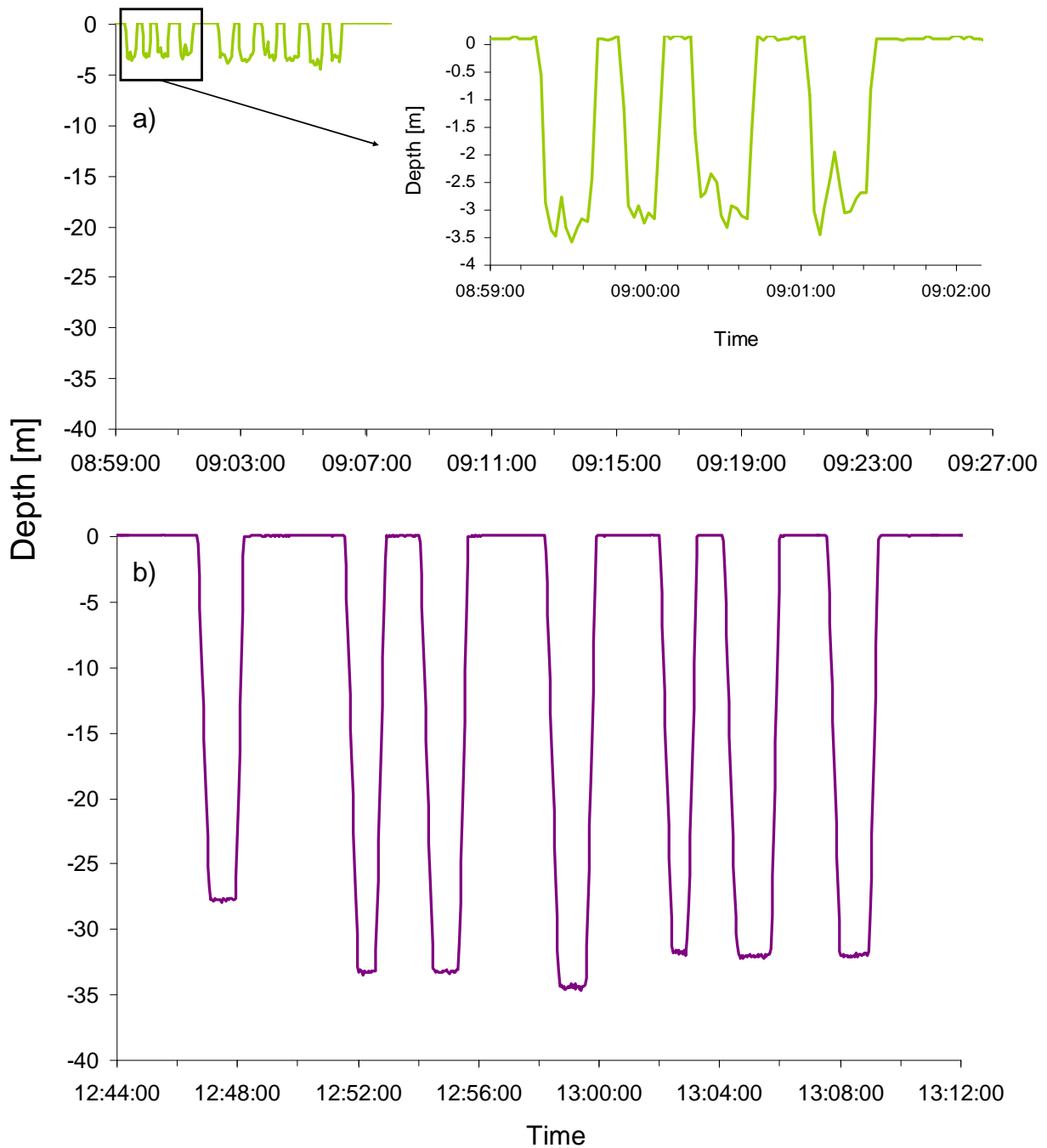


Figure 3.7. Typical dive profiles of a) shallow, near-surface dives, and b) deep, benthic dives of Pelagic Cormorants, illustrating the relative “flatness” of deep dives at the ocean floor.

Discussion

To our knowledge, our study is the first to investigate concurrently the foraging range and diving behaviour of Pelagic Cormorants with data loggers. The technology revealed foraging activity in much greater detail than was previously possible in the few studies based on observations from land or ships (Cooper 1986; Dow 1964; Hobson and Sealy 1985; Holm and Burger 2002).

Though the behaviour of birds equipped with loggers did not change noticeably, and the breeding success of equipped and non-equipped cormorants was statistically similar, it was higher for non-equipped birds. The difference might be random and independent of the loggers, but it could also be an effect of disturbance and stress on this sensitive species associated with capture, handling, or the device itself, even if outward behaviour did not change appreciably (Phillips et al. 2003; Wilson and McMahon 2006). Therefore, in further studies on this species, precaution should be taken to minimize any adverse effects.

An unexpected finding of our study on Middleton Island was the Pelagic Cormorants' near-total reliance for feeding on a small area north of the island throughout the study. All birds frequented the same area, and each bird used it on consecutive foraging trips and days. This pattern suggests that birds learned and remembered the foraging area over time and applied their knowledge on successive foraging trips (Hamer et al. 2001). Such learned behavior likely increases foraging efficiency and individual fitness (Grémillet et al. 1999; Irons 1998; Weimerskirch 2007). Other seabirds, such as the Blue-eyed Shag (*Phalacrocorax atriceps*), European Shags (*P. aristotelis*), Northern Gannets (*Morus bassanus*), Thick-billed Murre (*Uria lomvia*), or Cory's Shearwater (*Calonectris diomedea*) also have fidelity to foraging sites but typically vary more than Pelagic Cormorants on Middleton Island in their choice of feeding sites (Camphuysen 2005; Hamer et al. 2001; Mehlum et al. 2001; Navarro and González-Solís 2009; Wanless and Harris 1993). Faithfulness to a foraging site implies that prey is highly predictable in space and time. Thus, the feeding ground we identified seems to be consistently rich in prey, especially in comparison with other potential foraging areas around the colony.

It is known that seabirds forage in areas with high prey concentrations caused by interactions of currents and underwater topography (Bost et al. 2009; Ladd et al. 2005;

Piatt and Springer 2003). Yet bathymetry reveals no prominent features at the cormorants' foraging site on Middleton. The bottom topography in the primary feeding area is, if anything, slightly flatter than at other areas within the same distance of Middleton Island. The same can be said for the smaller and lesser-used feeding area to the northwest of the island, where were recorded three birds diving. Wanless et al. (1997) found that the efficiency of diving of the European Shag is greatest in areas within the range of maximum depths to which the shag dives and that offer a sediment type suitable for burrowing lesser sandeels (*Ammodytes marinus*). Similarly, we believe the relatively featureless sites Pelagic Cormorants used afford habitat that supports abundant prey—for instance, a substrate well suited for burrowing by the Pacific sand lance (*Ammodytes hexapterus*), a major prey item of the cormorants on Middleton (J. Kotzerka, unpubl. data). On the other hand, though the bathymetry of the Pelagic Cormorant's restricted foraging area shows no particular features, there might be rip currents or upwellings, which promote high concentration of nutrients and thus abundant prey.

Our results and those of Camphuysen (2005), Wanless and Harris (1993) and Wanless et al. (1997) support a general conclusion that foraging-site fidelity is common in cormorants, while some studies report reduced foraging-site fidelity owing to depletion or changing distributions of prey (Birt et al. 1987; Wanless et al. 1991). Further investigations, including diet analysis, deployment of data loggers over multiple years, direct sampling of the substrate, and measurements of primary and secondary production will be needed to explain the selection of foraging sites by Pelagic Cormorants on Middleton fully.

Like other cormorants, such as the European and Imperial Shags (Croxall et al. 1991; Wanless et al. 1999), Great Cormorant (*Phalacrocorax carbo*; Grémillet et al. 2004a) and Rock Shags (*Phalacrocorax magellanicus*; Quintana 2001), the Pelagic Cormorant feeds only by day. We recorded scarcely any dives between dusk and dawn, suggesting that this species is a visual predator exclusively. An exception to the rule was reported by Grémillet et al. (2005), who observed Great Cormorants diving in darkness through the polar night in western Greenland.

We found two peaks of diving, one in the morning and a second in the afternoon. Both peaks reflected a high frequency of dives shallower than 6 m. This diving behaviour might be related to diurnal vertical migration of the sand lance (Ainley et al. 1981; Robertson 1974). Sand lance schools migrate vertically through the day, spending the

daytime in the water column and burrowing themselves in the sediment at night (Robards et al. 1999). Freeman et al (2004) found schools of lesser sandeels in the water column at the same times of the day that Pelagic Cormorants made more shallow dives. Higher frequencies of deep dives in the late afternoon could be a result of birds following the sand lance back to the sea floor, where they pick them out of the substrate. Cormorants did at times obtain prey directly from the substrate, as attested by the occasional appearance of small particles of gravel in regurgitated pellets (J. Kotzerka, pers. obs.).

The foraging range, maximum distance to colony, and trip duration of the Pelagic Cormorants we studied agree generally with values for close relatives like the European Shag (Camphuysen 2005; Daunt et al. 2007; Wanless et al. 1991; 1998) and Rock Shag (Frere et al. 2008), although at some colonies the latter species' foraging range is more restricted (Sapoznikow and Quintana 2003). We found Pelagic Cormorants' dive depths to be similar to and their dives to be slightly briefer than those of the European Shag (Camphuysen 2005; Wanless et al. 1998; Wanless et al. 1999) but that their dive depths were much greater than and their dives to last somewhat longer than those of the Great Cormorant (Grémillet et al. 1999). Durations of Pelagic Cormorant dives measured by Dow (1964) , Hobson and Sealy (1985) and Cooper (1986) were shorter on average than those on Middleton, and the maximum durations we recorded were twice as long. Data from the previous studies pertain mostly to cormorants diving in shallow water, where briefer dives are expected. The relationship is evident in our data, in which dive duration was positively correlated with dive depth. If we are considering shallow dives only, the mean dive duration on Middleton was similar to that reported by the previous studies.

We found a prevalence of two very distinct dive types—shallow near-surface dives (33%) and deep benthic dives (36%). Foraging both benthically and pelagically opens up a potentially very wide spectrum of prey (Grémillet et al. 1999). European Shags, Blue-eyed Shags, and Great Cormorants also forage by both strategies, but in those species near-surface dives appear to be used less common (Grémillet et al. 1998; Grémillet et al. 1999; Wanless and Harris 1993). Furthermore, both preferred dive depths were subject to individual preferences and could be seen as an individuals' specialization in foraging habitat, especially in a colony with a very restricted foraging area. The tendency for cormorants on Middleton Island to specialize on either near-surface or benthic foraging

may help to reduce intraspecific competition for food but could also be related to the birds' age or diving experience (Ainley et al. 1981; Ropert-Coudert et al. 2003; Stephens and Krebs 1987). Individual specialization in foraging behaviour has been reported in other cormorants (Ainley et al. 1981) and in diving petrels (Bocher et al. 2000). Sexual differences in diving behaviour are known in some species of cormorants (Kato et al. 1999), but we excluded that explanation as we sampled only males.

In summary, we found that foraging of Pelagic Cormorants on Middleton Island was highly concentrated in a small area. The cormorants had high fidelity to the foraging site throughout chick rearing. Birds had flexibility in their choice of diving depths, and many had an individual preference for either near-surface or benthic dives. Learning and consistent feeding in patches with abundant prey save time and energy allocated to foraging. They enable birds to spend more time guarding their young at the nest site, which should promote breeding success. But over-reliance on a narrow range of foraging substrates and prey species may not be sustainable in the event of changes in habitat or prey populations. We hypothesize that the fluctuations of the cormorant population on Middleton Island arise in part because of the narrow scope of the foraging behaviour we observed. Research on the distribution and behaviour of the Pelagic Cormorant's prey on Middleton is needed, as is an assessment of foraging-site fidelity over multiple years. An inability of the cormorants to change to other foraging areas in years of reduced prey abundance would make them vulnerable to changing environmental conditions.

Acknowledgements

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Chapter IV



***Individual specialization in the diving behaviour of a widespread
North Pacific marine predator***

Individual specialization in the diving behaviour of a widespread North Pacific marine predator

Abstract

Foraging behaviour in many seabird species is specialized with different species exhibiting different prey capture techniques, using different prey search locations or foraging at different times of the day. This species-specific specialization is mainly due to morphological constraints but also controls interspecific competition for prey. But competition for food resources can also occur between individuals of the same species when the foraging habitat is limited. This is especially true during the breeding season when seabirds are central-place foragers and have to search for food in a limited area around their colonies. Therefore, individual specialization is widespread in seabirds and is a major aspect of foraging ecology. This individual specialization is often gender or age related and is potentially high in diving seabird species.

In this study we examined the foraging behaviour of Pelagic Cormorants (*Phalacrocorax pelagicus*) on Middleton Island in the Gulf of Alaska over three successive years, with special attention on individual birds that were tagged during two or three consecutive years, respectively. All cormorants showed high foraging-site fidelity over all study years but foraging trip parameters and diving behaviour differed in some aspects between the three years. The reliance on that restricted foraging site seems to evolve individual-specific diving behaviour. Nearly half (46%) of the individually observed birds did not differ in their diving behaviour or foraging trip parameters between the study years, indicating a individual specialization of their foraging behaviour not only during one season but also in consecutive years. Such specialization might be a strategy to avoid intraspecific competition when relying on a narrow foraging area. Thus, individual specialization might be advantageous for the breeding effort but the inability to use or move to other foraging areas could also be critical in case of changing environmental conditions.

Keywords: GPS data logger, diving behaviour, foraging behaviour, foraging-site fidelity, Gulf of Alaska, individual specialization, Pelagic Cormorant, *Phalacrocorax pelagicus*, time-depth recorder

Introduction

One basic principle of animal ecology predicts that species can only coexist in the same place when their ecology differs (Gause 1934). If two species or individuals of the same species have the same requirement for a specific resource interspecific or intraspecific competition plays a major role in the daily routine of survival, growth and reproduction. This can result in the reduction in numbers of one species or individuals by resource exploitation or interference with each other and influences population dynamics and distribution (Begon et al. 2006). With that it plays a major role in structuring avian communities (Cody 1974). Competition can be reduced by having different geographical distributions, using different habitats or by feeding on different prey organism (Lack 1971).

Seabird colonies are often large due to the limitations of suitable nesting habitat, predator defence, socialization and information transfer (Coulson 2002). But consequently, food shortage around the colony may become a major issue as a result of individuals competing for the same prey species and -size (Forero et al. 2002; Lewis et al. 2001; Ronconi and Burger 2011). Seabirds developed a multitude of different foraging strategies in order to prey successfully on patchy marine food. They have evolved different species-specific morphological and physiological adaptations to exploit the various food resources of their marine environment. They forage coastal, inshore, or offshore for food, and search for prey using different diving or surface feeding techniques, use different prey species or forage during night or day (Shealer 2002). During the breeding season seabirds are central-place foragers searching for food in a limited range around their nests or colonies. This range is restricted by oceanographic conditions that predict prey abundances (e. g. bathymetry, ocean productivity) and the capabilities of movements of a given species (Ballance et al. 2001; Burke and Montevecchi 2009; Paiva et al. 2010b; Shaffer et al. 2009).

An important aspect of foraging ecology is the extent to which individuals of a given population differ in their foraging behaviour (Bearhop et al. 2006). Individual specialization is widespread and has important implications for evolutionary, ecological and conservational aspects. It is one factor which contributes to intrapopulation niche variation and can be expressed as physiological, behavioural and ecological mechanisms (Bolnick et al. 2003).

