HABITAT SELECTION BY FORAGING NORTHERN FUR SEALS: ASSESSING IN-SITU OCEAN TEMPERATURE AND LINKS TO OCEANOGRAPHIC FEATURES IN THE EASTERN BERING SEA

by

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Abstract

Habitat characteristics and mechanisms that enable predators to successfully forage are poorly understood in open marine ecosystems. I addressed this problem in the eastern Bering Sea using animal-born data-loggers carried by lactating northern fur seals (*Callorhinus ursinus*) from two populations breeding in distinct oceanographic zones — a declining population on St. Paul Island on the continental shelf, and an increasing population on Bogoslof Island over the oceanic basin. The data-loggers recorded water temperatures, dive depths and animal locations throughout foraging trips that lasted as long as 17 days and extended as far as 460 km from the islands. I contrasted tag-derived ocean temperatures with concurrent shipboard measurements and found that the fur seal data revealed finer-scale hydrographic processes with less estimated error than ship-derived data, particularly in dynamic oceanographic areas. I also identified probable foraging hotspots using first-passage time analysis of at-sea locations of individual females, and linked them to fine-scale hydrographic data using habitat selection models. I found that hot spots were related to thermoclines and surface fronts (although not with water temperature), and that the relationships differed between populations and among foraging strategies. St. Paul Island fur seals that mixed epipelagic and benthic dives focused their effort in areas with deeper thermoclines that may concentrate prey closer to the ocean floor, while strictly epipelagic foragers tended to use waters with shallower thermoclines allowing prey to migrate closer to the surface. Fur seals from Bogoslof Island foraged almost exclusively over the Bering Sea basin and appeared to hunt intensively along the fine-scale fronts that surrounded the island while fur seals from St. Paul Island extended their trips off-shelf to forage in areas with similar oceanographic features. It appears that lactating females rely on fine-scale boundaries in the open ocean to effectively concentrate prey, and that the relative distribution and accessibility of these oceanographic features account for the inter-island differences in foraging patterns. Collectively, my thesis shows that wide-ranging, diving animals such as fur seals can be used to produce detailed maps of marine habitat and demonstrates the importance of fine-scale habitat characteristics to top predators foraging in dynamic oceanographic environments.

Preface

Chapters 2 and 3 include data collected from instrumented northern fur seals in 2009 as part of a research program developed by my supervisor, Dr. Andrew Trites. I was the field-team leader on St. Paul Island while concurrent deployments on Bogoslof Island were led by Dr. Brian Battaile. I was responsible for quality control of all tag data, for creating a telemetry database and for conducting all analyses related to this research.

Chapters 2 and 3 include hydrographic data collected by Dr. K. J. Benoit-Bird (Oregon State University) as chief-scientist of the Bering Sea Integrated Ecosystem Research Program oceanographic cruise in 2009. Chapter 2 uses temperature at depth data while Chapter 3 uses both temperature and chlorophyll at depth data. I was responsible for binning the data at the resolution of interest, deriving new variables, creating interpolated maps, performing all analyses, and writing the chapter.

A version of Chapter 2 has been submitted for publication. Nordstrom, C.A., Benoit-Bird, K.J, Battaile, B.C., Trites, A.W. Temperature data collected by northern fur seals exceed that of traditional shipboard sampling methods in the eastern Bering Sea.

Chapter 3 also includes data on fine-scale ocean fronts prepared by Dr. C. Cotté (Université Pierre et Marie Curie). I was responsible for creating maps of surface fronts in my study area, converting their positions/strengths into variables of interest, performing all analyses, and writing the chapter.

A version of Chapter 3 has been submitted for publication. Nordstrom, C.A., Battaile, B.C., Cotté, C., Trites, A.W. Foraging habitats of lactating fur seals from increasing and decreasing populations in the eastern Bering Sea are structured by thermocline depths and submesoscale fronts.

Fieldwork abided by the guidelines of the Committee on Animal Care at the University of British Columbia. Animal capture and handling was conducted under UBC animal care permit no. A09-0345 and the United States National Oceanographic and Atmospheric Administration (NOAA) permit no. 14329.

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I must also thank David Rosen and Rebecca Barrick for their support as I transitioned from technician to student within the Marine Mammal Research Unit. Their encouragement made a difficult decision a much easier one. David has also graciously reviewed my work throughout the course of my degree and helped me make many professional connections that will benefit me for years to come.

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Dedication

To Gwyneth and Jace: your patience and love made this work possible.

"As the days dwindle to the end of July the Golden Seal is far at sea on her third fishing trip. If by magic an unseen recorder could have been scribing the life of this little mother with a first-born young, the record would read as follows…"

Victor B. Scheffer, "The Year of The Seal", © 1970

Chapter 1: General introduction

Understanding the relationships between predators and their habitat is a major focus in animal ecology. How an animal uses its environment, specifically the food resources consumed and the habitats occupied, are central to understanding its population ecology (Johnson, 1980). These two factors are not independent — the physical habitat can directly limit potential foraging locations either through physical barriers or cues and also indirectly through its effect on prey distribution. Hence, physical habitat characteristics can influence foraging patterns to a large degree and can ultimately impact population dynamics through changes to vital rates such as survival and reproduction (Lande et al., 2003). It is therefore important to adequately measure key habitat variables and derive the mechanisms by which environments structure foraging patterns to project the impact of habitat on predator populations.

The division of prey resources in marine habitats varies spatially and temporally according to many physical processes that determine the distribution of nutrients and subsequent productivity. These processes play an important role in ocean mixing and aggregating prey in many pelagic systems, and can therefore impact foraging patterns of marine predators at a variety of spatial scales (Mann and Lazier, 2006). In theory, localized areas where prey are retained and enhanced can create dense resource patches that can be efficiently exploited by marine predators. However, the relationships between fine-scale oceanographic features, prey aggregations, and predator populations remain poorly understood in many systems. Quantifying these relationships requires fine-scale data typically lacking for studies of top-level predators. Mismatches in the scale of measurements obtained from animals and their environment are common, and can compound the challenges faced by researchers studying wide-ranging predators that interact with ephemeral features within highly dynamic marine systems. High-quality data generated by solid methodologies and acquired at a scale relevant to the predator are required to quantify connections between marine predators and their foraging habitats.

1.1 Biologging

Biologging is an inter-disciplinary field emerging from collaborations among ecologists, physiologists, oceanographers, engineers, and others (Rutz and Hays, 2009). The discipline is focused on animal-borne instruments capable of recording animal movements and other aspects of their biology and environment. The techniques have been embraced by those studying marine species and by the marine mammal community in particular, as many fundamental questions remain unanswered for cryptic species that forage in dynamic environments which are logistically challenging to describe (Bograd et al., 2010; Ropert-Coudert et al., 2010). Biologging is well-suited to quantifying key habitat parameters at a scale relevant to the animal, and these measurements can contribute concomitantly to ecological and physical science studies.

Instrumented animals have proven to be valuable platforms for oceanographic data collection. Under-sampled polar regions have benefitted in particular as animals have traced currents, identified water masses and tracked ocean fronts in areas rarely accessible by ships or autonomous profilers (Charrassin et al., 2002; Lydersen et al., 2002; Lydersen et al., 2004; Biuw et al., 2007; Charrassin et al., 2008). Similar high-resolution data could supplement traditional measurements in sub-polar and temperature regions to describe marine habitat on a finer scale. Deploying biologging tags in more equatorial seas would also allow for additional assessments of animal-borne sensors with concomitant shipboard sampling to both validate tag data and to employ the methodologies in tandem to describe oceanographic regions.

Animal-borne sensors have gathered large numbers of high-resolution oceanographic profiles over wide areas and long time periods but with an inherently different sampling strategy than the regularized data collection protocols (*e.g.* transects) generally used by ships, moorings or satellites (Boehme et al., 2009). Despite temporal and spatial differences in sampling, oceanographic data collected by animals have contributed to models of ocean heat fluxes, predictions of frontal strengths, and deep-water turnover estimates (Boehme et al., 2008; Charrassin et al., 2008; Costa et al., 2008; Grist et al., 2011). Technical validations of the tags have been performed in the field and in the lab (Hooker and Boyd, 2003; Simmons et al., 2009; Roquet et al., 2011), but there have been no comprehensive comparisons to date of data derived from platforms employing standard data collection techniques with those from animal-borne instruments sampling according to highly individualized spatiotemporal use. Animal-borne sensors can be powerful tools to collect habitat data, but only if the data can be assumed to be comparable to habitat descriptions previously obtained from more traditional ocean profiling techniques. This has yet to be examined on a large spatial scale.

1.2 Eastern Bering Sea

The eastern Bering Sea (Fig. 1.1) is a model system in which to compare hydrographic profiles collected by free-ranging animals with traditional measurements and to explore relationships between the physical environment and foraging patterns in top marine predators. The high-latitude region is a seasonally productive and hydrographically complex system where the coupling of physical and biological processes supports large aggregations of seabirds and marine mammals (Hunt Jr. and Stabeno, 2002; Sinclair et al., 2008; Sigler et al., 2012). The physical oceanography of the area has also been well documented using traditional methods and includes studies of water masses, circulation, transport, and stratification (see reviews by Loughlin and Ohtani, 1999; Stabeno and Hunt Jr., 2002 and references therein).

The eastern Bering Sea is characterized by year-to-year physical variability within more generalized climate regimes described in terms of "cold" versus "warm" periods. These regime shifts are driven by atmospheric teleconnections and are described by indices such as the Pacific Decadal Oscillation and the Arctic Oscillation (e.g., Overland et al., 1999a; Mantua and Hare, 2002). Despite the fluctuations in ocean temperature and productivity, distinct differences can

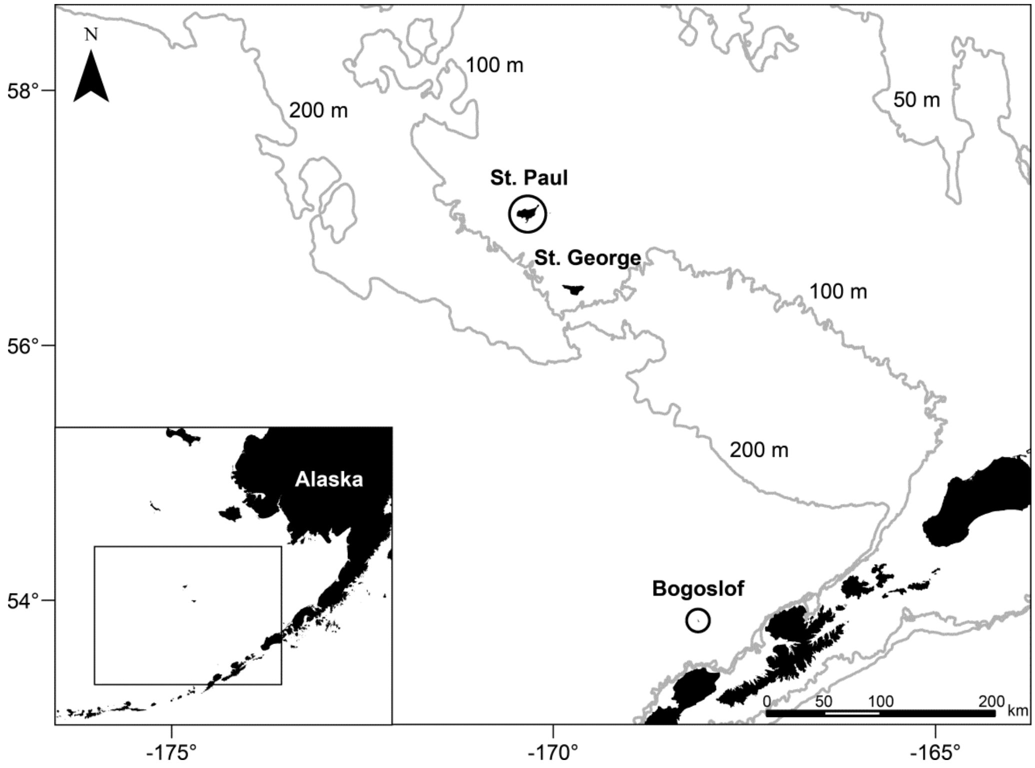


Figure 1.1 Map of the eastern Bering Sea highlighting St. Paul I. and Bogoslof I. Grey lines: major bathymetric isobaths.

be reliably found within zones over the continental shelf and also between the shelf and the deep oceanic basin. During summer the region is typically divided into three distinct hydrographic zones separated by thermal fronts along major bathymetric isobaths (Coachman, 1986): middle shelf with bottom depths less than 100 m; outer shelf with bottom depths between 100 and 200 m; and slope/basin with depths greater than 200 m (Fig. 1). Stratified waters are common over the shelf region while more mixed waters typify the basin (Ladd and Stabeno, 2012). In addition, a tongue of cold water (<2 °C) remnant from the spring ice melt (the cold pool) typifies the bottom waters of the central shelf while eddies are common over the more oceanic basin (Napp et al., 2000). These dramatic differences in thermal structure provide notable contrasts to facilitate comparisons of oceanographic profiles from different sources.

The exact positions of the thermal fronts and the cold pool are not static, but are dependent upon the strength of the winds and the tides which are the dominant physical forcing mechanisms (Stabeno et al., 1999; Napp and Hunt Jr., 2001). This variability is now known to have a pronounced effect on the role of the fronts as sites for prolonged production that supports zooplankton and fish communities (Brodeur et al., 2000; Brodeur et al., 2002; Swartzman et al., 2002; Schabetsberger et al., 2003; Ciannelli et al., 2004). Temperature is therefore thought to be an important factor in the distribution of plankton and fish in the eastern Bering Sea (Napp and Hunt Jr., 2001; Mueter et al., 2006; De Robertis and Cokelet, 2012). Walleye pollock (*Theragra chalcogramma*) are a major prey species within the ecosystem and have been shown to be horizontally distributed across the shelf and vertically distributed within the water column (Schabetsberger et al., 2000; Ciannelli et al., 2002; Winter and Swartzman, 2006). Young of the year (Age-0) and age-1 pollock are important forage fish for groundfish as well as a variety of seabirds and marine mammals (Livingston, 1993; Hunt Jr. et al., 2002; Sinclair et al., 2008). They are generally considered epipelagic, occupying the mid to upper portions of the water column while cannibalistic adults tend to be concentrated nearer the shelf bottom (Swartzman et al., 1994).

The spatial distributions of pollock have been described on-shelf, but it is not known whether the relationships hold at the immediate scale at which predators hunt or whether similar processes structure other fish populations. Pollock tend to be strong diel vertical migrators, as are other key prey of upper predators in the system. Cephalopods (squid, octopus), myctophids (lanternfish), and bathylagids (deep-sea smelt) are also well represented in the diets of seabirds and marine mammals that breed in the eastern Bering (Sinclair et al., 2008; Zeppelin and Orr, 2010; Renner et al., 2012). They are typically found over the slope and basin regions, and are a key link in transferring energy from ocean depths to upper trophic levels (Beamish et al., 1999; Sinclair and Stabeno, 2002). While the broad scale relationships between habitat and pollock have been tentatively described there have been no such connections made for most of these other, non-commercial species.

Oceanographic features such as eddies, meanders of the major currents, and disturbances created by bottom topography are common in the eastern Bering Sea and are all important mechanisms that can concentrate nutrient rich waters (Schumacher and Stabeno, 1994; Stabeno and van Meurs, 1999; Stabeno and Hunt Jr., 2002). These dynamic features could create boundaries capable of spatially shaping populations across multiple taxa (e.g. Schabetsberger et al., 2000; Brodeur et al., 2002; Flint et al., 2002) as areas where zooplankton would be aggregated and retained are likely to concentrate a range fish species and in turn attract piscivorous top-predators. As such, these features should be incorporated into any habitat selection modeling at the finest scale possible.

1.3 Northern fur seals

Northern fur seals (*Callorhinus ursinus*) are ecologically important apex predators in the Bering Sea. They migrate to the Bering Sea from the North Pacific to breed and raise their pups from July through November during which time female fur seals behave as central place foragers, alternating foraging trips at-sea with periods of nursing ashore (Gentry, 1998). Lactating females employ multiple foraging strategies (Goebel et al., 1991) and exhibit a large degree of inter-individual difference in terms of where animals travel in search of prey. While they appear to show some fidelity to areas where they previously foraged (Robson et al., 2004; Call et al., 2008), they do not appear to target specific foraging grounds as commonly seen in other species (e.g., Campagna et al., 2001; Chilvers et al., 2005; Weise et al., 2010). Lactating females do, however, rely on predictable and profitable foraging areas to maintain their energy reserves throughout the nursing process. Shifts in the location or timing of preferred prey could have a detrimental impact on fur seal health, productivity, and ultimately survival.

Population sizes of northern fur seals on different islands in the eastern Bering Sea are diverging. The population in the Pribilof Islands Archipelago (on St. Paul and St. George Islands) constitutes roughly half of the world population and has declined since the 1950's

(Trites, 1992; Testa, 2011). The decline in fur seal numbers through the 1970s are attributed to an experimental harvest of females that took place in the 1950s (York and Hartley, 1981) and to a high mortality of juveniles (Trites and Larkin, 1989). However, the population continues to decline for unknown reasons following a limited interval of stability (Towell et al., 2006). In contrast, a relatively small population of northern fur seals established itself on Bogoslof Island with pups first noted in 1980 (Lloyd et al., 1981) and with rapid increases in numbers since 1995 (Loughlin and Miller, 1989; Ream et al., 1999; Allen and Angliss, 2011).

While the causes of these divergent population trends in the eastern Bering Sea are currently unknown, there are notable differences between the breeding colonies which are separated by only 400 km (Fig. 1.1). St. Paul Island lies on the continental shelf in the central portion of the eastern Bering Sea surrounded by waters <100 m deep and with the shelf-break within foraging distance. In contrast, Bogoslof Island (a volcanic spire) projects above the southeastern basin north of the Aleutian archipelago over deep oceanic waters. Fur seals from the Pribilof Islands prey primarily (>80%) on walleye pollock and gonatid squid (*Cephalopoda*) (Sinclair et al., 1994; Gudmundson et al., 2006; Sinclair et al., 2008; Call and Ream, 2012) while limited data from Bogoslof suggests fur seals there target squid and northern smoothtongue (*Leuroglossus schmidti*) (Zeppelin and Orr, 2010). Recent tagging efforts using the Argos satellite system have also revealed differences in foraging trips with lactating females from St. Paul averaging 6.9 days at-sea while those from Bogoslof left their dependant pups for an average of 2.5 days in 2006 (Springer et al., 2008).

Regional differences in prey abundance, composition, and distribution may explain the contrasting foraging patterns between fur seal populations and are likely affected by physical oceanography. Data for northern smoothtongue are limited but strong evidence exists that pollock, and to a lesser extent squid, are concentrated in patches by shifting fronts and eddies (Springer et al., 1996; Brodeur et al., 2002; Schabetsberger et al., 2003) and these patches may represent reliable foraging areas in dynamic environments. Shifts in the distribution or concentration of preferred prey could detrimentally affect foraging success and ultimately population numbers by decreasing reproductive success, lowering pup survival, or reducing the number of offspring a female will have over her lifetime (e.g., Baker and Fowler, 1992). Such reductions in the availability, aggregation, and retention of prey are likely a function of oceanographic processes occurring at a variety of scales (Mann and Lazier, 2006). Thus, the contrasting population trends, trip durations, and island geographies in the eastern Being Sea provide a natural experiment in which to test the hypothesis that oceanographic conditions may be impacting the foraging patterns of northern fur seals by mediating their foraging opportunities.

1.4 Study goals and thesis structure

Despite long-term studies of the physical oceanography of the eastern Bering Sea and the biology of northern fur seals, the links between fine-scale hydrographic features and fur seal foraging patterns have not been established. Nor has there been a quantitative assessment of habitat mapping using newer biologging techniques with the more regularized data collection protocols employed by ships, moorings, and satellites.

My thesis goals were to evaluate ocean temperature data collected by animal-borne sensors in a complex marine environment and to investigate whether foraging patterns of northern fur seals from two breeding colonies with contrasting population trajectories were associated with fine-scale oceanographic features. To answer these questions I took a biologging approach to track lactating, foraging northern fur seals at high-resolution in the eastern Bering Sea during the breeding period in 2009. Fine-scale GPS enabled time-depth recorders fitted with a fast-response thermistor were attached to female fur seals on St. Paul and Bogoslof Islands. In this respect the fur seals became oceanographers as they collected ocean temperature profiles while diving during foraging trips. I supplemented the temperature and fur seal movement data with additional fine-scale hydrographic data collected concurrently by ships and with high-resolution frontal maps derived from ocean observing satellites.

I had two goals for the data: 1) compare ocean temperature profiles collected by seals with traditional measurements obtained by ships in the eastern Bering Sea; and 2) identify any temperature-specific regions, chlorophyll concentrations, eddies/filaments, or thermoclines that may structure at-sea fur seal distribution. My analysis looked to confirm that oceanographic data collected by seals was comparable to standard shipboard collections and to investigate how fine-scale oceanographic features influenced foraging habitat selection for northern fur seals from islands with diverging population trends.

My thesis consists of two data chapters written in manuscript style for submission to peer-reviewed journals. As such, there is some repetition in content to allow each chapter to stand alone independently of the thesis. Chapter 2 focuses on the oceanography of the eastern

Bering Sea and a detailed comparison of thermal habitat maps as derived from instrumented northern fur seals or standard shipboard sampling. Chapter 3 concentrates on the at-sea habitat selection of lactating, foraging fur seals to investigate how differences in foraging patterns between two populations with diverging population trends may be related to physical oceanographic features. Collectively, my thesis aims to measure key habitat variables for northern fur seals in the eastern Bering Sea and derive the mechanisms by which environments structure the foraging patterns of this top piscivorous predator.

Chapter 2: Temperature data collected by northern fur seals exceed that of traditional shipboard sampling methods in the eastern Bering Sea

2.1 Summary

Oceanographic data collected by marine vertebrates are increasingly being used in biological and physical studies under the assumption that data recorded by free-ranging animals are comparable to those from traditional vertical sampling. I tested this premise by comparing the water temperatures measured during a 2009 oceanographic cruise with those measured during 82 foraging trips by instrumented northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. The animal-borne data loggers were equipped with a fast-response temperature sensor and recorded 6,492 vertical profiles to depths ≥ 50 m during long distance (up to 600 km) foraging trips. Concurrent sampling during the oceanographic cruise collected 247 CTD casts in the same 5-week period. Average temperature differences between ship casts and seal dives (0.60 ± 0.61 °C), when the two were within 1 day and 10 km of each other (*n* = 32 stations), were comparable to mean differences between adjacent 10 km ship casts (0.46 ± 0.44 °C). Isosurfaces were evaluated at region wide scales at depths of 1 m and 50 m while the entire upper 100 m of the water column was analyzed at finer-scales in highly sampled areas. Similar trends were noted in the temperature fields produced by ships or seals despite the differences in sampling frequency and distribution. However, the fur seal dataset was of higher temporal and spatial resolution and was thereby able to visualize finer-detail with less estimated error than ship-derived data, particularly in dynamic areas. Integrating the ship and seal datasets provided temperature maps with an unprecedented combination of resolution and coverage allowing fine-scale processes on-shelf and over the basin to be described simultaneously. Fur seals (*n* = 65 trips) also collected 4,700 additional profiles post ship cruise which allowed ≥1 °C warming of the upper 100 m to be documented through mid-September, including regions where ship sampling has traditionally been sparse. My data show that hydrographic information collected by wide-ranging, diving animals such as fur seals can contribute physical data comparable to, or exceeding those, of traditional sampling methods at regional or finer scales when the questions of interest coincide with the ecology of the species.

2.2 Introduction

Traditional oceanographic sampling has been increasingly supplemented with data collected by free-ranging marine vertebrates (Boyd et al., 2001; Charrassin et al., 2002; Lydersen et al., 2004; Biuw et al., 2007; Roquet et al., 2009; Simmons et al., 2010). Animal-borne sensors have gathered large numbers of high-resolution vertical profiles over wide areas and long time periods but with an inherently different sampling strategy than the regularized data collection protocols (*e.g.* transects) generally used by ships, moorings or satellites. Despite temporal and spatial differences in sampling, oceanographic data collected by animals have contributed to models of ocean heat flux, predictions of frontal strength, and deep-water turnover estimates (Boehme et al., 2008; Charrassin et al., 2008; Costa et al., 2008; Grist et al., 2011). Technical validations of the tags have been performed in the field and the lab (Simmons et al., 2009; Roquet et al., 2011), but to date there have been no large scale comparisons of data derived from platforms employing standard data collection techniques with those from animal-borne instruments sampling according to highly individualized spatiotemporal use. Animal-borne sensors can be powerful tools to collect habitat data, but only if the data can be assumed to be, at minimum, comparable to habitat descriptions previously obtained from more traditional ocean profiling techniques, and this has yet to be examined on a large scale.

The eastern Bering Sea is a hydrographically complex region north of the Aleutian arc comprised of a broad, shallow (<200 m) continental shelf with a deep oceanic basin (>3,000 m) separated by a narrow shelf break (Fig. 2.1). The region is a seasonally productive high-latitude system where the coupling of physical and biological processes supports large aggregations of sea-birds and marine mammals (Hunt Jr. and Stabeno, 2002; Sinclair et al., 2008). Well described temperature regimes at the mesoscale are defined by the major isobaths but at the sub-mesoscale (<10 km) conditions are highly dynamic (Stabeno et al., 2001; Stabeno et al., 2008; Sullivan et al., 2008). For example, the middle continental shelf (< 100 m) typically consists of two well-structured temperature layers compared to the three diffuse layers on the outer shelf (<200 m), but the position of the sharp transition between the two fluctuates over space and time. In addition, a subsurface layer of water <2 °C (cold-pool) that is remnant from the spring ice melt occupies the middle-shelf, but its extent shifts inter-annually. Eddies, meanders of the major northward currents, and disturbances created by bottom topography all introduce fine-scale variability within the region's large expanse (Schumacher and Stabeno, 1994; Stabeno and van Meurs, 1999; Okkonen et al., 2004).

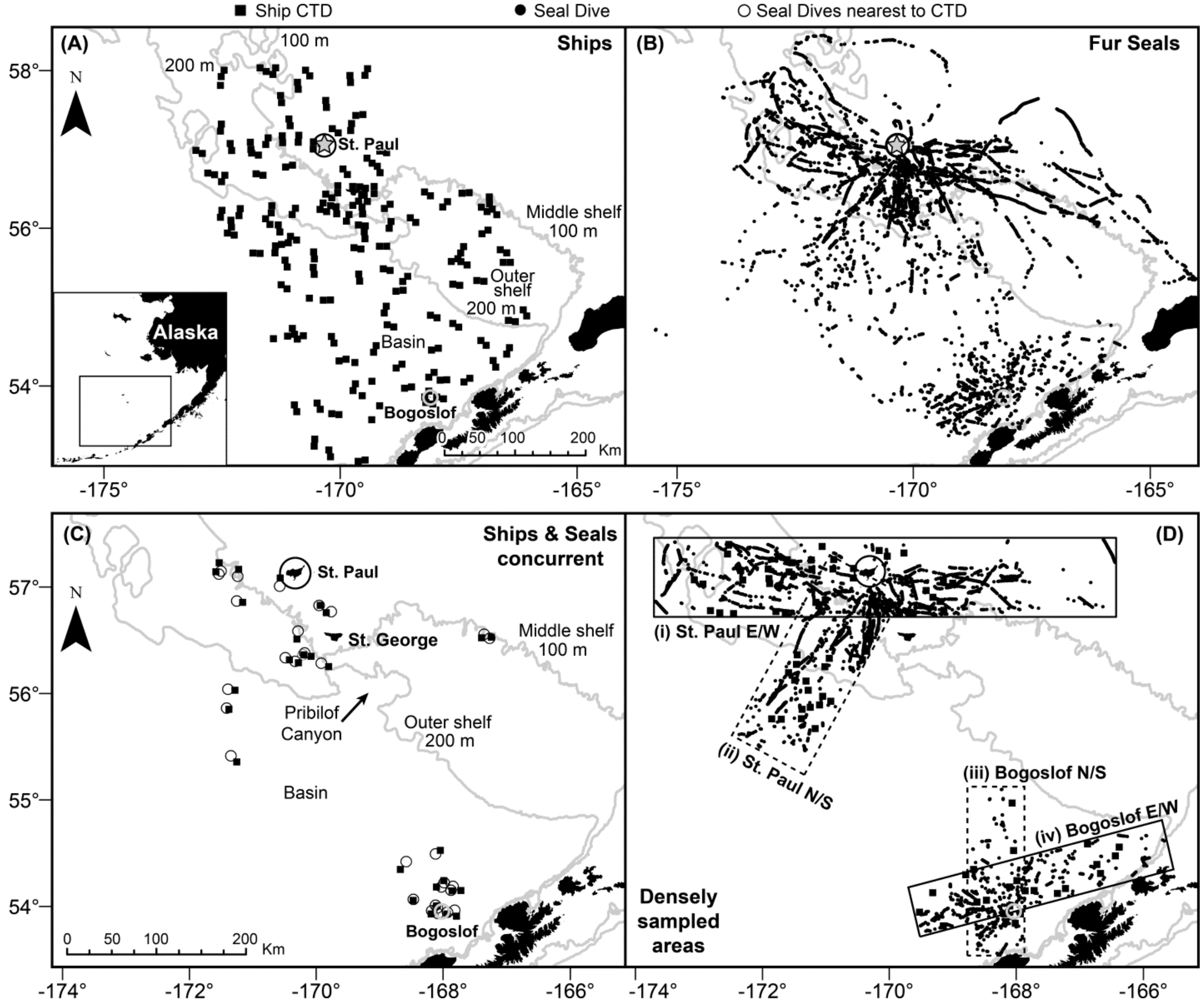


Figure 2.1 Sampling stations with ocean temperature profiles ≥50 m in the eastern Bering Sea: (A) ship CTD casts (*n*=247) from July 18–Aug 14, 2009; (B) fur seal dives from July 15–Sept 17, 2009 (*n*=11,192); (C) concurrent CTD casts (black squares) and seal dives (open circles) within 10 km and 1 day of each other (*n*=32); and D) delineated sub-regions where ships (black squares) and seals (black circles) sampled most frequently. The 200 m isobaths marks the approximate location of the shelf-break dividing the Bering Sea basin (west) from the continental shelf (east).