In many species, including seabirds, specialization is often revealed as gender-related differences due to sexual dimorphism and associated foraging capacities (e. g. deeper diving ability of heavier individuals, different breeding behaviour, unequal nutritional or energetic requirements) or age-related differences, like experience or dominance (Greig et al. 1983; Hudson 1989; Ishikawa and Watanuki 2002; Magurran and Garcia 2000; Weimerskirch et al. 2006). But individual specialization within a population can also vary in their foraging behaviour regardless of their age or sex due to variation in their morphology, physiology, dominance or limited memory capacity (see in Woo et al. 2008) or as a result of intraspecific competition. Especially among diving seabirds, which are often highly colonial and have limited foraging ranges, the potential for intraspecific competition is high and might be predictable (Bearhop et al. 2006). Particularly for shags *Phalacrocorax* spp. sex-specific foraging behaviour could be shown in several studies (Casaux et al. 2001; Ishikawa and Watanuki 2002; Kato et al. 1999; Kato et al. 2000). Individual foraging specialization was observed in Blue-eyed Shags (*Phalacrocorax atriceps*) at South Georgia (Wanless et al. 1992a; Wanless and Harris 1993). But these studies were only performed during one breeding season and cannot give evidence about the consistency of such behaviour. From those studies it is not possible to derive whether the specialization is due to environmental circumstances in one breeding season (as shown for Japanese Cormorants *Phalacrocorax capillatus*, Ishikawa and Watanuki 2002) or whether it is consistent over several years and thus an individual specific specialization, as shown for Thick-billed Murres *Uria lomvia* (Elliott et al. 2009; Woo et al. 2008).

In this paper, we examine the foraging behaviour of Pelagic Cormorants (*Phalacrocorax pelagicus*) on Middleton Island in the Gulf of Alaska over three successive years in general, and with emphasis on individual birds that were tagged during two or three consecutive years, respectively. During an earlier study of the foraging behaviour of Pelagic Cormorants covering only one season, we found an indication of individual

specialization in the diving behaviour and strong foraging-site fidelity of this species (Kotzerka et al. 2011). The observed high foraging-site fidelity, and thus possible limited foraging space, may lead to individual specialization in foraging behaviour. This evidence was further investigated regarding the consistency of the individual specialization over longer time periods to unravel the degree of individual specialization. Hence, we compared general foraging trip parameters and diving behaviour of each individual between the study years and tested these with Generalized Linear Mixed Effect Models.

Methods

Study area

We studied the foraging and diving behaviour of Pelagic Cormorants on Middleton Island in the northern Gulf of Alaska (59.4° N, 146.3° W, Fig. 4.1) during three consecutive breeding seasons from 2006 to 2008. The island is situated at the edge of a broad unsheltered continental shelf area and close to a steep submarine slope (about 10 – 15 km south of the island).

During each of the breeding seasons from 2006 to 2008 about 1300 pairs of Pelagic Cormorants were breeding on the island. One part of this breeding population is nesting on an old U.S. Air Force radar tower that was decommissioned and derelict since the 1960s, and to which artificial nest sites have been constructed for research purposes. This artificial nest sites supported between 152 and 206 Pelagic Cormorant nests in each of the study years, mainly using wooden ledges viewable from inside the building through sliding panes of one-way mirror glass (Gill and Hatch 2002).

We caught 14 (all males), 22 (18 males, 4 females) and 28 birds (15 males, 10 females) rearing chicks between June and August of each breeding season. The sex was determined by their bands applied in previous studies or by bill size (Hobson 1997). The higher male ratios in 2006 and 2007 were due to the logger size used during the study (see next paragraph). Males have a larger body size than females and thus a more favourable ratio of body mass to device mass. All nests of the tower breeding colony were checked each morning for their status of eggs and chicks and the presence of the adults.

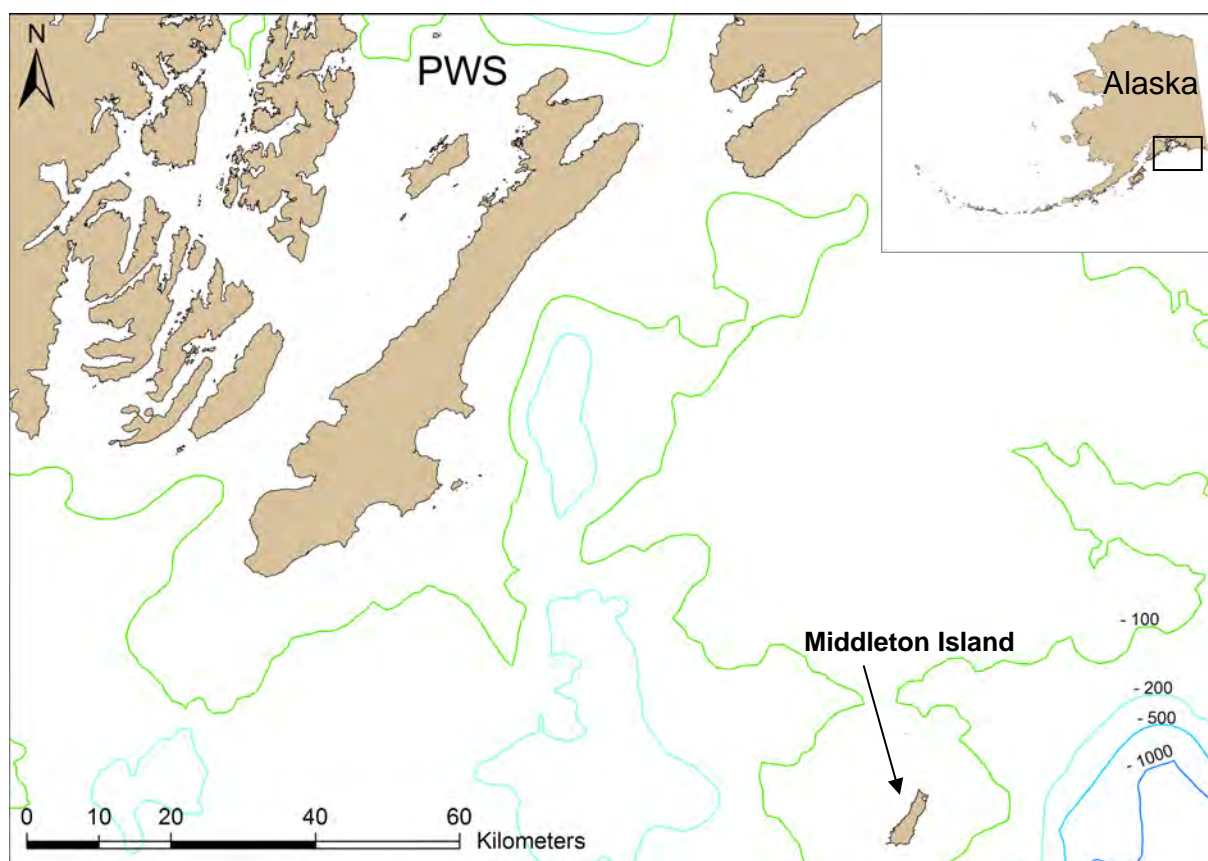


Figure 4.1. Study area in the Gulf of Alaska showing the locations of Middleton Island and Prince William Sound (PWS). Middleton Island is located about 80 km south of the Alaska mainland. Depth contours are shown as indicated in the figure.

Data loggers

During the first season in 2006 we deployed GPS data loggers (70 g, dimensions 100 × 48 × 24 mm) with integrated pressure and temperature sensors (earth & Ocean Technologies, Kiel, Germany). In addition, during the following two seasons we also used MiniGPS loggers (26 g, dimensions 46.5 × 32 × 18.5 mm) and PreciTD's (Precision Temperature-Depth recorders; 16 g, Ø 19 mm, length 75 mm), both also from earth & Ocean Technologies, Kiel, Germany. The GPS data loggers were deployed on males; females were equipped with MiniGPS loggers and PreciTD's. All those loggers were temporarily attached to feathers of the lower back with waterproof TESA® tape (Wilson et al. 1997).

Both types of GPS loggers had the same positional accuracy. Usually 65 % of all positions were within a circle of 10 m around the actual position and 90 % were within

19 m. During the first season in 2006 the GPS loggers sampled the date, time, longitude, latitude and speed at intervals of 1, 2 or 3 min (different birds had different intervals). The integrated pressure and temperature sensors of the GPS data loggers were set to record the pressure and temperature (with corresponding date and time) every 1 or 2 seconds (different birds had different sampling intervals). In the following seasons 2007 and 2008 all GPS loggers sampled the above mentioned parameters at 2 min intervals and the integrated pressure and temperature sensors as well as the PreciTD's sampled the pressure and temperature (with corresponding date and time) at 1 s periods.

Upon capture, we weighed each bird to the nearest 10 g using a spring balance. The mean body mass for males was 1.86 kg (range: 1.6 – 2.13 kg) and the mean body mass for females was 1.43 kg (range: 1.28 – 1.5 kg). The loggers represented around 3.8 % (range: 3.3 – 4.4 %) for the males and about 3.0 % (range: 2.9 – 3.4 %) of the females body weight. These body mass – device mass ratios are within the range where device induced effects on birds are usually minor (Phillips et al. 2003). After 1 – 11 days (mean 4 days) birds were re-captured and the loggers removed. In order to exclude capture biased foraging behaviour all loggers had a delayed start. Recording of GPS positions and diving parameters began only the next morning after capture. To compare the breeding success of equipped and non-equipped birds we used 77, 106 and 72 unmanipulated nests of the tower colony as control groups in 2006, 2007 and 2008, respectively.

Statistical analysis

We plotted the obtained GPS positions in ArcGIS® 9.2 (ESRI, Redlands, CA) for visualization of the foraging areas and calculated the maximum foraging range (km; maximum distance in a straight line from the nest), total distance travelled (km; summed distance between start and end position for each individual foraging trip) and trip duration (h; elapsed time between start and end of a foraging trip). For the analysis of the data on dive parameters we used an individually written Matlab script by T. Mattern. Vertical immersions deeper than 1 m were considered as a foraging dive. With this analysis of the dive data we then calculated the maximum dive depth (m; most distant dive depth from the water surface during a dive), dive duration (min; time between start

and end of a dive), bottom duration (min; time spend at the max. dive depth) and surface duration (min; time between consecutive dives during a dive bout).

We statistically compared individual foraging and diving behaviour between different years using the open source software R 2.10.1 (R Development Core Team 2009) applying Generalized Linear Mixed Effect Models (GLMM's, Faraway 2006). Differences in breeding success were analysed using a Generalized Linear Model (GLM's, Faraway 2006). Mean values are reported \pm SD.

Results

All birds sampled in 2006, 2007 and 2008 showed high foraging-site fidelity to the same area in all three years (Fig. 4.2a - c). The foraging areas in 2006 and 2007 were nearly identical. All birds foraged in north-western direction of the colony. In the following year (2008) the birds used the same area as in both years before. They mainly foraged to the north and north-west of their colony, but additionally expanded that area slightly to the east. Although the foraging area appears to have been the same in all three years, foraging trip duration and max. distance to the colony were significantly different between all three years. Mean trip duration was longest in 2008, and shortest in 2007. Mean max. distance to colony was furthest in 2006 and closest in 2007. Total distance travelled was only similar among 2006 and 2008, but significantly different between 2006 and 2007 and between 2007 and 2008. It was shorter in 2007 than in both other years (Table 4.1).

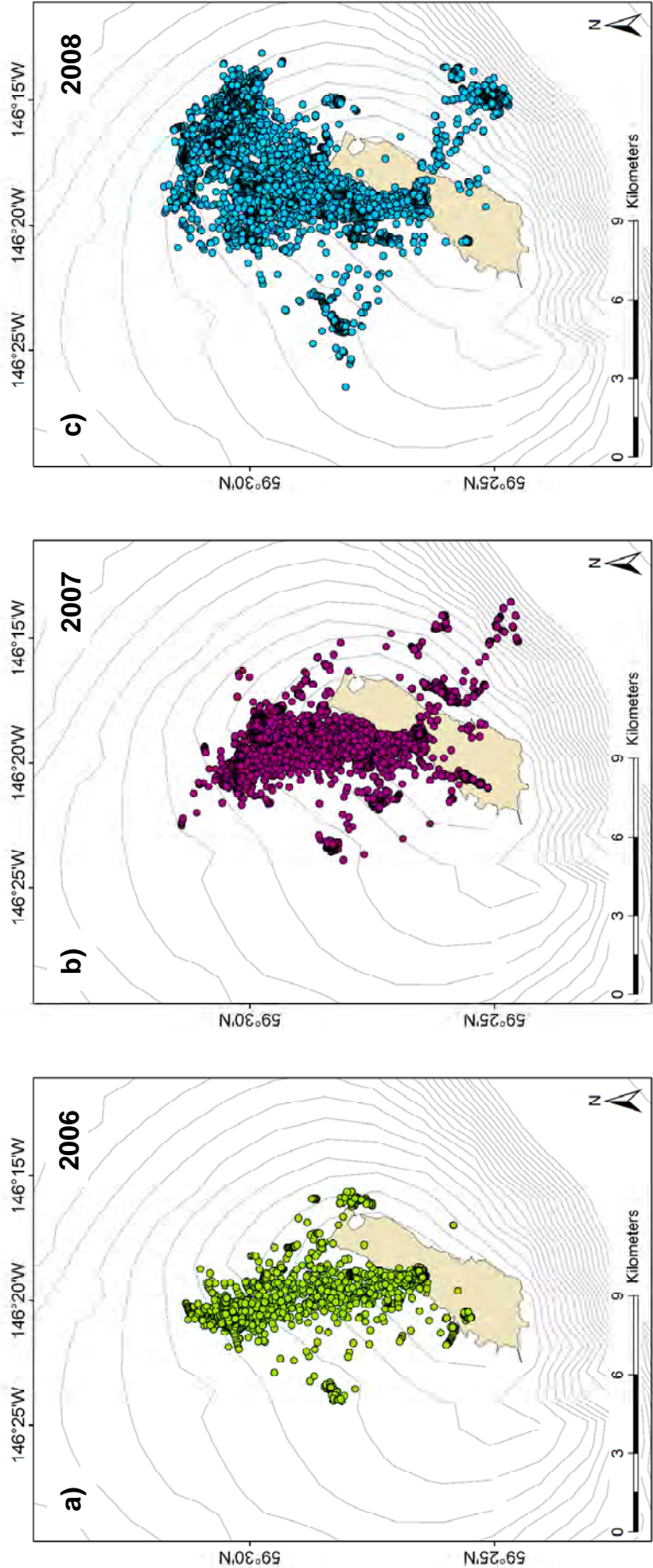


Figure 4.2. Foraging locations of all Pelagic Cormorants during the breeding seasons 2006 (a), 2007 (b) and 2008 (c) on Middleton Island, Gulf of Alaska, indicating the high foraging site fidelity during all three study years Depth contours indicate bathymetric isobars in 10-m intervals.

Table 4.1. Foraging and diving behaviour of individual and all Pelagic Cormorants sampled in consecutive years. The P-value explains the difference between the two or three samples years. n. s. = not significant, n. t. = not tested due to too small sample size, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, 1) Order of P-values: difference between 2006 and 2007, 2006 and 2008, 2007 and 2008

Bird		2006	2007	2008	P-value
		mean \pm SD (n)	mean \pm SD (n)	mean \pm SD (n)	
O-1	trip duration (h)	1.6 \pm 1.3 (3)	0.9 \pm 0.2 (8)	-	n. s
	max. dist. (km)	8.1 \pm 0.5 (3)	6.4 \pm 0.3 (8)	-	*
	total dist. (km)	16.3 \pm 1.0 (3)	15.4 \pm 4.1 (8)	-	n. s
	max. dive depth (m)	26.5 \pm 7.7 (64)	21.5 \pm 4.0 (152)	-	***
	dive dur. (s)	60.8 \pm 17.4 (64)	56.8 \pm 11.7 (152)	-	n. s
	bottom dur. (s)	20.1 \pm 13.2 (64)	26.2 \pm 11.0 (152)	-	**
	surface dur. (s)	131.6 \pm 109.9 (54)	68.7 \pm 51.3 (139)	-	**
O-14	trip duration (h)	no data	1.1 \pm 0.4 (15)	-	-
	max. dist. (km)	no data	4.2 \pm 1.3 (15)	-	-
	total dist. (km)	no data	11.7 \pm 5.4 (15)	-	-
	max. dive depth (m)	6.8 \pm 7.7 (229)	10.0 \pm 4.9 (459)	-	n. s
	dive dur. (s)	30.5 \pm 15.8 (229)	38.4 \pm 9.9 (459)	-	n. s
	bottom dur. (s)	16.9 \pm 9.8 (229)	21.4 \pm 7.4 (459)	-	**
P-6	surface dur. (s)	35.2 \pm 80.3 (218)	32.1 \pm 26.0 (442)	-	n. s
	trip duration (h)	1.5 \pm 0.5 (10)	1.2 \pm 1.1 (12)	-	n. s
	max. dist. (km)	7.0 \pm 2.0 (10)	6.1 \pm 1.4 (12)	-	n. s
	total dist. (km)	16.5 \pm 5.8 (10)	17.1 \pm 12.7 (12)	-	n. s
	max. dive depth (m)	20.3 \pm 12.1 (250)	21.4 \pm 5.0 (164)	-	n. s
	dive dur. (s)	45.4 \pm 20.8 (250)	65.5 \pm 13.9 (164)	-	***
	bottom dur. (s)	13.7 \pm 9.5 (250)	34.0 \pm 12.5 (164)	-	***
P-13	surface dur. (s)	84.2 \pm 93.6 (238)	93.7 \pm 70.1 (149)	-	n. s
	trip duration (h)	1.8 (1)	1.4 \pm 0.4 (11)	-	n. s
	max. dist. (km)	3.9 (1)	5.8 \pm 0.9 (11)	-	n. s
	total dist. (km)	21.9 (1)	16.1 \pm 5.4 (11)	-	n. s
	max. dive depth (m)	14.5 \pm 7.6 (60)	15.7 \pm 5.3 (303)	-	n. s.
	dive dur. (s)	54.1 \pm 16.3 (60)	48.0 \pm 11.4 (303)	-	*
	bottom dur. (s)	31.5 \pm 8.4 (60)	23.9 \pm 8.5 (303)	-	**
K-10	surface dur. (s)	83.9 \pm 117.4 (57)	58.6 \pm 64.8 (291)	-	n. s.
	trip duration (h)	-	1.4 \pm 0.2 (9)	2.2 \pm 0.5 (10)	*
	max. dist. (km)	-	5.6 \pm 0.7 (9)	7.4 \pm 1.3 (10)	n. s.
	total dist. (km)	-	15.5 \pm 5.0 (9)	22.5 \pm 9.8 (10)	n. s.
	max. dive depth (m)	-	17.3 \pm 5.8 (349)	28.9 \pm 9.8 (435)	**
	dive dur. (s)	-	45.8 \pm 10.3 (349)	73.2 \pm 19.7 (435)	***
	bottom dur. (s)	-	20.2 \pm 8.8 (349)	33.2 \pm 13.3 (435)	***
L-10	surface dur. (s)	-	36.3 \pm 37.6 (340)	89.5 \pm 62.1 (424)	**
	trip duration (h)	-	1.3 \pm 0.5 (9)	3.0 \pm 2.5 (10)	n. s.
	max. dist. (km)	-	6.6 \pm 0.5 (9)	7.9 \pm 1.4 (10)	n. s.
	total dist. (km)	-	17.8 \pm 4.8 (9)	22.8 \pm 10.4 (10)	n. s.
	max. dive depth (m)	-	15.8 \pm 9.4 (139)	27.3 \pm 7.9 (377)	**
	dive dur. (s)	-	41.9 \pm 22.0 (139)	86.1 \pm 22.1 (377)	***
	bottom dur. (s)	-	21.8 \pm 18.2 (139)	45.2 \pm 15.5 (377)	***
L-12	surface dur. (s)	-	66.9 \pm 84.8 (128)	125.8 \pm 74.0 (365)	**
	trip duration (h)	-	1.0 \pm 0.3 (11)	2.1 \pm 0.4 (11)	***
	max. dist. (km)	-	6.4 \pm 0.6 (11)	7.9 \pm 0.2 (11)	***
	total dist. (km)	-	15.0 \pm 3.0 (11)	20.8 \pm 3.0 (11)	***
	max. dive depth (m)	-	16.3 \pm 8.8 (229)	31.9 \pm 5.1 (352)	*
	dive dur. (s)	-	44.8 \pm 18.5 (229)	81.3 \pm 12.9 (352)	***
	bottom dur. (s)	-	19.6 \pm 10.0 (229)	35.5 \pm 12.1 (352)	***
O-13	surface dur. (s)	-	61.6 \pm 68.9 (215)	112.6 \pm 51.9 (340)	***
	trip duration (h)	-	0.9 \pm 0.1 (9)	1.9 \pm 0.7 (9)	**
	max. dist. (km)	-	4.4 \pm 0.4 (9)	4.6 \pm 1.0 (9)	n. s.
	total dist. (km)	-	10.6 \pm 3.6 (9)	17.6 \pm 9.1 (9)	n. s.
	max. dive depth (m)	-	11.6 \pm 3.6 (181)	12.8 \pm 2.3 (478)	*
	dive dur. (s)	-	48.4 \pm 12.6 (181)	51.8 \pm 7.6 (478)	*
	bottom dur. (s)	-	30.7 \pm 10.3 (181)	31.3 \pm 7.1 (478)	n. s.
surface dur. (s)	-	63.3 \pm 71.9 (172)	56.1 \pm 44.0 (469)	n. s.	

Table 4.1. continued...

Bird	Year			P-value	
	2006	2007	2008		
	mean ± SD (n)	mean ± SD (n)	mean ± SD (n)		
O-10	trip duration (h)	2.3 ± 0.8 (3)	1.0 ± 0.4 (10)	2.0 ± 0.8 (10)	*, n. s., ** ¹⁾
	max. dist. (km)	8.2 ± 0.2 (3)	5.5 ± 1.3 (10)	6.9 ± 1.9 (10)	*, n. t., * ¹⁾
	total dist. (km)	26.1 ± 15.0 (3)	12.1 ± 2.8 (10)	18.3 ± 5.9 (10)	n. s., n. s., ** ¹⁾
	max. dive depth (m)	24.5 ± 9.8 (43)	16.0 ± 6.5 (145)	21.4 ± 10.3 (294)	***, n. s., * ¹⁾
	dive dur. (s)	67.3 ± 21.7 (43)	49.1 ± 17.0 (145)	72.0 ± 28.1 (294)	** , n. s., ** ¹⁾
	bottom dur. (s)	29.7 ± 12.8 (43)	28.6 ± 21.1 (145)	41.9 ± 17.9 (294)	n. s., n. s., * ¹⁾
	surface dur. (s)	130.6 ± 94.5 (38)	67.4 ± 84.0 (133)	102.2 ± 85.7 (281)	** , n. s., ** ¹⁾
all birds combined	trip duration (h)	1.7 ± 1.1 (65)	1.2 ± 0.9 (203)	2.4 ± 1.2 (193)	** , * , *** ¹⁾
	max. dist. (km)	7.2 ± 1.6 (65)	5.7 ± 1.5 (203)	6.3 ± 2.0 (193)	*** , * , ** ¹⁾
	total dist. (km)	17.3 ± 5.5 (65)	14.1 ± 5.6 (203)	17.3 ± 8.0 (193)	*** , n. s., *** ¹⁾
	max. dive depth (m)	19.7 ± 11.4 (1746)	13.9 ± 6.7 (7538)	18.1 ± 9.6 (12542)	* , n. s., *** ¹⁾
	dive dur. (s)	52.9 ± 22.8 (1746)	45.5 ± 15.2 (7538)	61.2 ± 23.5 (12542)	n. s., n. s., *** ¹⁾
	bottom dur. (s)	21.7 ± 17.0 (1746)	23.7 ± 12.6 (7538)	33.7 ± 14.8 (12542)	** , *** , *** ¹⁾
	surface dur. (s)	89.6 ± 94.7 (1629)	46.5 ± 55.5 (7236)	68.1 ± 70.2 (12287)	*** , n. s., *** ¹⁾

Diving behaviour was also not consistent among the three study years. Bottom duration was different in all years. Mean max. dive depth and surface duration were only alike in 2006 and 2008, but not between 2006 and 2007 or 2007 and 2008. Dive duration varied only among 2007 and 2008, but not between 2006 and 2007 or 2006 and 2008. There was high variability in all of these parameters in all years (Table 4.1).

Of those birds equipped during the three study years we were able to sample 8 birds in two consecutive years. Four birds were sampled in both years 2006 and 2007 (O-1, O-14, P-6, P-13) and another 4 birds were sampled in both years 2007 and 2008 (K-10, L-10, L-12, O-13). One additional individual was sampled in all three years (O-10). All of these birds were males.

The individual-based foraging-site faithfulness was high, although it was higher between 2006 and 2007 than between 2007 and 2008. Individual birds, which were sampled in 2006 and 2007, had more or less the same foraging site in both years (Fig. 4.3). Birds, which were sampled in 2007 and 2008 also had the same foraging site in both years, but in addition also used an area northeast of the colony and thus reflect the overall pattern of the foraging areas used by of all birds in all three years (Fig. 4.4). The same pattern of foraging areas used throughout 2006, 2007 and 2008 is shown by bird O-10 (Fig. 4.5). The diving behaviour and foraging trips of these 9 birds were in many parts similar during the study years. Nearly half of the birds sampled in consecutive years (46%) were consistent in their foraging trips and diving behaviour throughout the years (Table 4.1).

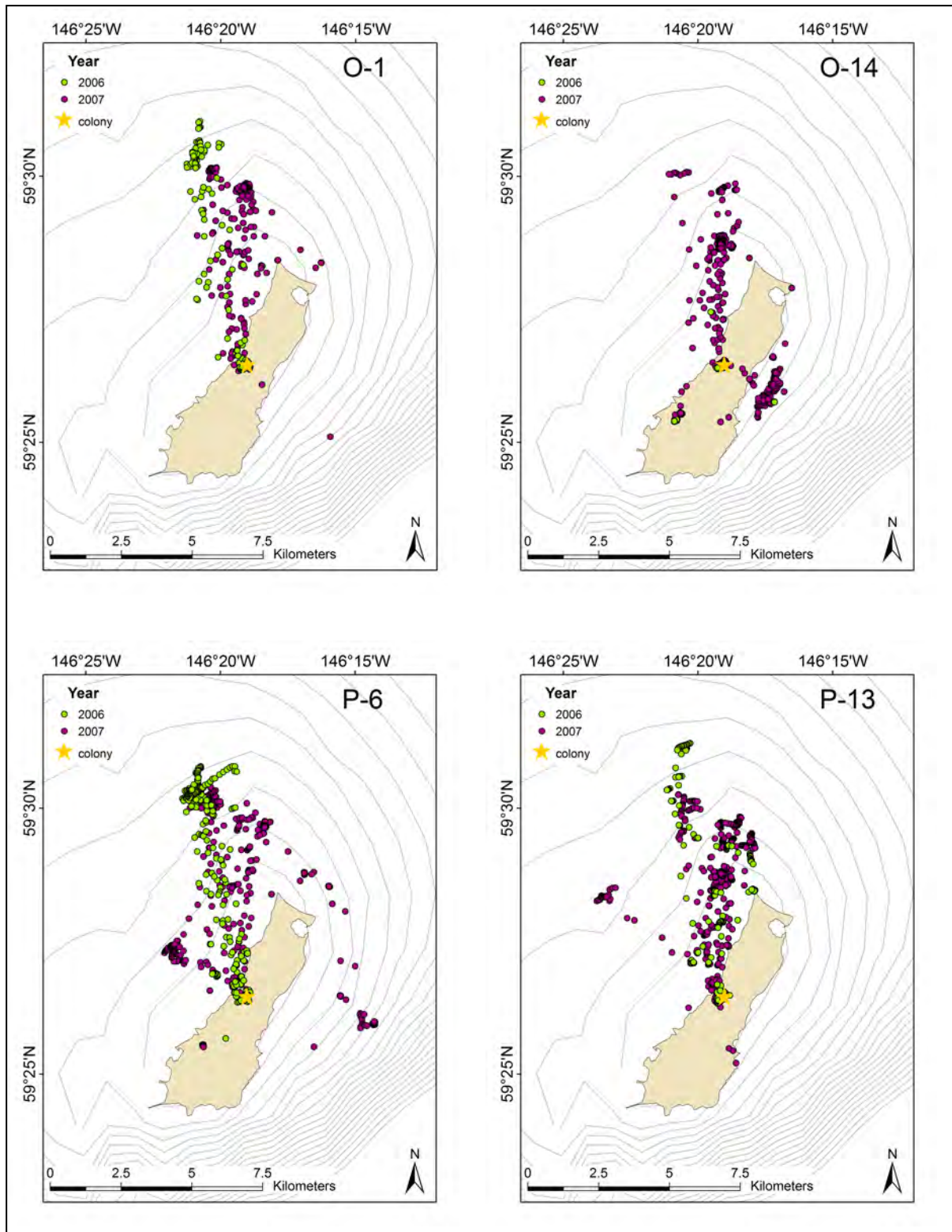


Figure 4.3. Foraging locations of four Pelagic Cormorants O-1, O-14, P-6 and P-13 sampled during the consecutive breeding seasons 2006 and 2007 on Middleton Island, Gulf of Alaska indicating high individual foraging-site fidelity during both study years.

In particular, of the four birds sampled in 2006 and 2007, bird O-1 had no significant differences in trip duration and total distance travelled. But the max. distance to the colony was significantly higher in 2006 than in 2007. Birds P-6 and P-13 showed no significant differences in trip duration, max. distance to the colony or total distance travelled between both sampled years 2006 and 2007. For the fourth bird sampled in 2006 and 2007, O-14, a comparison of the foraging trip parameters trip duration, max. distance to the colony and total distance travelled is not possible due to too fragmented GPS positions in 2006. Regarding the diving behaviour birds O-14, P-6 and P-13 had no significant differences in the max. dive depth and surface duration between 2006 and 2007. For both birds O-1 and O-14 the dive duration was not different among these two years, but it was significantly different for the birds P-6 and P-13. Furthermore, O-1 had significant greater max. dive depths and longer surface durations in 2006 than in 2007 and all four birds sampled in 2006 and 2007 showed different bottom durations. Bottom duration was significantly shorter in 2006 for the birds O-1, O-14 and P-6, and significantly longer for bird P-13.

Of the four birds sampled in 2007 and 2008 one bird (L-10) showed no significant differences in trip duration, max. distance to the colony and total distance travelled between both years. In contrast, for bird L-12 these three parameters were significantly longer and further in 2008 than in 2007. The remaining two birds K-10 and O-13 showed significant differences in trip duration (longer in 2008 than in 2007) but max. distance to colony and total distance travelled were not significantly different. The diving behaviour of the three birds K-10, L-10 and L-12 was different in 2007 than 2008. All three birds had deeper max. dive depths, longer dive durations and bottom durations as well as surface durations in 2008. Bird O-13 performed also significantly deeper and longer dives in 2008, but bottom duration and surface duration were not different between 2007 and 2008.

The one bird that was sampled in all three years, O-10, showed a variable foraging and diving behaviour throughout the three years. Foraging trip duration and max. distance to colony were similar between 2006 and 2008, but not between 2006 and 2007 or 2007 and 2008. Trips lasted longer and were farther from the colony in 2006 and 2008 than in 2007. Total distance travelled was only significantly different between 2007 and 2008, with having greater total distances in 2008. The diving behaviour showed a likewise pattern.