Northern fur seals (*Callorhinus ursinus*) are apex predators in the Bering Sea with an ecology that makes them well-suited platforms for fine-scale sampling across varied habitats and large distances. These small otariids return to islands in the Bering Sea to breed, give birth and rear pups for 4 months each summer. During this period, lactating females intersperse wide-ranging (up to 600 km) foraging trips at-sea with nursing bouts ashore (Gentry, 1998). As a result, complete data records can be recovered following foraging trips instead of necessitating the use of sub-sampled data typically relayed through satellites, thereby facilitating examination of fine-scale oceanographic data from complex environments. Lactating northern fur seals also employ multiple foraging strategies (Goebel et al., 1991) and exhibit a large degree of inter-individual difference in terms of where animals travel in search of prey. While females appear to show some fidelity to areas where they previously foraged (Robson et al., 2004; Call et al., 2008), they do not appear to target specific foraging grounds as commonly seen in other species (e.g., Campagna et al., 2001; Chilvers et al., 2005; Weise et al., 2010). From a sampling perspective, the routes used by the fur seals appear almost random at the island population level. This fine-scale heterogeneous sampling, in conjunction with their wide-ranging movements and predictable returns to the rookery for instrument recovery should make the northern fur seal an excellent animal platform from which to study the physical parameters of the eastern Bering Sea.

The overall objective of my study was to compare the upper water temperatures collected by ships with similar data collected by northern fur seals in the eastern Bering Sea. More specifically, I deployed fast-response temperature sensors (thermistors) on 31 northern fur seals concomitantly with ship-board sampling designed to support studies of upper trophic predators. This provided a unique opportunity to collect point-sampled oceanographic data from different platforms operating independently but over the same geographical region and time period. Not only could the information be compared to examine differences between ship and fur seal collections but the data could also be combined to describe the oceanography of the region more completely. My goals were to 1) compare water temperatures measured during a 2009 oceanographic cruise with those from instrumented fur seals, 2) evaluate interpolated temperature maps derived from each data source, and 3) describe summer conditions in the eastern Bering Sea using the novel, integrated dataset.

2.3 Materials and methods

2.3.1 Ship sampling

The eastern Bering Sea between St. Paul I. (57.1°N, 170.3°W) and Bogoslof I. (53.9°N–168.0°W) was simultaneously sampled from July 18th – Aug 14th, 2009 from the 43 m M/V Frosti and the 32 m M/V Gold Rush. Sampling was designed primarily to sample the distributions and habitat conditions of forage fish and krill and consisted of a series of paired stations separated by 10 km long transects. A total of 247 stations were stratified among three, hydrographically distinct zones (Coachman, 1986): middle shelf with bottom depths less than

100 m (45 stations); outer shelf with bottom depths between 100 and 200 m (81 stations); and slope/basin with depths greater than 200 m (121 stations) (Benoit-Bird et al., 2011). The first station in each pair was randomly located and the direction of the transect to the next station was randomly oriented so that transects were not allowed to cross region boundaries or other transects (Fig. 2.1A). Note that odd numbers of stations represent data loss from individual CTD deployments but at least one profile was collected for each transect.

A CTD (conductivity, temperature, depth) profile was conducted at each station (at the beginning and end of each 10-km transect). A Sea-Bird SBE19plus CTD was guided by a real time remote pressure sensor (Simrad PI60) and lowered to a depth of 100 m or 5 m from the bottom if the sea floor was <100 m from the surface. Each CTD was also equipped with a dissolved oxygen sensor, a transmissometer within the visible spectrum for most fish, and a fluorometer. Data were low pass filtered, aligned to account for instrument lags, and edited for loops (to account for ship heaving) before the raw data were converted to variables of interest using factory calibrations.

2.3.2 Seal sampling

Lactating fur seals at St. Paul I. (57.1°N, 170.3°W, Reef rookery, *n*= 44 females) and Bogoslof I. (53.9°N–168.0°W, *n*=43 females) were instrumented with Mk10-F GPS enabled time-depth recorders equipped with fast-response thermistors (Wildlife Computers, WA, USA) from July 11th to September 19th, 2009 (Table A1.1). Each GPS tag was paired with a VHF transmitter to assist with instrument recovery (Advanced Telemetry Systems, MN, USA). The archival Mk10-F tags recorded depth (0.5 m resolution), external temperature (0.52 s response, 0.05 °C resolution, 0.1 °C accuracy, Hill *pers. comm.*), and light level once per second. Fastloc™ GPS fixes were attempted every 15 minutes while the animal was at the surface.

Females on St. Paul were tagged at Reef rookery because fur seals from this location have been shown to forage in all hydrographic domains around St. Paul (Robson et al., 2004). Instruments were deployed on fur seals from 3 rookeries on Bogoslof with different geographic orientations to ensure tracks were representative for the island. Seals were captured using a mobile blind (July) or via hoop-net (August and September). Individual females were chosen based on size and the presence of a healthy pup and/or adequate milk production. These criteria increased the likelihood that females would return to the rookery for instrument recovery and redeployment. Animals were physically restrained using custom restraint-boards and neoprene wraps to allow devices to be glued to the dorsal pelage along the seal's midline using 5-minute epoxy (Devcon®, MA, USA). Hoop-netted females were weighed (± 0.1 kg) using an MSI-7200 Dyna-Link digital scale (Measure Systems International, Seattle, WA). Standard lengths (± 1 cm) and girths (± 1 cm) were also measured whenever possible for all animals but were generally more challenging to obtain from the mobile blind. Animals were recaptured, physically restrained, re-measured, and devices were removed following foraging trips (deployment interval = 5–39 days, Table A1.1). Capture teams based on each island redeployed instruments on successive animals after the data were recovered to increase the sample size of tagged individuals.

Profiles collected from fur seals were divided into 2 time periods: 1) July 15–August 15 (to match the ship cruise), and 2) from August 16–September 17 (post-cruise until last profile). GPS locations were filtered to remove points with unlikely travel speeds at sea (>3 m/s) and the tag's salt-water switch was used to determine the start and end of each foraging trip. Tracks were linearly interpolated between points as temporal resolution was generally very high (mean = 17.4 post filtered locations per day) (Tremblay et al., 2006).

Dive data were zero-offset corrected using Wildlife Computer's DAP program (v.2.063) with dives defined as those reaching at least 5 m. Each dive was enumerated and broken into descent, bottom, or ascent portions using 80% of the maximum dive depth as the transition points. Maximum depth (m) was recorded and dives > 50 m were retained for comparison with ship profiles. Locations for the start and end of each dive were determined by matching them to the interpolated tracks via the tag's clock (Fig. 2.1B).

The Mk10 external temperature data were processed according to Simmons et al. (2009). Briefly, external temperature readings were aligned with the depth sensor by applying a 1-second time lag and corrected by subtracting 0.05°C. Dives were binned at 1-m intervals and temperature values were interpolated using a hermite spline. As most seal dives occurred at <1 m/s, temperature measures were averaged more often than interpolated for a given depth.

2.3.3 *In-situ* temperature comparisons

Temperatures from CTD casts and the corresponding nearest seal dives were directly compared at 1, 25, 50, 75, and 100 m (as dives permitted) when they co-occurred within 10 km and 24 hours (Fig. 2.1C). Previous, side-by-side validations have shown good agreement between the thermistor in the Mk10 and CTD sensor (Simmons et al., 2009). Temperature values from data-loggers were regressed against CTD values at paired depths and summary statistics were calculated for absolute differences using the *R* software package (R Development Core Team, 2009). All reported values include ± standard deviation unless otherwise noted.

2.3.4 Comparing temperature fields: ship vs. seal sampling

Region wide temperature isosurfaces were generated separately from data collected by ships or by seals at 1 m and 50 m depth slices for the area covering -174.25° to -164.0° longitude, 58.75° to 53.25° latitude using the Ocean Data View software package (Schlitzer, 2011a, http://odv.awi.de) at the default projection (see 2.3.6 Gridding details). This allowed us to estimate temperature at layers routinely sampled by both platforms for the whole sampling region. I compared isosurfaces in 3 general ways by 1) qualitatively assessing broad temperature patterns, 2) quantitatively examining fits and errors within surfaces (two methods), and 3) quantitatively comparing interpolated values between surfaces (two methods).

First, regional temperature maps were examined visually to assess how features such as the cold pool and transitions along the isobaths compared between maps produced from ship or seal data. Second, I measured the quality of each interpolated surface via cross-correlation (estimated goodness of fit) using *a priori* estimates of correlation length and signal-to-noise ratio generated by the data-interpolating variational analysis (DIVA) fit routine (see 3.3.6 Gridding details) (Barth et al., 2010). Third, error estimates obtained for individual surfaces from Ocean Data View were mapped using ArcGIS 9.3.1 software for additional within surface assessment. Ocean Data View uses error estimates to restrict mapping to areas with error values below a user-defined tolerance and I retained the default setting of 0.25 for my analyses (see 2.3.6 Gridding details).

Fourth, I directly compared temperature/error estimates extracted from ship and seal fields at 1 km intervals along a 300 km transect across the continental shelf (-173.35° to -166.0°

at 51.1° latitude) and along a 220 km transect from the basin across the shelf-break to St. Paul (55.5° to 57.1° latitude, -172.0°-170.3° longitude). Extract transects were placed along the mid-line of densely sampled sub-regions (see next section). Fifth, regional surface maps were contrasted using a difference surface and a normalized difference surface for each depth slice that I generated by overlaying the ship derived field on the seal derived field and subtracting them. The normalized difference surface examined where differences between the fields was larger than the estimated errors and was defined as:

$$\text{Normalized difference} = \frac{\text{Ship temperature} - \text{Seal temperature}}{\sqrt{(\text{ship error}^2 \ + \ \text{seal error}^2)}} \qquad \text{Eqn. 2.1}$$

2.3.5 Temperature fields: fine-scale comparisons, seasonal differences and merged data

Finer scale cross-sections (side-profiles of temperature fields) were interpolated from complete CTD profiles and from entire fur seal dives in sub-regions that were sampled most often (Fig. 2.1D). This allowed us to examine the variability of the water column in highly sampled regions as described by either platform and to examine changes in temperature between two time-periods using data collected by the fur seals.

Difference cross-sections were created from seal derived data for each of the 4 sub-regions by overlaying fields from July–August 15 with those from August 15–September and subtracting their gridded values. I calculated the standard deviation of the gridding errors over the whole section and doubled that value (2x SD) to obtain a threshold above which any temperature changes were likely to be real differences between time periods as opposed to artifacts of the gridded interpolation. Further summary statistics on smaller patches within the difference section were calculated in Ocean Data View.

Datasets were merged and isosurfaces at 1 and 50 m were again produced using integrated data from ships and seals. This allowed us to describe the eastern Bering Sea using all available data for the period of July 15–August 15. Supplementary data describing the positions of fine-scale fronts over the basin on July 29 was added to provide a snapshot of frontal activity at the mid-point of the composite temperature maps and to provide context for the patterns observed over the basin. The frontal positions were estimated from 4-day maps of surface Lagrangian coherent structures (*e.g.* transport barriers, filament edges, or eddy boundaries).

These maps were derived from geostrophic current anomalies (produced by Aviso, France, *http://www.aviso.oceanobs.com*) using the finite-size Lyapunov exponent (FSLE) method which is well suited to study the properties of transport in fluid flow (Boffetta et al., 2001; d'Ovidio et al., 2004). Low FSLE values coincide with areas of low dispersion rates (*e.g.* eddy cores) while regions of large Lyapunov exponents are associated with areas of high dispersion such as the outer part of eddies and strong fronts (d'Ovidio et al., 2004; Resplandy et al., 2009). I contoured the FSLE values at 0.25 FSLE/d to reproduce the edges of the strongest fronts which was suitable for comparison with the aggregated temperature data.

2.3.6 Gridding details

Gridding allowed us to create composite temperature maps for the study region from the point-sample data collected by ships and seals. All surfaces and cross-sections were interpolated using the data-interpolating variational analysis (DIVA) method (Brasseur et al., 1996; Rixen et al., 2000; Troupin et al., 2010) as implemented in the Ocean Data View software package. The DIVA algorithm is akin to optimal interpolation techniques but incorporates directional constraints and barriers such as bottom topography. All re-created fields are sensitive to correlation length and, as with other gridding algorithms, the smoothness of the estimated field is controlled by adjusting the correlation length (Schlitzer, 2011b). Larger values allow for the assimilation of data from points further apart and result in smoother fields but at the expense of potentially losing fine-scale detail. The correlation length is set as the percent of *x* (*e.g.* longitude) and *y* (*e.g.* latitude or depth) in Ocean Data View therefore the areal extent of each surface was fixed prior to gridding. For example, I set a correlation length of 1% over a depth range of 110 m for all cross-sections to consistently allow each sample to influence the gridded value of vertically neighboring samples out to 1.1 m. Correlations lengths are reported as percentages with their equivalent linear distance in km.

All isosurfaces used in ship *vs*. seal comparisons were generated using a conservative correlation length of 1.3% (7.5 km latitude x 8.3 km longitude) that was based on the 10 km separation between nearest ship casts. Cross-sections used in finer-scale and seasonal comparisons were generated using either 1% (3.0 km) or 2% (4.4 km) of *x* (depending on the sub-region) but the correlation length was kept consistent within a sub-region. A correlation length of 1% (1.1 m) was used for *y* (depth) in all cross-sections. DIVA, as enabled within

Ocean Data View, employed a basic or poor man's error field (Barth et al., 2010; Troupin et al., 2010) to hide regions with estimated errors > 0.25. This created irregularly shaped temperature isosurfaces or left "gaps" within surfaces/cross-sections but it retained only those estimates with errors below the defined threshold. Errors are presented as the standard deviation relative to the field variance. The default quality limit of 0.25 was used as it produced relatively contiguous temperature maps without extrapolating estimates beyond the sampling region.

2.4 Results

2.4.1 Ship sampling

All 247 ship casts sampled depths >50 m and were therefore included in all subsequent analyses. Temperatures ranged from -0.10 °C (measured in the cold-pool to the north-east of St. Paul I.) to 10.57 °C (measured at 1m along the shelf break to the south-west of St. Paul). While stations were selected randomly within the study area, they were relatively well distributed at the regional scale (Fig. 2.1A) compared to the clumped, non-random distribution exhibited by the fur seals (Fig. 2.1B). The delineated sub-regions in Fig. 2.1D covered 30.8% of the area sampled by ships and incorporated 36% of all ship casts, further highlighting the relatively even spatial sampling achieved by the ships within the study region.

2.4.2 Seal sampling

St. Paul (*n*=44) and Bogoslof I. (*n*=41) fur seals completed 147 foraging trips (82 July–August, 65 August–September) that recorded at least one 50 m temperature profile (Table A1.2). Fur seals collected 11,192 profiles to depths ≥50 m during foraging dives at-sea between July 15th – Sept 17th, 2009 (6,492 July–August; 4,700 August–September; Fig. 2.1B). Recorded temperatures ranged from -0.80°C (in the cold pool east of St. Paul) to 10.45 °C (in the 1m surface waters along the 100 m isobath south-east of St. Paul).

Profiles were collected relatively evenly between the middle domain (*n*=3,497), the outer domain (*n*=4,060), and the slope/basin (*n*=3,635). Dives were nonetheless clumped within regions as the sub-regions delineated in Fig. 2.1D encompassed 21.6% of the area sampled by fur seals yet incorporated 50.9% of all sampling dives >50 m.

St. Paul fur seals foraged widely as expected, radiating in all directions from the island with a notable concentration of southward trips. Seals originating from St. Paul travelled further, were at-sea longer, and dove >50 m more regularly (Nordstrom et al., 2012) and in doing so collected more profiles (*n*=9,325) than seals from Bogoslof (*n*=1,867). Some trips from St. Paul were restricted to the continental shelf and sampled the middle and outer shelf domains only while trips that reached the basin sampled all three hydrographic zones as they had to cross the shelf to reach the slope and basin regions.

Bogoslof fur seals did not pass through the Aleutian chain but constrained their foraging trips primarily to the Bering Sea basin with occasional dives along the continental margins. Fewer sampling dives, generally restricted to the basin or slope regions, were recorded despite the greater number of trips performed by fur seals from Bogoslof. This was to be expected given Bogoslof Island's location over the basin when coupled with their shorter trips and their propensity for shallow diving (Nordstrom et al., 2012).

2.4.3 *In-situ* temperature comparisons

Seal dives ≥50 m coincided with ship-borne CTD casts within 10 km and 24 h of each other on 48 occasions. Of these, 32 unique casts were directly compared to the nearest seal dive (Fig. 2.1C) as depths permitted (*e.g.* Fig. 2.2). Overall there was good agreement between paired ship casts and seal dives (*e.g.* Fig. 2.2A–C) when comparing absolute temperature differences at pre-determined depths (0.32 median, 0.60 average ± 0.61 °C). Differences were comparable to sequential CTD casts (within 10 km of each other) at those same depths (0.36 median, 0.46 average ± 0.44 °C)

Regression analysis of paired temperature values (*n*=87 pairs) showed significant correlations between values recorded from either platform ($F_{1,85} = 516.1$, $p < 0.001$, adj. $R^2 = 0.87$; Fig. 2.3) and confidence intervals (95%) showed little uncertainty about predicted values. Most points were within 0.6 °C (the mean absolute difference between temperature pairings) of predicted values, particularly when temperatures were <4 and >8 °C which was typical of stable water masses well below or above the thermocline respectively.

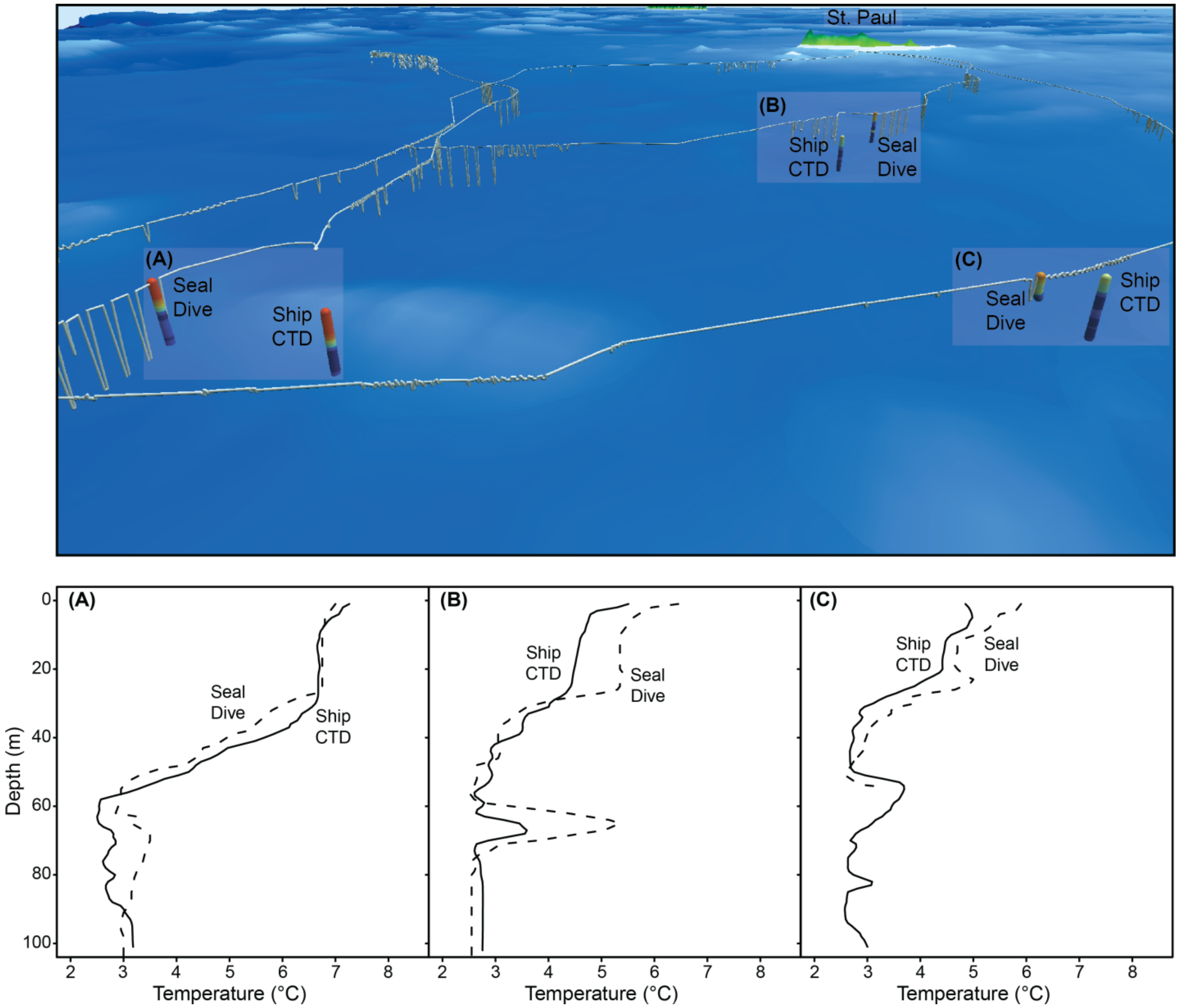


Figure 2.2 Examples of paired temperature profiles collected by concurrent ship CTD casts and instrumented northern fur seals when sampling occurred within 10 km and 24 h. The upper panel depicts 3 pairs of *in-situ* profiles (coloured vertical lines) on the continental shelf south of St. Paul I. White lines: fur seal surface track and additional dives. The lower panels compare the temperature-depth profiles from each ship cast (solid lines) and fur seal dive (dashed lines) pairing respectively (A: Dive SP09-0207 *vs*. CTD-34; B: Dive SP04B-0072 *vs*. CTD-32; C: Dive SP06-1466 *vs*. CTD-36).

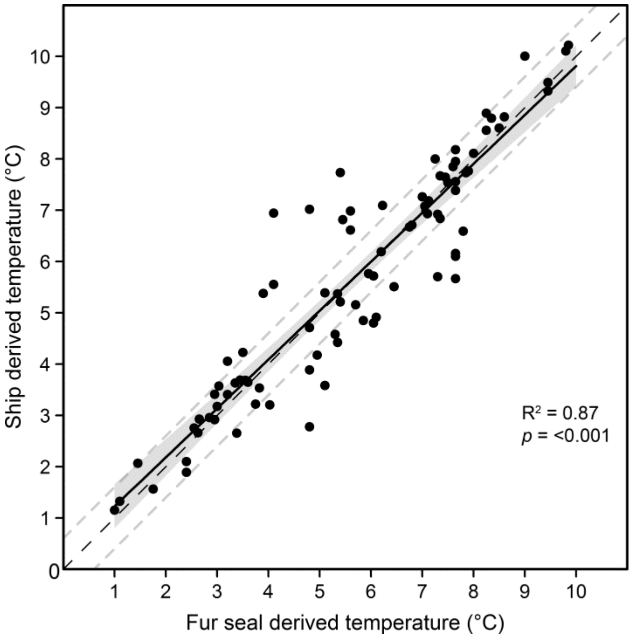


Figure 2.3 Regression of temperature (°C) values collected at 1, 25, 50, 75, and 100 m by instrumented northern fur seals (when dives permitted) in relation to the nearest ship CTD cast within 10 km and 1 day (see Fig. 2.1C). Shading: 95% model confidence interval; black dashed line: 1 to 1 line; grey dashed lines: ± 0.6 °C from 1 to 1 line (mean absolute difference between temperature pairings). There are 87 points comparing 32 stations/dives as collected by 20 individual fur seals.

2.4.4 Comparing temperature fields: ship vs. seal sampling

Each of the five different methods used to compare interpolated temperature surfaces illustrated that those created from the seal data were equivalent or exceeded those produced from ship data.

2.4.4.1 Qualitative comparisons

Seal derived temperature fields at depths of 1 m and 50 m were qualitatively very similar to fields generated by standard CTD profiling despite obvious differences in the extents of the areas sampled (Fig. 2.4). The CTD data provided a nearly contiguous surface from north of St. Paul to south of Bogoslof thanks to the relatively even distribution of sampling stations over the study area. In contrast, seal surfaces were irregularly shaped polygons as they were generated from clumped sampling dives restricted along widely dispersed foraging tracks. While I did not detect any overlap in the foraging areas between islands, a sufficient number of sampling dives existed along the periphery of the fur seal ranges to bridge the surfaces into collective wholes rather than generating disjointed maps for each island. Instrumented seals provided highly detailed temperature data over a large expanse of the eastern Bering Sea with the early summer surfaces (Fig. 2.4C and D) providing more coverage over the continental shelf east of the Pribilofs while later summer surfaces provided a more contiguous picture over the basin (Fig. 2.4E and F) .

Isosurfaces from both ships and seals highlighted similar features at the regional scale including cooler waters (~3–4 °C) surrounding the Pribilof Islands' at 1m depth from July through August (Fig. 2.4A and B). They also delineated the cold-pool (waters <2 °C) north and east of the archipelago at 50 m although seals did not sample north of St. Paul until late August (Fig. 2.4F). Both data collection platforms also revealed a band of cool (~3 °C) water extending along the 100 m isobath across the outer shelf south of St. George I.

Seal derived temperature surfaces showed greater variability than ship derived surfaces and revealed finer scale heterogeneity of temperature within areas both on and off the continental shelf (Fig. 2.4A–D). For example, the large numbers of samples taken on the shallow plateau between St. Paul and St. George showed that well-mixed waters at 1m surrounded and connected both islands despite intrusions of warmer surface waters. Seals also revealed greater temperature fluctuations along the 100 and 200 m isobaths (particularly around the Pribilof Canyon) as well north and west of Bogoslof.

Isosurfaces from later summer (Fig. 2.4E and F), when only seals were sampling, showed generalized warming at both 1 and 50 m, however the cold pool appeared to remain relatively stable. Waters at 1m around the Pribilofs increased to ~7–8 °C and the outer shelf west of St. George increased to ~9–10 °C. The band of cool water at 50 m in the outer shelf persisted, however; it was less continuous as 4–5 °C water intersected it along the shelf-break.

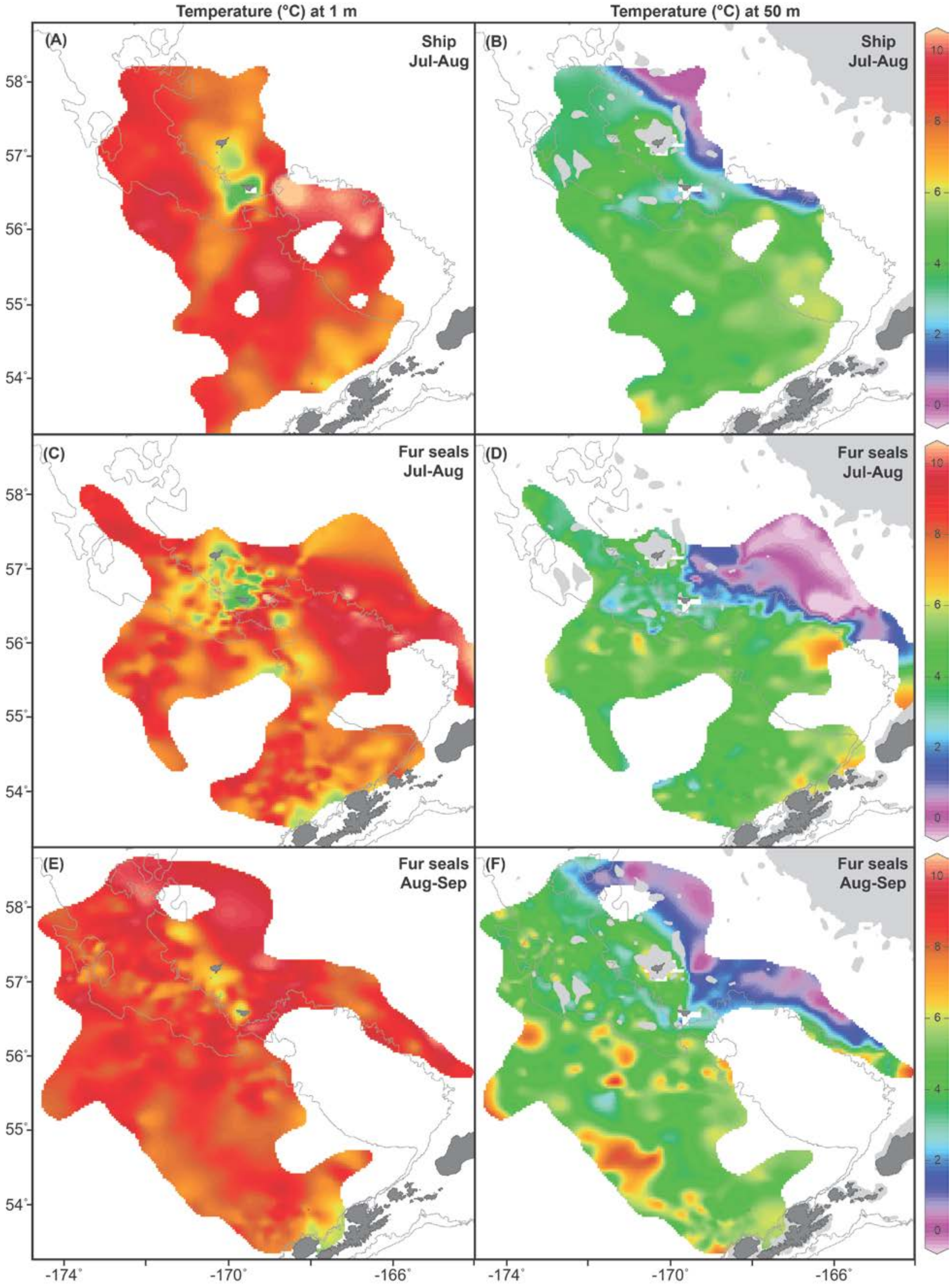


Figure 2.4 Comparing interpolated temperature surfaces (°C) of the eastern Bering Sea at 1m and 50m generated by ship CTD (panels A, B) or instrumented northern fur seal data (panels C, D) during Jul 15–Aug 15, 2009. Fur seals continued to collect data from Aug 16–Sep 17, 2009 (panels E, F).