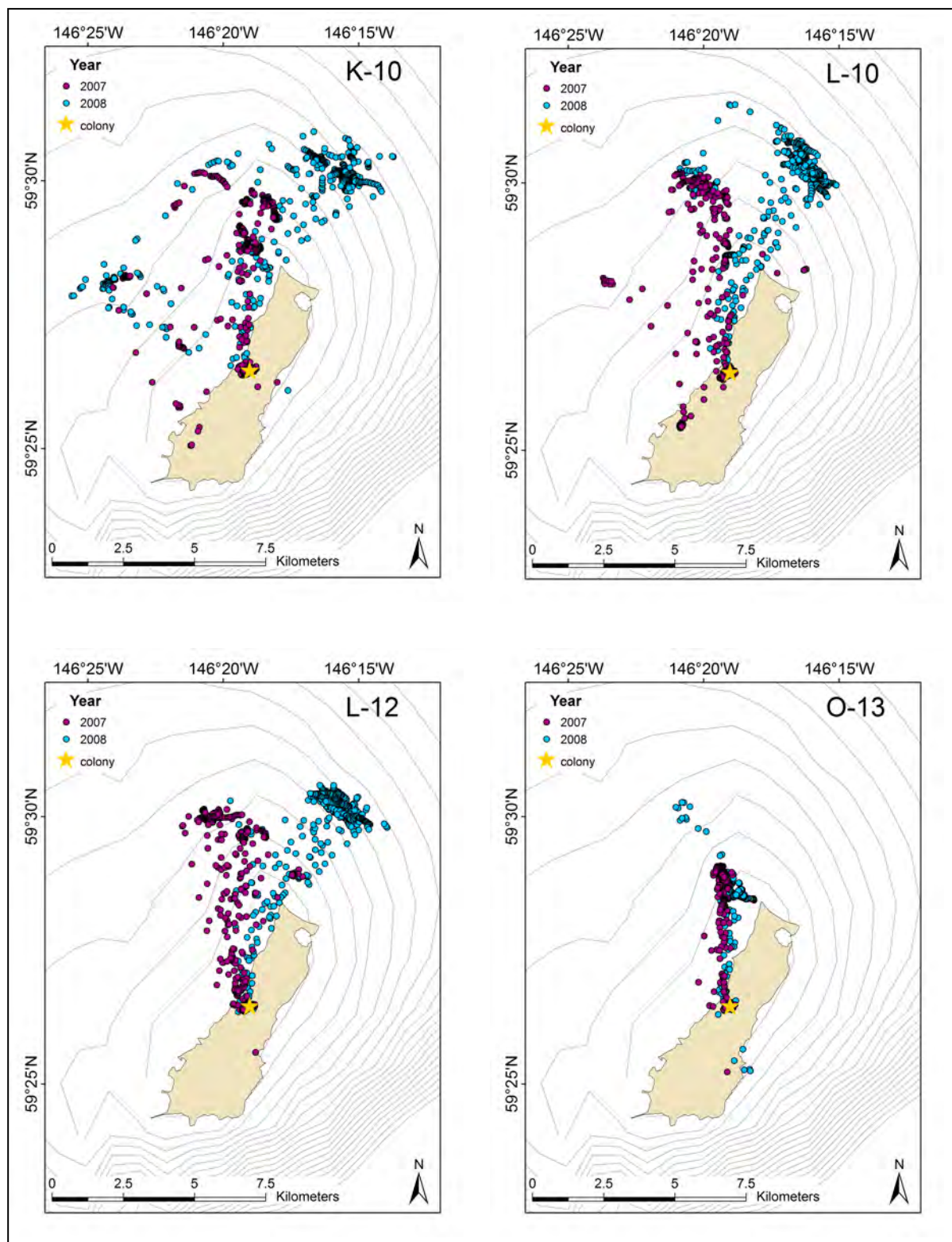


Figure 4.4. Foraging locations of four Pelagic Cormorants K-10, L-10, L-12 and O-13 sampled during the consecutive breeding seasons 2007 and 2008 on Middleton Island, Gulf of Alaska indicating partly high individual foraging-site fidelity during both study years and the slight shifting of the foraging locations to the east during the breeding season 2008.

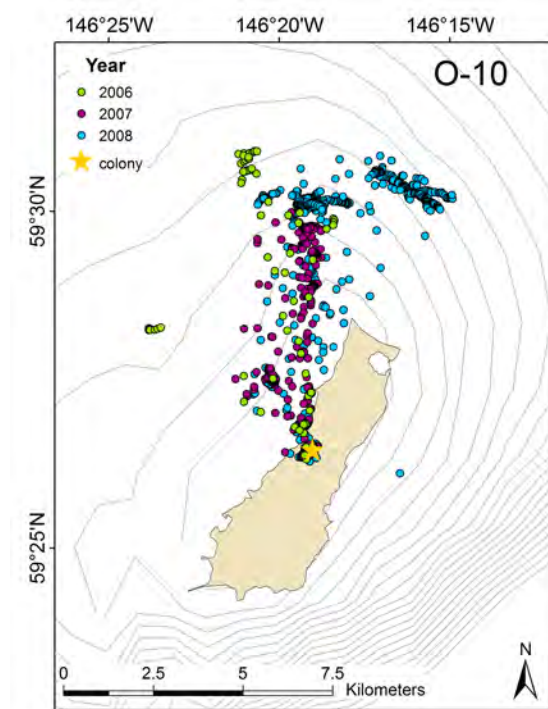


Figure 4.5. Foraging locations of the one Pelagic Cormorants O-10 sampled during the three consecutive breeding seasons 2006, 2007 and 2008 on Middleton Island, Gulf of Alaska indicating high individual foraging-site fidelity during all three study years and the slight shifting of the foraging locations to the east during the breeding season 2008.

Max. dive depth, dive duration and surface uration were similar between 2006 and 2008 but not between 2006 and 2007 or 2007 and 2008. These three parameters were deeper and lasted longer in 2006 and 2008 than in 2007. The bottom duration was not different between 2006 and 2007 or 2006 and 2008. But it lasted significantly longer in 2008 than in 2007.

In Table 4.1 the mean values \pm standard deviations over all sampled days are shown for each of the nine individuals sampled in two or three consecutive years as well as combined for all birds sampled in all three years.

The breeding success (no. of birds fledged/ no. birds hatched) was not different between the nine twice or threefold sampled birds and between all birds during the three study years, although it was slightly lower for all birds in 2008 (0.6) than in 2006 and 2007 (both years 0.7).

Discussion

During the first season of studying the foraging and diving behaviour of Pelagic Cormorants on Middleton Island in 2006 we found an indication of individually specific diving behaviour and a strong foraging-site fidelity of all sampled birds to a small feeding area north of the colony (Kotzerka et al. 2011). Based on those findings we further examined if this individual behaviour was consistent over several years or only applied during one breeding season. From our findings of the foraging behaviour of Pelagic Cormorants in two (8 birds) and three (1 bird) consecutive years we can state that nearly half (46 %) of the observed individuals were consistent in their foraging and diving behaviour in consecutive years. Nevertheless, there was partly high variability (with many outliers) in each parameter of their foraging trips and diving behaviour. Though several of these parameters are statistically different among the years, evidently only small differences appear and the behaviour seem to be more or less equal. Therefore significance values should be treated carefully.

All of the observed birds in our study used the same foraging area, even throughout different breeding seasons. This reliance to a restricted foraging site may indicate (1) that prey must be highly abundant in this area, (2) that this area is the only one that provides prey for Pelagic Cormorants or (3) that other areas are already “occupied” by other seabird species or other cormorant colonies on Middleton Island. Pelagic Cormorants (and other seabird species) breed all along the northwestern, western, southern and eastern cliffs on Middleton Island. Feeding areas of neighbouring seabird colonies may typically not overlap as is already discussed in the hinterland model (Cairns 1989). Such behaviour was already described for Blue-eyed Shags (= Imperial Cormorants) (Sapoznikow and Quintana 2003; Wanless and Harris 1993), penguins (Masello et al. 2010) and kittiwakes (Bull et al. 2004) and is also known for sympatric species (Frere et al. 2008; Weimerskirch et al. 1988; Wilson 2010). Thus, it might be possible that birds breeding in the south use other foraging areas than birds breeding in the northwestern part in order to avoid competition for foraging habitat and prey species. Further studies should therefore also focus on those parts of the colony. This spatial segregation of foraging areas is classified as interference competition with niche partitioning by processes and activities of one species/population that prevent the usage of the same resource by another species/population (Maniscalco et al. 2001). Intra-

specific competition is thought to be more powerful than interspecific competition because of the lack of niche separation between conspecifics (Begon et al. 2006). Thus, it might be possible that Pelagic Cormorants breeding in the southern part of Middleton Island use other foraging areas than birds from the investigated colony. But such considerations can only be speculative for this study as we only investigated birds of one colony on Middleton Island. Further studies should be carried out in order to unravel the question whether all Pelagic Cormorants of this island use the same foraging area or if different parts of the population forage in different regions. The more birds with similar prey species forage in one particular area, the higher is the competition for their prey and may result in food depletion around colonies (Ashmole 1971; Birt et al. 1987; Forero et al. 2002; Furness 1984; Lewis et al. 2001).

To conquer problems associated with food competition seabirds display species-specific adaptations to exploit the various food resources in their marine environment. These can be variations in the breeding time, different prey species or size, nocturnal or daylight foraging or different foraging areas (Casaux et al. 2001; Croxall and Prince 1980; Ronconi and Burger 2011). Furthermore, also within-species specialization is common. It can be expressed as physiological, behavioural and ecological mechanisms and has important implications for ecological and evolutionary aspects as well as conservation. Within-species specialization is one factor which contributes to intrapopulation niche variation (Bolnick et al. 2003). The individual specialization in diving behaviour of at least some individuals of the observed Pelagic Cormorants give an indication that birds compete for food resources in their restricted foraging area. Different birds had different preferred diving depths. The diving depth of most birds was reliable at least throughout one season and three of the observed birds preferred the same diving depth in consecutive years. Bird P-13 performed in both studied years mainly dives to intermediate depths, bird P-6 performed mainly deep dives and bird O-14 dived mainly shallow in both years. Two other birds also showed preferred diving depths throughout both study seasons (O-13 preferred intermediate diving depths and O-1 favoured deep dives), but statistically seen both study years were not similar for these two birds. The remaining 4 birds did not show a preference for a specific dive depth (O-10) or were only consistent in their diving depth during one season and changed their preference in the following season (K-10, L-10, L-12). Individual specific diving depth could be related to individually preferred prey species (Wanless et al. 1992a), although we can not prove

this assumption for our study as we did not analyse diet samples, yet. In a study on the individual foraging behaviour of Thick-billed Murres Woo et al. (2008) could show that different individuals had specialized foraging behaviour and preferred certain prey species, but only few individuals had extreme specialization over longer time scales. The majority of their studied individuals showed specialization in foraging and diving behaviour only over short time scales (days). But regarding diet specialization of the same population Elliott et al. (2009) found individually evolved patterns for different individuals investigated over a period over 15 years. They could show that some of the murres exhibited extreme prey species fidelity using a unique dive pattern to obtain their preferred prey. But even in that study specialization seem to have been higher over shorter time scales. Birds, which could be observed over more than four years, had lower specialized prey species frequencies than birds that could only be observed over two years (Elliott et al. 2009).

Individual specific foraging behaviour can also be related to sex (Bearhop et al. 2006; Durell 2000; Elliott et al. 2010; Kato et al. 1999; Quintana et al. 2010) or age (Bertellotti and Yorio 2000; Daunt et al. 2007; Gomes et al. 2009) as shown in many studies on shags or other bird species. In our study sex could be ignored as a determinant of foraging behaviour as only males were studied in consecutive years. Whether age plays a role in the practice of different diving behaviour can not be clarified since all of the nine birds were only banded as adults and thus their age could not be determined.

Our findings lead to the assumption that Pelagic Cormorants breeding at the old military tower on Middleton Island rely on a narrow foraging area during the breeding season and are altering this area according to possible changes in prey availability only to a minor extent. Such dependence on a restricted foraging site can have major impacts on population changes and is important for conservation plans. In order to avoid too intense intraspecific competition while depending on a small specific foraging area, many individuals seem to have evolved individually specialized diving behaviour, at least during one season. Using specialized foraging tactics these birds may avoid conspecific competition and leaving the individual bird more time and energy for self-feeding and capturing prey for their chicks. Specialized diving behaviour might result in certain preferred prey species that are not exploited by other conspecifics and thus provide a better and reliable food resource. On the other hand, not being flexible enough in foraging and diving behaviour will make individuals, as well as the whole population,

vulnerable to changes in prey availability, which could in turn be disadvantageous for breeding success. Flexibility could buffer against interannual oder interseasonal changes in principle prey availability (Miller et al. 2009). An indication that flexible foraging behaviour is favourable against too narrow specialization might be bird O-10. This bird was the only one observed that did not show any dive depth preference, suggesting a very broad range of possible prey species in different foraging locations. In all of the three study years this bird was one of the first that laid eggs and that always had high breeding success in comparison to other birds.

In conclusion we can state that the Pelagic Cormorants studied were strongly restricted to a relatively small foraging area during the breeding season. The reliance on this location seems to lead to individual specific adaptations in diving behaviour at least of a fundamental part of the population and might be a strategy to avoid intraspecific competition when using a limited area of suitable prey species and sufficient abundance. This behaviour may also lead to individually preferred prey species, but investigations on this still need to be carried out in further studies. Though the individual specialization in foraging behaviour might generally be advantageous for breeding performance, it could also be fatal in case of changing environmental conditions. If birds are unable to adapt to altering foraging habitats or prey species it may have profound effects on population structures and is therefore also important for conservational issues.

Acknowledgements

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Chapter V



First insights into the diving behaviour and foraging areas of chick-rearing Tufted Puffins (Fratercula cirrhata)

First insights into the diving behaviour and foraging areas of chick-rearing Tufted Puffins (*Fratercula cirrhata*)

Abstract

The Tufted Puffin (*Fratercula cirrhata*) is a conspicuous seabird species widespread in the eastern and western North Pacific. It is well studied in many aspects of its breeding biology but information on the foraging behaviour is limited. Here we present for the first time data on their diving and foraging activities obtained by data loggers. During the breeding season 2007 and 2008 we deployed a temperature-depth-recorder (TDR) and MiniGPS logger, respectively, to a chick-rearing Tufted Puffin breeding on Middleton Island in the Gulf of Alaska. We obtained dive data of nearly 3 complete days in 2007 and positional data of 2.5 days in 2008. The bird equipped in 2007 performed a high number of 923 dives during this time, reaching up to nearly 60 m (mean: 17.3 m) and lasting up to 192 sec (mean: 72 sec). Half of all dives were not deeper than 11 m. Dives in the early morning and late evening were shallower than during the rest of the day. There were three major peaks of diving activity, in the early morning, before noon and in the late evening. These peaks correspond well with high numbers of shallow and short dives. In 2008 we recorded 5 foraging trips with the MiniGPS data logger. The maximum foraging range was at least 53 km, with a total distance travelled of at least 135 km and at least 29 h duration. Mean flight speed was 52 km·h⁻¹. While these are only very limited data, they show for the first time diving and foraging behaviour of a free-ranging Tufted Puffin. But further studies are necessary to underline this first successful approach.

Keywords: diving behaviour, foraging, *Fratercula cirrhata*, GPS data logger, Gulf of Alaska, time-depth recorder, Tufted Puffin

Introduction

Knowledge on seabird foraging ranges and feeding areas is essential to understand both the ecological roles of seabirds and constraints acting upon them in marine ecosystems (Monaghan 1996; Wilson et al. 2002). The search for unevenly distributed prey in the surrounding ocean plays a major role in their daily activities. Especially during the breeding season when the energy demand is very high to feed themselves and raise their chicks, seabirds have to make the right decision where to forage successfully in an appropriate time span. To understand the relationship between predators and prey it is crucial to study their foraging behaviour and determine their feeding and home ranges as well as movement patterns. But information on this behaviour is difficult to obtain, especially as foraging behaviour can be variable across time and space. Furthermore, many pelagic seabirds even travel long distances to forage during the breeding season and are thus difficult to observe.

The Tufted Puffin (*Fratercula cirrhata*) is the most pelagic member of the auk family (Alcidae), ranging widely from their colonies to search for prey, even during the breeding season (Davis et al. 2009; Piatt and Kitaysky 2002). The breeding range of this medium sized auk covers a vast range in the North Pacific. It is the most abundant puffin species in the Pacific (del Hoyo et al. 1996). Breeding colonies are found from southern California to arctic Alaska and from Japan (Hokkaido) to the Chukchi Peninsula. But beside that broad distribution and abundance its foraging ecology is scarcely known. Information about their foraging behaviour at sea is limited to direct observations from ship-based surveys (Ladd et al. 2005; Ostrand et al. 1998; Piatt 2002) and diet analyses (Baird 1991; Golubova 2002). These observations at sea are not able to distinguish between individual birds or between breeders and nonbreeders nor can it give details about the diving behaviour of this species. Descriptions of their diving behaviour are only known from captive Tufted Puffins. Duffy et al. (1987) observed on birds in captivity that they foraged near the bottom more often than other alcids.