2.4.4.2 Quantitative comparisons within surfaces

DIVA cross-correlation values were high for all isosurfaces with quality of the fits ranging from 0.80–0.94 (where min=0 and max=1). Seal surfaces at 1 m had better fits (0.89 for Jul–Aug, 0.94 for Aug–Sep) than the 1 m ship surface while the ship fit was better (0.90) than the respective seal fits at 50 m (0.80 for Jul–Aug, 0.86 for Aug–Sep). The July–August seal surfaces generated the highest (1 m field) and lowest (50 m field) fits.

Isosurface error fields derived from ships and seals were notably different both in the distribution and the relative amount of error within the temperature surfaces (Fig. 2.5). Given that surfaces were masked, all resulting polygons were ringed with relatively large errors resulting from the cut-off at 0.25. The ship error field contained wide areas of relatively large errors (>0.20) and the surface itself was pocked with small zones where the errors exceeded the threshold (Fig. 2.5A). In contrast, seal error fields generally comprised contiguous areas of relatively low error (<0.10). Rare exceptions occurred in areas where the temperatures were interpolated between the southern limits of St. Paul fur seal tracks and the northern extent of Bogoslof trips (Fig. 2.5C and E) or in areas sampled by a lone fur seal. Overall, the ship surface had a greater degree of estimated error (median=0.08; Fig. 2.5B) compared to either seal surface (medians=0.02–0.03; Fig. 2.5C and F).

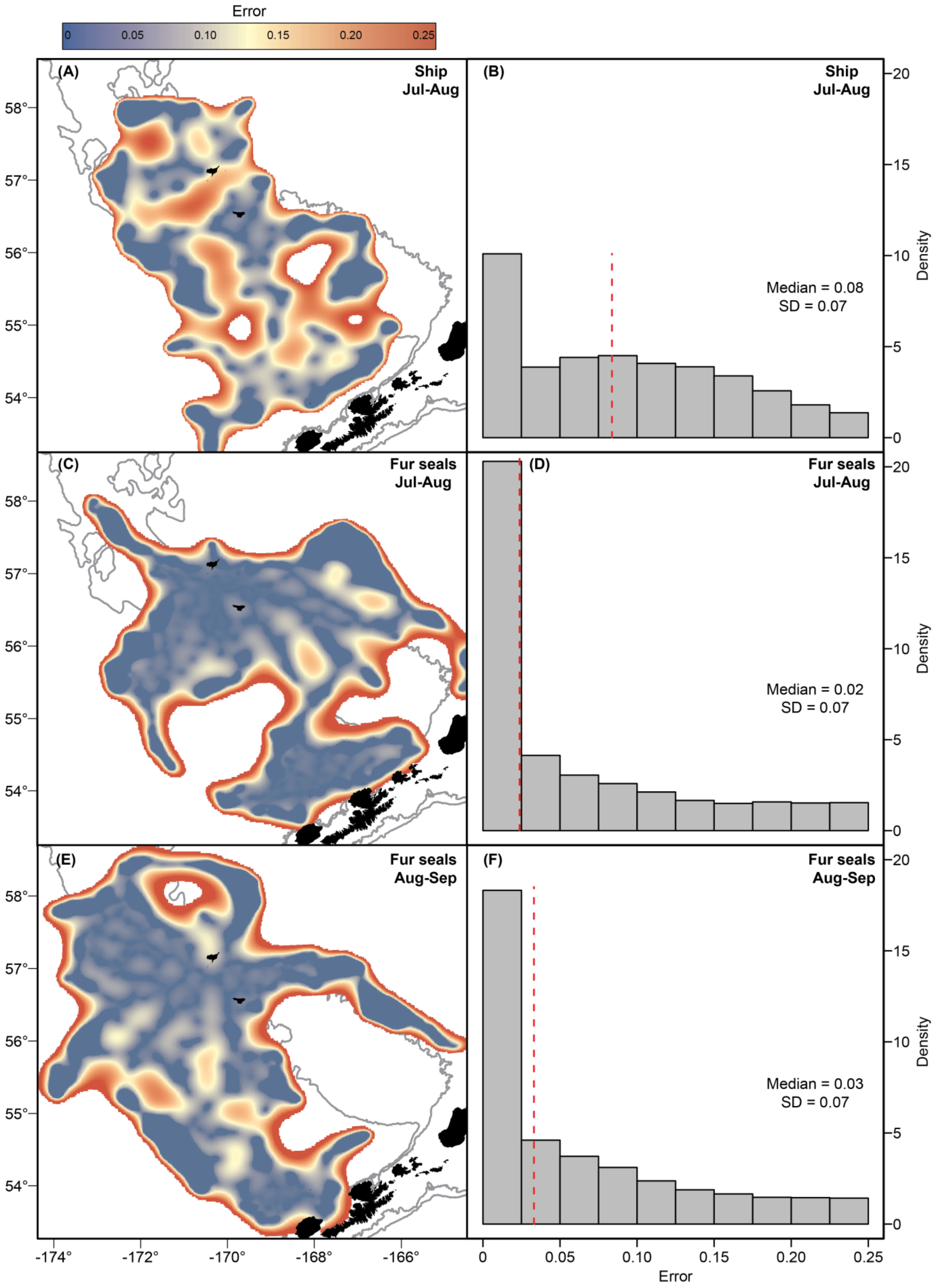


Figure 2.5 Comparing temperature error fields in the eastern Bering Sea at 1m generated by ship CTD (panels A,B) or instrumented northern fur seal data (panels C,D) during Jul 15–Aug 15, 2009. Fur seals continued to collect data from Aug 16–Sep 17, 2009 (panels E,F). Median errors are highlighted with a red dashed line. Note: errors > 0.25 are masked from the analysis.

2.4.4.3 Quantitative comparisons between surfaces

Extracted values from isosurfaces highlighted that both ship and seal maps tracked temperature changes across hydrographic domains (Fig. 2.6). However, seal derived temperature estimates revealed finer details in the field compared to the smoothed estimates obtained from sparser ship data. The amount of error associated with the seal estimates was also noticeably less than ship estimates on both transects and at both 1 m and 50 m depths. Errors within transects from ship surfaces were not restricted to the terminuses, where increased error was expected as they coincided with the isosurface edge (due to the aforementioned error mask cutoff), and instead flared intermittently throughout the extracted length.

Difference surfaces highlighted areas where interpolated fields from ships and seals diverged (Fig. 2.7A–B) and summarized the magnitude of the discrepancies (Fig. 2.7C–D). Raw differences between 1 m surfaces ranged from -5.1 (where ship fields were cooler) to +4.8 °C (where ship fields were warmer) but 50% of the differences were within -0.17 and 1.13 °C (Q1–Q3). The largest raw differences occurred around St. George: 1) south along the 100 m isobath and over the Pribilof Canyon; 2) northeast on the 50 m plateau, and 3) west along the 200 m isobath (Fig. 2.7A). The raw differences approximated a normal distribution but overall the ship surface was slightly warmer than the seal surface (median = 0.40 ±1.14 °C).

Normalized differences between 1 m surfaces highlighted the inconsistencies remaining between temperature fields after attempting to account for the error within the respective ship and seal surfaces. Normalized differences between -1 and 1 indicated where fields were consistent within the estimated errors while differences < -1 (cooler) and > 1 (warmer) indicated where the fields were notably different. Half of the differences were within -0.17 and 1.23 (Q1–Q3) and again the ship surface was slightly warmer than seal surface (median = 0.36 ± 3.22). Large differences were again apparent around St. George coinciding with the previously described band of cooler water south of the island and with cooler but variable surface waters on the plateau between the Pribilof archipelago. Additionally, a narrow band north-east of Bogoslof was identified as a dissimilar zone (Fig. 2.7B).

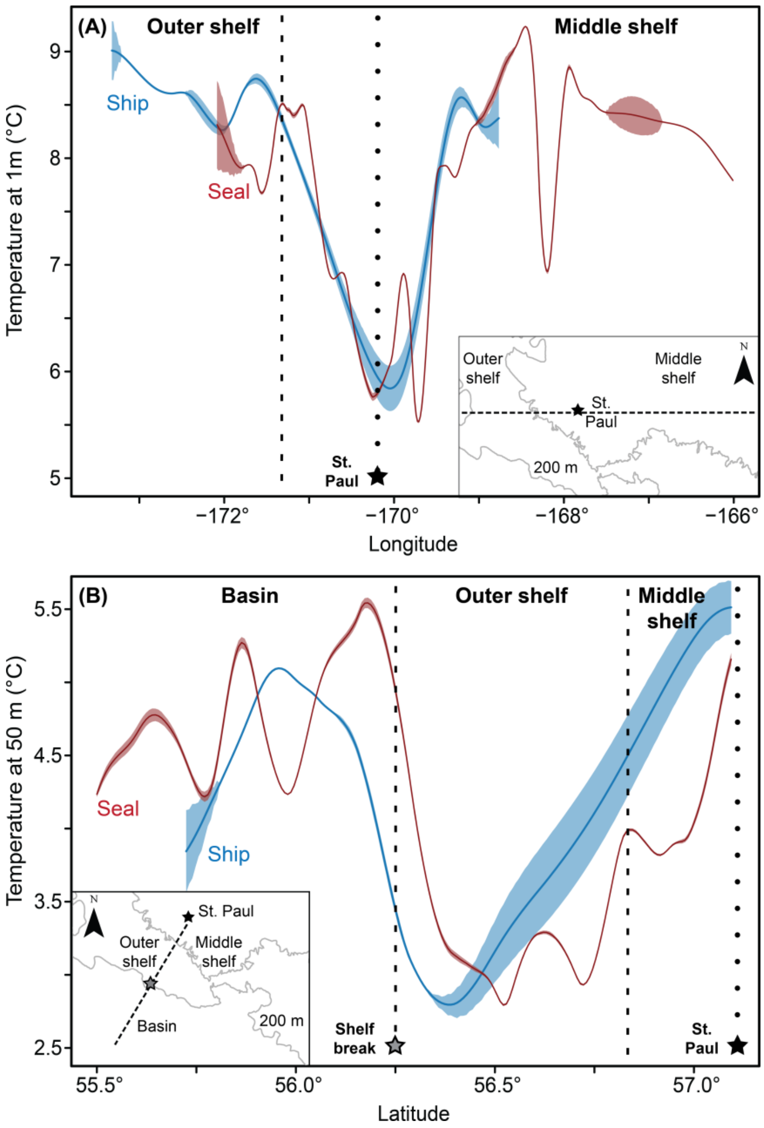


Figure 2.6 Temperatures estimates (°C, solid lines) and associated errors (ribbons) extracted from isosurfaces (Figs. 2.4 and 2.5) at 1 km intervals across the continental shelf of the eastern Bering Sea at 1 m depth (panel A) and from St. Paul I. south across the shelf-break to the basin at 50 m depth (panel B). Blue lines: ship derived surface; red lines: seal derived surface; dashed lines: isobath location; dotted line: St. Paul location. Isosurfaces were sampled along the mid-line of densely sampled sub-regions (insets, Fig. 2.1D i and ii). Note the relatively smoothed temperatures and wider-errors from ship-derived estimates compared to those from instrumented seals.

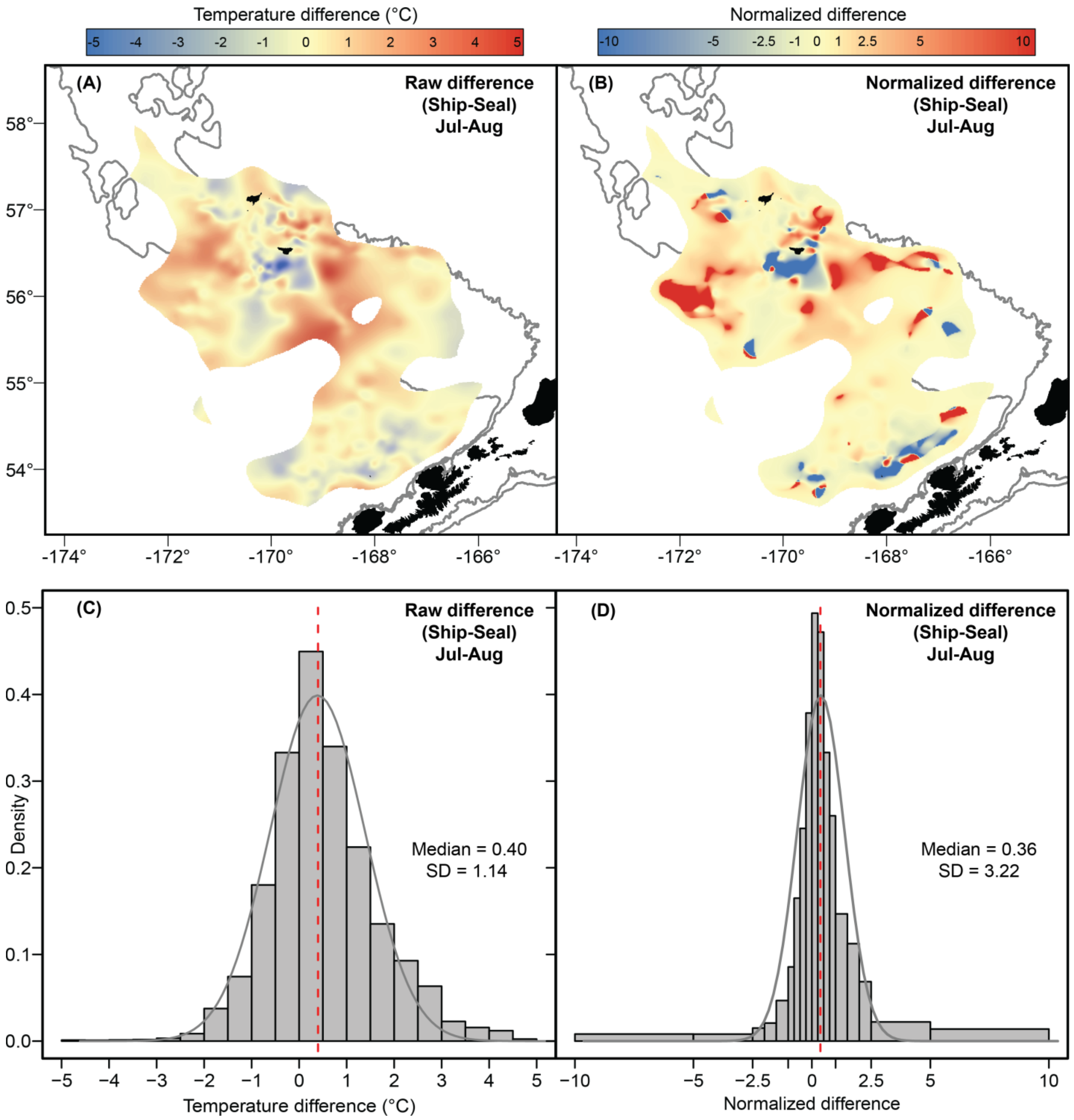


Figure 2.7 Interpolated surfaces and histograms describing the differences between temperature fields generated at 1m by ship CTD and instrumented northern fur seals in the eastern Bering Sea from Jul 15–Aug 15, 2009. Temperature (°C) differences resulting from subtracting the seal surface (Fig. 2.5B) from the ship surface (Fig. 2.5A) are described in panels A and C while normalized differences (where temperature differences are corrected for error estimates) are depicted in panels B and D. Note: normalized differences between -1 to 1 indicate where fields are consistent within the estimated errors (yellows) and differences <-1 and >1indicated where the fields are notably different (blues and reds).

2.4.5 Temperature fields: fine-scale comparisons, seasonal differences and merged data

Ship derived temperature cross-sections showed less detail and covered less area than those derived from seals (*e.g.* Figs. 2.8 and 2.9) in areas highly sampled by both platforms (Fig. 2.1D). Nonetheless, the side-profiles generated near Bogoslof (data not shown) and St. Paul tracked similar large scale shifts in the water column. For example, both ship (Fig. 2.8A) and seal (Fig. 2.8B) sections documented the abrupt transition from a weakly stratified 3-layer water column typical of the outer domain, to the strongly stratified 2-layer water column characteristic of the middle-domain (although the seal section was more informative thanks to increased sampling due east of St. Paul). Increased sampling by seals also likely made it possible to properly co-locate a shift in water column structure with the shelf-break south-west of St. Paul (Fig. 2.9B) as opposed to the same shift being documented more inshore on the outer shelf when using ship data (Fig. 2.9A).

Fur seals documented the warming of the eastern Bering Sea in all hydrographic regions due to continued sampling following the end of the ship cruise (*e.g.* Figs. 2.8C and 2.9C). The sub-region bracketing St. Paul from east to west warmed intermittently. On average, temperatures in the top 40 m increased over the outer shelf (mean = 0.61 ±1.04 °C, max = 4.30 °C), around St. Paul (mean = 1.06 ±1.46 °C, max = 7.30°C) but not over the middle shelf east of St. Paul (mean = -0.05 ±1.04 °C) as the water column remained strongly stratified and the cold-pool persisted throughout the summer (Fig. 2.8D). The sub-region intersecting the Bering Sea shelf and basin on a roughly north to south line also showed signs of warming with the most dramatic increases occurring on the outer shelf to depths of 100 m (mean = 1.7 ±1.11 °C, max = 5.25 °C; Fig. 2 9D).

Seal dives over the basin south-west of St. Paul (Fig. 2.9B and C) occurred within a persistent anticyclonic eddy (Nordstrom et al., 2012; Paredes et al., 2012) and they recorded ~7 °C water, more typical of waters at 20 to 30 m depth, being drawn to the surface and segmenting the ~9 °C surface waters from 55.5° – 56.25°. The regularized, banded pattern was similar to the concentric density ridges commonly observed in altimeter data and were notable particularly during the July to mid-August period when the eddy was strongest. The same pattern was not detected using the coarser ship data (Fig. 2.9A).

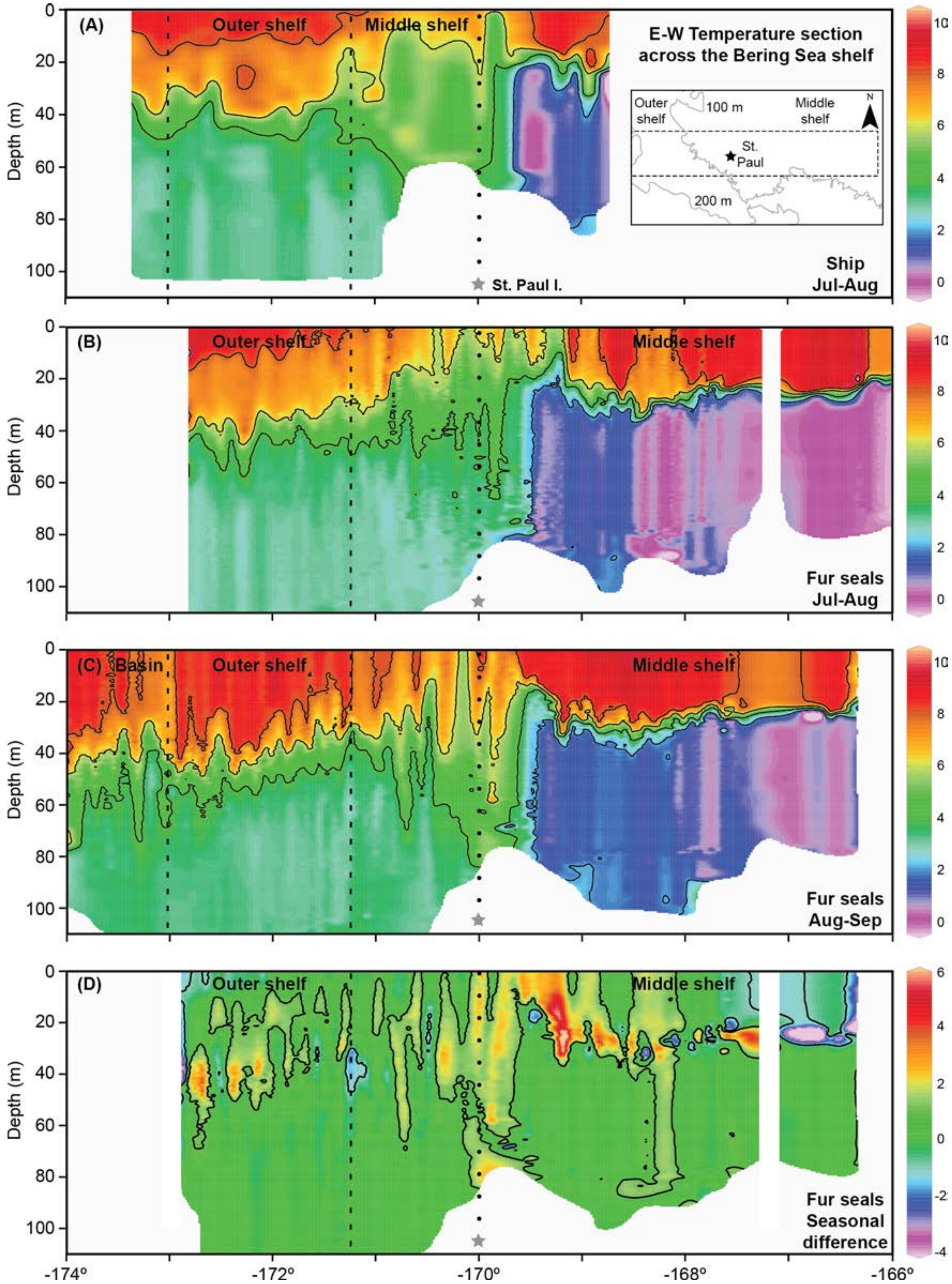


Figure 2.8 Comparing interpolated temperature (°C) cross-sections along a band crossing the eastern Bering Sea shelf at St. Paul I. (see inset and Fig. 2.1D i) generated by ship CTD (panel A) or instrumented northern fur seals (panel B) from Jul 15–Aug 15, 2009. Fur seals also collected data from Aug 16–Sep 17, 2009 (panel C) and the difference section (panel D) shows the patchy increase in temperature through to late summer in the upper 40 m of the water column changes >1 °C are contoured in panel D). Dashed lines: isobath locations; dotted line: St. Paul location.

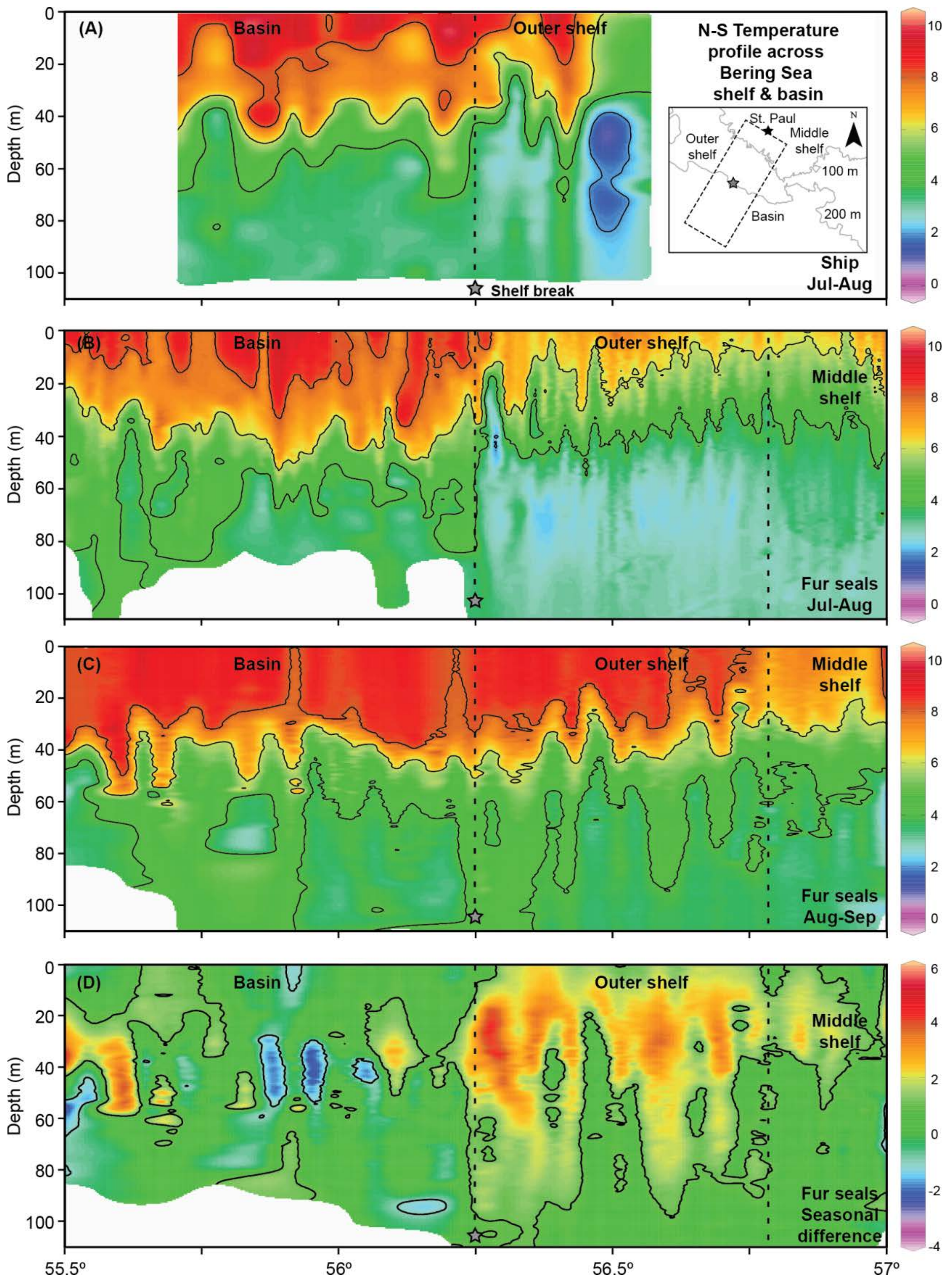


Figure 2.9 Comparing interpolated temperature (°C) cross-sections along a band from St. Paul I. (on-shelf) southwest to an area over the eastern Bering Sea basin (see inset and Fig. 2.1D ii) generated by ship CTD (panel A) or instrumented northern fur seals (panel B) from Jul 15–Aug 15, 2009. Fur seals also collected data from Aug 16–Sep 17, 2009 (panel C) and the difference section (panel D) shows the warming in the upper 40–60 m of the water column north of the shelf-break (located at ~56.25°; changes >1 °C are contoured in panel D). Dashed lines: isobath locations.

Given that temperature fields were similar at the regional scale, I integrated data collected by both platforms to produce isosurfaces that combined the sampling breadth of ships with the sampling resolution of fur seals (Fig. 2.10). Fine-scale temperature details were retained, and in some cases were enhanced, in the resulting maps. For example, a cluster of CTD casts north of St. Paul linked previously disparate bands of ~3 °C water collected by fur seals on the east and west sides of the Pribilofs' (Fig. 2.4D) into a coherent ribbon surrounding the islands at 50 m (Fig. 2.10B, see 3.5.2 Comparing temperature fields: ship vs. seal sampling). Those same casts better-defined the position of the cold-pool north of the Pribilof plateau.

Merged temperature maps also documented the cores of both anticyclonic and cyclonic eddies over the basin (Fig. 2.10). Anticyclonic (clockwise rotation) eddies commonly entrain warmer surface waters to deeper depths while cyclonic (counter-clockwise) eddies tend to transport colder water to the surface and this pattern has been documented in the southern Bering Sea (Mizobata et al., 2002) and the nearby Gulf of Alaska (Ladd et al., 2005). Temperature gradients at 1m depth were too small in regional maps to adequately define these features from temperature only (*e.g.* Fig. 2.10C); however, that was not the case at 50 m depth. The warm, downwelling core of the persistent eddy south-west of St. Paul was delineated (Fig. 2.10B i) as was an extension of the same feature that bordered the shelf-break further east (Fig. 2.10B ii). Two suspected cold-core (upwelling) eddies were also outlined over the central basin, albeit less sharply (Fig. 2.10B iii and iv). The temperature anomalies were confirmed as eddy cores by plotting the positions of encircling fronts which were derived from satellite altimeter measures of sea-surface height (Fig. 2.10D). Matching the temperature cores to the eddy rotation with the coarser altimeter data was possible for three of four eddies (Fig 2.10B and D, i–iii), and in these cases the warm eddy cores were correctly associated with an anticyclonic rotation while the cold-core aligned with a cyclonic circulation. The fine-scale surface fronts did not perfectly enclose eddy cores although this was not to be expected given the fronts were highly dynamic and a single snapshot was overlaid on a month-long temperature composite.

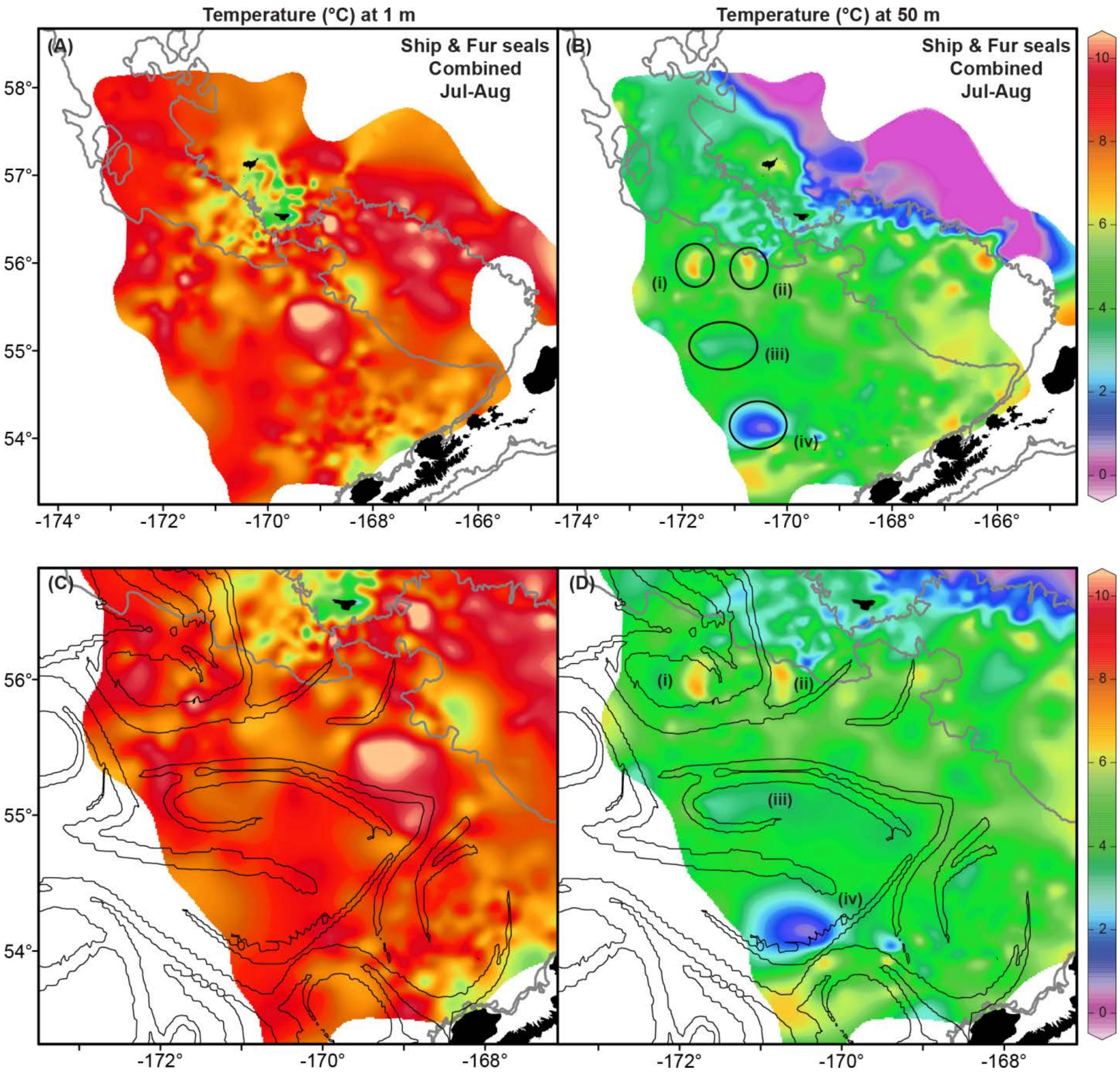


Figure 2.10 Integrated temperature surfaces (°C) of the eastern Bering Sea at 1 m (panels A and C) and 50 m (panels C and D) generated by interpolating ship CTD and instrumented northern fur seal data from Jul 15–Aug 15, 2009. Contoured surface fronts (black lines, 0.25 FSLE/d) are overlaid in panels C and D and are derived from geostrophic current data from Jul 29, 2009. Note the warm and cold cores of confirmed downwelling (i, ii) and upwelling (iii only) eddies observed within the temperature field over the basin at 50 m.

2.5 Discussion

I used *in-situ* profiles, regional isosurfaces, error maps, difference surfaces, and side-profile fields to compare temperature data collected from ship-based CTDs with those collected by free-ranging, instrumented northern fur seals. Data from casts and dives relatively concurrent in time and space were similar as were regional temperature maps depicting well-described temperature structure in the eastern Bering Sea. Maps produced using fur seal data included more detail, less estimated error, and provided an additional 5-week period than those available from the ship dataset. Maps produced using the integrated dataset preserved the fine-scale detail in the fur seal data while improving coverage thanks to the improved distribution of the ship stations, particularly north of St. Paul and over the basin. I propose that diving predators such as fur seals can provide high quality physical data products either to support studies of their own ecology or to answer hydrographic questions provided that the instrumented species lend themselves to the questions of interest.

2.5.1 *In-situ* temperature comparisons

Temperature profiles taken *in-situ* in a variety of hydrographic regions were strikingly similar regardless if the thermistors were carried by ships or seals, particularly since the recordings could be separated by as much as 10 km and 24 hours (*e.g.* Fig. 2.2). Relationships were similarly tight when ship derived temperatures were regressed against seal derived temperatures (Fig. 2.3). A nearly 1:1 relationship was found (slope = 0.95) with only 13% error which suggested instrument performance was similar after binning temperature values to 1 m. Profiled reading between 4 and 8 °C were the most variable when compared likely because these temperatures were typical of the mid-water column where rapid shifts associated with the thermocline were more common and where temperature-depth pairings would be more affected than those well above or below the thermocline. Slight changes in the location and/or timing of the measurements, inherent to the paired ship casts and seal dives, likely contributed real temperature differences between sampling and would exacerbate instrument differences between readings.

2.5.2 Comparing temperature fields: ship *vs*. seal sampling

Each surface polygon was the product of the correlation length, the specified error limit, and the sampling distribution. Correlation lengths and the error cut-off were kept consistent leaving the data coverage as the factor responsible for the different shapes and resolutions of the temperature surfaces. Regional maps were qualitatively similar where coverage was similar; however, fur seal isosurfaces revealed greater detail, particularly over the shelf region. For example, fur seals sampled the plateau between the Pribilofs intensively as they departed and returned to the rookery revealing chaotic, well-mixed surface waters in the early portion of the study followed by wide-spread warming as high as 6 °C in some areas as the summer progressed. Fur seals also traced a cool (~3 °C) band of water along the 100 m isobath at 50 m depth that persisted throughout the study period. The band bifurcated east of St. George to surround the Pribilofs and may form part of a transient front enveloping the islands (Kowalik and Stabeno, 1999; Sullivan et al., 2008).

The benefits of high-resolution sampling were most apparent in areas that were highly physically dynamic. Given these areas typically coincided with known bathymetric features on-shelf, they are generally predictable and could be targeted in advance for additional study. Near-real time satellite altimetry and satellite-linked drifters have also been used successfully to direct detailed sampling in more pelagic environments (e.g., Whitney and Robert, 2002; Ladd et al., 2005). Future hydrographic work supporting upper trophic level studies, similar to the cruises in my study, could benefit from incorporating highly adaptive sampling schemes that would allow for additional casts or for towed CTD sampling in dynamic areas which would be akin to the fur seal sampling I observed in the study. Changes to physical sampling protocols could also be extended to net tows, acoustic sampling, or other biological collections to better describe relationships between prey and their environment at the finer scales at which predators commonly exploit them.

Goodness of fit and error estimates provided a quantitative assessment of the within surface variability for each individual isosurface. The DIVA fit cross-correlation values have been shown to be overly optimistic for fields fit with the poor-man’s error routine (Troupin et al., 2010) such as those used in this study but I restricted them to relative comparisons only. The error estimates within the interpolated temperature fields depended on two factors: the data coverage (again) and instrument error. The ship-board CTD’s were more precise and more accurate instruments than the Mk-10 thermistors despite post-deployment corrections and limited sensor drift on the tags over time (Simmons et al., 2009). There was also more inherent variability within the 24 multi-purpose recorders deployed on seals than the two dedicated instruments deployed by the vessels. Given that error on data was negligible for ship instruments, the larger errors within the ship derived isosurfaces were primarily driven by their relatively limited sampling (Fig. 2.6).

High-resolution sampling by seals was also responsible for revealing finer temperature fluctuations (with less estimated error), than ship measures along identical transects extracted from temperature maps. The extracted data was predisposed to contain less error than other areas of the maps as transects were placed along the centre line of sub-regions previously identified as highly sampled areas for both platforms. Data extracted from alternative transects could show ships and seals as having similar temperature resolution and/or error rate depending on the placement. However, I observed subtle variations in temperature, an improved alignment of temperature with mapped isobaths, and limited error on the estimates in seal data both across the shelf near St. Paul (Fig. 2.6A) and across multiple domains (Fig. 2.6B) which were likely typical given the sheer number of seal samples in most areas. In addition, data extracted at 50 m over the basin revealed a regularized temperature inversion likely related to the surface currents layered within a young eddy (Fig. 2.9C, see 2.5.3: Temperature fields: fine-scale comparisons, seasonal differences and merged data).

The difference surfaces were difficult to interpret as the underlying sampling was not identical between ships and seals. Notable inconsistencies remained between the datasets despite 61% of the values in the normalized surface falling within -1 and +1 (indicating little difference). Outstanding differences could be related to the aforementioned instrument error of the tags, to sampling bias by fur seals, or to differences in the sampling time of particular locations. Fur seal dives showed remarkable heterogeneity in their locations both between individuals and within seals tracked over multiple trips thereby limiting their sampling bias. Most discrepancies ± 3 °C were however, consistent with dynamic regions such as along isobaths, over canyons, in areas of high vertical mixing, or even within an eddy core (Fig. 2.7) which would be sensitive to differences in sampling time.

Both ships and seals detected large temperature changes in dynamic areas at the regional scale but the specific boundaries placed by the spatial interpolations were strongly affected by the nearest casts or dives. Our composite maps (generated over a month) were presented as static snapshots but such temporally aggregated data would clearly mute dynamics occurring on a finer time scale which would be exacerbated in areas of rapid flux. The large inconsistencies remaining in the difference surfaces were not indicative of measures taken at the same time/locations (see 2.4.1 In-situ temperature comparisons) but rather I suspect they were the result of differences between predicted surfaces generated from datasets with very different spatial and temporal sampling strategies.

2.5.3 Temperature fields: fine-scale comparisons, seasonal differences and merged data

Seals recorded 4,700 additional temperature profiles ≥50 m deep after the completion of the 5-week ship cruise which permitted us to examine sub-regions sampled most often at a finer-scale and over two time periods. The 2-layer structure of the water column over the middle shelf east of St. Paul went largely unchanged throughout the study unlike the waters surrounding St. Paul itself or over the outer shelf as those areas experienced a deepening of the warm surface layer (*e.g.* Fig. 2.8B–D). Dramatic warming and increased structuring of the previously cooler and moderately mixed outer shelf waters was also documented south-west of St. Paul (*e.g.* Fig. 2.9B–D). Fur seal derived observations agree with those from a recent study where the spatial distributions of stratification generally reflect the traditional boundaries of the middle and outer shelf domains (Ladd and Stabeno, 2012). However, the data were unique in that they track the development of shoaling over a large area on the outer shelf and within the Pribilof domain as opposed to describing fully established stratification in the early fall.

Seals repeatedly sampled an anticyclonic eddy situated beyond the shelf-break and I suspect the temperature banding observed in the upper 20 m was indicative of concentric eddy currents drawing cooler waters to the surface (Fig. 2.9B). However, I cannot confirm my suspicion without the density contours used to define similar structures within eddies spawned in the Gulf of Alaska (Ladd et al., 2005; Janout et al., 2009; Ladd et al., 2009) although the presence of the eddy itself was confirmed with satellite altimeter derived data. The cooler intrusions were noted with less frequency and the upper 20 m was more homogenous (Fig. 2.9C) as the eddy core abutted the shelf break and began to wane in September.

Fur seals tracked temperature changes throughout the study period highlighting sometimes dramatic increases in specific locales. Longitudinal temperature records within a 2-month span (outside of mooring data) are relatively rare for most of the region as fisheries-based surveys rarely repeat transects. Recurring, short-term sampling of the basin, the slope, and even the outer shelf has been absent due to survey designs which are focused on the shallow continental shelf whereas moorings have been difficult to place in depths even approaching 200 m (but see Stabeno et al., 2009). The repeated measurements collected by fur seals across the region were therefore relatively unique and documented the continued warming of much of the eastern Bering, particularly the outer shelf waters to 100 m, over a relatively short span.

The hybrid mapping approach using ships and seals appeared to balance the strengths and weaknesses of each data collection platform. Ship sampling locations could be chosen in advance within pre-defined regions creating a relatively well-distributed but small dataset to describe a large and varied oceanographic area. Fur seal sampling locations were entirely opportunistic (from a data collection perspective) but frequent dives from a large number of wide-ranging individuals created a large but occasionally clumped dataset describing the eastern Bering Sea. Merging data collected from ships and seals thereby produced temperature maps of the upper surface waters with an unparalleled combination of coverage and resolution, particularly beyond the 200 m isobath. Many studies have examined the water properties of the Bering Sea but have been typically confined to a limited area or feature. In contrast, the merged maps provided a contiguous view of some ephemeral summer processes as varied as the presence of the Pribilof front, the extent of the cold-pool, and the onset of stratification over the shelf while also delineating eddy cores over the basin.

Merging the ship and seal collected datasets provided the most complete temperature description of the region and highlights how traditional oceanographic measurements and animal-borne sampling can complement one another. For example, warm core (downwelling) eddies were evident at 50 m in the merged temperature record that were either poorly defined (seals only) or absent entirely (ships only) in the July-August isosurfaces derived from a single platform. Cold core (upwelling) eddies were less well defined as the surrounding waters were similarly cool and they were sampled less frequently resulting in a more diffuse definition of the core proper. In all cases, the addition of CTD profiles, taken in a more regular pattern over the basin, provided the missing data required to definitively isolate eddies from the background field. Supplemental ship-casts were not available, but were also less necessary to identify features over the basin during the August-September time period when fur seals increased their sampling in the area (*e.g.* Fig. 2.4F).

The observations I made from the merged regional maps were not novel and specific features may not have been recognized if not for the variety of oceanographic work previously conducted on smaller scales in various domains across the region. Well-mixed surface waters around the Pribilofs, the inner Pribilof front, the expansive cold-pool, and temperature domains delineated along major isobaths were all observed over the continental shelf while a high-degree of eddy activity was concurrently observed over the basin. The physical processes observed here all require continued dedicated study using a variety of *in-situ* and remote-sensing tools; however, the combination of ship and seal temperature data provided a unique snapshot of the processes at work across the whole of the southeastern Bering Sea and this hybrid approach may be applicable to a variety of oceanographic scenarios.

Cost could be a determining factor when considering any combination of traditional and bio-logging data collection. While each situation will be unique, the operational costs of ship-sampling and fur seal sampling were very similar for this study. I examined a range of financial assumptions but cost differences were within 10% under any given scenario. Costs were dependent upon the time estimated to solely collect the CTD casts and the financial break-down of establishing the field camp on Bogoslof which was shared with other groups. The similarity was driven by the large number of instruments acquired for fur seal tagging thereby increasing bio-logging costs, in conjunction with lower than anticipated ship-time fees which decreased the ship sampling expenditure. The comparisons only cover the overlapping 5-week sampling period from Jul–Aug 2009, after which ship costs would begin to outpace the expense required to maintain field crews. The disparity would continue to grow for multi-year sampling programs, even with the relatively high logistical costs of sub-polar work, as many times instruments can be recovered whereas ships must be re-chartered.

2.5.4 Limitations

The fast-response thermistor was the only oceanographic quality sensor onboard the fur seal borne packages which restricted the comparison with ships to temperature only. Ships carried a wide variety of instrumentation, thereby allowing them to sample additional physical and biological characteristics of the water column which can in turn help draw connections with other levels of the ecosystem, including top predators. Other tags exist that can alternatively include conductivity sensors or fluorometers (*e.g.* Sea Mammal Research Unit's CTD- SRDL) although their increased size restricts them to deployments on marine animals larger than small otariids such as female northern fur seals. Animal-borne sensors must also be minimized and hardened to withstand the rigors of the deployment which typically results in reduced sampling rates, response time, and resolutions.

My study had a relatively large sample size (87 females) and the tagging effort focused on deployments that would maximize the spatial coverage at-sea yet there were areas that remained under sampled by fur seals. Obvious gaps included north of St. Paul and over the central basin, particularly in the July-August period. Deploying instruments on the northern rookeries would certainly improve sampling north of St. Paul as females there show high site fidelity to the shelf areas north of the island. In contrast, little could be done to improve central basin coverage as animals from Reef rookery (the study deployment site) typically forage over the central basin more than any other group of female fur seals. Northern fur seals are known to be relatively shallow, nocturnal divers which limited their sampling to the upper water column. Sampling the upper 100 m was expected, but the number of fur seal dives deeper than 50 m decreased rapidly (*n* dives ≥75 m = 5,620; ≥100 m = 2,456) and became increasingly constricted to the outer shelf south of St. Paul. The comparisons I could make with ships and the extent to which I could describe the vertical structure of the Bering Sea was therefore limited. This was particularly evident for fur seals instrumented on Bogoslof as the majority of their dives were generally <30 m. The physical limitations of the tags and the biological characteristics of the target species must be weighed alongside a project's goals and budget to determine whether bio-logging would be appropriate for any given application. In my case, a large number of northern fur seals were able to record a single environmental variable (temperature) and did it incredibly well across a vast area and over an extended time period.

2.5.5 Conclusions

Northern fur seals instrumented in the study collected high-quality temperature profiles at unprecedented spatial resolution in the upper water column of the eastern Bering Sea. They collected 26-times as many profiles as the ships over the same 5-week period and produced interpolated maps with finer detail and less estimated error than similar surfaces produced by standard CTD casts. Inconsistencies between regional maps typically occurred in isolated clumps along isobaths or in high-mixing areas where subtle differences in the plotting of abrupt temperature shifts led to large differences in raw and normalized difference surfaces. Fur seals repeatedly sampled a range of hydrographic regions throughout their nursing period which tracked the continued warming of the upper water column in areas, such as the outer shelf, where longitudinal sampling has traditionally been challenging. Areas sampled intensively by fur seals were, by definition, biologically relevant areas to top predators and typically occurred where water masses mixed which were difficult to sample via ship. For example, some individuals repeatedly sampled temperatures within an anticyclonic eddy south-west of St. Paul and appeared to reveal subtle temperature intrusions associated with the eddy's concentric currents when the eddy was at peak strength. Integrated temperature maps simultaneously depicted phenomenon previously described in separate studies on-shelf or over the basin and therefore provided unbroken coverage over most of the region with high-resolution data clustered in dynamic areas.

Our animal-borne dataset benefitted by deploying a large number of instruments from two widely separated sources (*i.e.* rookeries) on a species with wide ranging foraging trips in order to match the vessels' sampling distribution and to compensate for the limited individual sampling at depths >50 m. Northern fur seals also exhibited a high-dive frequency and were relatively non-selective in their foraging distribution at-sea (from a population sampling perspective). This produced a dataset with limited bias in terms of coverage which may not be true for other pinnipeds which show fidelity to highly specific areas (although these species would be well-suited to track changing oceanographic conditions in particular locales over time). Clearly, care must be taken to match the characteristics of potential instrument carriers with the data requirements in any bio-logging study. Our data show that hydrographic information collected by wide-ranging, diving animals such as fur seals can provide physical data products comparable to, and exceeding those provided by traditional sampling methods at regional or finer scales when the questions of interest coincide with the ecology of the species.

Chapter 3: Foraging habitats of lactating northern fur seals are structured by thermocline depths and submesoscale fronts

3.1 Summary

Northern fur seal (*Callorhinus ursinus*) populations in the eastern Bering Sea are declining at St. Paul Island and increasing at Bogoslof Island. The population differences may be related to foraging trip duration, but the cause of such trip differences are unidentified. I hypothesized that fur seals on St. Paul were forced to travel further to reach adequate foraging grounds, and that elevated prey concentrations were created by dynamic oceanographic features. I tested this by tracking a record number of lactating, foraging northern fur seals at high-resolution and linking individual areas of high-use to fine-scale oceanographic features within a rigorous statistical habitat selection framework. Probable foraging hotspots were identified with first-passage time analysis on tracks from 87 lactating females instrumented with bio-logging tags (44 St. Paul I., 43 Bogoslof I.) during July–September, 2009. I found no overlap in foraging areas between islands, but a difference in the duration of foraging trips—St. Paul trips were twice as long (7.9 d average) and covered 3-times the distance (600 km average) compared to trips from Bogoslof. St. Paul animals also foraged at double the scale (mean radius = 12 km) compared to Bogoslof animals (6 km), which suggests that prey were more diffuse near St. Paul than prey near Bogoslof. Comparing first passage times with oceanographic covariates using mixed-effects Cox-proportional hazard models revealed that foraging hotspots were linked to thermocline depth and occurred near fine-scale surface fronts (eddies and filaments). St. Paul fur seals that mixed epipelagic and benthic dives focused their effort in areas with deeper thermoclines that may concentrate prey closer to the ocean floor, while strictly epipelagic foragers tended to use waters with shallower thermoclines allowing prey to migrate closer to the surface. Fur seals from Bogoslof foraged almost exclusively over the Bering Sea basin and appeared to hunt intensively along fine-scale fronts that may constrain prey within narrow bands near the surface. Bogoslof fur seals foraged close to the island which was surrounded by strong fronts, while fur seals from St. Paul travelled >100 km and extended their trips off-shelf to forage at similar oceanographic features. It appears that the relative distribution and accessibility of prey-concentrating oceanographic features accounts for the observed inter-island foraging patterns, and that these differences may explain the current diverging population trends of the two fur seal colonies.

3.2 Introduction

The distribution and abundance of prey resources varies spatially and temporally in dynamic marine environments. Physical processes can play an important role in ocean mixing and aggregating prey in many pelagic systems (Mann and Lazier, 2006). In theory, localized areas where prey are retained and enhanced can create dense resource patches that can be efficiently exploited by marine predators. However, the relationships between fine-scale oceanographic features, prey aggregations, and predator populations remain poorly understood in many systems.

The eastern Bering Sea is a model system in which to explore relationships between the physical environment and foraging patterns in top marine predators. It supports large breeding aggregations of marine birds and marine mammals across a wide range of habitats. The highly productive region is characterized by strong and variable currents, eddies, and shifting fronts that regulate the distribution of nutrients from the deep basin to the shallow continental shelf (Stabeno et al., 2001; Brodeur et al., 2002; Hunt Jr. et al., 2002; Okkonen et al., 2004; Stabeno et al., 2008). The position and width of the fronts are not static, but vary significantly depending upon the strength of the winds and tides which are the dominant physical forcing mechanisms (Overland et al., 1999b; Kachel et al., 2002). This variability has a pronounced effect on the role of fronts as sites for prolonged production, and occasionally as a barrier to the exchange of nutrients between hydrographic regions. Eddies, meanders of the major northward currents, and disturbances created by bottom topography are all important mechanisms that introduce nutrient rich slope water onto the shelf (Schumacher and Stabeno, 1994; Stabeno and van Meurs, 1999) and are features that influence the positions of fronts from year to year. Areas where such production is aggregated and retained (Brodeur et al., 2002; Flint et al., 2002) are locations that are likely to attract top-predators.

Northern fur seals (*Callorhinus ursinus*) are important apex predators in the Bering Sea. The population in the Pribilof Islands Archipelago (on St. Paul Island and St. George Island, Fig. 3.1) constitutes roughly half of the world population and has declined since the 1950s (Trites, 1992; Testa, 2011). Declining fur seal numbers through the early 1970s are attributed to an experimental harvest of females that took place in the 1950s (York and Hartley, 1981) and to a high mortality of juveniles (Trites and Larkin, 1989) while a sharp decline through the late 1970's and early 1980's were correlated with rapid environmental changes (regime shift) and increasing commercial fishing in the region (National Research Council, 1996). The population stabilized temporarily from the mid 1980’s to mid 1990’s however, the population has since continued to decline at roughly 6% per year for unknown reasons (Towell et al., 2006; Allen and Angliss, 2011). In contrast to the declining Pribilof population, a relatively small population of northern fur seals was discovered on Bogoslof Island (Fig. 3.1) in 1980 (Lloyd et al., 1981) and has rapidly increased in numbers since 1995 (Loughlin and Miller, 1989; Ream et al., 1999; Allen and Angliss, 2011). While the causes of these divergent population trends at different breeding colonies in the eastern Bering Sea are unknown, recent tagging efforts on both islands have revealed notable differences in foraging trips (Springer et al., 2008) that may provide some insight into the current phase of the Pribilof decline.

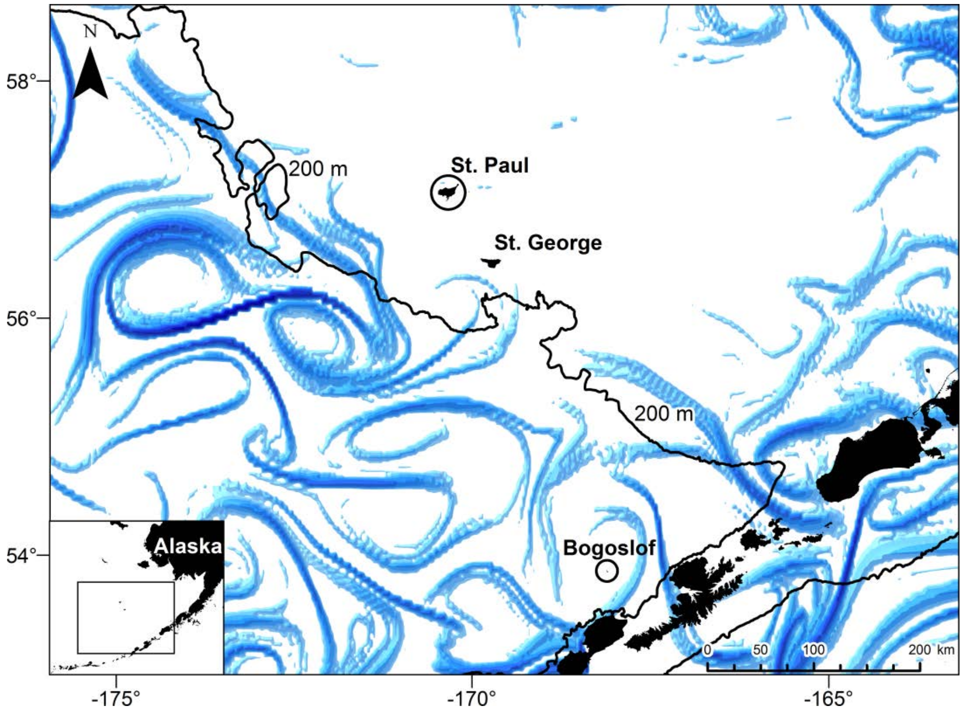


Figure 3.1 Map of the eastern Bering Sea showing the locations of St. Paul I. and Bogoslof I. in relation to the positions of submesoscale surface fronts (Lagrangian coherent structures) on Aug 1, 2009. The Lagrangian coherent structures had a resolution of 4 km over 4 days, and fronts were defined as >0.2 finite-size Lyapunov exponents per day. The 200 m isobath marks the approximate location of the shelf-break dividing the Bering Sea basin (west) from the continental shelf (east). Note the lack of strong surface fronts around St. Paul I.

Regional differences in prey abundance (quantity), composition (quality), and distribution (accessibility) may explain the contrasting foraging patterns between fur seal populations and are likely affected by physical oceanography. Such differences would be most acute for lactating fur seals during this energetically costly life-history stage (Gittleman and Thompson, 1988; Trillmich, 1996; Arnould, 1997) and differences in their foraging patterns may emphasize disparities in their environment (Costa et al., 1989; Trillmich, 1990). Northern fur seals migrate to the Bering Sea from the North Pacific to give birth and raise their pups from July through November during which time female fur seals behave as central place foragers, alternating foraging trips with periods of nursing (Gentry, 1998). This income provisioning strategy relies on predictable and profitable foraging areas to maintain their energy reserves and support their pup throughout the nursing process. Shifts in the distribution or concentration of preferred prey could detrimentally affect foraging success and ultimately population numbers by decreasing reproductive success, lowering pup survival, or reducing the number of offspring a female will have over her lifetime (e.g., Baker and Fowler, 1992). Such reductions in the availability, aggregation, and retention of prey are likely a function of oceanographic processes occurring at a variety of scales (Mann and Lazier, 2006).