Tufted Puffins feed themselves on different prey (invertebrates, like squid and euphausiids, fish) than they provide to their young (fish, like Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea pallasii*, Capelin *Mallotus villosus* and juvenile Pollock *Theragra chalcogramma* or Rockfish *Sebastes spp.*) (Gjerdrum 2004;

Golubova 2002; Hatch and Sanger 1992; Hobson et al. 1994). These bimodal foraging forces them to exploit a wide range of ocean habitat.

Therefore, the aim of this study was to characterize the diving behaviour and foraging areas of this widespread seabird species. We show, to our knowledge the first data, on Tufted Puffins foraging behaviour obtained by data loggers. We were able to examine the diving activities of one bird and the foraging behaviour of the other one. This new approach for Tufted Puffins shows a quite variable home range and intensive diving activities.

Methods

Within a bigger study approach to investigate the foraging behaviour of different seabird species on Middleton Island, Alaska, we equipped Tufted Puffins with data loggers to examine their foraging behaviour. Middleton Island (59.4° N, 146.3° W) is situated at the edge of the continental shelf in the northern Gulf of Alaska (Fig. 5.1). Middleton Island supports a large colony of several thousand of Tufted Puffins (probably 12,000 – 14,000 pairs; S. A. Hatch & T. van Nuus, unpubl. data), divided into different subcolonies. Yearly counts indicate a stable population at this island (S. A. Hatch, unpubl. data).

During the breeding season 2007 we deployed three Temperature-Depth-Recorders (TDR; 16 g, L 75 mm x ϕ 19 mm) and one Compass-Temperature logger (Compass TDlog; 14 g, L 65 mm x ϕ 16 mm) on chick-rearing Tufted Puffins. One of these TDRs could be recaptured. During the breeding season 2008 we equipped one incubating and one chick-rearing Tufted Puffins with a TDR and two chick-rearing Tufted Puffins with a MiniGPS logger (25 g, L 46.5 mm x W 32 mm x H 18.5 mm). One MiniGPS logger could be recaptured. All of these loggers were manufactured by earth & Ocean Technologies, Kiel, Germany. The spatial accuracy of the MiniGPS logger shows 65 % of the positional fixes within a circle of 10 m and 90 % within 20 m of the true location. Data stored in the device memories and used for this analysis included date, time, temperature and depth for the TDR, and date, time, latitude, longitude and speed for the MiniGPS logger.

The loggers were temporarily attached to the feathers of the lower back using waterproof TESA[®] tape (Wilson et al. 1997). Before deployment, each bird was weighed

to the nearest 10 g using a spring balance. The loggers equalled 2.1% and 3.3 % of mean body mass (760 g and 740 g), respectively. After 3 – 5 days of deployment the birds were recaptured and the loggers were removed.

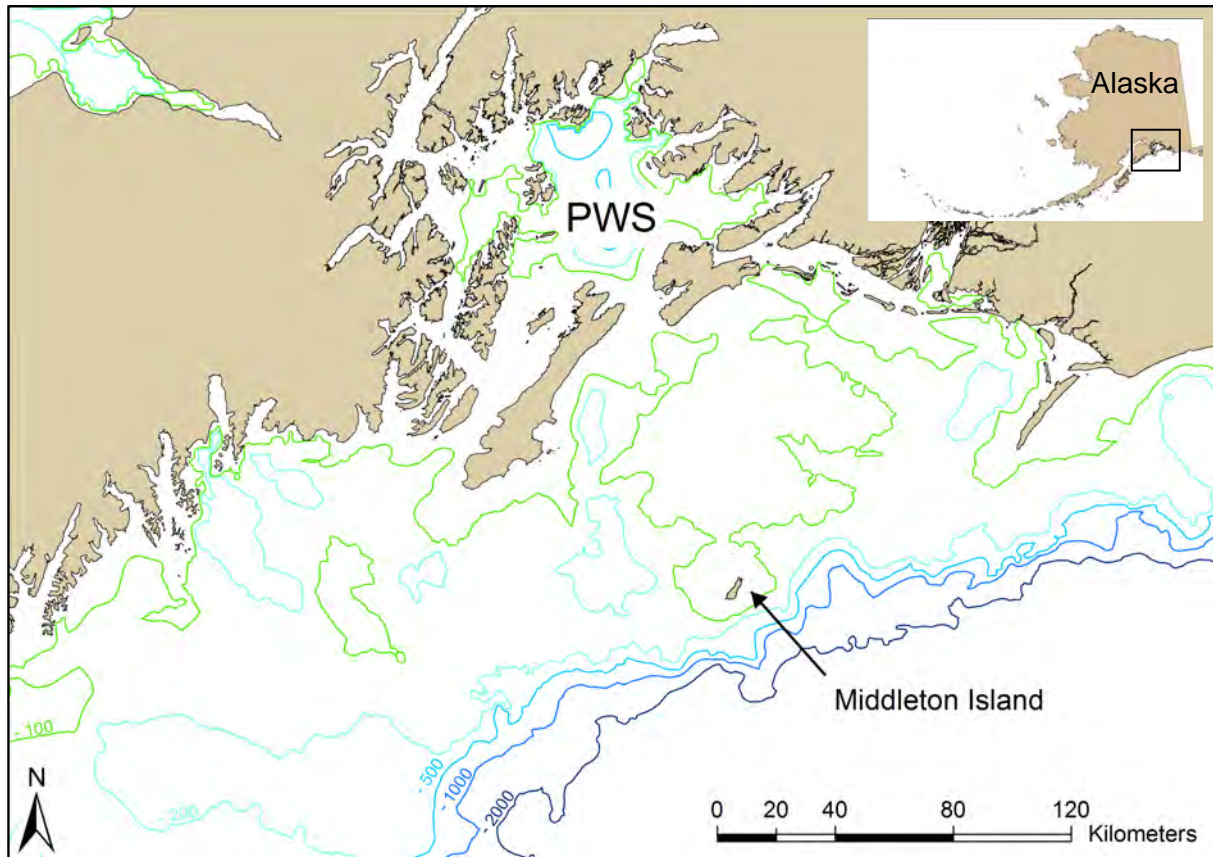


Figure 5.1. Study area in the Gulf of Alaska showing the locations of Middleton Island and Prince William Sound (PWS). Middleton Island lies about 80 km south of the Alaska mainland. Depth contours indicate the shelf region and the continental slope.

Both recaptured Tufted Puffins were actively chick rearing. As Tufted Puffins are highly sensitive to human disturbance (Pierce and Simons 1986) we tried to keep handling time of the birds as short as possible, and no measurements were taken in 2007. Therefore, sex of this bird was not determined. In 2008 we used a different approach while handling the bird. During logger deployment and removal the bird was anesthetized (Kotzerka, unpubl. data) and thus we could measure it upon recapture. These measurements indicate a female according to Piatt and Kitaysky (2002).

While the birds were equipped with data loggers we did not observe their nests until the day of proposed recapture in order to reduce disturbance. That's why we can only hypothesize times at the nest of the bird equipped with a TDR in 2007 by using temperature records of the logger. With those temperature records it is possible to describe the activity of the birds from thermal fluctuations as explained by Wilson et al (1995) and Garthe et al (1999). Relatively constant temperatures well above the air temperature were considered to be temperatures when the bird was in its burrow. Reasonably constant temperatures close to the ambient air temperature were considered swimming or resting at the water surface and when the temperatures were more fluctuating it was regarded as flying with varying orientations of the temperature sensor to the sun.

The first and the last of these trips are incompletely recorded. The incompleteness of the first trip is due to the bird leaving the nest prior to the loggers preset start time. The last trip is incomplete due to the logger running out of battery power. To analyse the data of all trips we interpolated both incomplete trips back to the colony.

Dive data obtained in 2007 were analyzed using the software MultiTrace-Dive (Jensen Software Systems, Laboe, Germany). Vertical immersions were considered dives when they were deeper than 0.5 m. From positional data obtained by the MiniGPS logger in 2008 flight paths were plotted in ArcGIS® 9.2 (ESRI, Redlands, CA). The total distance travelled per foraging trip applies to the summed distances between all positions from the start to the end of each trip. The maximum foraging range was defined as the most distant position in a straight line from the colony. Elapsed time from start to end of a trip is trip duration. Start and end of a trip were defined using GPS data. Trips started when a positional fix was at least 300 m away from the colony and subsequent positions were progressively farther away. In calculating mean velocity (ground speed), we used only flight speeds greater than 10 km·h⁻¹. Speeds less than 10 km·h⁻¹ were probably associated with swimming or feeding (Weimerskirch et al. 2006). To analyse the total max. distance travelled per foraging trip and the trip duration of incomplete foraging trips we corrected the values by adding the missing distances to the colony from the first or last position at sea (in a straight line) and by adding the duration for these distances using our observed mean flight speed.

Results

During the breeding seasons 2007 and 2008 we obtained data of one bird equipped with a TDR or MiniGPS logger, respectively. With the TDR we acquired data about the diving behaviour over nearly three complete days, resulting in 923 individual dives. Temperature measurements of the data logger indicate that these dives were distributed over several foraging trips with returns to the colony in between. The bird performed a maximum of 353 dives per day. The deepest dives occurred between 06:30 and 22:30. Dives were shallower in the early morning and late evening. The maximum dive depth was 59.7 m with a mean of $17.3 \text{ m} \pm 14.8 \text{ m}$. About 50% of all dives were spent in the upper 11 m (Fig. 5.2). Though these are only data of one bird, there seem to be three major peaks of diving activity, in the early morning between 04:00 – 05:00, between 10:00 – 11:00 and in the late evening between 22:00 – 23:00 (Fig. 5.3a). These peaks correspond well with high numbers of shallow dives (Fig. 5.3b).

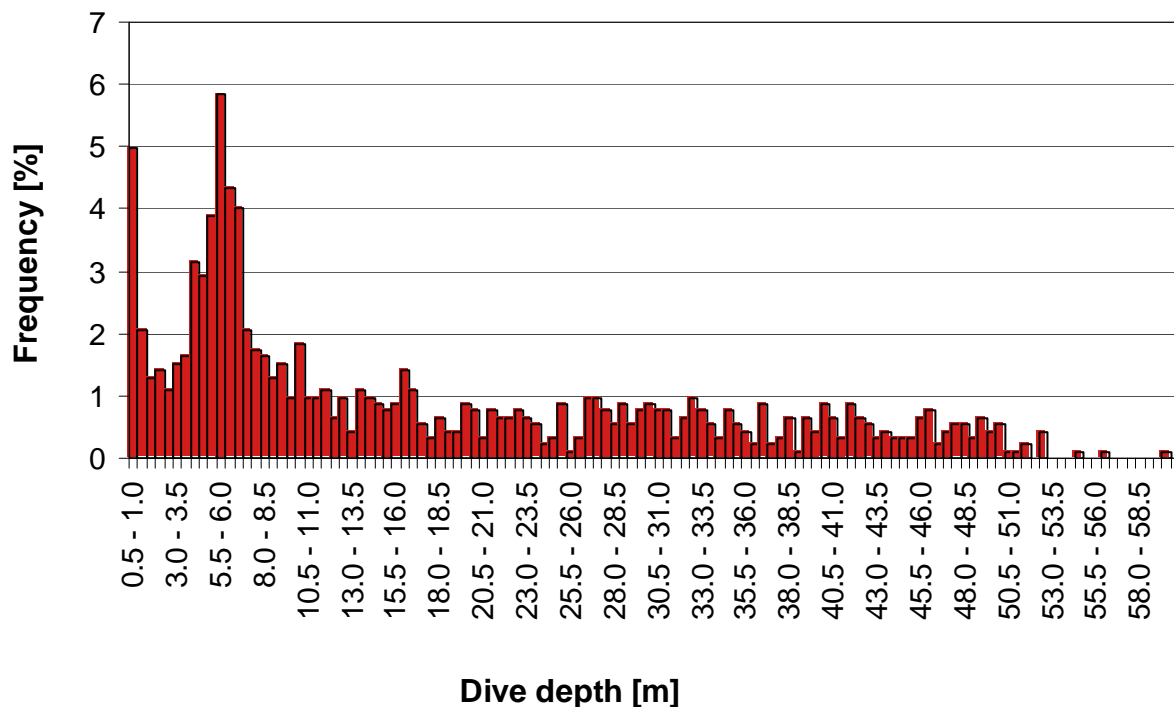


Figure 5.2. Dive depth frequencies of a Tufted Puffin obtained by a TDR during chick-rearing in 2007 on Middleton Island, Gulf of Alaska.

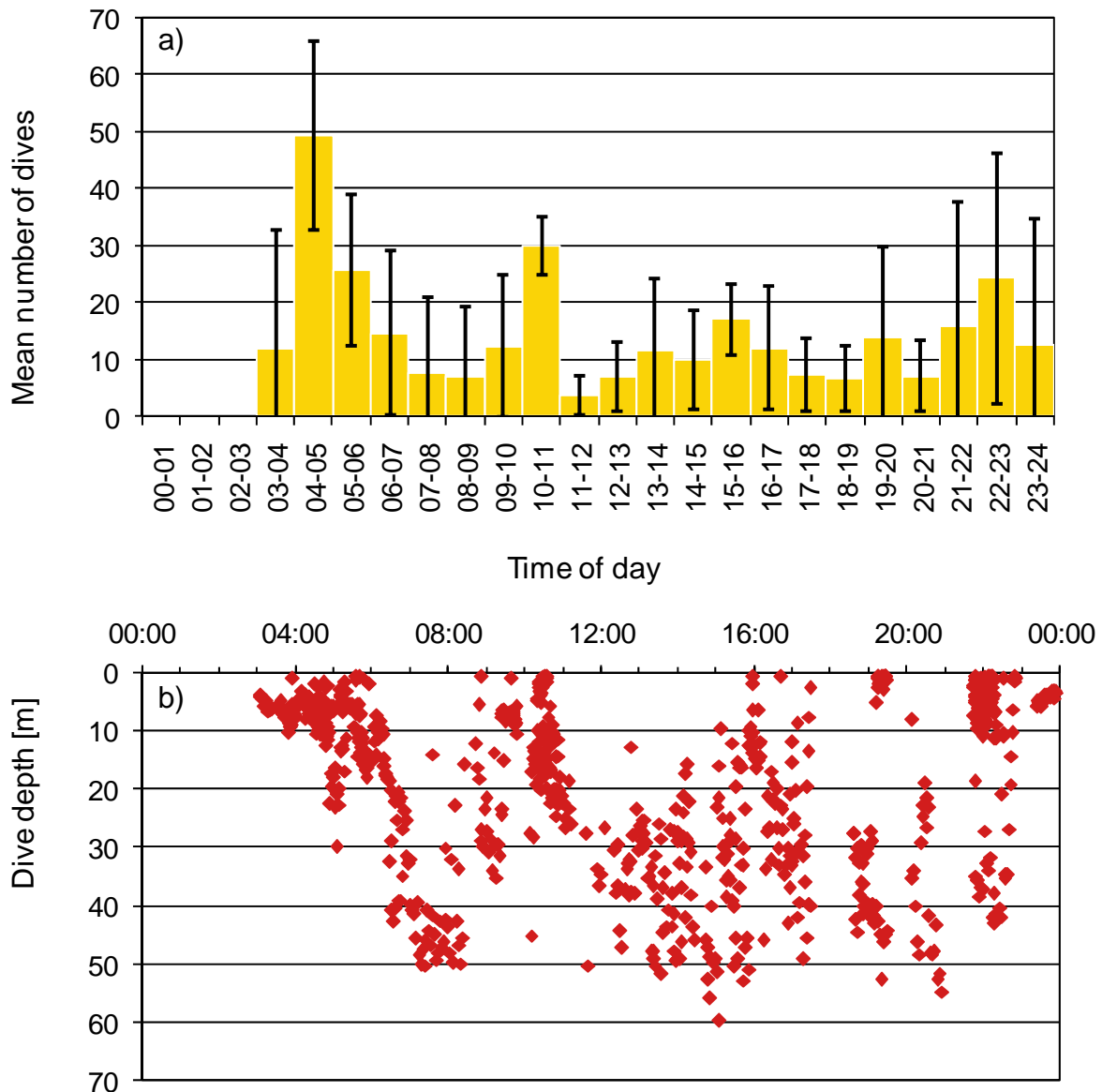


Figure 5.3. Number of dives (a) and dive depth (b) of a Tufted Puffin during the daily cycle obtained by a TDR during chick-rearing in 2007 on Middleton Island, Gulf of Alaska. Vertical bars in (a) represent \pm SD.