A number of pinniped species have been recently documented interacting with mesoscale (~50–300 km) oceanographic features (e.g., Guinet et al., 2001; Lea and Dubroca, 2003; Bradshaw et al., 2004; Arnould and Kirkwood, 2008; Baylis et al., 2008; Bailleul et al., 2010; Dragon et al., 2010; Simmons et al., 2010), including northern fur seals (Ream et al., 2005; Sterling, 2009). Linking foraging in marine predators to finer scale oceanographic features (submesoscale) has been more challenging because of the difficulty of precisely knowing the positions and activities of animals at sea relative to oceanographic parameters (but see Trathan et al., 2008; Tew Kai et al., 2009; Kuhn, 2011). However, continued advances in animal-borne telemetry, environmental data resolution, and statistical frameworks now allows for the collection and analysis of finer-scale data to better address population level questions from tagged individuals.

The goal of the study was to investigate whether foraging patterns of northern fur seals from two breeding colonies with contrasting population trajectories could be associated with submesoscale oceanographic features. I tested this by tracking a record number of lactating, foraging northern fur seals at high-resolution and linking individual areas of high-use to fine-scale oceanographic features within a rigorous statistical habitat selection framework. More specifically, I tracked lactating females during summer to (1) compare foraging behaviours; (2) determine areas of high use along foraging trips; (3) quantify the influence of fine-scale oceanography on foraging intensity; and (4) relate habitat selection to diverging population trends at islands situated in different geographic domains.

3.3 Material and methods

3.3.1 Animal handling and instrumentation

Lactating fur seals were instrumented at St. Paul Island (57.1°N, 170.3°W, Reef rookery, n=44 females) and Bogoslof Island (53.9°N–168.0°W, n=43 females), Alaska, with Mk10-F GPS enabled time-depth recorders (Wildlife Computers, WA, USA) from July 11th to September 19th, 2009 (Table A1.1). Each GPS tag was paired with a VHF transmitter to assist with instrument recovery (Advanced Telemetry Systems, MN, USA). The archival Mk10-F tags recorded depth (0.5 m resolution), external temperature (0.52 s response, 0.05 °C resolution, 0.1 °C accuracy, Hill *pers. comm.*), and light level. Fastloc™ GPS fixes were attempted every 15 minutes while the animal was at the surface.

Females on St Paul were tagged at Reef rookery as females from this location have been shown to be the most variable of the 13 rookeries on the island and forage in all hydrographic domains around St. Paul (Robson et al., 2004). Instruments were deployed on fur seals from 3 rookeries on Bogoslof to ensure tracks were representative for the island. Seals were captured using a mobile blind (July) or with a hoop-net (August and September) and transferred to a custom-made restraint board. Animals were physically restrained and devices were glued to the dorsal pelage along the seal's midline using 5-minute epoxy (Devcon®, MA, USA). Hoop-netted females were weighed (± 0.1 kg) using an MSI-7200 Dyna-Link digital scale (Measure Systems International, Seattle, WA). Standard lengths (± 1 cm) and girths (± 1 cm) were also measured whenever possible for all animals but were generally more challenging to obtain from the mobile blind. Animals were recaptured, physically restrained, re-measured, and devices were removed following foraging trips (deployment interval = 5–39 days, Table A1.1). Capture teams based on each island redeployed instruments on successive animals after the data were recovered to increase the sample size of tagged individuals.

3.3.2 GPS and dive data analysis

GPS fixes were filtered to remove locations resulting from unlikely travel speeds (*i.e.*, >3 m/s), and the salt-water switches on the tags were used to determine the start and end of each foraging trip. The GPS locations had a high temporal resolution (mean = 17.4 post filtered locations per day) and were linearly interpolated to reconstruct the tracks (Tremblay et al., 2006). Metrics for each foraging excursion included time away from the rookery (± 0.1 d), total distance travelled, and maximum distance from the rookery (± 0.1 km). Distance travelled was calculated by summing distances between GPS points while maximum distance was defined as the straight-line distance from the rookery to the furthest point on the track. All length calculations used the great-circle distance (WGS84-geoid) option in the *sp* package (Bivand et al., 2008) for *R* software (R Development Core Team, 2009).

Dive data were zero-offset corrected using Wildlife Computer's DAP program (v.2.063) with dives defined as those reaching a minimum of 5 m. Dives were further classified as foraging dives for behavioural analyses if they exceeded 20 seconds (Baylis et al., 2008; Kuhn et al., 2010; Kuhn, 2011). Each dive was enumerated and broken into descent, bottom, or ascent portions using 80% of the maximum dive depth as the transition points. Maximum depth (m), duration (s), bottom duration (s), as well as ascent and descent rates (m/s) were calculated for each dive. Bottom deviations (*i.e.*, vertical deviations >1.0 m during the bottom segment of each dive) were counted as they may be indicative of feeding behaviour. The position of each dive was determined by interpolating their start and end times (as recorded by the tag's clock) along the reconstructed swimming track. The total number of dives, total number of bottom deviations, as well as the mean dive duration, bottom duration, ascent rate and descent rate were calculated for 12 km (St. Paul fur seals) and 6 km (Bogoslof fur seals) intervals along each foraging track to compare dive-based feeding proxies with first-passage time (see section 3.3.3).

The Mk10 external temperature data were processed according to Simmons et al. (2009). External temperature readings were aligned with the depth sensor by applying a 1-second time lag and corrected by subtracting 0.05°C. Dives were binned at 1-m intervals and temperature values were interpolated using a hermite spline. As most seal dives occurred at <1 m/s, temperature measures were averaged more often than interpolated for a given depth. Each dive was classified as occurring during daylight hours or at night using the civil twilight tables (where the sun is 6° below the horizon) for St. Paul (for fur seals originating from St. Paul) and Dutch

Harbor (for fur seals originating from Bogoslof (http://www.usno.navy.mil/USNO/astronomical-applications/data-services). All dive classifications and statistics were accomplished using custom scripts in *R*.

The timing of diving within a day/night cycle appears to reflect alternative foraging strategies in northern fur seals (Goebel et al., 1991). Fur seals from Bogoslof made 98% (± 0.5%) of their foraging dives during the night. However, two foraging strategies were evident for St. Paul fur seals based on the proportion of time they spent diving at night. The first group resembled animals from Bogoslof as they made 95% (group mean ± 0.8%) of their foraging dives at night and were termed the Nocturnal group. The second group was termed the Cathemeral group since they made substantial use of both the dark and light portions of the day cycle by foraging throughout the night and into the next morning. This Cathemeral group only made 69% (group mean ± 2.7%) of their foraging dives at night with all individuals making a minimum of 18% of their dives during the day which were typically to the ocean bottom.

3.3.3 First-passage time

First-passage time (FPT) is the time required for a tracked seal to cross a circle of a given radius (Fauchald and Tveraa, 2003). I used this scale dependent measure of search effort to identify areas along each track that were intensively used by the fur seals. I assumed that increased habitat use was indicative of increased foraging effort and verified this assumption by comparing dive behaviours with FPT (see section 3.3.2). Direct and faster movements across a defined area resulted in low FPT values (*i.e.*, low residency times), while tortuous or slower movements produced relatively high FPTs (*i.e.*, high residency times). Using FPT in statistical habitat models violates the assumptions underlying traditional parametric models such as Gaussian generalized linear models (Freitas et al., 2008b). However, FPTs are continuous event-time measurements, and therefore can be used in survival models such as Cox proportional hazards models (section 3.3.5)

I interpolated a position every 2 km along the GPS derived track to spatially standardize the foraging tracks and remove potential biases associated with oversampling some areas or with animals that provided a greater number of locations. A two km interval was chosen because it was the mean and median distance between successive filtered GPS locations at sea for both St. Paul and Bogoslof groupings. FPT was thus calculated for each of the generated positions for radii ranging from 2–40 km at 2 km intervals using the *adehabitat* software package in *R* (Calenge, 2006).

FPT values will increase as the radii increases as more of the path is included in the FPT calculation (Fig. 3.2A). However, the variance of the mean FPT calculated for each radius should reflect the consistency with which the fur seals spent time in each circle. Thus the radius with the maximum FPT variance should be the one that best differentiates between low and high FPT, and reflects the spatial scale within which animals concentrated their time (Fauchald and Tveraa, 2003, 2006; Freitas et al., 2008b).

Mean log-transformed FPT variances were plotted by island of origin and dive strategy (*i.e.*, St. Paul Nocturnal, St. Paul Cathemeral, and Bogoslof) to determine the maximum variance for each grouping. I chose the radius with the maximum variance as a common length-scale for fur seals in each foraging group. This facilitated comparing individuals within groups, removed some of the stochasticity from individual differences, and defined the minimum resolution for the environmental covariates. FPTs from the interpolated tracks from each island (at 12 km intervals for St. Paul trips, and 6 km for Bogoslof) were used to compare the time spent in different areas as a response to changes in the environment. These radii reflected the sizes of the areas within which the mean variances of FPTs were the highest (*i.e.*, at 12 km for both foraging strategies observed from St. Paul fur seals and a 6 km radius for Bogoslof fur seals; Fig. 3.2B). Given the majority of fur seal dives took place after civil twilight, plots correlating FPT and habitat variables were created using either all FPT points (including likely resting behaviour) or a subset of night time FPT points only for the St. Paul Nocturnal group and the Bogoslof group (see section 3.3.5).

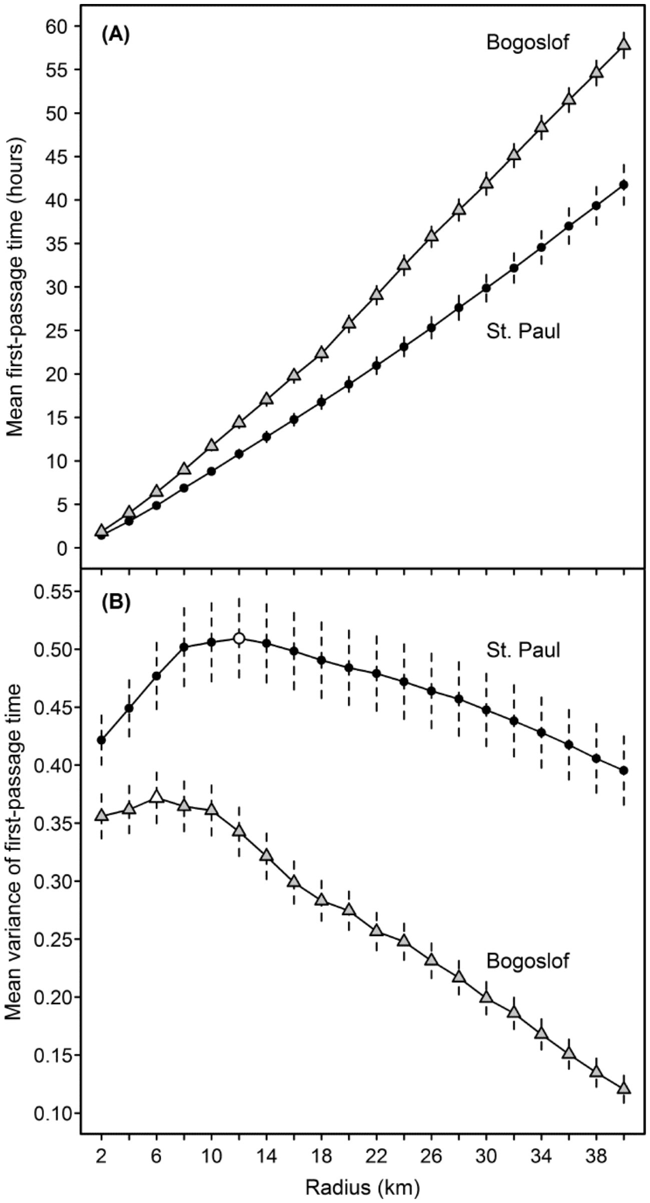


Figure 3.2 Mean first passage time and the mean variance of logged first passage time (± SE) in relation to area radius for northern fur seals foraging from St. Paul I. (*n* = 44) and Bogoslof I. (*n* = 43). First-passage time is the time required for a tracked seal to cross a circle of a given radius. Peak variance occurred at radiuses of 12 km for St. Paul trips and 6 km for Bogoslof trips.

3.3.4 Environmental co-variates

A number of environmental parameters may explain the time that fur seals spent foraging along their tracks. I therefore tested (section 3.3.5) whether the relative foraging intensity could be explained by six environmental parameters: water temperature at 1 m (°C), thermocline depth (m), mean temperature above the thermocline (°C), total chlorophyll concentration (mg/m^3), ocean depth (m), and distance to the nearest front (km). Temperature measured by the Mk10 at 1 m was considered to be a proxy for sea surface temperature, and was interpolated to the nearest FPT location. Constraining the temperatures to those obtained at 1 m ensured that they were from the water column and were not biased by air temperatures when the tag was exposed while the animals surfaced to breathe.

Thermocline depth, mean temperature above the thermocline, and total chlorophyll in the upper 100 m of the water column were derived from 247 CTD profiles obtained via ship sampling in the study area from July 18–August 14, 2009 (Fig. 3.3). A Sea-Bird SBE19plus CTD with a WetLabs ECO-flntu fluorometer was lowered to a depth of 100 m or 1 m from the bottom if the sea floor was <100 m from the surface. Data were low pass filtered and edited to account for heaving of the ship before the raw data were converted to variables of interest using factory calibrations. Thermoclines were defined as the greatest slope in temperature data from each cast and gradients were confirmed visually. Fluorometer calibration equations were confirmed from periodic samples of water filtered for chlorophyll in the area of the experiment. CTD variables were converted into predicted surface rasters using inverse distance weights in ArcGIS geospatial analyst (v. 9.3.1) and values were extracted to FPT points. Inverse distance interpolation was used as it is a conservative method well suited to smoothly varying variables such as temperature, and it retains the original sampled values. Ocean depth was extracted for each FPT location from a 30 arc-second gridded global bathymetry model (GEBCO_08 Grid, *http://www.gebco.net*)

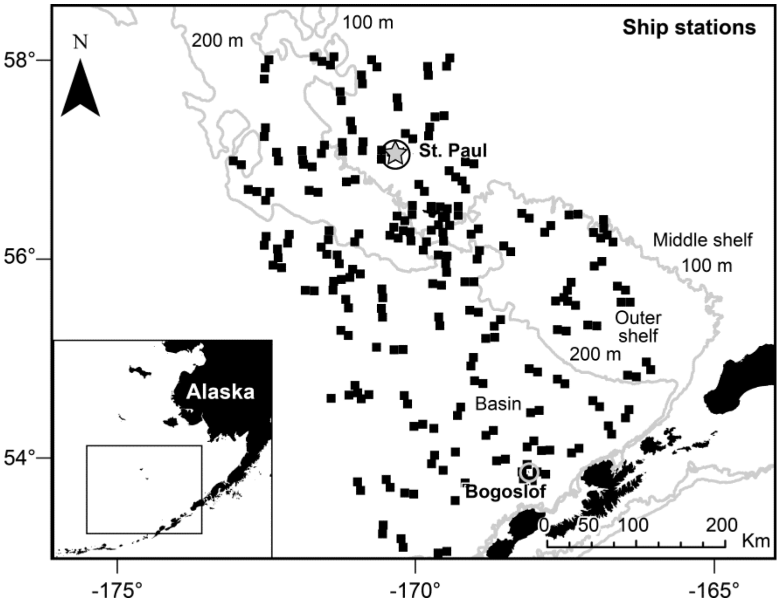


Figure 3.3 Ship sampling stations in the eastern Bering Sea (n=247) from July 18–Aug 14, 2009

Distance to the nearest front was calculated from 4-day maps of surface Lagrangian coherent structures (*e.g.* transport barriers, filament edges, or eddy boundaries). These maps (*e.g.* Fig. 3.1) were derived from absolute geostrophic current velocities using the finite-size Lyapunov exponent (FSLE) method. The method is well suited to study the properties of transport in fluid flow (Boffetta et al., 2001; d'Ovidio et al., 2004) and low FSLE values coincide with areas of low dispersion rates (e.g. eddy cores) while regions of large Lyapunov exponents are associated with areas of high dispersion such as the outer part of eddies or strong fronts (d'Ovidio et al., 2004; Resplandy et al., 2009). As such, frontal boundaries can be detected retrospectively when the calculation is performed over a time-series of geostrophic currents. Geostrophic velocities used to produce frontal maps were in turn produced by gridded, sea-surface height data merged from multi-mission, delayed-time satellite altimetry (Aviso, France, *http://www.aviso.oceanobs.com*).

FSLEs measure the exponential speed at which fluid particles separate from an initial set distance to a final prescribed distance, and were computed at position x and time t as:

$$\lambda = \frac{1}{\tau} \log \frac{\delta_f}{\delta_0} \qquad \text{Eqn. 3.1}$$

where δ_0 is the initial separation distance of two tracers, δ_f is the final separation distance, and τ is the first time the δ_f distance is reached. When computing submesoscale structures in the ocean, typical FSLE values along filament boundaries fall in the range of 0.1–1.0 FSLE/d, indicating that a large scale tracer anomaly can be structured into a submesoscale filament or front within a few days (Cotté et al., 2011). Separation values were set as δ_0 = 0.04° latitude (which is equivalent to approximately 4 km in the south eastern Bering Sea) and as δ_f = 0.6° latitude (~67 km). FSLEs >= 0.2 were retained to be conservative when defining filaments or fronts capable of influencing fur seal foraging. The position of the nearest frontal edge was extracted for each FPT point using ArcGIS from temporally aligned FSLE rasters and fur seal tracks. Distance (km) to the feature was calculated in *R* to quantify the association between FPT locations and fronts. Serial autocorrelation of the data was avoided by limiting sampling of environmental covariates along fur seal tracks to intervals equal to the maximum FPT variance for each island (6 km Bogoslof; 12 km St. Paul) as these intervals were larger than the 4 km minimum resolution of the data (Freitas et al., 2008b).

3.3.5 Habitat selection modelling

The six habitat variables (water temperature at 1 m, thermocline depth, mean temperature above the thermocline, total chlorophyll concentration, ocean depth, and distance to the nearest front) were first categorized and plotted against FPTs to explore potential correlations in the data *sensu* Freitas (2009). The associated 95% confidence intervals were calculated via the adjusted percentile method with 5000 bootstrapping samples. I then evaluated the effect of the six candidate variables on fur seal movements (as quantified via FPT) using mixed-effects Cox proportional hazards (CPH) models (Pankratz et al., 2005; Freitas et al., 2008b). The CPH model was defined as:

$$h(t) = \exp\left(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots + \beta_P X_P + b\right) h_0(t) \qquad \text{Eqn. 3.2}$$

where $h(t)$ is the risk or likelihood an animal will leave an area (defined as a circle of 6 or 12 km radius in this case) at time t, X_x are the explanatory oceanographic covariates in the model, β_x are the regression coefficients fit to each variable by the modeling process, b is the per-subject random effect, and $h_0(t)$ is the baseline hazard function (*i.e.* the hazard when all covariates equal zero or a pre-defined baseline). Including the b random-effect term allowed the model to account for some of the individual variability exhibited by the fur seals.

CPH models assume that hazards are proportional throughout the study period (*i.e.*, variables have the same influence on FPT throughout the course of the foraging trip). I tested this assumption visually by plotting Shoenfeld residuals for each covariate against log(time) and by testing if slopes were zero (Kleinbaum and Klein, 2005). Non-proportional continuous variables were categorized based on their quantile distributions and re-tested to satisfy model assumptions. All possible combinations of the six variables were fit during model selection. I also included an interaction term between distance to fronts and chlorophyll concentration to investigate whether FPTs at different distances to fronts were affected by the level of chlorophyll. The fur seals from St. Paul and Bogoslof Islands had different FPT scales and were modeled separately to compare habitat selection differences between them.

CPH models were evaluated and fit in *R* using the *survival* and *coxme* packages (Therneau, 2009; Therneau and Lumley, 2009). Model selection was performed using AIC corrected for effective sample size:

$$\text{AICc} = -2\log(L) = 2k + \frac{2k(k+1)}{n-k-1} \qquad \text{Eqn. 3.3}$$

where $\log(L)$ is the penalized log likelihood and k is the penalized degrees of freedom from the CPH model, while n is the sample size (number of FPT points). After appropriate models were chosen, hazard ratios (expβ) were calculated from the coefficients of all retained covariates. In this context, they provided quantitative assessment of the relative influence that specific habitat features had on FPT (Freitas et al., 2008b). Values less than one implied that the habitat variable was advantageous for foraging while values greater than one implied that the feature or category had a negative influence. Coefficients with values close to zero or with confidence intervals that span zero were considered to have little to no impact on foraging time as they produced neutral hazard ratios ($\exp^{\beta} = 1$). Summary statistics are presented as means ± standard error unless otherwise noted.

3.4 Results

3.4.1 Animal movements and dive analysis

A total of 182 foraging trips were recorded from instrumented seals (Table A1.2) with 54 from St. Paul Island and 128 from Bogoslof Island. Trips (days and distance) from St. Paul were significantly different from those from Bogoslof (two sample t-tests, p <0.001). Trips from St. Paul took longer (mean = 7.9 *vs*. 3.3 d; range = 4.2–16.9 *vs*. 0.2–13.16 d), covered a greater distance (mean = 604.5 *vs*.197.1 km; range = 243.5–1267.0 *vs*. 0.46–519.7 km), and went further from the rookery (mean = 227.8 *vs*. 73.5 km*;* range = 78.7–462.4 *vs*. 0.2–189.7 km) compared to trips from Bogoslof. As a result, I recorded many more repeat trips from Bogoslof fur seals (85 repeat trips from 39 seals, range = 2–9 trips per seal) than from St. Paul fur seals (10 repeat trips from 5 seals, range = 2–4 trips per seal) during the study period. St. Paul fur seals foraged widely as expected (Fig. 3.4), radiating in all directions from the island with a notable concentration of southward trips. Trips from the Nocturnal group were often directed beyond the shelf-break while Cathemeral fur seals generally foraged over the continental shelf. Bogoslof fur seals did not pass through the Aleutian chain but constrained their foraging trips to the south eastern Bering Sea basin (Fig. 3.4).

Given the large disparity in trip duration between islands, I standardized trip length (km per d) to compare distances covered by animals making multiple short trips from Bogoslof with those making single trips from St. Paul over an equivalent time period. On average, St. Paul fur seals travelled 26% further per day (mean = 76.0 *vs*. 60.4 km) after accounting for variable times at-sea. St. Paul fur seals also conducted fewer foraging dives (dives >20 s) per km when foraging trips were standardized (median = 2.1 *vs.* 2.9 dives/km).

I recorded 139,032 foraging dives (72,202 St. Paul I., 66,830 Bogoslof I.). They showed St. Paul Nocturnal fur seals (*n* = 29 trips) to be primarily shallow, epipelagic divers (Q_1–Q_3 depth range = 10–22 m) that foraged widely over the shelf, slope and basin. In contrast, St. Paul Cathemeral fur seals (*n* = 25 trips) dove primarily on-shelf and over a wider depth range (Q_1–Q_3 = 8–49 m) by clustering many short dives in the upper water column throughout the night followed by longer, deeper dives to the sea floor during the early daylight hours. Foraging dives by Bogoslof fur seals were consistently shallow (Q_1–Q_3 depth range = 10–21 m) and took place primarily over the basin with rare exceptions along the margins of the continental shelf or the Aleutian slope.

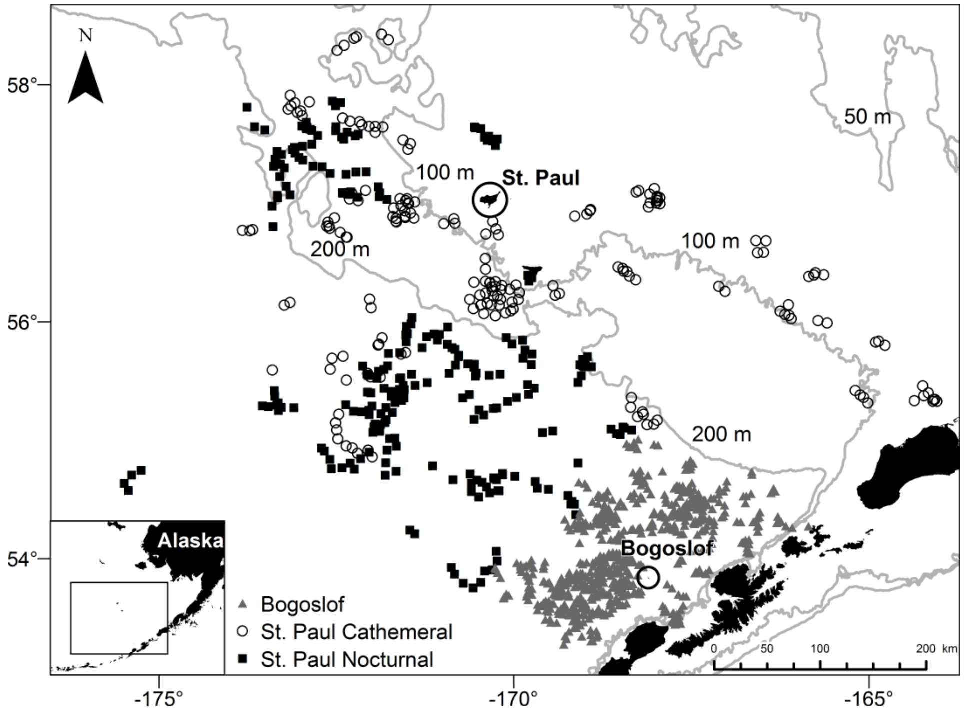


Figure 3.4 Areas used intensively by lactating northern fur seals instrumented at St. Paul I. (*n* = 44 females) and Bogoslof I. (*n* = 43, filled triangles) from Jul–Sep, 2009. St. Paul trips were subdivided into those consisting of >90% night dives (Nocturnal, filled squares); and those that made < 90% nighttime dives (Cathemeral, open circles). Areas of intense use were defined as areas with the top 16.7% (sextile) of first-passage times calculated for foraging trips from each island (St. Paul >15.9 h; Bogoslof > 9.5 h). First passage times were calculated within a radius of 6 km for Bogoslof fur seals (*n* = 660 intense-use FPTs) and 12 km for St. Paul fur seals (*n* = 437 intense-use FPTs).

3.4.2 First-passage time

The scale of area-restricted searches for foraging trips from St. Paul (12 km) was double the size of trips from Bogoslof (6 km). A total of 2,618 FPTs were used to model St. Paul trips and ranged from 2.2–70.3 h at a 12 km radius, which translated to average transiting speeds of 10.9–0.34 km/h (3.0–0.1 m/s). Average FPTs were similar between the St. Paul fur seal groups (Nocturnal group mean = 9.9 ± 0.3 h; Cathemeral group mean = 10.2 ± 0.3 h).

Of the 128 total foraging trips from Bogoslof, 111 trips (3,923 FPTs) were deemed to provide sufficient track resolution (>4 FPTs per trip) for modeling habitat selection. FPTs ranged from 1.29–44.0 h at a radius of 6 km which is equivalent to average transit durations of 9.3–0.27 km/h (2.6–0.08 m/s). Average FPT for Bogoslof trips was 6.0 ± 0.2 h, but must be doubled (~12 h) for a relative comparison of residence times with St. Paul based trips due to the differences in FPT spatial scale. However, the average swim speed between island groupings could be directly compared side by side and was notably slower for fur seals from Bogoslof (1.7 *vs*. 2.8 m/s).

High FPTs were associated with high numbers of dives >20 s (Fig. 3.5) for trips from both islands. In addition, high FPTs were correlated with increased numbers of bottom deviations, relative bottom time and dive ascent rates (data not shown). Sextiles (6-quantiles) were calculated for each island separately, and the top 16.7% of FPT values (St. Paul trips >15.9 h; Bogoslof trips > 9.5 h) were defined as areas of high use (*e.g.*, Fig. 3.4) for visualization purposes. Percentile values >83.3% therefore represented only the areas used most intensively by foraging northern fur seals. Variances of log FPT over 2–40 km radii ranged from 0.41–0.51 for northern fur seals from St. Paul while those from Bogoslof ranged from 0.13–0.37 (Fig. 3.2B).

Comparing mean FPTs against categorized covariates using either all FPT values or just a subset of those values obtained at night revealed similar trends for both the St. Paul Nocturnal group and the Bogoslof population (see section 3.4.3). All FPT points were therefore included in their respective habitat selection analysis. Raw, not mean or categorized, FPT values were used as the response variable for all habitat selection modeling.