Dive depth was positively correlated with dive duration, ($p < 0.01$, $t = 45.63$, $df = 922$). The maximum dive duration was 192 sec (mean 72 sec \pm 36 sec).

In 2008 we achieved positional data of 2.5 days from the bird equipped with a MiniGPS logger. During this time the bird performed 5 foraging trips (Fig. 5.4). The maximum range per foraging trip was at least 52.9 km (incomplete trip), covering a total distance travelled during this trip of at least 135 km and lasting at least 29.4 h. Mean and

maximum flight speeds were similar in all 5 recorded foraging trips, ranging from 49.8 – 55.6 km·h⁻¹ and 55.8 – 73.4 km·h⁻¹, respectively (Table 5.1).

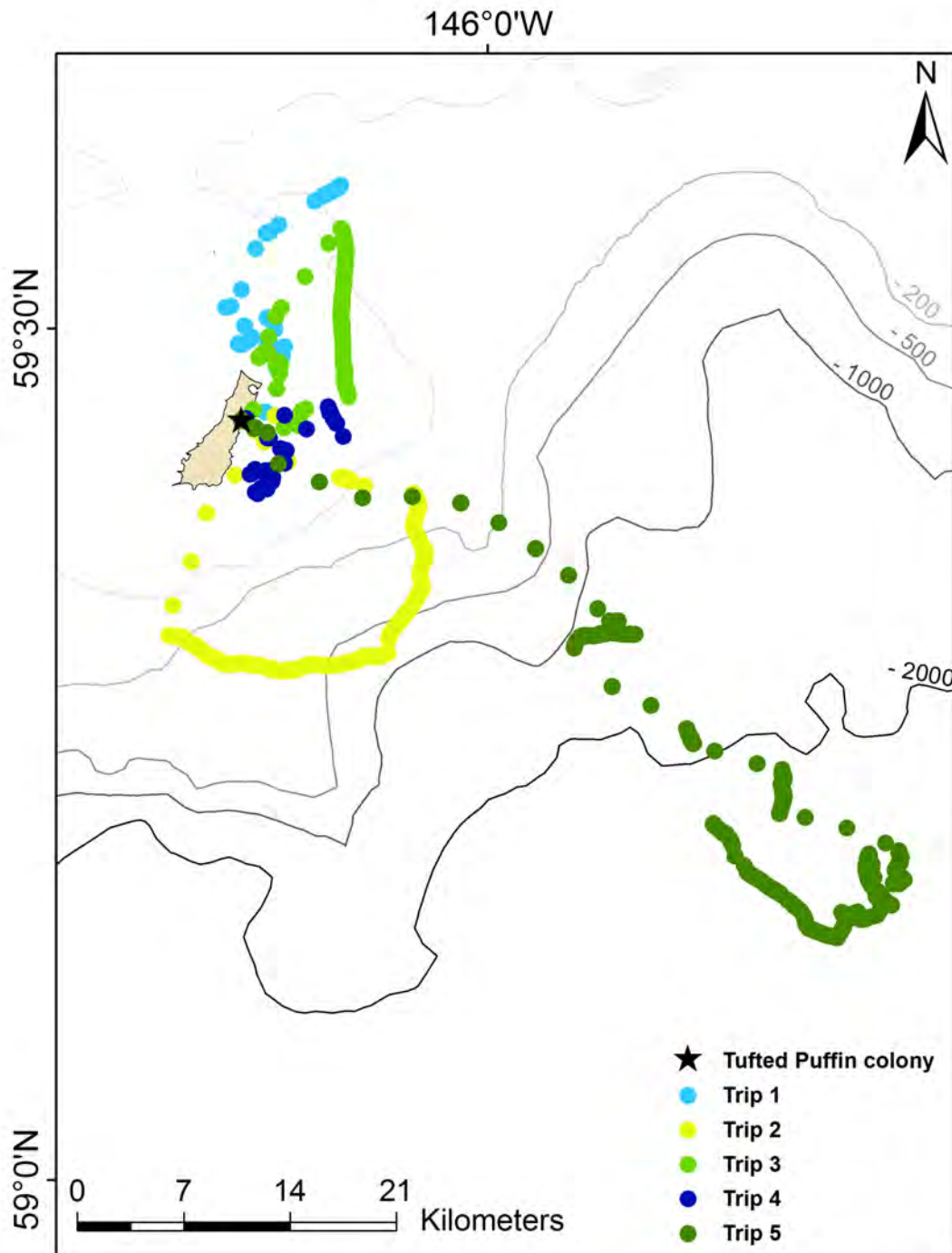


Figure 5.4. Foraging trips of a Tufted Puffin obtained by a MiniGPS-data logger during chick-rearing in 2008 on Middleton Island, Gulf of Alaska. Different colours indicate the five foraging trips.

Table 5.1. Foraging behaviour of a Tufted Puffin breeding on Middleton Island, Gulf of Alaska during chick-rearing 2008. Range indicates maximum straight-line distance from the colony. Total distance travelled is distance covered during one foraging trip. Grey shadowed rows reveal completely recorded foraging trips, white rows are incomplete trips.

trip no.	max. range (km)	max dist. travelled/trip (km)	trip dur. (h)	max. speed (km/h)	mean speed (km/h)	% speed > 10 km/h
1	16.6	47.8	4.6	65.4	55.6	20.8
2	18.0	58.4	15.1	73.4	49.8	6.2
3	14.1	36.0	6.5	55.8	50.2	8.6
4	6.7	30.5	3.4	66.3	49.9	29.7
5	52.9	135.0	29.4	68.8	55.3	5.2

Using speed as a measurement of activity, the bird spent 92 % of all trips with non-active flight activities (drifting, swimming, diving, or at the colony) and only the remaining 8 % in active flight (Fig. 5.5).

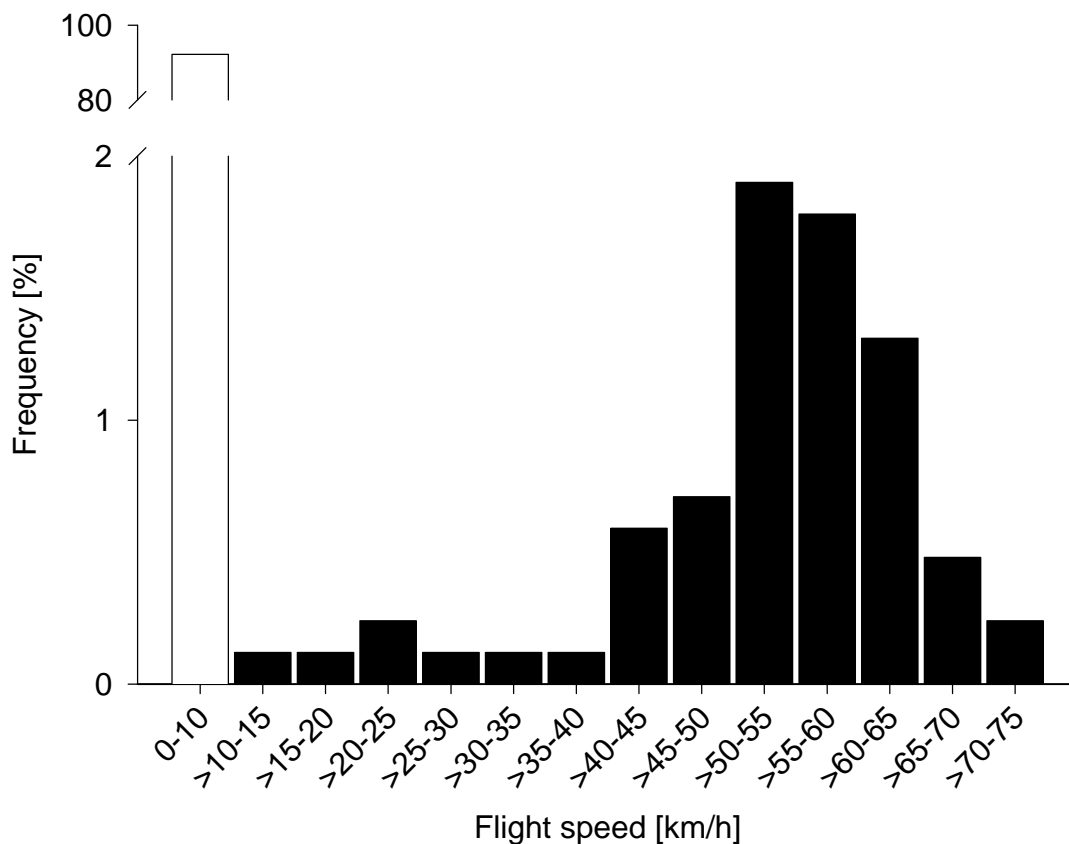


Figure 5.5. Flight speed frequencies of a Tufted Puffin obtained by a MiniGPS-data logger during chick-rearing in 2008 on Middleton Island, Gulf of Alaska.

Though these data are only of one bird, according to the measured speeds, the bird might have performed two different types of foraging trips. During one type of foraging trips the bird flew into a certain area, spent the main proportion of the foraging trip sitting and drifting at the water surface or diving, and then flew straight back to the colony. The second type of foraging trip is characterized by more flight activity throughout the whole foraging trip (Table 5.1, Fig. 5.6).

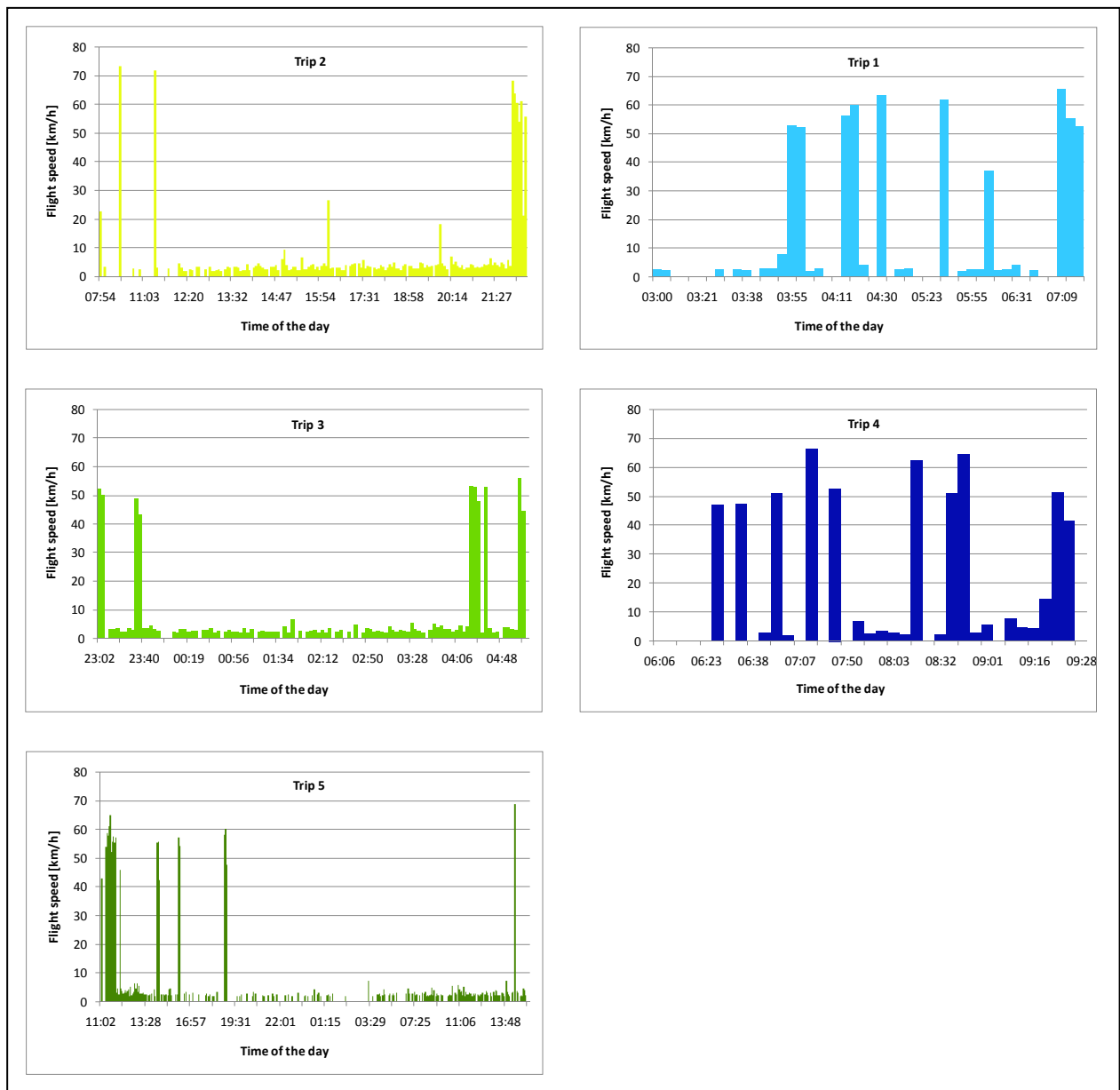


Figure 5.6. Flight speed during single foraging trips of a Tufted Puffin obtained by a MiniGPS-data logger during chick-rearing in 2008 on Middleton Island, Gulf of Alaska. Green diagrams indicate foraging trips with flight activity only at the beginning and end of the trip. Blue diagrams indicate trips with flight activity throughout the whole trip.

Discussion

To our knowledge, this is the first study on Tufted Puffins using data loggers to determine their foraging and diving behaviour successfully during the breeding season. These technologies enabled us to obtain first in situ information on diving behaviour, home range, and movement patterns during their foraging trips.

Tufted Puffins are very sensitive to disturbance during the breeding season and thus should be handled very carefully, especially when external devices are going to be attached (Hatch et al. 2000; Pierce and Simons 1986; Whidden et al. 2007). During the breeding season 2007 we lost three of four data loggers due to nest abandonment after logger deployment. Thus, we developed a new approach to reduce disturbance of the birds by anesthetizing them directly after capturing (Kotzerka, unpubl. data) during the breeding season 2008. First tests with this new method promised good results and markedly reduced nest abandonment rates. Nevertheless, we still lost three of four data loggers. Further investigations are necessary to improve this method and precisely adjust it to the birds.

In 2007, the Tufted Puffin performed a high number of dives per day, at depths up to 60 m. Nearly the same maximum dive depth was assumed and measured for Atlantic Puffins (Burger and Simpson 1986; Piatt and Nettleship 1985), although the body weight of this species, 300 – 500 g, is only about half of the weight of a Tufted Puffin, 700 – 900 g, (Gaston and Jones 1998). Therefore it could be assumed that Tufted Puffins dive deeper than Atlantic Puffins (*Fratercula arctica*). But our measured dive data coincide well with estimated dive depths by Piatt and Kitaysky (2002). They calculated the maximum dive depth for the Tufted Puffin of maximum 102 m and 110 m for females and males, respectively, from a function of body size (Burger 1991), but assumed that this species probably usually dives < 60 m. Although our data are only from one bird, the high number of more than 900 dives suggests that 60 m is approximately the maximum dive depth of Tufted Puffins. Dive duration calculated by Watanuki and Burger (1999) for a 1 kg alcid agrees nearly exactly with our measured dive duration. Mean dive depth of Tufted Puffins is shallower than in Rhinoceros Auklets (*Cerorhinca monocerata*) and Common Murres (*Uria lomvia*) and similar to Razorbills (*Alca torda*), but dive duration is to some extent longer in the Tufted Puffin than in the auklet and Razorbills, respectively. Dive durations of Common Murres are despite their

greater dive depths similar to puffins (Benvenuti et al. 2001; Burger et al. 1993; Hedd et al. 2009; Kato et al. 2003). Dive durations of the closely related Atlantic Puffin are much shorter than in the Tufted Puffin (Wanless et al. 1988). These differences in diving behaviour in different alcid species may indicate different foraging strategies to capture similar prey and to prevent interspecific competition, especially in areas where more than one of the alcid species is breeding (Benvenuti and Dall'Antonia 2004). Wanless et al (1990) also found different foraging ranges for three alcid species breeding in the same colony in Scotland, all of them still had smaller foraging ranges than the Tufted Puffin. In comparison to our observed puffin, Tufted Puffins in Prince William Sound, Alaska, had slightly shorter feeding ranges (Ostrand et al. 1998). Not only within the alcid family, but also to prevent interspecific competition between seabirds with similar prey in general, each species seem to have an own specific foraging behaviour. The foraging areas of the Tufted Puffin are overlapping to some extent those of other seabird species on Middleton Island (Black-legged Kittiwakes *Rissa tridactyla* and Pelagic Cormorants *Phalacrocorax pelagicus*) preying on the same species, sand lance (Hatch, unpubl. data, Kotzerka pers. obs.), but mean foraging ranges are different (Kotzerka et al. 2010; Kotzerka et al. 2011). But these results have to be regarded carefully and should not be generalized as these are only data of one Tufted Puffin.