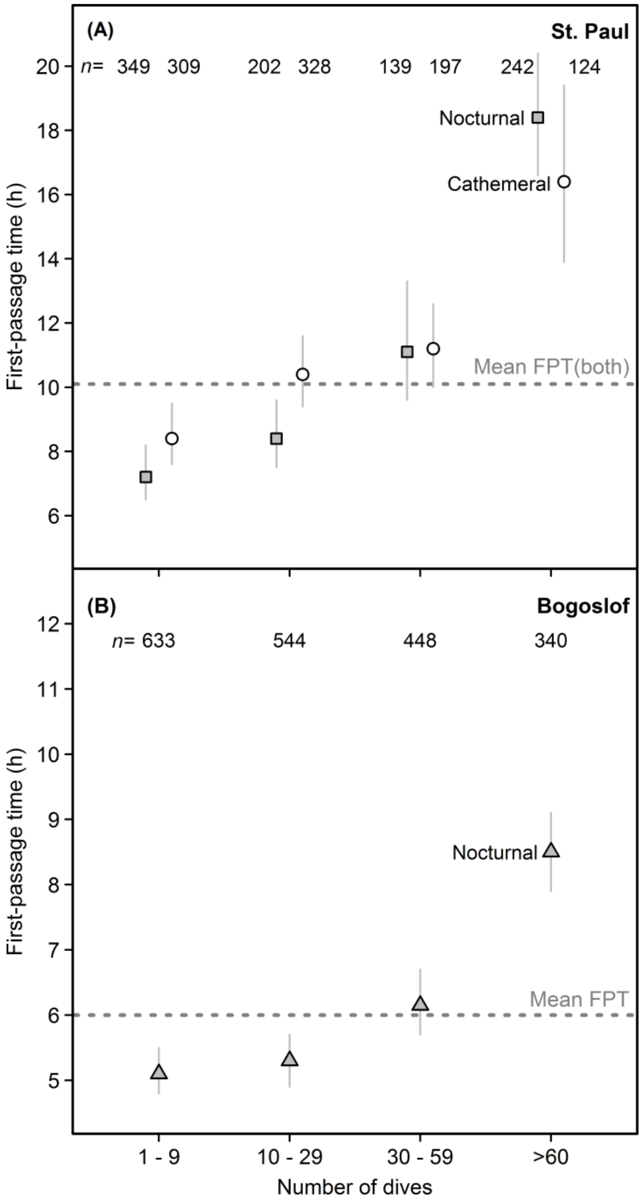


Figure 3.5 Increasing first-passage time (FPT) with increasing numbers of dives lasting >20 s along foraging tracks of northern fur seals tagged on St. Paul I. (A) and Bogoslof I. (B). St. Paul trips were subdivided into those consisting of >90% nighttime dives (Nocturnal, filled squares); and those that made <90% nighttime dives (Cathemeral, open circles). Mean FPTs, bootstrapped 95% confidence intervals, and number of FPT points (*n*) are shown for each island and dive category. Overall mean FPTs are displayed as dashed lines. Note that the FPT scale for the Bogoslof panel is half that of the St. Paul panel as the Bogoslof FPT area radius (6 km) was half that of St. Paul (12 km).

3.4.3 Habitat selection modeling

The relative importance of covariates varied between fur seals foraging in different regions despite groups having similar top CPH models (Fig. 3.6). Two models were given similar weighting for the St. Paul Nocturnal fur seals (Table A2.1), but only hazards for the first model are reported in Table 3.1. The influence of chlorophyll as an additional covariate in the second model was extremely limited (hazard ratio = 1.08, CI(β) = -0.08–0.23) and had no effect on other covariates.

Areas of intense use (visualized as top 16.7% of FPTs) occurred closest to fronts when trips took place near the shelf-break or over the basin (*e.g.*, Figs. 3.7A and B) and a corresponding higher risk (likelihood) of leaving was noted for areas >10 km from frontal edges. For example, the risk of a fur seal moving to the next 12 km portion of its path was 55% greater in areas >20 km from a front than in areas <4 km from a front. Intense use of areas near the shelf break and over the basin where frontal activity was greatest resulted in a coincidental lowering of risk (increasing habitat selection) in increasingly deeper waters. Fur seals in this group tended to transit quickly through areas with thermoclines >35 m deep and trends were similar whether daytime FPT points were included or excluded (Fig. 3.8A).

Pockets of shallow thermoclines were encountered off-shelf but were primarily exploited when foraging on-shelf (*e.g.*, Fig. 3.9B). Fittingly, higher risks of moving to the next 12 km portion of the track (reduced habitat selection) were progressively greater when thermoclines deepened. Mean temperature above the thermocline was retained in the model but had no discernible influence on animal movements (see confidence intervals in Table 3.1). Increasing risk was noted for increasing surface temperatures over the observed range (4.0–10.0 °C).

All covariates were included in the top-ranked model for the St. Paul Cathemeral fur seal group (Table A2.2). Chlorophyll concentration again had no clear effect on animal movements. Neither did the interaction between high relative chlorophyll and increasing distances to the nearest front (see respective CI in Table 3.2). Their exclusion from the two next best models had negligible impacts on remaining model coefficients or hazard ratios (Table 3.2). Distances >4 km away from fronts had a limited effect on area use (<28% increase over baseline risk) but there was no trend with increasing distance. Cathemeral trips rarely encountered fronts (hence their limited effect) but a few intersected them at the shelf-break or just beyond resulting in some increased selection for deeper depths but only >200 m.

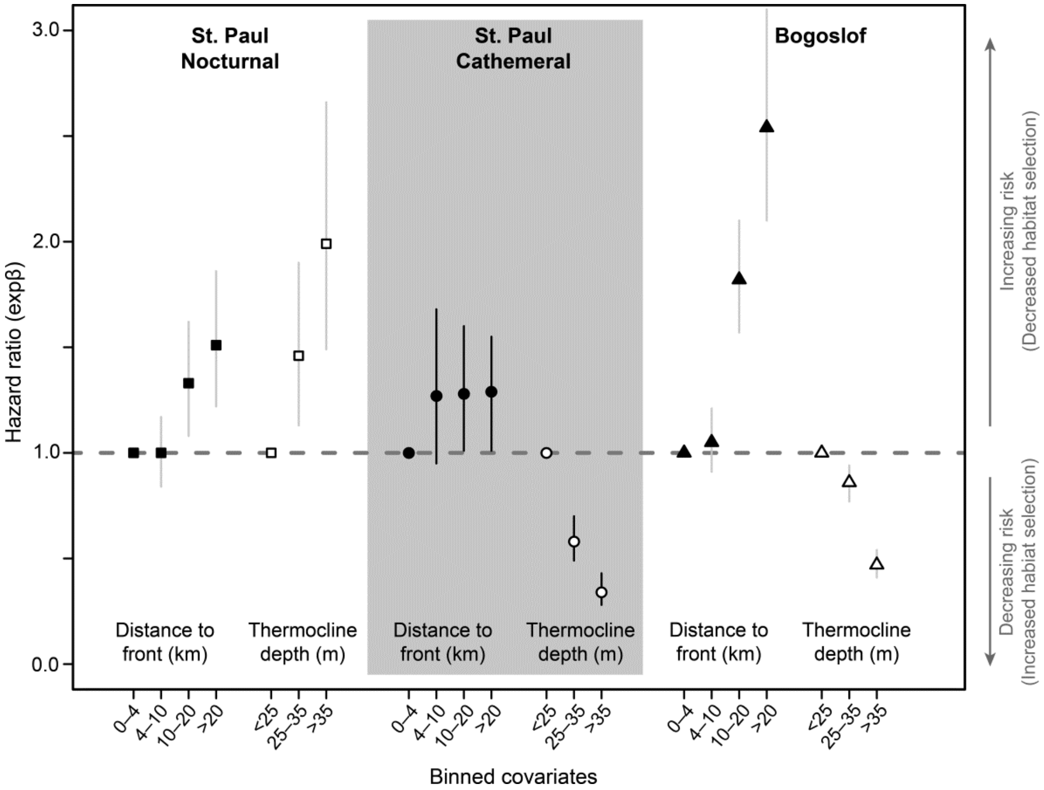


Figure 3.6 Summary of key hazard ratio estimates (expβ) and 95% confidence intervals (expβ(CI)) from top-ranked Cox proportional hazards models describing habitat use (time spent within a specified radius) by 3 groups of foraging, lactating northern fur seals (see Tables 3.1–3.3). Estimates are relative to the first binned category of each covariate (distance to nearest front and thermocline depth) which is the baseline hazard (dashed line, HR=1.0). Hazard ratios >1.0 indicate increasing risk (likelihood) of fur seals leaving an area (reduced habitat selection) while ratios <1.0 infer decreasing risk (increased habitat selection).

Table 3.1 Estimates from the top-ranked Cox proportional hazards model predicting habitat use (time spent within a 12 km radius) by foraging, lactating northern fur seals from the St. Paul I. Nocturnal group as determined by AICc (see Table A2.1). Number of first passage time points (n), coefficients (β), hazard ratios ($\exp^{\beta}$), and 95% confidence intervals (CI(β)) are shown for each covariate/category affecting the risk of fur seals moving to the next 12 km portion of their track. Categorical values are relative to their first class. Front: distance to nearest front; Depth: ocean depth; TC: thermocline depth; TempTC: mean temperature above thermocline; Temp1m: temperature at 1 m; Chl: total chlorophyll in upper 100 m. Note: β-values > 0 ($\exp^{\beta}$ >1.00) indicate increased risk (likelihood) of leaving, while β-values < 0 ($\exp^{\beta}$ <1.00) infer decreased risk (*i.e.* increasing habitat selection).

Model covariate	n	β	$\exp^{\beta}$	CI (β)
Front + Depth + TC + TempTC + Temp1m; (AIC w_i = 0.54)				
Front (0–4 km)	752	–	–	–
Front (>4–10 km)	209	0.00	1.00	-0.17 to 0.16
Front (>10–20 km)	153	0.28	1.33	0.08 to 0.48
Front (>20 km)	352	0.41	1.51	0.20 to 0.62
Depth (0–100m)	325	–	–	–
Depth (>100–200 km)	377	-0.52	0.59	-0.72 to -0.32
Depth (>200–350 km)	44	-0.78	0.46	-1.15 to -0.41
Depth (>350 km)	720	-1.46	0.23	-1.74 to -1.18
TC (<25 m)	144	–	–	–
TC (25–35 m)	969	0.38	1.46	0.12 to 0.64
TC (>35 m)	353	0.69	1.99	0.40 to 0.98
TempTC	1466	-0.07	0.93	-0.17 to 0.03
Temp1m	1466	0.13	1.14	0.03 to 0.22

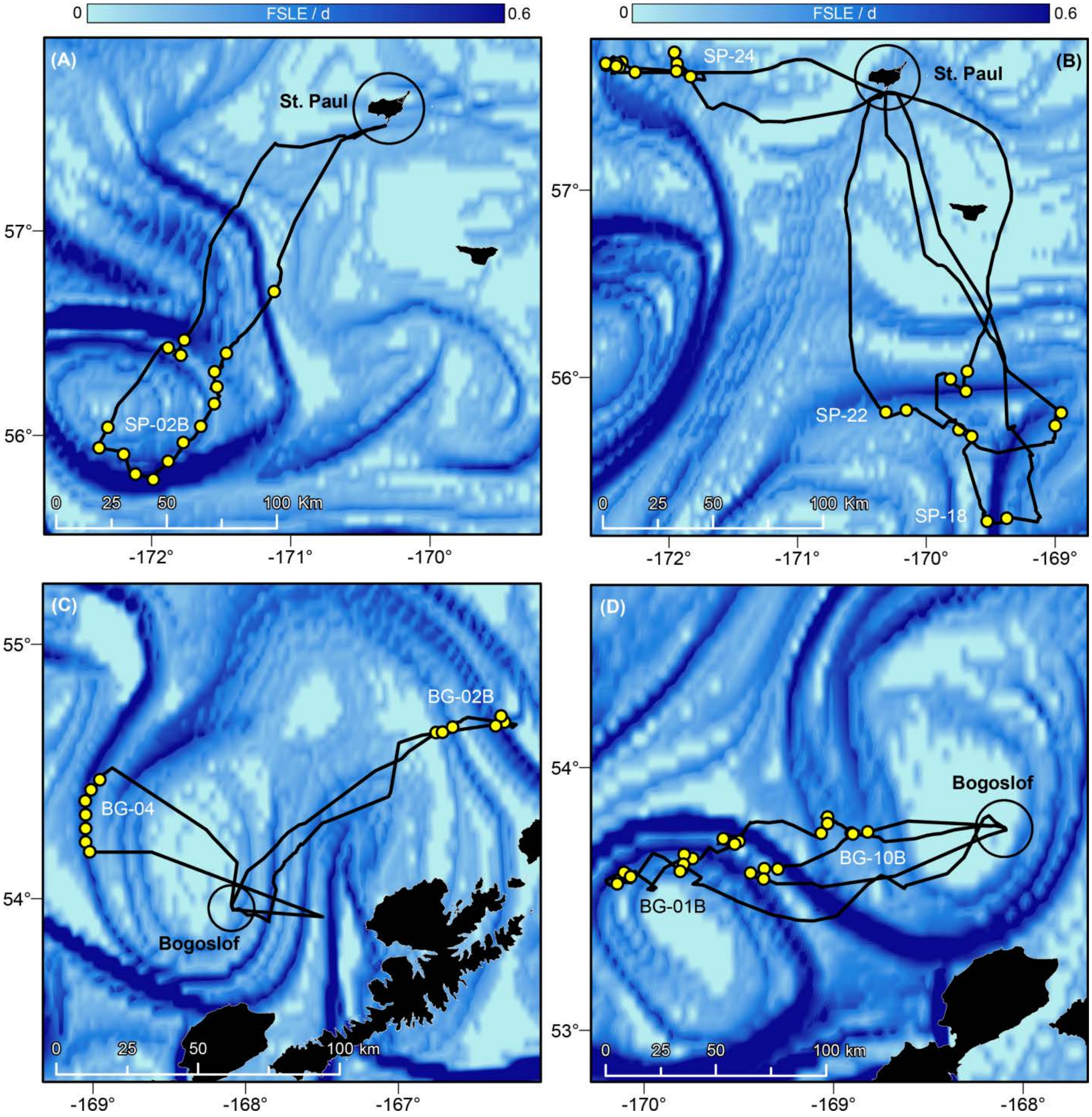


Figure 3.7 Examples of northern fur seals foraging locations in relation to submesoscale fronts (Lagrangian coherent structures >0.2 finite-size Lyapunov exponents per day). Complete foraging tracks are shown with continuous lines for each numbered individual, and areas of intense use are shown by yellow points during A) Jul 23–31, B) Aug 13–27, C) Jul 17–26 , and D) Jul 22–28, 2009. Intense use was defined as the top 16.7% (sextile) of first-passage times, and time spent by fur seals was calculated within areas having radiuses of 6 km for trips from Bogoslof I. and 12 km for trips from St. Paul I. Lagrangian coherent structure maps have a resolution of 4 km over 4-days. The tracks shown are among the clearest examples showing the interaction between high-use areas and fronts. Note that the panels are a snapshot of a dynamic system.

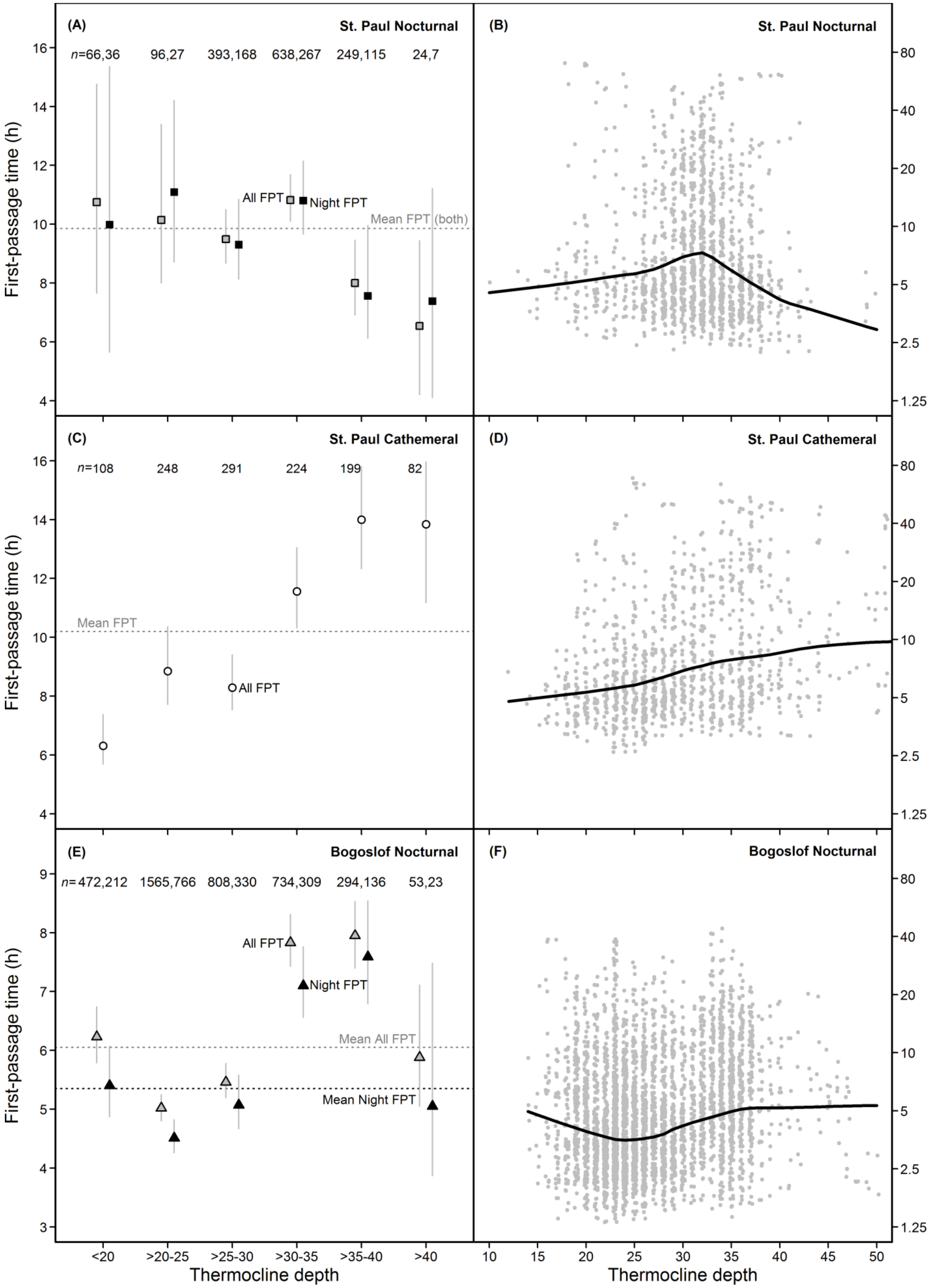

(A)
St. Paul Nocturnal
n=66,36
96,27
393,168
638,267
249,115
24,7
All FPT
Night FPT
Mean FPT (both)
(B)
St. Paul Nocturnal
(C)
St. Paul Cathemeral
n=108
248
291
224
199
82
Mean FPT
All FPT
(D)
St. Paul Cathemeral
(E)
Bogoslof Nocturnal
n= 472,212
1565,766
808,330
734,309
294,136
53,23
All FPT
Night FPT
Mean All FPT
Mean Night FPT
(F)
Bogoslof Nocturnal
First-passage time (h)
16
14
12
10
8
6
4
9
8
7
6
5
4
3
80
40
20
10
5
2.5
1.25
<20
>20-25
>25-30
>30-35
>35-40
>40
Thermocline depth
10
15
20
25
30
35
40
45
50
Thermocline depth

Figure 3.8 Contrasting relationships between first-passage time (FPT) and thermocline depth for northern fur seals foraging from St. Paul I. and Bogoslof I. St. Paul trips were subdivided into those consisting of >90% nighttime dives (Nocturnal, squares); and those that made <90% nighttime dives (Cathemeral, circles). Mean FPTs are shown with bootstrapped 95% confidence intervals, and the number of FPT estimates (*n*) per depth category (panels A, C, E) both including (All FPT) and excluding (Night FPT) daytime FPT estimates. Cathemeral trips show All FPT estimates only as >18% of dives on these trips occurred in the daytime. Overall mean FPTs are displayed as horizontal dashed lines. Additional depth bins are shown than were included in the Cox models to better highlight FPT trends. Note that the untransformed scale for Bogoslof panels are half those for St. Paul animals as the Bogoslof FPT area radius (6 km) was half that of St. Paul (12 km). Also shown are panels of jittered FPT values on a $\log_{10}$ scale plotted against jittered depth values with fitted loess curves for each trip grouping (panels B, D, F). The log scale was used to depict the full range of FPT data and did not affect the loess statistic.

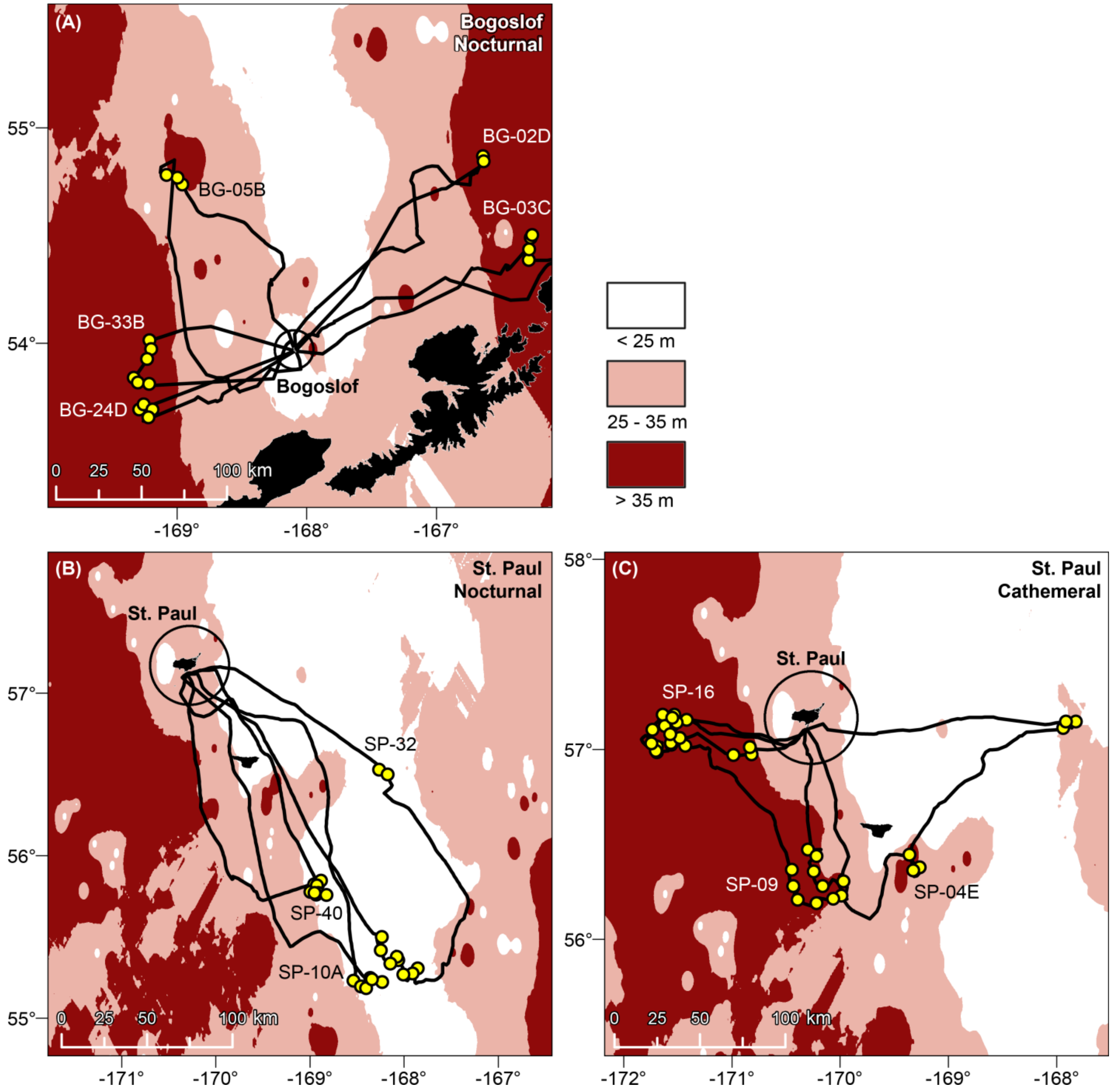


Figure 3.9 Examples of foraging locations of northern fur seals in relation to three thermocline depths classes (<25m in white, 25–35 m medium, and >35 m in dark). Complete trips are shown for the numbered lactating females by the continuous lines, and areas of intense use are shown with the yellow points. St. Paul trips were subdivided into those consisting of >90% nighttime dives (Nocturnal, panel B); and those that made <90% nighttime dives (Cathemeral, panel C). Intense use was defined as the top 16.6% (sextile) of first-passage time (FPT) with FPT calculated within a radius of 6 km for Bogoslof fur seals and 12 km for St. Paul fur seals. The plotted tracks are among the clearest examples showing the interaction with different thermocline depths.

Table 3.2 Estimates from the top three ranked Cox proportional hazards models predicting habitat use (time spent within a 12 km radius) for foraging, lactating northern fur seals from the St. Paul I. Cathemeral group as determined by AICc (see Table A2.2). Number of first passage time points (n), coefficients (β), hazard ratios (exp$^{\beta}$), and 95% confidence intervals (CI(β)) are shown for each covariate/category affecting the risk of fur seals moving to the next 12 km portion of their track. Categorical values are relative to their first class. Front: distance to nearest front; Depth: ocean depth; TC: thermocline depth; TempTC: mean temperature above thermocline; Temp1m: temperature at 1 m; Chl: total chlorophyll in upper 100 m. Note: β-values > 0 (exp$^{\beta}$ >1.00) indicate increased risk (likelihood) of leaving, while β-values < 0 (exp$^{\beta}$ <1.00) infer decreased risk (*i.e.* increasing habitat selection).

Model covariate	n	β	exp$^{\beta}$	CI (β)
Front + Depth + TC + TempTC + Temp1m + Chl + (Front x Chl); AIC $w_i = 0.62$				
Front (0–4 km)	296	–	–	–
Front (>4–10 km)	166	0.24	1.27	-0.05 to 0.52
Front (>10–20 km)	196	0.24	1.28	0.01 to 0.47
Front (>20 km)	494	0.23	1.25	0.01 to 0.44
Depth (0–100m)	628	–	–	–
Depth (>100–200 km)	362	-0.09	0.92	-0.25 to 0.08
Depth (>200–350 km)	37	-0.58	0.56	-0.98 to -0.19
Depth (>350 km)	125	-1.03	0.36	-1.37 to -0.69
TC (<25 m)	293	–	–	–
TC (25–35 m)	537	-0.54	0.58	-0.72 to -0.36
TC (>35 m)	322	-1.07	0.34	-1.29 to -0.85
TempTC	1152	-0.14	0.87	-0.21 to -0.07
Temp1m	1152	0.01	1.01	-0.07 to 0.10
Chl (<350 mg/m^3)	817	–	–	–
Chl (>350 mg/m3)	335	0.14	1.15	-0.16 to 0.44
Front (0–4 km) x Chl (>350 mg/m^3)	137	–	–	–
Front (>4–10 km) x Chl (>350 mg/m^3)	74	-0.55	0.57	-0.96 to -0.15
Front (>10–20 km) x Chl (>350 mg/m^3)	70	0.00	1.00	-0.40 to 0.40
Front (>20 km) x Chl (>350 mg/m^3)	54	0.14	1.15	-0.28 to 0.57
Front + Depth + TC + TempTC + Temp1m; AIC $w_i = 0.13$				
Front (0–4 km)	296	–	–	–
Front (>4–10 km)	166	0.20	1.22	-0.01 to 0.41
Front (>10–20 km)	196	0.22	1.25	0.01 to 0.44
Front (>20 km)	494	0.19	1.22	0.00 to 0.39
Depth (0–100m)	628	–	–	–
Depth (>100–200 km)	362	-0.05	0.95	-0.22 to 0.12
Depth (>200–350 km)	37	-0.52	0.59	-0.91 to -0.13
Depth (>350 km)	125	-0.96	0.38	-1.28 to -0.64
TC (<25 m)	293	–	–	–
TC (25–35 m)	537	-0.58	0.56	-0.76 to -0.40
TC (>35 m)	322	-1.09	0.33	-1.31 to -0.87
TempTC	1152	-0.15	0.86	-0.22 to -0.08
Temp1m	1152	0.00	1.00	-0.08 to 0.08

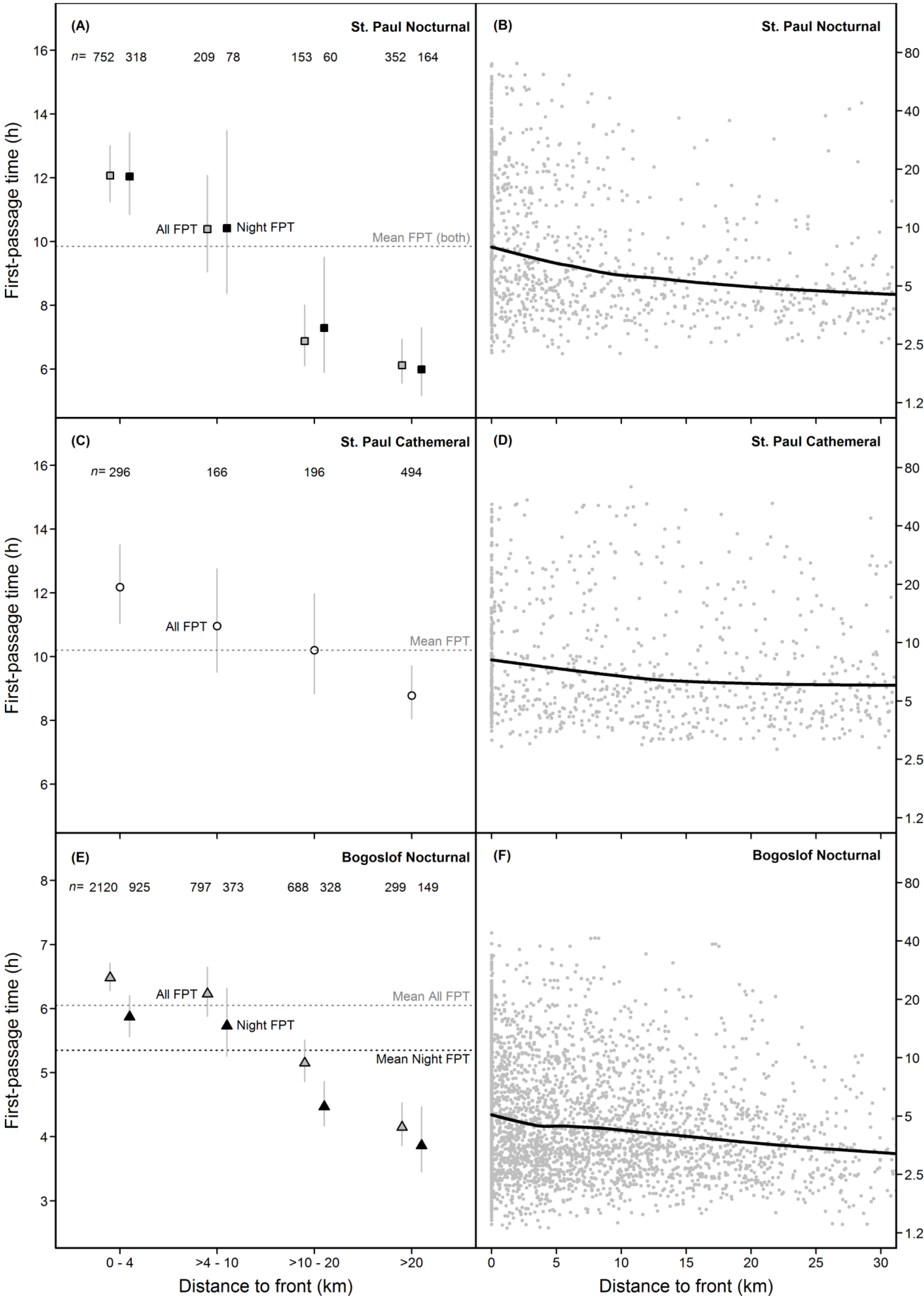
Model covariate	n	β	$\exp^{\beta}$	CI (β)
Depth + TC + TempTC + Temp1m; AIC w_i = 0.12				
Depth (0–100m)	628	–	–	–
Depth (>100–200 km)	362	-0.05	0.95	-0.22 to 0.11
Depth (>200–350 km)	37	-0.55	0.58	-0.93 to -0.16
Depth (>350 km)	125	-1.07	0.34	-1.37 to -0.77
TC (<25 m)	293	–	–	–
TC (25–35 m)	537	-0.59	0.56	-0.77 to -0.41
TC (>35 m)	322	-1.17	0.31	-1.38 to -0.96
TempTC	1152	-0.15	0.86	-0.22 to -0.08
Temp1m	1152	0.00	1.00	-0.08 to 0.09

In contrast to the Nocturnal group, high FPT areas were associated with the deepest thermoclines (Figs. 3.8B and 3.9A). Progressively decreasing risk corresponded with deepening thermoclines (*e.g.* 66% less risk in areas where thermoclines >35 m deep compared to <25 m deep). Surface temperature was consistently retained yet had no effect on where fur seals concentrated their foraging time (see CI, Table 3.2). Reduced risk was noted for increasing mean temperatures above the thermocline (observed range = 2.4–9.7 °C).