The observed bird in 2007 showed a unique pattern of diving activity with higher frequencies, shallower and shorter dives at certain times of the day. These patterns correspond well with high puffin activity observed in the colony which usually resulted in chick feeding activities. Main chick feeding on Middleton Island takes place around 05:00, between 11:00 – 12:00 and 22:00 – 23:00 (pers. obs.). The temporal proximity of these diving patterns with high chick feeding rates also leads to the assumption that prey items to feed chicks are caught in close proximity to the colony and are not carried over long distances. Our results from GPS data in 2008 seem to support this suggestion for some of the foraging trips. Although we recorded only 5 trips from only one bird there might be an indication for two different types of foraging trips. Trips of one type show higher densities of bird positions close to the colony and more flight activity than trips of the other type. A similar behaviour of such foraging trip types is known from razorbills (Benvenuti et al. 2001; Dall'Antonia et al. 2001). Thus, it is possible that trips are either allocated to feed their chicks (trips with higher flight activity and more positions close to the colony) or for self-feeding (trips with less flight activity). This special diving behaviour

just prior to high chick feeding rates supports the finding from other studies that adult Tufted Puffins prey on different species than they feed to their chicks (Gjerdrum 2004; Hobson et al. 1994). But because we did not observe the puffin burrows while birds were quipped with data loggers, we can not determine any such details but further investigations may focus on such patterns.

Although the data presented in this paper are very limited, and should hence be handled carefully with respect to generalization, they give first detailed information on Tufted Puffin's foraging behaviour at sea on an individual level. Further studies are needed to reveal if there are different types of foraging trips and if these are correlated with chick feeding occurrences.

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General Conclusion



General conclusion

The present study aimed at investigating the foraging strategies of three sympatric seabird species in the North Pacific and to identify and characterize their foraging areas and their feeding and diving behaviour. These three seabird species (Black-legged Kittiwake, Pelagic Cormorant, Tufted Puffin) included birds that have a wide range of possible habitat requirements, as they included planktivorous (Tufted Puffins, partly Black-legged Kittiwakes) and piscivorous species (Black-legged Kittiwakes, Pelagic Cormorants, Tufted Puffins) as well as species that usually forage offshore (Tufted Puffins, partly Black-legged Kittiwakes) and inshore (Black-legged Kittiwakes, Pelagic Cormorants). With those selected species it was possible to study different marine habitats used by seabirds. Thus, with this thesis our knowledge of these widely distributed but partially only rarely studied seabird species could be substantially improved and the understanding of their foraging ecology could be enhanced. By applying new data logger technologies for the first time on these species I gained detailed information about their foraging and diving behaviour. Main results of this thesis are general information and detailed description of the foraging behaviour during the breeding season of those chosen seabird species (chapter I, III and V), as information on that was not available before for free-ranging Pelagic Cormorants and Tufted Puffins. For Black-legged Kittiwakes information on the foraging ecology was already available, though only from other regions in the North Pacific (Prince William Sound, Irons 1998; Suryan et al. 2000), or the Atlantic (Camphuysen 2005; Daunt et al. 2002). Furthermore, details of the foraging areas were often lacking due to limits of conventional radio telemetry or only calculations of their maximum foraging range, or the sampling was dependent on vessels and thus causing possible disturbance and thereby affecting their foraging rates or flushing them (Rodgers and Schwikert 2003; Schwemmer et al. 2011; Stolen 2003). Additional investigations resulted in a comparison of the foraging behaviour of Black-legged Kittiwakes during the pre-breeding and the breeding season (chapter II) and distinct diving behaviour of individual Pelagic Cormorants in consecutive years (chapter IV). Considerable gaps in the understanding of relationships of these seabird species, but also of seabirds in general, with their marine environment could be filled with this thesis. In the following, the four questions addressed in the “General Introduction” should be answered:

1. How are the foraging areas of the selected seabird species distributed in the study area?
2. Which detailed foraging strategies are they exhibiting?
3. How do the individual seabird species cope with interspecific competition for prey?
4. How are the distribution and the foraging strategies driven by the oceanographic and bathymetric parameters?

Distribution of foraging areas of selected and representative seabird species breeding in the Gulf of Alaska

Some of the main results of this thesis describe the foraging areas of three selected seabird species (Black-legged Kittiwakes, Pelagic Cormorants and Tufted Puffins) in the Gulf of Alaska. Seabird distribution belongs to the most crucial information of seabird biology and is essential to understand comprehensively their biology and interaction with the environment. This is especially true for the at-sea distribution, as seabirds spend the preponderance of their life at sea. Further, they rely completely on marine food to survive and thus, studying the marine distribution of seabirds can give additional information about the marine environment and thus seabirds can also act as indicator species for changing environmental conditions (Ballance 2007). But seabirds are not evenly distributed and they can widely disperse from their colonies, even during their breeding season, so that information on their distribution is difficult to obtain. For that reason I used novel data logger technologies attached to the birds during the pre-breeding and breeding season to unravel some very important aspects of seabird ecology. With that I was able to identify, to my knowledge for the first time, the foraging areas of breeding Pelagic Cormorants (chapter III and IV) and Tufted Puffins (chapter V) in general and of Black-legged Kittiwakes in the Gulf of Alaska (chapter I and II).

During the breeding season, kittiwakes foraged mainly over the continental shelf region and rarely visited the continental shelf slope. They did not forage over the abyssal zone during that breeding stage. In contrast, birds equipped during the pre-breeding season showed a completely different foraging behaviour, than those birds foraged

nearly exclusively over deep pelagic waters. Furthermore, foraging trips during the breeding season were conducted usually during the daytime whereas trips during the pre-breeding season were mainly nocturnal. These contrasting foraging areas and foraging times are obviously linked to different prey species exploited during the two breeding stages, as it was already shown by Gill and Hatch by diet analysis (2002). Because the Gulf of Alaska lies in the northern Pacific Ocean it is part of the mid-latitude oceanic climate zone and thus influenced by different seasonal climatic characteristics. Consequently, prey species for seabirds are not evenly distributed throughout the year but rather fluctuate with changing seasonal environmental conditions (Brown 2002; Spies 2007). Therefore, foraging strategies and foraging areas vary in relation to prey abundance and distribution around their colonies (Baduini and Hyrenbach 2003). At different breeding stages they rely on different prey species according to their availability, easiness of accessibility and energy gain in relation to time spent foraging and energy consumption by themselves or by their chicks. During pre-breeding they often feed on high-energy lampfish (Myctophidae), which is only abundant in the surface water layer during night time in the pelagic ocean (Beamish et al. 1999). Later during the breeding season, capelin and other schooling fishes (e. g. sand lance) become available to kittiwakes on the continental shelf region. The birds can forage on these fish species during day time and at shorter distances to the colony. That is probably advantageous as the birds can spend more time for breeding activities like nest and brood defence or chick feeding. The identification of this contrasting foraging behaviour during the pre-breeding and breeding season results in the appraisal that not only the foraging area used during chick-rearing seems to be sufficient, and thus important, for good breeding performance.

This study was the first that investigated the foraging and diving behaviour of Pelagic Cormorants concurrently using GPS data loggers. Older studies based only on observations from land or boats (Hobson and Sealy 1985; Holm and Burger 2002), and were therefore not as precise as data collected in this study. The most surprising and unexpected finding of this study was that Pelagic Cormorants in the Gulf of Alaska showed an extremely strong preference for a very restricted foraging area throughout all foraging trips and all three study seasons. During the first two seasons in 2006 and 2007, this foraging area was more or less identical while in the third season the birds started to disperse slightly, even though the main foraging area was still the same as in both previous years. Such a strong reliability on a very restricted foraging area has rarely been

observed before. Other seabird species (European Shag (*P. aristotelis*), Northern Gannet (*Morus bassanus*), or Cory's Shearwater (*Calonectris diomedea*)) also show foraging-site fidelity, but typically not to the same extent as the Pelagic Cormorants (Camphuysen 2005; Hamer et al. 2001; Navarro and González-Solís 2009). Foraging-site faithfulness assumes that prey is very abundant and highly predictable in space and time and that the birds remember this from day to day and from one breeding season to the next. But it could also mean that other profitable feeding sites are lacking in the vicinity of the colony. Hence, foraging-site fidelity might be beneficial for breeding activities as long as preferred prey is abundant, but also makes the birds very sensitive to changing environmental conditions.

Another novelty of this thesis was the first successful deployment of a tracking device that logs the foraging positions of a breeding Tufted Puffin, although I have only data of one bird fitted with a MiniGPS-logger. The data of this bird show foraging positions of 2.5 days encompassing 5 foraging trips. This bird foraged over the continental shelf region in relative proximity to the colony as well as over the abyssal zone in greater distances to its nest site. These findings only partly coincide with results of Tufted Puffin feeding locations in Prince William Sound, which is situated about 130 km north of Middleton Island, and where Tufted Puffins were observed feeding close to colonies (Ostrand et al. 1998). But the Prince William Sound is an embayment with different hydrographic, oceanographic and bathymetric conditions, hence a comparison of my results with those is difficult. Furthermore, my results represent only foraging tracks of one bird and thus should be handled carefully regarding generalizations. Further studies are needed to fortify my first results for foraging ranges of Tufted Puffins at an oceanic island like Middleton Island.

Foraging strategies of selected seabird species breeding on Middleton Island

All three seabird species investigated in this study used different foraging strategies that are (partly) caused by their species specific physiological and morphological constraints. Foraging areas, foraging ranges and diving behaviour differed markedly, even within

both diving species (Pelagic Cormorant and Tufted Puffin). Although foraging-site fidelity is a characteristic that is independent from body condition, and therefore could possibly be performed by all three species, it was only observed in the Pelagic Cormorant and especially not only on individual level but also on population level. All observed cormorants used the same foraging site in consecutive foraging trips and throughout all three study years. Data on their diving behaviour illustrated that the birds exhibited shallow and deep dives representing feeding on benthic and pelagic prey. Furthermore, some of the sampled individuals showed individual specific diving behaviour with having a preference for certain diving depths. Although the Pelagic Cormorants seem to be restricted to a relatively small foraging area they probably used the whole water column to search for food. With that the birds could probably increase the probability to encounter sufficient prey to fulfil their own energy demands and to raise their chicks successfully (Grémillet et al. 1999). With foraging on the ocean floor and in the water column Pelagic Cormorants probably followed one of their principal prey species, the Pacific sand lance (pers. obs.).

In contrast, faithfulness of all observed birds to such a specific feeding area could neither be detected for the Black-legged Kittiwake nor the Tufted Puffin. Instead, kittiwakes used a much greater area for foraging. During breeding, they exhibited foraging trips on the continental shelf region, encompassing an area from the colony at the continental slope northward to the southern coast of the Prince William Sound. By using that big area their trips lasted in general around 7 h (2007) and 4.5 h (2008) and the birds travelled usually a total of 73 km (2007) and 61 km (2008) during each trip. Mean max. distance to their colony was in both years 26 km. On the other hand, during the pre-breeding season kittiwakes foraged only over deep pelagic waters, mainly during night. During those trips the birds reached mean max. distances to the colony of 41.6 km and travelled up to 105.7 km during single trips. With these both distinct foraging areas they used a wide range of ocean habitat. As surface feeders, kittiwakes depend more on less predictable prey species than diving species, and thus need a larger foraging area than those species (e. g. cormorants) (Montevicchi 1993). Therefore, especially during the breeding season surface feeder have less time to buffer increased foraging activities caused by reduced prey availability (Monaghan et al. 1996). Otherwise, being able to fly great distances, the birds are able to avoid areas with low prey density and search for food in more productive regions. With that strategy they can probably compensate for

low prey abundance in one area. But if prey is scarce on broader scales, this advantage will be overridden by the longer flight time they have to spend in large areas for prey search.

For the single Tufted Puffin GPS data set in 2008 it is not possible to make any statements on foraging-site fidelity, but the 5 foraging trips that could be recorded with the GPS logger, and of which 3 were complete, were all in different directions of the colony. These 5 foraging trips lasted between 3.4 h and at least 29.4 h and reached maximum distances from the nest site of 7 km to at least 53 km. During those trips the bird travelled between 31 km and at least 135 km. During the previous field season in 2007 it was possible to receive one data set of diving activity of another Tufted Puffin. These data show high diving activities throughout the nearly three days of data recording. The bird performed a maximum of 353 dives per day and reached a maximum dive depth of nearly 60 m. The mean dive depth was substantially shallower with only 17 m. The longest dive lasted more than 3 minutes, but in general mean dives were only 1.2 minutes long. Though these data are only from one bird each, general assumptions of the foraging strategies of Tufted Puffins are not possible and conclusion can only be speculative. But these data are the first ones available on the real diving activity and foraging areas and are therefore important for the understanding of the ecology of Tufted Puffins, especially during the breeding season. Hatch et al. (2000) observed greater distances from the colony than were observed in this study. But their data probably did not reflect the foraging areas of breeding birds, as they assumed that all birds abandoned their nest after the satellite transmitters were implanted. From the few data obtained in this study (this thesis) their might be an indication of performing two different kinds of foraging trips. That might point to different foraging behaviour for self maintenance and chick rearing. From studies of puffin diets it is already known that adult birds feed on different prey items than they deliver to their chicks (Baird 1991; Gjerdrum 2004). As no other detailed foraging and diving data of breeding Tufted Puffins are existing so far (besides observations from ships; e.g. Ostrand et al. 1998), the data of this study are a first step to unravel the foraging behaviour of this conspicuous seabird species.

How the selected seabird species might avoid interspecific competition?

Seabirds spend an essential part of their life at sea, often far from the mainland. But during breeding they have to find places that are suitable to raise their chicks. In many parts of the world chick-raising is time limited due to climatic and oceanographic conditions. Therefore, breeding sites have to be in regions with high and predictable prey abundances. Additionally, the establishment of colonies require the appropriate habitat for breeding (e. g. burrowing habitat, trees or open areas) and should preferable be predator free. Consequently, when regarding all these constraints, breeding habitat is limited and many seabird species (over 96 %) breed in colonies (mixed species and single species) that are huge and consist of thousands or millions of breeding pairs. Besides the many advantages of colonial breeding, like socialization, information transfer for feeding areas, adjustment of the breeding season and predator defence, food competition is one of the main disadvantages (Coulson 2002). Competition for certain prey species may be high around colonies and could lead to a depletion of some prey species (Forero et al. 2002; Lewis et al. 2001), even in temperate regions (Birt et al. 1987; Furness 1984). Seabird populations on Middleton Island are high. Alone the three species studied account already for more than 44,000 birds (S. A. Hatch and T. v. Nus unpubl. data). Black-legged Kittiwakes (Gill and Hatch 2002; Hatch et al. 1993b; Hatch et al. 2009), Tufted Puffins (Baird 1991; Hatch and Sanger 1992; S. A. Hatch unpubl. data) and Pelagic Cormorants (Ainley et al. 1981; Hobson 1997; J. Kotzerka & S. A. Hatch unpubl. data) on Middleton Island all feed, at least in some years, primarily on the same fish species, Pacific sand lance and capelin. Hence, this could lead to a reduction of their principal prey species around the colony. Strategies to avoid interspecific competition could therefore be to feed at different times of the day or night (Lance and Thompson 2005), in different water depths (Piatt 1990), in different foraging areas (Croxall and Prince 1980) or a combination of these three. Besides their different foraging feasibilities based on their morphological constraints, e. g. diving versus surface-plunging or surface-dipping, the studied seabird species seem to exhibit the strategy of foraging habitat segregation in order to avoid interspecific competition (Fig. GC-1).