All covariates were retained for CPH modeling for trips from Bogoslof (Table A2.3) but as with the other groups, relative chlorophyll concentration had no effect on fur seal foraging (Table 3.3). Areas near fronts were sites of intense use (*e.g.*, Figs. 3.7C and D) with lower FPT observed >10 km from the features regardless of the inclusion or exclusion of daytime FPT (Fig. 3.10). Corresponding higher risks were noted for locations >10 km from fronts. For example, the probability of a fur seal moving to the next 6 km section of the track was 154% greater in areas >20 km from a front compared to areas <4 km from the feature. Depth was retained, yet had no influence on fur seal movements ($\exp^{\beta}$ = 1.0) which was not surprising for animals diving <30 m on average in areas typically >400 m deep. Areas with deeper thermoclines coincided with regions of concentrated fronts and, accordingly, with decreased risk of leaving these areas. Area use intensified with increasing mean temperature above the thermocline (observed range = 0.4–8.6 °C) and with increasing surface temperature (observed range = 5.4–9.5 °C). Relatively high chlorophyll areas at increasing distances from fronts showed increasing habitat selection contrary to expectations that higher chlorophyll values nearer to fronts would engender increased use.

Table 3.3 Estimates from the top-ranked Cox proportional hazards model predicting habitat use (time spent within a 6 km radius) by foraging, lactating northern fur seals from Bogoslof I. as determined by AICc (see Table A2.3). Number of first passage time points (n), coefficients (β), hazard ratios ($\exp^{\beta}$), and 95% confidence intervals (CI(β)) are shown for each covariate/category affecting the risk of fur seals moving to the next 6 km portion of their track. Categorical values are relative to their first class. Front: distance to nearest front; Depth: ocean depth; TC: thermocline depth; TempTC: mean temperature above thermocline; Temp1m: temperature at 1 m; Chl: total chlorophyll in upper 100 m. Note: β-values > 0 ($\exp^{\beta}$ >1.00) indicate increased risk (likelihood) of leaving, while β-values < 0 ($\exp^{\beta}$ <1.00) infer decreased risk (*i.e.* increasing habitat selection).

Model covariate	n	β	$\exp^{\beta}$	CI (β)
Front + Depth + TC + TempTC + Temp1m + Chl + (Front x Chl); AIC w_i = 1.00				
Front (0–4 km)	2124	–	–	–
Front (>4–10 km)	799	0.05	1.05	-0.09 to 0.19
Front (>10–20 km)	697	0.60	1.82	0.45 to 0.74
Front (>20 km)	309	0.93	2.54	0.74 to 1.13
Depth	3929	0.00	1.00	0.00 to 0.00
TC (<25 m)	1739	–	–	–
TC (25–35 m)	1644	-0.16	0.86	-0.26 to -0.06
TC (>35 m)	546	-0.75	0.47	-0.88 to -0.62
TempTC	3929	-0.18	0.83	-0.23 to -0.14
Temp1m	3929	-0.23	0.80	-0.29 to -0.16
Chl (<450 mg/m^3)	1782	–	–	–
Chl (>450 mg/m^3)	2147	-0.01	0.99	-0.12 to 0.11
Front (0–4 km) x Chl (>450 mg/m^3)	1236	–	–	–
Front (>4–10 km) x Chl (>450 mg/m^3)	472	0.01	1.01	-0.18 to 0.20
Front (>10–20 km) x Chl (>450 mg/m^3)	341	-0.53	0.59	-0.73 to -0.33
Front (>20 km) x Chl (>450 mg/m^3)	120	-0.65	0.52	-0.94 to -0.37



(A)
St. Paul Nocturnal
n= 752 318 209 78 153 60 352 164
All FPT
Night FPT
Mean FPT (both)
First-passage time (h)
16
14
12
10
8
6
(B)
St. Paul Nocturnal
80
40
20
10
5
2.5
1.25
(C)
St. Paul Cathemeral
n= 296 166 196 494
All FPT
Mean FPT
First-passage time (h)
(D)
St. Paul Cathemeral
(E)
Bogoslof Nocturnal
n= 2120 925 797 373 688 328 299 149
All FPT
Night FPT
Mean All FPT
Mean Night FPT
First-passage time (h)
8
7
6
5
4
3
(F)
Bogoslof Nocturnal
0 - 4
>4 - 10
>10 - 20
>20
Distance to front (km)
0
5
10
15
20
25
30
Distance to front (km)

Figure 3.10 Decreasing first-passage time (FPT) with increasing distance to the nearest fine-scale front along foraging tracks of northern fur seals tagged on St. Paul I. and Bogoslof I. St. Paul trips were subdivided into those consisting of >90% nighttime dives (Nocturnal, filled squares); and those that made <90% nighttime dives (Cathemeral, open circles). Mean FPTs are shown with bootstrapped 95 % confidence intervals, and number of FPT estimates (*n*) for each distance category (panels A, C, E) both including (All FPT) and excluding (Night FPT) daytime FPT estimates. Cathemeral trips show All FPT estimates only as >18% of dives on these trips occurred in the daytime. Overall mean FPTs are displayed as dashed lines. Note that the FPT scale for the Bogoslof seals is half that of the St. Paul seals as the Bogoslof FPT area radius (6 km) was half that of St. Paul (12 km). Also shown are panels of jittered FPT values on a $\log_{10}$ scale plotted against jittered distance values with fitted loess curves for each trip grouping (panels B, D, F). The log scale was used to depict the full range of FPT data and did not affect the loess statistic.

3.5 Discussion

Using data collected by fur seals, ships, and satellites, I showed that northern fur seals from two different colonies had significant differences in foraging behaviour that could be tied to the presence of fine-scale oceanographic features. Hotspots for lactating female northern fur seals occurred near dynamic submesoscale surface fronts and were linked to thermocline depth classes that generally matched a preferred dive strategy. Trips were longer and the size of area-restricted searches was larger for fur seals foraging from St. Paul Island compared to those from Bogoslof Island. I propose the relative use of these features by northern fur seals changed with their regional availability. In particular, the accessibility of submesoscale surface fronts available to lactating northern fur seals differed between the two breeding populations and may be impacting the foraging patterns observed on St. Paul and Bogoslof Islands.

3.5.1 Animal movements and dive analysis

The 87 lactating females instrumented during the study period represent the largest single season tag deployment to date on adult northern fur seals. This large number of tagged individuals revealed significant foraging trip differences between islands, but no overlap in their respective foraging areas (Fig. 3.4). St. Paul based trips were twice as long (7.9 d average), 3-times as far (228 km average max distance from rookery), and covered 3-times greater distance (600 km average) compared to trips from Bogoslof. Ranges of these metrics barely overlapped, indicating substantial biological differences between colonies.

Fur seals from Bogoslof travelled 26% less per day while at sea and returned more frequently to shore to nurse their pups compared with those from St. Paul. This difference in time spent at-sea between nursing bouts could significantly affect milk delivery rates to pups and thereby impact pup size at weaning or the timing of weaning between populations. This is consistent with the finding of others that pups on Bogoslof gained more mass per day during the lactation period and were heavier than pups on St. Paul in mid-October (Springer et al., 2008). Foraging longer and further from rookeries to obtain prey may reflect reduced prey availability (Costa, 2008) and suggests that fur seals from St. Paul had more difficulty obtaining prey compared to conspecifics from Bogoslof. (see section 3.5.3).

Our large sample size re-affirms the understanding that northern fur seals in the eastern Bering Sea are generally nocturnal divers. Nocturnal diving has been thoroughly documented for female fur seals from the Pribilofs (Goebel et al., 1991; Gentry, 1998; Kuhn et al., 2010) which are presumed to primarily target juvenile walleye-pollock (*Theragra chalcogramma*) that migrate vertically to the upper portion of the water column (Antonelis et al., 1997; Gudmundson et al., 2006; Sinclair et al., 2008; Zeppelin and Orr, 2010). Similarly, I found that fur seals foraging almost exclusively at night (the Nocturnal group) exhibited a shallow diving pattern (< 30 m) and did so primarily off-shelf or over the shelf-break as shown by Goebel *et al*. (1991). In contrast, fur seals that foraged at night and also during the day (the Cathemeral group) did so primarily over the continental shelf. They exhibited the typical shallow dive pattern at night followed by deeper dives that typically reached the ocean-bottom during early morning. Such benthic dives would allow fur seals to target and trap prey against the sea-floor, and is a strategy that could be more successful during daylight hours, particularly if prey migrated below the deep scattering layer during the day (Schabetsberger et al., 2000). Adult pollock are also typically found nearer the ocean bottom and such larger prey may be targeted during bottom dives. Other semi-demersal prey such as Pacific sandlance (*Ammodytes hexapterus*) and Atka mackerel (*Pleurogrammus monopterygius*) begin their diurnal vertical migration in the early daylight hours (Hobson, 1986; Nichol and Somerton, 2002) when they would be available and vulnerable to deeper diving fur seals as they move off the bottom. Females from Bogoslof foraged primarily in the deep basin waters surrounding Bogoslof I. and were predominantly shallow, night-time divers. Their dive behaviour matches the strongly diel pattern of their nearly exclusive prey: northern smoothtongue and squid (Sinclair et al., 2008; Zeppelin and Orr, 2010).

3.5.2 First-passage time

FPT peaks were detected for foraging northern fur seals and areas of intense use were identified for each trip at the spatial scales that best differentiated low and high FPTs. St. Paul animals doubled the scale at which they foraged (mean radius = 12 km) compared to Bogoslof animals (6 km), which indicated that their area-restricted search pattern was wider and suggests that prey were more diffuse near St. Paul than prey near Bogoslof.

Mean variances in FPTs were low while the standard errors were high for northern seals between radii of 2–40 km (Fig. 3.2B). I attribute this to the lack of distinct northern fur seal foraging grounds and the constrained nature of foraging trips during the pup rearing season. As income breeders and central place foragers, females must balance the competing demands of foraging and lactation over a brief period. Therefore they tend to travel at high-speed, foraging throughout the trip and slowing rarely on their circuit away from the rookery. This type of travel, coupled with high inter-animal variability led to low overall variance between areas of increasing radii along the tracks. This was particularly notable for trips from St. Paul where Nocturnal and Cathemeral strategies were identified. Our FPT variance structure was narrower than similar FPT analyses of long-term deployments on arctic marine mammals (Freitas et al., 2008a; Freitas et al., 2009) and short-term deployments on seabirds (Suryan et al., 2006; Weimerskirch et al., 2007; Pinaud, 2008). Those FPT variances were wider and are likely indicative of extended foraging in well-defined areas between long stretches of direct travel.

Concern has been raised that track-based measures of area use intensity such as FPT fail to coincide with areas defined by other feeding proxies for diving predators at fine scales (Robinson et al., 2007) but this was not the case in the study. The number of dives (Fig. 3.5), the number of bottom deviations, and the relative dive bottom time all increased in areas with increasing FPT for trips from both islands. Ascent rates were also positively associated with trips from St. Paul but not for trips from Bogoslof. These dive metrics have been previously used to infer foraging behaviour in marine predators (Trathan et al., 2008; Dragon et al., 2010; Scheffer et al., 2010) including northern fur seals (Kuhn, 2011) and provides confirmation that increasing FPTs in the study are indicative of increased foraging activity at least at scales of 6 and 12 km.

Despite verification of the FPT technique with correlates of foraging behaviour, short sleep bouts along the paths could inflate FPT values. I suspect some limited travel devoid of dive activity observed immediately following intense diving bouts may indicate resting or sleep, but this behaviour was generally within 6 km of high-use areas and therefore still highlighted those locations where foraging took place. Interestingly, neither mean dive duration nor mean bottom duration increased with an increasing number of hours spent in a defined area (6 or 12 km). This supports the idea that individual search and foraging strategies are relatively fixed for lactating northern fur seals. Increased frequency of habitual dive behaviour within an area is seemingly indicative of intense foraging as opposed to increasing dive-time or bottom-time at the scale of this study.

Using all FPT values or just values obtained at night showed similar patterns in how fur seals concentrated their time relative to oceanographic variables (*e.g.*, Figs. 3.8 and 3.10). Nightfall may have triggered the epipelagic foraging strategy employed by nocturnal foragers, but changes in key oceanographic parameters appear to drive the overall intensity of area use independent of whether dives occurred exclusively at night.

3.5.3 Habitat selection modeling

A similar set of environmental parameters explained the foraging behaviours of fur seals from both islands. This suggests that a common set of mechanisms structured northern fur seal foraging in the eastern Bering Sea during the study (Tables 3.1–3.3). However, the relative importance of these oceanographic parameters on residency times (primarily foraging time) along foraging tracks was notably different between trips originating from St. Paul and Bogoslof and also between Nocturnal and Cathemeral strategies of St. Paul fur seals (Fig. 3.6).   Areas of intense use (high FPTs) were associated with short distances to submesoscale fronts, with thermocline depths that tended to coincided with group specific dive strategies, and occasionally with somewhat elevated temperatures in the upper portion of the water column. The importance of these variables changed in relation to their relative presence within the oceanographic domains exploited by different groups of fur seals. For example, strong fronts were concentrated over the Bering Sea basin (Fig. 3.1) while stratified waters producing sharp thermoclines (at shallow and mid-water depths) were primarily located over the shelf.

The Nocturnal group from St. Paul (>95% night dives) adhered strictly to foraging at night and employed shallow pelagic dives over the shelf, off-shelf, or near the shelf-break (Fig. 3.4). These wide ranging fur seals regularly encountered submesoscale fronts as they left shelf waters (Figs. 3.1, 3.7A and B). CPH analysis showed risks of leaving were similar for areas less than 4 km and 10 km after which risks increased with increasing distance from these features. This suggests fur seals hunted intensively along fine-scale fronts when foraging off-shelf, ostensibly targeting highly constrained prey in these narrow ribbons. Areas over deeper water were increasingly used (Table 3.1) but there was no concurrent increase in dive depth in the TDR records. This suggests that ocean depth is not a driving feature *per se* for this group but rather is a static indicator for dynamic features, such as eddy-derived fronts, that develop inter-annually along the shelf-break due to topographic interactions with the northward flowing Bering Slope Current (Ladd, pers. comm.; Stabeno et al., 1999; Stabeno et al., 2001).

Fur seals in the St. Paul Nocturnal group were influenced most strongly by thermocline depth (Table 3.1). They concentrated foraging efforts in areas where thermoclines were shallowest, presumably where diel migrating juvenile pollock were most abundant and easily accessible from the surface at night. There was some evidence that fur seals in this group adjusted their max dive depth as thermoclines deepened (mean max depth: 21 m at thermoclines <25 m; 27 m at thermoclines >25–35 m; 37 m at thermoclines >35 m) which could explain the wide confidence intervals observed for this covariate (Fig. 3.8A). Nonetheless, these fur seals clearly spent the least amount of time in areas where thermoclines were deepest and where prey would be less likely to be encountered by fur seals that constrained the vast majority of their dives to the upper 30 m of the water column.

The Cathemeral group from St. Paul (>18% day dives) regularly mixed shallow night dives with deeper benthic day dives during foraging trips that primarily remained over the continental shelf (Fig. 3.4). Trips constrained to the shelf rarely intersected filaments with the exception of some animals who ventured over the shelf-break to the south-west of St. Paul where they interacted with surface fronts. As a result, there was no trend in the risks of leaving areas beyond 4 km (one map pixel) from fronts for the group as a whole (Table 3.2). There was also no difference in the risks between areas less than 100 or 200 m deep as foraging hotspots were generally evenly distributed between the isobaths on-shelf. Increased habitat selection for waters beyond the shelf-break (>200 m) were driven by the few animals foraging pelagically along fronts over the basin and did not represent an affinity for deeper water.

Fur seals in the St. Paul Cathemeral group were impacted most strongly by thermocline depth (Table 3.2) but they increasingly selected habitats with deeper thermoclines in contrast to the Nocturnal group. Presumably this allowed the fur seals to forage effectively by trapping prey between the thermocline and the benthos during deeper daytime dives on the shelf. Interestingly, Cathemeral fur seals did not appear to adjust their mean maximum dive depths as thermocline depth changed (mean max depth: 49 m at thermoclines <25 m; 45 m at thermoclines >25–35 m; 52 m at thermoclines >35 m) which would typify daytime dives targeting the ocean bottom as opposed to the thermocline itself.

Northern fur seals from Bogoslof showed little variation in foraging behaviour as trips consisted primarily of shallow night diving restricted to the basin (Fig. 3.4). Fine-scale fronts resulting from interactions of topographic features with the eastward flowing Aleutian North Slope Current (Stabeno et al., 1999) dominated the waters around the island (*e.g.*, Fig. 3.1). Consequently, foraging fur seals in this population were influenced most strongly by distance to fronts (Table 3.3). Risk of moving to the next 6 km of their foraging track was similar for areas <4 km and <10 km from fronts but increased rapidly at distances beyond 10 km. The increasing use of areas with deeper thermoclines contrasted with the shallow diving recorded for the group. The relationship may be confounded as overlaying frontal maps (*e.g.* Fig. 3.1) on the thermocline surface (*e.g.* Fig. 3.9C) revealed a ring of deeper thermoclines coinciding with persistent frontal edges.

I suspect strong currents and winds maintained well-mixed surface waters in the vicinity of the fronts in the south-eastern Bering Sea and restricted thermoclines to depths >35m. Fur seals foraging intensively along fronts in these areas would coincidently be using waters with deeper thermoclines. This likely explains why the fur seals seemingly failed to adjust their maximum dive depth under different conditions (max dive depth: 18–20 m for thermocline depths <25 m, >25-35 m, or >35 m).

Chlorophyll and temperature parameters were often included in top models yet their impact on fur seal foraging was difficult to interpret. Increased chlorophyll levels showed some minor trends with increasing FPT when plotted as a single covariate (hence its inclusion as a parameter in the CPH models) but it failed to influence fur seal foraging movements when other parameters were set to base levels of risk. The interaction term between fronts and chlorophyll was also inconsequential when quantifying relative habitat use for most northern fur seals. As such, fronts may better serve to aggregate fur seal prey where they can be efficiently exploited as opposed to stimulating local primary production. Increasing temperature of the water column above the thermocline or at the surface had limited correlation with FPT in exploratory plots. Temperature may play a role in shaping the distribution of fur seal prey (notably pollock) at the broad scale (Ciannelli et al., 2002; Swartzman et al., 2002; Bacheler et al., 2010), but correlations of near surface temperature or temperature integrated above the thermocline with fur seal foraging were inconsistent at the finer scale of this study. Unfortunately, similar habitat preference data are lacking for non-commercial species such as gonatid squid and northern smoothtongue.

3.5.4 Considerations

Dividing trips from St. Paul was appropriate to distinguish which parameters influenced habitat selection for two different groups at a coarse level in the study but it oversimplified the segregation between nocturnal and cathemeral foraging strategies. Fur seals from St. Paul likely adopt a continuum of additional daylight dives to target deeper prey as opposed to the discrete classification employed in the study. Such vertical partitioning of the water column within a rookery complex could compliment existing inter-rookery segregation of the waters around the Pribilof Islands (Robson et al., 2004) and help alleviate intra-specific competition for a single dominant resource (*e.g.* diel-migrating walleye pollock). I also wish to emphasize that the methods by which northern fur seals detect fronts and thermoclines remain unclear. Females tracked for multiple trips showed high fidelity to foraging paths and diving patterns as previously reported (Call et al., 2008), yet the lack of direct travel to hotspots encountered earlier suggests that they do not perceive these boundaries from a distance *per se* as speculated for some marine predators (Nevitt, 2008; Tew Kai et al., 2009). Rather, I propose that northern fur seals respond opportunistically to increased prey density in areas where oceanographic features have concentrated prey in a manner that matched their pre-existing search tactics.

Differences in the quality of primary prey and in the population sizes of the two colonies could influence foraging behaviour alongside differences in oceanographic parameters. Walleye pollock has a relatively low energy density compared to northern smoothtongue or gonatid squid (Van Pelt et al., 1997; Whitman, 2010; Vollenweider et al., 2011), and fur seals consuming pollock may have to travel further or longer to replenish their energy reserves than fur seals consuming more energy rich prey. Nutritional studies involving northern fur seals have been limited, but work with Steller sea lions (*Eumetopias jubatus*) has demonstrated that pinnipeds eating pollock can compensate energetically for low energy fish if sufficient quantities were available (Rosen, 2009). While fur seals from St. Paul may need to eat more pollock to acquire a similar energetic return as Bogoslof fur seals consuming higher energy prey, I argue that trip differences between populations would be minimized if juvenile pollock were concentrated closer to the island. Increased intra-specific competition on St. Paul I. may also increase trip duration and trip distance relative to Bogoslof I. where the population is much smaller. Nonetheless, trip durations reported here are consistent with other studies covering the current phase of decline from the mid-1980's until more recently (Loughlin et al., 1987; Goebel et al., 1991; Robson et al., 2004; Springer et al., 2008; Kuhn et al., 2010) when the population differences were even greater but when environmental parameters aggregating prey were also likely uniform.

Despite extensive geographic coverage of the eastern Bering Sea, the data represent a single, one-year snapshot of the linkages between oceanographic parameters and the foraging trips of lactating northern fur seals during the pup rearing period. This limits my ability to predict how fur seals will respond to future oceanographic scenarios. However, the differences in population-level habitat selection described herein could provide some insight. For example, foraging trips from St. Paul may decrease in length if enhanced frontal activity was closer to the Pribilofs based on the extensive use of fronts by Bogoslof fur seals. Conversely, Bogoslof seals may need to forage longer if frontal activity weakens over the basin despite their access to high-energy prey based on trips by St. Paul females. Strong surface fronts were distributed unequally around the different colonies (*e.g.*, >100 km from St. Paul I.) but clearly focussed the foraging efforts of fur seals that encountered them, particularly on the outbound portion of their foraging trips. I surmise that these horizontal bands extended from the surface through the shallow depths where most females were diving and formed an effective retainer of fur seal prey along their lengths. Thermoclines were ubiquitous around both islands and may be a weaker concentrating feature than submesoscale fronts despite being an important vertical impedance for fur seal prey.

3.5.5 Conclusions

Lactating northern fur seals from different colonies in the eastern Bering Sea had notable differences in at-sea habitat selection consistent with the physical features most prevalent in their respective hydrographic domains. Thermoclines dominated over the highly stratified continental shelf while strong surface fronts were generally restricted to the shelf-break and over the basin. Cathemeral fur seals from St. Paul with a benthic diving component focused their effort in areas with deeper thermoclines that presumably concentrated prey between them and the ocean floor, while epipelagic nocturnal foragers focused on shallower thermoclines which presumably provided easier access to diel migrating prey closer to the surface. Fur seals from Bogoslof foraged primarily over the Bering Sea basin and hunted intensively along fine-scale fronts that likely constrained prey via mechanical convergence near the surface. In contrast, fur seals from St. Paul needed to extend their trips off the shelf to access similar fronts, but concentrated their foraging near them when they were encountered. Trips from St. Paul were longer and areas of high use were larger which suggests that the prey they encountered were less aggregated in comparison to prey consumed by Bogoslof fur seals. It appears that most northern fur seals foraged along the physical features that were available to them. I propose that differences in the relative distribution and accessibility of oceanographic features that concentrate prey in an effective manner account for the observed differences in foraging patterns between colonies, which in turn may partially explain the current contrasting population trends for this piscivorous top-predator.

Chapter 4: General conclusions

4.1 Summary of findings

My goals were to assess temperature data collected by animal-borne sensors in reference to standard CTD casts within the eastern Bering Sea and to investigate whether foraging patterns of northern fur seals from two breeding colonies with contrasting population trajectories were associated with fine-scale oceanographic features. To do so, I instrumented lactating, foraging northern fur seals on St. Paul and Bogoslof Islands with high-resolution GPS enabled time-depth recorders equipped with oceanographic grade thermistors. I then compared thermal habitat maps generated by the free-ranging fur seals with those derived from concurrent shipboard sampling to assess the reliability of animal-borne sampling in describing a complex marine environment (Chapter 2). I also constructed hindcast habitat selection models for fur seals with different foraging strategies and from different populations using high-resolution data collected by seals, ships, and satellites within a rigorous statistical framework (Chapter 3). My findings include oceanographic and ecological elements and as such my thesis informs both physical oceanography (habitat description) and northern fur seal foraging ecology (habitat selection).

Northern fur seals instrumented in my study collected high-quality temperature profiles at unprecedented spatial resolution in the upper water column of the eastern Bering Sea (Chapter 2). They collected 26-times as many profiles as the ships over the same 5-week period and produced interpolated maps with finer detail and less estimated error than similar surfaces produced by standard CTD casts. Inconsistencies between regional maps typically occurred in isolated clumps along isobaths or in high-mixing areas where subtle differences in the plotting of abrupt temperature shifts led to large differences in raw and normalized difference surfaces. Seals repeatedly sampled a range of hydrographic regions throughout their nursing period which tracked the continued warming of the upper water column in areas, such as the outer shelf, where longitudinal sampling has traditionally been challenging. Seals also repeatedly sampled temperatures within an anticyclonic eddy south-west of St. Paul Island and appeared to reveal subtle temperature intrusions associated with the eddy’s concentric currents when the eddy was at peak strength. Integrated temperature maps simultaneously depicted phenomenon previously described in separate studies on-shelf or over the basin and therefore provided unbroken coverage over most of the region with high-resolution data clustered in dynamic areas. Areas sampled intensively by fur seals were, by definition, the most important to these top predators.

The biologging dataset benefitted from the large number of instruments deployed from two widely separated sources (*i.e.* rookeries) on a species with wide ranging foraging trips in order to match the vessels' sampling distribution and to compensate for the limited individual sampling at depths >50 m. The northern fur seals also had a high-dive frequency and were relatively non-selective in their foraging distribution at sea (from a sampling perspective). This produced a dataset with limited bias in terms of coverage which may not be true for other pinnipeds species that have higher foraging-site fidelity (although these species would be well-suited to track changing oceanographic conditions in particular locales over time). Clearly, care must be taken to match the characteristics of potential instrument carriers with the data requirements in any bio-logging study. My data show that hydrographic information collected by wide-ranging, diving animals such as fur seals can provide physical data products comparable to, and exceeding those provided by traditional sampling methods at regional or finer scales when the questions of interest coincide with the ecology of the species.