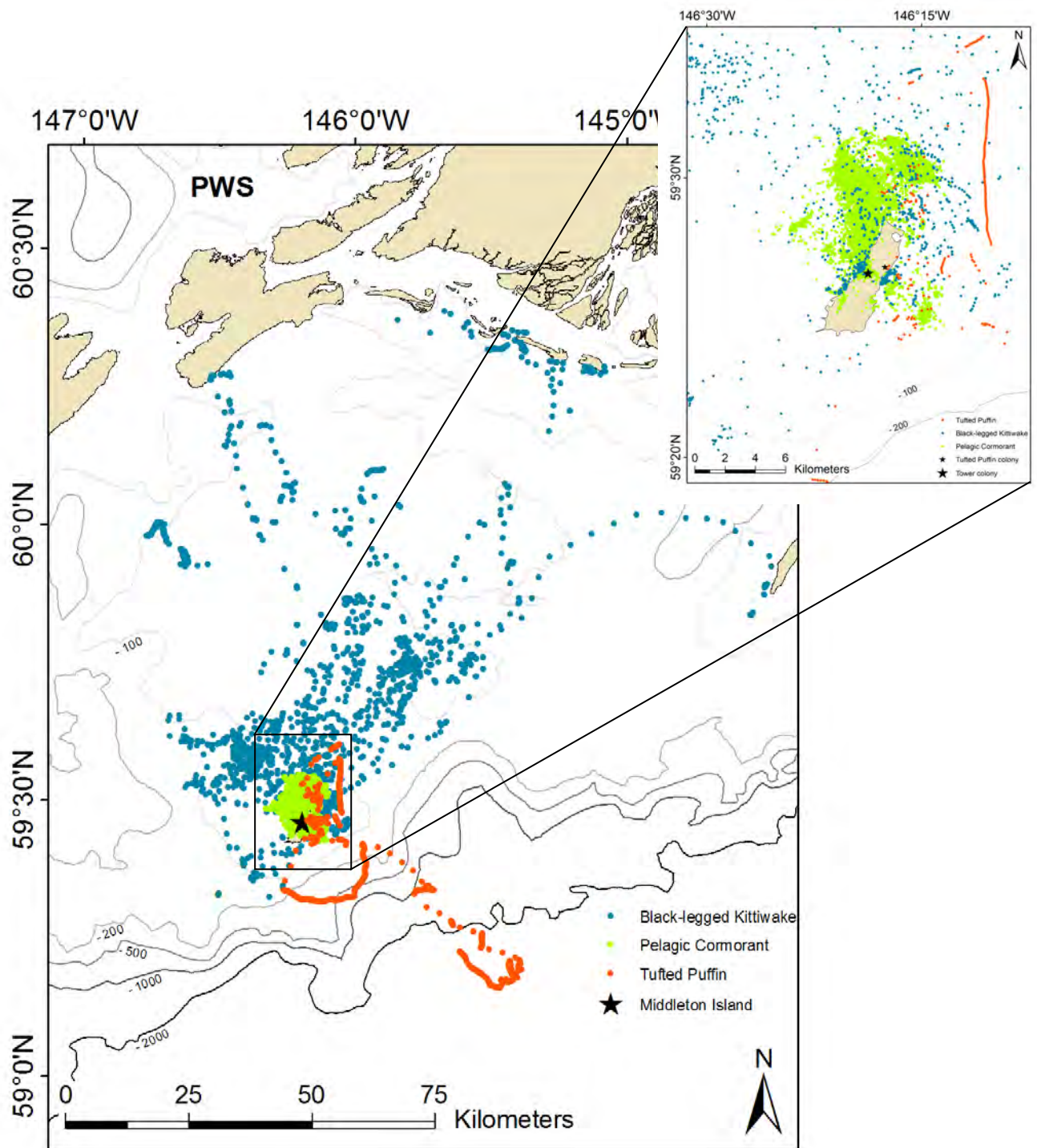


Figure GC-1. Distributions obtained with GPS data loggers of a) all sampled individuals of Black-legged Kittiwakes, Pelagic Cormorants and Tufted Puffins during the breeding seasons 2006, 2007 and 2008 on Middleton Island in the Gulf of Alaska. PWS indicates the Prince William Sound. b) Enlargement of the area around the colony to illustrate the GPS positions of all sampled individuals in that area in more detail. The tower colony refers to the sampled colony of Black-legged Kittiwakes and Pelagic Cormorants.

In this figure it is apparent that all three species use different foraging regions. Their foraging trips overlap in close proximity to the colony but their final foraging destinations, and thus probable feeding locations, are diverse. Black-legged Kittiwake foraged widely over the continental shelf region, Pelagic Cormorants only in northern direction in close proximity to their colony and the Tufted Puffin foraged north and southeast in intermediate distances of its nest site. A similar finding is described by Weimerskirch et al. (1988), who could show that three albatross species use separated foraging zones as an extensive means of resource partitioning. Furthermore, individual Pelagic Cormorants with their restricted foraging area showed, to some degree, distinct diving behaviour. Such individual specialization could be an additional indication to prevent intraspecific competition when foraging in a very limited foraging area and where habitat segregation does not seem possible.

Modelling foraging distributions of seabirds with oceanographic and bathymetric parameters

The distribution of seabirds is closely related to the physical properties of the oceans. Oceanographic and bathymetric conditions indirectly influence seabird abundances through prey availability (Fauchald 2009; Hunt 1991; Shealer 2002). Recently, more and more studies investigated the relationship of seabird abundances and foraging areas with sea surface temperatures or chl *a* concentrations using remotely sensed satellite data (e. g. Catry et al. 2009; Freeman et al. 2010; Paiva et al. 2010b). In this thesis the foraging distribution of Black-legged Kittiwakes could be modelled in conjunction with remote sensing data of the sea surface temperature and chl *a* concentration. Since the Pelagic Cormorants had a very restricted foraging area in close proximity to their colony modelling of their preferred feeding zone was not possible due to the spatial resolution of the remote sensing data. This resolution was not high enough for such small scale modelling. With having data on the foraging areas of only one Tufted Puffin developing a bird-habitat-relationship-model would not have been meaningful for this species.

Modelling of abiotic factors (SST and chl *a*) with kittiwake distributions did not show any relationship during the pre-breeding season. During that time of the year the

water masses in the open ocean are well mixed. Only along the coast waters are stratified and a phytoplankton bloom may develop in the cold and nutrient rich water. But in spring no considerable fish abundances have established yet on the continental shelf (Brown 2002; Doyle et al. 2009) and thus kittiwakes forage on oceanic waters where myctophids are available at the sea surface during night (Mundy 2005), and which are a main food source during this breeding stage (Gill and Hatch 2002). The positive correlation of kittiwake foraging areas and deep pelagic waters during the pre-breeding season underlines this assumption. Later during the breeding season kittiwakes changed their foraging area and were found over the continental shelf where they probably fed on capelin or sand lance (Gill and Hatch 2002). The spring phytoplankton bloom on the shelf is at this time already grazed off by zooplankton organisms (that in turn are the food source for forage fish species), and thus the modelling of Black-legged Kittiwake foraging areas with chl *a* concentrations were negatively correlated and positively with shallow waters. The SST on the continental shelf was intermediate between warmer inshore waters (e. g. the Prince William Sound) and colder pelagic deep sea waters. The flexibility to change their foraging areas quickly seems to be an advantage and might explain the wide distribution of Black-legged Kittiwakes, rendering it the most widely distributed gull species in the northern hemisphere (Springer et al. 1996). Referring to the results of this modelling one should carefully link data of areas with high primary production directly to high densities of higher trophic levels like seabirds or marine mammals, at least in regions with strong seasonal changes. Those predictions should rather be made under consideration of additional components of the surrounding environment.

Synopsis and future perspectives

The present thesis provides substantial new insights into the foraging ecology of three abundant seabird species of the North Pacific. Most results are utterly new for the particular species and the innovative technologies used in this study have never been applied on seabirds before in this region. With that, the thesis contributes to an improved ecological knowledge of these species and shows important details on their foraging areas and foraging behaviour.

Despite some limitations in this study due to small sample sizes of some investigated aspects, the present work revealed unique data sets to better understand the investigated seabird species in their marine environment. Especially for two of the studied species (Pelagic Cormorant and Tufted Puffin) such information was barely available before. Although these results are already very valuable for the identification of the different habitats used by seabirds many parts of their ecology are still unknown. Specifically, investigations on the foraging behaviour of the Tufted Puffins should be continued in order to be able to assign the findings of this study to the Middleton Island population of this species in general and not only to rely on two individuals. Additionally, the monitoring of the foraging behaviour should be further continued, to obtain data of longer time series that comprise more years with different environmental conditions. It is well known that seabirds react to changes of their marine environment quickly and they are often used as indicators of altering conditions in the surrounding oceans (Frederiksen et al. 2007). Moreover, dietary studies could further enhance the results of this study and give more detailed information on the foraging ecology of all of the investigated species. Those analyses would especially contribute to the understanding of individual-specific foraging behaviour of the Pelagic Cormorants and could also improve our assessment of the habitat requirements of Black-legged Kittiwakes. Advances in tracking logger technologies applied on seabirds in such a remote marine region in conjunction with oceanographic parameters would be particularly suitable for the establishment of models of seabird-habitat-relationships. Such seabird-habitat-models are also important for the analysis of anthropogenic influences on seabird distributions, like impacts of fishery, oil and gas exploration or offshore wind farms. Hence, those models are of particular interest for conservation issues and the development of environmental management plans. Human overexploitation of the marine environment has profound negative effects on seabirds and other marine animals by spatial competition for resources and certain areas. Areas of extensive fisheries often overlap widely with foraging areas of seabirds, making seabirds highly vulnerable to bycatch mortality by long-line fishing (Dietrich et al. 2009; Fischer et al. 2009) or gill nets (Furness 2003; Zydalis et al. 2009), or causing temporal habitat loss by displacing the birds from their natural foraging habitats (Schwemmer et al. 2011). Offshore drilling platforms may also block seabirds from their primary foraging areas or have negative effects on seabirds through pollution of those feeding zones (Boersma et al. 2002). Nowadays, there is concern about offshore wind

farms that may further influence the at-sea behaviour and distribution of seabirds. Knowledge of where and when seabirds forage, especially in combination with information about the habitat requirements, is therefore important in order to map and protect sensitive areas. Models of seabird-habitat-relationships can help to define such areas and should be considered for the establishment of Marine Protected Areas (MPA's).

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Description of the individual scientific contributions to the multiple-author papers

The chapters of this thesis are either already published in peer-reviewed journals (chapter I and III) or written as manuscripts with multiple-authorship and will be prepared soon for submission to international peer-reviewed journals. The following list specifies my personal contributions to the individual papers:

Chapter I: GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes

Authors: Jana Kotzerka¹, Stefan Garthe¹, Scott A. Hatch²

¹ *Research and Technology Center Westcoast Büsum, University of Kiel, Hafentörn 1, 25761 Büsum, Germany*

² *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA*

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Scott Hatch developed the idea of the study. Jana Kotzerka conducted the field work and carried out data analysis. Stefan Garthe and Jana Kotzerka developed the idea for the manuscript. The manuscript was written by Jana Kotzerka. Scott Hatch and Stefan Garthe reviewed and approved the manuscript.

Chapter II: Contrasting foraging strategies of Black-legged Kittiwakes between pre-breeding and breeding and their relationship to oceanography

Authors: Jana Kotzerka¹, Stefan Garthe¹, Scott A. Hatch²

¹ *Research and Technology Center Westcoast Büsum, University of Kiel, Hafentörn 1, 25761 Büsum, Germany*

² *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA*

prepared for submission

Scott Hatch and Jana Kotzerka developed the idea of the study. Most of the field work was conducted by Jana Kotzerka. Data analysis was carried out by Jana Kotzerka. Stefan Garthe and Jana Kotzerka developed the idea for the manuscript. Jana Kotzerka wrote the manuscript. Scott Hatch and Stefan Garthe reviewed the paper.

Chapter III: Evidence for foraging-site fidelity and individual foraging behaviour of Pelagic Cormorants rearing chicks in the Gulf of Alaska

Authors: Jana Kotzerka¹, Scott A. Hatch², Stefan Garthe¹

¹ *Research and Technology Center Westcoast Büsum, University of Kiel, Hafentörn 1, 25761 Büsum, Germany*

² *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA*

published in *Condor* 2011, Vol. 113 (1), pp 80-88

Jana Kotzerka developed the idea of this study, conducted field work and carried out data analysis. Jana Kotzerka, Scott Hatch and Stefan Garthe discussed the results. Jana Kotzerka and Stefan Garthe developed the idea of the manuscript. The manuscript was written by Jana Kotzerka. Stefan Garthe and Scott Hatch reviewed and approved the paper.

Chapter IV: Individual specialization in the diving behaviour of a widespread North Pacific marine predator

Authors: Jana Kotzerka¹, Scott A. Hatch², Stefan Garthe¹

¹ *Research and Technology Center Westcoast Büsum, University of Kiel, Hafentörn 1, 25761 Büsum, Germany*

² *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA*

will be prepared soon for submission

Jana Kotzerka developed the idea of this study and discussed field work with Scott Hatch. Jana Kotzerka conducted field work and data analysis. The results were discussed by Jana Kotzerka, Stefan Garthe and Scott Hatch. Jana Kotzerka and Stefan Garthe developed the idea for the manuscript. The manuscript was written by Jana Kotzerka. Stefan Garthe reviewed the paper.

Chapter V: First insights into the diving behaviour and foraging areas of chick-rearing Tufted Puffins (*Fratercula cirrhata*)

Authors: Jana Kotzerka¹, Scott A. Hatch², Stefan Garthe¹

¹ *Research and Technology Center Westcoast Büsum, University of Kiel, Hafentörn 1, 25761 Büsum, Germany*

² *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA*

will be prepared soon for submission

Jana Kotzerka, Stefan Garthe and Scott Hatch developed the idea of this study. Jana Kotzerka conducted field work and carried out data analysis. The results were discussed by Jana Kotzerka, Scott Hatch and Stefan Garthe. Jana Kotzerka and Stefan Garthe developed the idea for the manuscript. Jana Kotzerka wrote the manuscript. Stefan Garthe reviewed the paper.

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Curriculum vitae

Personal data

Name: Jana Kotzerka
Birthday: 12.09.1975 in Magdeburg

Scientific career

WS 1996 – WS 2002 Study of biology at Christian-Albrechts-University of Kiel
Subjects: zoology, marine biology, geography

Oct. 2002 Diploma in zoology
Diploma thesis at the Institute of Marine Science (IFM-Geomar),
Kiel with the title “Spatial and temporal activity patterns of the
Dominican Gull (*Larus dominicanus*) in Northern Chile“

Sept. – Dec. 2002 Institute of Marine Science (IFM-GEOMAR), Kiel
Research associate in a project to seabird ecology

Feb. – Dec. 2003 Research and Technology Center Westcoast (FTZ), Buesum
Research associate in a project to seabird ecology

Dec. 2003 – Dec. 2004 Institute for Avian Research, Wilhelmshaven
Research associate in a project to bird migration

Jan. – Dec. 2005 Research and Technology Center Westcoast (FTZ), Buesum
Research associate in a project to seabird ecology

Since Jan. 2006 Research and Technology Center Westcoast (FTZ), Buesum
PhD student with thesis” Identification of foraging behaviour and
feeding areas of three seabird species breeding sympatrically in a
highly productive regime, the northern Gulf of Alaska”

Jan. 2009 – Sept. 2010 Biola, Consulting Agency, Hamburg
Research associate in projects concerning environmental impact
assessments of offshore wind farms

Since Oct. 2010 Research and Technology Center Westcoast (FTZ), Buesum
Research associate in a project to data base management and
seabird ecology

Publications

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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 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

Jana Kotzerka