I also quantified the relative importance of fine-scale habitat variables to female northern fur seals foraging in the eastern Bering Sea. Lactating fur seals from different colonies had notable differences in at-sea habitat selection consistent with the physical features most prevalent in their respective hydrographic domains. Temperature was a poor predictor of fur seal foraging intensity at the scale of my study suggesting that broad characterizations of their prey may not hold at the finer-scales at which fur seals forage. Thermoclines dominated over the highly stratified continental shelf while strong surface fronts were generally restricted to the shelf-break and over the basin.

Cathemeral fur seals from St. Paul with a benthic diving component focused their effort in areas with deeper thermoclines that presumably concentrated prey between them and the ocean floor, while epipelagic nocturnal foragers focused on shallower thermoclines which presumably provided easier access to diel migrating prey closer to the surface. Fur seals from Bogoslof foraged primarily over the Bering Sea basin and hunted intensively along fine-scale fronts that likely constrained prey via mechanical convergence near the surface. In contrast, fur seals from St. Paul needed to extend their trips off the shelf to access similar fronts, but concentrated their foraging near them when they were encountered. Trips from St. Paul were longer and areas of high use were larger which suggests that the prey they encountered were less aggregated in comparison to prey consumed by Bogoslof fur seals. It appears that most northern fur seals foraged along the physical features that were available to them. It further appears that differences in the relative distribution and accessibility of oceanographic features that concentrate prey in an effective manner may account for the observed differences in foraging patterns between colonies, which in turn may partially explain the contrasting population trends for this piscivorous top-predator.

Despite extensive geographic coverage of the eastern Bering Sea, my data represent a single, one-year snapshot of the linkages between oceanographic parameters and the foraging trips of lactating northern fur seals during the pup rearing period. This limits my ability to predict how fur seals will respond to future oceanographic scenarios. However, the differences in population-level habitat selection described in Chapter 3 could provide some insight. For example, foraging trips from St. Paul may decrease in length if enhanced frontal activity was closer to the Pribilofs' based on the extensive use of fronts by Bogoslof fur seals. Conversely, Bogoslof seals may need to forage longer if frontal activity weakens over the basin despite their access to high-energy prey based on trips by St. Paul females. Fronts were distributed unequally around the different colonies (*e.g.*, >100 km from St. Paul I.) but clearly focused the foraging efforts of fur seals that encountered them, particularly on the outbound portion of their foraging trips. I surmise that these horizontal bands extended from the surface through the shallow depths where most females were diving and formed an effective retainer of fur seal prey along their lengths. Thermoclines were ubiquitous around both islands and may be a weaker concentrating feature than submesoscale fronts despite being an important vertical impedance for fur seal prey.

4.2 Future research

Despite the volume of data generated from my field study, it covers only a single breeding season and as such represents a snapshot of the oceanographic processes and how lactating northern fur seals respond to them in the eastern Bering Sea. Both the oceanography and the biology of upper predators has been well studied in the region, including telemetry studies employing different generations of time-depth recorders and positional tags (Goebel et al., 1991; Ream et al., 2005; Sterling, 2009; Kuhn et al., 2010). Therefore, many opportunities exist to expand on my findings either through collecting new data in subsequent field seasons or through mining older but comparable datasets from oceanographic cruises, seabirds, and northern fur seals.

Instrumented fur seals were able to describe ocean temperatures across much of the eastern Bering Sea and animal based sampling should continue during future telemetry studies. Merging data derived from fur seals with standard ship-board sampling created a rich dataset and future measurements by animal-borne instruments could contribute to ongoing sampling in the region. Annual groundfish surveys collect hydrographic data according to a fixed grid across the majority of the eastern shelf and could be better informed about the finer-scale ocean characteristics between broadly spaced stations by incorporating data from free-ranging fur seals. Instrumenting animals from the north-east rookeries of St. Paul Island would provide the most value in that regard given their general fidelity to the shelf region. I recommend deploying multifunction instruments with environmental sensors in lieu of standalone time-depth recorders during future telemetry studies of northern fur seals whenever possible to increase the value of the data returned. In particular, sub-adult males have received little attention and their larger size would allow for deploying a complete CTD sensor suite (*e.g.*, SMRU CTD-SRDL). Such a study would provide ecological insights into another sex class in addition to producing more informative hydrographic data.

Areas sampled most often by fur seals allowed me to describe thermal characteristics of the upper 100 m of the water column similar to ships collecting data on transect lines. The sub-regions or "lines" generated from St. Paul fur seal data crossed several hydrographic zones and could be repeated by dedicated surveys to track inter-annual variation across different domains. The roughly north-south swath from St. Paul (sub-region ii) may be the simplest to incorporate as its position is similar to pre-existing survey lines. In contrast, the data informing the surfaces from the immediate vicinity around Bogoslof Island are valuable in that they cannot be easily reproduced as a 6 nautical mile buffer around the island reserve prevents near-shore ship based sampling.

Lactating female northern fur seals responded to both vertical (thermoclines) and horizontal (surface fronts) boundaries when foraging, presumably due to increased aggregations of prey compared to surrounding waters. Stratified waters are common over the shelf from year to year yet eddy activity and the strength of the major currents show high inter-annual variability. Sterling (2009) suggested that northern fur seals from St. Paul forage over the basin more often in years of increased eddy or storm activity. My results from 2009 could be merged with data collected in other years to test: 1) whether fur seals continue to make use of surface fronts across time and; 2) whether the population responds to shifts in the eddy or filament activity by foraging more or less over the basin. It may also be possible to test the ability of fur seals to detect fronts or other productive areas through the accumulation of dimethyl sulfide (released from aggregated plankton) within a captive setting, as such a mechanism has been proposed for procellariiform seabirds and harbour seals.

Given the possible differences in prey fields available over shelf and slope/basin habitats, studies of individual fur seal diet are warranted. Bogoslof fur seals appear to employ a single foraging strategy on trips largely restricted to basin waters surrounding the island. This presumably is the result of benefitting three-fold from a combination of high energy prey concentrated close to a rookery with relatively less intra-specific competition. In contrast, St. Paul fur seals have seemingly developed two foraging strategies which allow them to exploit different hydrographic zones (shelf and basin) and reduce intra-specific competition. The scenario on St. Paul provides an opportunity to compare foraging trips to different regions within an optimal foraging theory framework. Future studies should strive to collect diet data from instrumented individuals and analyze them on a per-individual basis to better relate prey consumed with foraging trip characteristics.

Future studies seeking to address questions of habitat selection in northern fur seals and other marine mammals will need to expand on the techniques, technologies, and insights from both the oceanographic and ecological communities that were applied in my thesis. Rapid advances in technologies have opened new opportunities to study the linkages between fine-scale oceanography, prey communities, foraging behaviour, and upper predator population dynamics—yet the ability to analyze this multifaceted data and make informed predictions about the ecosystem will require dedicated collaborations among the disciplines.

References

Allen, B.M., Angliss, R.P., 2011. Alaska marine mammal stock assessments, 2010. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-223, p. 292.

Antonelis, G.A., Sinclair, E.H., Ream, R.R., Robson, B.W., 1997. Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. J. Zool. 242, 435-451.

Arnould, J.P.Y., 1997. Lactation and the cost of pup-rearing in antarctic fur seals. Mar. Mamm. Sci. 13, 516-526.

Arnould, J.P.Y., Kirkwood, R., 2008. Habitat selection by female Australian fur seals (*Arctocephalus pusillus doriferus*). Aquat. Conserv.: Mar. Freshwat. Ecosyst. 17, S53-S67.

Bacheler, N., Ciannelli, L., Bailey, K., Duffy-Anderson, J., 2010. Spatial and temporal patterns of walleye pollock (*Theragra chalcogramma*) spawning in the eastern Bering Sea inferred from egg and larval distributions. Fish. Oceanogr. 19, 107-120.

Bailleul, F., Cotté, C., Guinet, C., 2010. Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. Mar. Ecol. Prog. Ser. 408, 251-264.

Baker, J.D., Fowler, C.W., 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. J. Zool. 227, 231-238.

Barth, A., Alvera-Azcárate, A., Troupin, C., Ouberdous, M., Beckers, J.-M., 2010. A web interface for griding arbitrarily distributed in situ data based on Data-Interpolating Variational Analysis (DIVA). Adv. Geosci. 28, 29-37.

Baylis, A.M.M., Page, B., Goldsworthy, S.D., 2008. Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central-place forager, the New Zealand fur seal. Can. J. Zool. 86, 774-789.

Beamish, R.J., Leask, K.D., Ivanov, O.A., Balanov, A.A., Orlov, A.M., Sinclair, B., 1999. The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. Prog. Oceanogr. 43, 399-442.

Benoit-Bird, K.J., Kuletz, K., Heppell, S., Jones, N., Hoover, B., 2011. Active acoustic examination of the diving behavior of murres foraging on patchy prey. Mar. Ecol. Prog. Ser. 443, 217-235.

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J.B., Roquet, F., Bailleul, F., Meredith, M., Thorpe, S., Tremblay, Y., McDonald, B., Park, Y.H., Rintoul, S.R., Bindoff, N., Goebel, M., Crocker, D., Lovell, P., Nicholson, J., Monks, F., Fedak, M.A., 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proc. Natl. Acad. Sci. USA 104, 13705-13710.

Bivand, R.S., Pebesma, E.J., Gomez-Rubio, V., 2008. Applied spatial data analysis with R. Springer, New York, NY, USA.

Boehme, L., Lovell, P., Biuw, M., Roquet, F., Nicholson, J., Thorpe, S.E., Meredith, M.P., Fedak, M.A., 2009. Technical Note: Animal-borne CTD-satellite relay data loggers for real-time oceanographic data collection. Ocean Sci. Discuss. 6, 1261-1287.

Boehme, L., Meredith, M.P., Thorpe, S.E., Biuw, M., Fedak, M., 2008. Antarctic Circumpolar Current frontal system in the South Atlantic: monitoring using merged Argo and animal-borne sensor data. J. Geophys. Res. 113, C09012.

Boffetta, G., Lacorata, G., Redaelli, G., Vulpiani, A., 2001. Detecting barriers to transport: a review of different techniques. Physica D: Nonlinear Phenomena 159, 58-70.

Bograd, S.J., Block, B.A., Costa, D.P., Godley, B.J., 2010. Biologging technologies: new tools for conservation. Endang. Species Res. 10, 1-7.

Boyd, I.L., Hawker, E.J., Brandon, M.A., Staniland, I.J., 2001. Measurement of ocean temperatures using instruments carried by Antarctic fur seals. J. Mar. Syst. 27, 277-288.

Bradshaw, C.J.A., Higgins, J., Michael, K.J., Wotherspoon, S.J., Hindell, M.A., 2004. At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. ICES J. Mar. Sci. 61, 1014.

Brasseur, P., Beckers, J.-M., Brankart, J.M., Schoenauen, R., 1996. Seasonal temperature and salinity fields in the Mediterranean Sea: Climatological analyses of a historical data set. Deep-Sea Res. I 43, 159-192.

Brodeur, R., Wilson, M., Ciannelli, L., 2000. Spatial and temporal variability in feeding and condition of age-0 walleye pollock (*Theragra chalcogramma*) in frontal regions of the Bering Sea. ICES J. Mar. Sci. 57, 256-264.

Brodeur, R., Wilson, M., Ciannelli, L., Doyle, M., Napp, J., 2002. Interannual and regional variability in distribution and ecology of juvenile pollock and their prey in frontal structures of the Bering Sea. Deep-Sea Res. II 49, 6051-6067.

Calenge, C., 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516-519.

Call, K.A., Ream, R.R., 2012. Prey selection of subadult male northern fur seals (*Callorhinus ursinus*) and evidence of dietary niche overlap with adult females during the breeding season. Mar. Mamm. Sci. 28, 1-15.

Call, K.A., Ream, R.R., Johnson, D.S., Sterling, J.T., Towell, R.G., 2008. Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. Deep-Sea Res. II 55, 1883-1896.

Campagna, C., Werner, R., Karesh, W., Marín, M.R., Koontz, F., Cook, R., Koontz, C., 2001. Movements and location at sea of South American sea lions (*Otaria flavescens*). J. Zool. 255, 205-220.

Charrassin, J., Park, Y., Maho, Y., Bost, C., 2002. Penguins as oceanographers unravel hidden mechanisms of marine productivity. Ecol. Lett. 5, 317-319.

Charrassin, J.B., Hindell, M., Rintoul, S.R., Roquet, F., Sokolov, S., Biuw, M., Costa, D., Boehme, L., Lovell, P., Coleman, R., Timmermann, R., Meijers, A., Meredith, M., Park, Y.H., Bailleul, F., Goebel, M., Tremblay, Y., Bost, C.A., McMahon, C.R., Field, I.C., Fedak, M.A., Guinet, C., 2008. Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. Proc. Natl. Acad. Sci. USA 105, 11634-11639.

Chilvers, B.L., Wilkinson, I.S., Duignan, P.J., 2005. Summer foraging areas for lactating New Zealand sea lions *Phocarctos hookeri*. Mar. Ecol. Prog. Ser. 304, 235-247.

Ciannelli, L., Brodeur, R.D., Swartzman, G., Salo, S., 2002. Physical and biological factors influencing the spatial distribution of age-0 walleye pollock (*Theragra chalcogramma*) around the Pribilof Islands, Bering Sea. Deep-Sea Res. II 49, 6109-6126.

Ciannelli, L., Robson, B.W., Francis, R.C., Aydin, K., Brodeur, R.D., 2004. Boundaries of open marine ecosystems: an application to the Pribiolf archipelago, southeast Bering Sea. Ecol. Appl. 14, 942-953.

Coachman, L.K., 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. Cont. Shelf Res. 5, 23-108.

Costa, D.P., 2008. A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. Aquat. Conserv.: Mar. Freshwat. Ecosyst. 17, S44-S52.

Costa, D.P., Croxall, J.P., Duck, C.D., 1989. Foraging energetics of antartic fur seals in relation to changes in prey availability. Ecology, 596-606.

Costa, D.P., Klinck, J.M., Hofmann, E.E., Dinniman, M.S., Burns, J.M., 2008. Upper ocean variability in west Antarctic Peninsula continental shelf waters as measured using instrumented seals. Deep-Sea Res. II 55, 323-337.

Cotté, C., d'Ovidio, F., Chaigneau, A., Lévy, M., Taupier-Letage, I., Mate, B., Guinet, C., 2011. Scale-dependent interactions of Mediterranean whales with marine dynamics. Limnol. Oceanogr. 56, 219-232.

d'Ovidio, F., Fernández, V., Hernández-García, E., López, C., 2004. Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. Geophys. Res. Lett. 31, L17203.

De Robertis, A., Cokelet, E.D., 2012. Distribution of fish and macrozooplankton in ice-covered and open-water areas of the eastern Bering Sea. Deep-Sea Res. II (*in press*).

Dragon, A.-C., Monestiez, P., Bar-Hen, A., Guinet, C., 2010. Linking foraging behaviour to physical oceanographic structures: Southern elephant seals and mesoscale eddies east of Kerguelen Islands. Prog. Oceanogr. 87, 61-71.

Fauchald, P., Tveraa, T., 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84, 282-288.

Fauchald, P., Tveraa, T., 2006. Hierarchical patch dynamics and animal movement pattern. Oecologia 149, 383-395.

Flint, M.V., Sukhanova, I.N., Kopylov, A.I., Poyarkov, S.G., Whitledge, T.E., 2002. Plankton distribution associated with frontal zones in the vicinity of the Pribilof Islands. Deep-Sea Res. II 49, 6069-6093.

Freitas, C., Kovacs, K.M., Ims, R., Fedak, M.A., Lydersen, C., 2008a. Ringed seal post-moulting movement tactics and habitat selection. Oecologia 155, 193-204.

Freitas, C., Kovacs, K.M., Ims, R.A., Fedak, M.A., Lydersen, C., 2009. Deep into the ice: over-wintering and habitat selection in male Atlantic walruses. Mar. Ecol. Prog. Ser. 375, 247-261.

Freitas, C., Kovacs, K.M., Lydersen, C., Ims, R., 2008b. A novel method for quantifying habitat selection and predicting habitat use. J. Appl. Ecol. 45, 1213-1220.

Gentry, R.L., 1998. Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, New Jersey, U.S.A.

Gittleman, J.L., Thompson, S.D., 1988. Energy allocation in mammalian reproduction. Am. Zool. 28, 863-875.

Goebel, M.E., Bengtson, J.L., DeLong, R.L., Gentry, R.L., Loughlin, T.R., 1991. Diving patterns and foraging locations of female northern fur seals. Fish. Bull. 89, 171-179.

Grist, J.P., Josey, S.A., Boehme, L., Meredith, M.P., Davidson, F.J.M., Stenson, G.B., Hammill, M.O., 2011. Temperature signature of high latitude Atlantic boundary currents revealed by marine mammal-borne sensor and Argo data. Geophys. Res. Lett. 38, L15601.

Gudmundson, C.J., Zeppelin, T.K., Ream, R.R., 2006. Application of two methods for determining diet of northern fur seals (*Callorhinus ursinus*). Fish. Bull. 104, 445-455.

Guinet, C., Dubroca, L., Lea, M.-A., Goldsworthy, S.D., Cherel, Y., Duhamel, G., Bonadonna, F., Donnay, J.-P., 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. Mar. Ecol. Prog. Ser. 219, 251-264.

Hobson, E.S., 1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: *Ammodytidae*), during the transition between day and night in southeastern Alaska. Copeia 1986, 223-226.

Hooker, S.K., Boyd, I.L., 2003. Salinity sensors on seals: use of marine predators to carry CTD data loggers. Deep-Sea Res. I 50, 927-939.

Hunt Jr., G.L., Stabeno, P.J., 2002. Climate change and the control of energy flow in the southeastern Bering Sea. Prog. Oceanogr. 55, 5-22.

Hunt Jr., G.L., Stabeno, P.J., Walters, G., Sinclair, E.H., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res. II 49, 5821-5853.

Janout, M.A., Weingartner, T.J., Okkonen, S.R., Whitledge, T.E., Musgrave, D.L., 2009. Some characteristics of Yakutat Eddies propagating along the continental slope of the northern Gulf of Alaska. Deep-Sea Res. II 56, 2444-2459.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65-71.

Kachel, N.B., Hunt Jr., G.L., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitledge, T.E., 2002. Characteristics and variability of the inner front of the southeastern Bering Sea. Deep-Sea Res. II 49, 5889-5909.

Kleinbaum, D.G., Klein, M., 2005. Survival Analysis: a self-learning text, 2nd ed. Springer, New York.

Kowalewsky, S., Dambach, M., Mauck, B., Dehnhardt, G., 2006. High olfactory sensitivity for dimethyl sulphide in harbour seals. Biol. Lett. 2, 106-109.

Kowalik, Z., Stabeno, P.J., 1999. Trapped motion around the Pribilof Islands in the Bering Sea. J. Geophys. Res. 104, 25,667-625,684.

Kuhn, C., 2011. The influence of subsurface thermal structure on the diving behavior of northern fur seals (*Callorhinus ursinus*) during the breeding season. Mar. Biol. 158, 649-663.

Kuhn, C.E., Tremblay, Y., Ream, R.R., Gelatt, T.S., 2010. Coupling GPS tracking with dive behavior to examine the relationship between foraging strategy and fine-scale movements of northern fur seals. Endang. Species Res. 12, 125-139.

Ladd, C., Crawford, W.R., Harpold, C.E., Johnson, W.K., Kachel, N.B., Stabeno, P.J., Whitney, F., 2009. A synoptic survey of young mesoscale eddies in the Eastern Gulf of Alaska. Deep-Sea Res. II 56, 2460-2473.

Ladd, C., Kachel, N.B., Mordy, C.W., Stabeno, P.J., 2005. Observations from a Yakutat eddy in the northern Gulf of Alaska. J. Geophys. Res. 110, C03003.

Ladd, C., Stabeno, P.J., 2012. Stratification on the Eastern Bering Shelf revisited. Deep-Sea Res. II (*in press*).

Lande, R., Engen, S., Sæther, B.-E., 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.

Lea, M.A., Dubroca, L., 2003. Fine-scale linkages between the diving behaviour of Antarctic fur seals and oceanographic features in the southern Indian Ocean. ICES J. Mar. Sci. 60, 990-1002.

Livingston, P.A., 1993. Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi* in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 102, 205-215.

Lloyd, D.S., McRoy, C.P., Day, R.H., 1981. Discovery of northern fur seals (*Callorhinus ursinus*) breeding on Bogoslof Island, Southeastern Bering Sea. Arctic 34, 318-320.

Loughlin, T.R., Bengtson, J.L., Merrick, R.L., 1987. Characteristics of feeding trips of female northern fur seals. Can. J. Zool. 65, 2079-2084.

Loughlin, T.R., Miller, R.V., 1989. Growth of the northern fur seal colony on Bogoslof Island, Alaska. Arctic 42, 368-372.

Loughlin, T.R., Ohtani, K., 1999. Dynamics of the Bering Sea: a summary of the physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea. University of Alaska Sea Grant, Fairbanks, Alaska, p. 839.

Lydersen, C., Anders Nost, O., Kovacs, K.M., Fedak, M.A., 2004. Temperature data from Norwegian and Russian waters of the northern Barents Sea collected by free-living ringed seals. J. Mar. Syst. 46, 99-108.

Lydersen, C., Nost, O., Lovell, P., McConnell, B.J., Gammelsrod, T., Hunter, C., Fedak, M.A., Kovacs, K.M., 2002. Salinity and temperature structure of a freezing Arctic fjord-monitored by white whales (*Delphinapterus leucas*). Geophys. Res. Lett. 29, 2119.

Mann, K.H., Lazier, J.R.N., 2006. Dynamics of marine ecosystems: biological-physical interactions in the oceans, Third ed. Blackwell Publishing, Malden, MA USA.

Mantua, N.J., Hare, S.R., 2002. The Pacific Decadal Oscillation. J. Oceanogr. 58, 35-44.

Mizobata, K., Saitoh, S.I., Shiomoto, A., Miyamura, T., Shiga, N., Imai, K., Toratani, M., Kajiwara, Y., Sasaoka, K., 2002. Bering Sea cyclonic and anticyclonic eddies observed during summer 2000 and 2001. Prog. Oceanogr. 55, 65-75.

Mueter, F.J., Ladd, C., Palmer, M.C., Norcross, B.L., 2006. Bottom-up and top-down controls of walleye pollock (*Theragra chalcogramma*) on the Eastern Bering Sea shelf. Prog. Oceanogr. 68, 152-183.

Napp, J.M., Hunt Jr., G.L., 2001. Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and Biology. Fish. Oceanogr. 10, 61-68.

Napp, J.M., Kendall, A.W., Schumacher, J.D., 2000. A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fish. Oceanogr. 9, 147-162.

National Research Council, 1996. The Bering Sea Ecosystem. The National Academies Press, Washington, D.C.

Nevitt, G.A., 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. J. Exp. Biol. 211, 1706-1713.

Nichol, D.G., Somerton, D.A., 2002. Diurnal vertical migration of the Atka mackerel *Pleurogrammus monopterygius* as shown by archival tags. Mar. Ecol. Prog. Ser. 239, 193-207.

Nordstrom, C.A., Benoit-Bird, K.J., Battaile, B.C., Trites, A.W., 2012. Foraging locations of lactating fur seals from increasing and decreasing populations in the eastern Bering Sea are related to thermocline depths and submesoscale fronts. Deep-Sea Res. II, *in review*.

Okkonen, S.R., Schmidt, G.M., Cokelet, E.D., Stabeno, P.J., 2004. Satellite and hydrographic observations of the Bering Sea 'Green Belt'. Deep-Sea Res. II 51, 1033-1051.

Overland, J.E., Adams, J.M., Bond, N.A., 1999a. Decadal variability in the Aleution low and its relation to high-latitude circulation. J. Clim. 12, 1542-1548.

Overland, J.E., Salo, S.A., Kantha, L.H., Clayson, C.A., 1999b. Thermal stratification and mixing on the Bering Sea shelf, in: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: A summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea. Alaska Sea Grant College Program, Fairbanks, AK.

Pankratz, V.S., de Andrade, M., Therneau, T.M., 2005. Random-effects Cox proportional hazards model: General variance components methods for time-to-event data. Genet. Epidemiol. 28, 97-109.

Paredes, R., Roby, D., Irons, D., Suryan, R., Orben, R., Renner, H., Kitasky, S., 2012. Proximity of a nesting colony to productive marine habitats influences the foraging strategy of a marine predator: evidence from the first GPS tracking of thick-billed murres (*Uria lomvia*). Mar. Ecol. Prog. Ser., *in review*.

Pinaud, D., 2008. Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems. J. Appl. Ecol. 45, 91-99.

R Development Core Team, 2009. R: A language and environment for statistical computing., 2.10.1 ed. R Foundation for Statistical Computing, Vienna, Austria.

Ream, R.R., Baker, J.D., Towell, R.G., 1999. Bogoslof Island studies, 1997, in: Sinclair, E.H., Robson, B.W. (Eds.), Fur seal investigations, 1997 U.S. Dep. Commer., pp. 81-91.

Ream, R.R., Sterling, J.T., Loughlin, T.R., 2005. Oceanographic features related to northern fur seal migratory movements. Deep-Sea Res. II 52, 823-843.

Renner, H., Mueter, F., Drummond, B., Warzybok, J., Sinclair, E.H., 2012. Patterns of change in diets of two piscivorous seabird species during 35 years in the Pribilof Islands. Deep-Sea Res. II (*in press*).

Resplandy, L., Lévy, M., d'Ovidio, F., Merlivat, L., 2009. Impact of submesoscale variability in estimating the air-sea CO2 exchange: Results from a model study of the POMME experiment. Global Biogeochem Cycles 23, GB1017.

Rixen, M., Beckers, J.-M., Brankart, J.M., Brasseur, P., 2000. A numerically efficient data analysis method with error map generation. Ocean Model. 2, 45-60.

Robinson, P.W., Tremblay, Y., Crocker, D.E., Kappes, M.A., Kuhn, C.E., Shaffer, S.A., Simmons, S.E., Costa, D.P., 2007. A comparison of indirect measures of feeding behaviour based on ARGOS tracking data. Deep-Sea Res. II 54, 356-368.

Robson, B.W., Goebel, M.E., Baker, J.D., Ream, R.R., Loughlin, T.R., Francis, R.C., Antonelis, G.A., Costa, D.P., 2004. Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). Can. J. Zool. 82, 20-29.

Ropert-Coudert, Y., Beaulieu, M., Hanuise, N., Kato, A., 2010. Diving into the world of biologging. Endang. Species Res. 10, 21-27.

Roquet, F., Charrassin, J.-B., Marchand, S., Boehme, L., Fedak, M., Reverdin, G., Guinet, C., 2011. Delayed-mode calibration of hydrographic data obtained from animal-borne satellite-relay data loggers. J. Atmos. Ocean. Tech. 28, 787-801.

Roquet, F., Park, Y.-H., Guinet, C., Bailleul, F., Charrassin, J.-B., 2009. Observations of the Fawn Trough Current over the Kerguelen Plateau from instrumented elephant seals. J. Mar. Syst. 78, 377-393.

Rosen, D.A.S., 2009. Steller sea lions *Eumetopias jubatus* and nutritional stress: evidence from captive studies. Mamm. Rev. 39, 284-306.

Rutz, C., Hays, G.C., 2009. New frontiers in biologging science. Biol. Lett. 5, 289-292.

Schabetsberger, R., Brodeur, R.D., Ciannelli, L., Napp, J.M., Swartzman, G.L., 2000. Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. ICES J. Mar. Sci. 57, 1283-1295.

Schabetsberger, R., Sztatecsny, M., Drozdowski, G., Brodeur, R.D., Swartzman, G.L., Wilson, M.T., Winter, A.G., Napp, J.M., 2003. Size-dependent, spatial, and temporal variability of juvenile walleye pollock (*Theragra chalcogramma*) feeding at a structural front in the Southeast Bering Sea. Mar. Ecol. 24, 141-164.

Scheffer, A., Trathan, P.N., Collins, M.A., 2010. Foraging behaviour of king penguins (*Aptenodytes patagonicus*) in relation to predictable mesoscale oceanographic features in the Polar Front Zone to the north of South Georgia. Prog. Oceanogr. 86, 232-245.

Schlitzer, R., 2011a. Ocean Data View 4.4.1 (http://odv.awi.de), 27568 Bremerhaven, Germany.

Schlitzer, R., 2011b. Ocean Data View 4.4.1 User's manual, 27568 Bremerhaven, Germany.

Schumacher, J.D., Stabeno, P.J., 1994. Ubiquitous eddies in the eastern Bering Sea and their coincidence with concentrations of larval pollock. Fish. Oceanogr. 3, 182-190.

Sigler, M.F., Kuletz, K.J., Ressler, P.K., Friday, N.A., Wilson, C.D., Zerbini, A.N., 2012. Marine predators and persistent prey in the southeast Bering Sea. Deep-Sea Res. II (*in press*).

Simmons, S., Tremblay, Y., Costa, D., 2009. Pinnipeds as ocean-temperature samplers: calibrations, validations, and data quality. Limnol. Oceanogr. Methods 7, 648-656.

Simmons, S.E., Crocker, D.E., Hassrick, J.L., Kuhn, C.E., Robinson, P.W., Tremblay, Y., Costa, D.P., 2010. Climate-scale hydrographic features related to foraging success in a capital breeder, the northern elephant seal *Mirounga angustirostris*. Endang. Species Res. 10, 233-243.

Sinclair, E.H., Loughlin, T.R., Pearcy, W., 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish. Bull. 92, 144-156.

Sinclair, E.H., Stabeno, P.J., 2002. Mesopelagic nekton and associated physics of the southeastern Bering Sea. Deep-Sea Res. II 49, 6127-6145.

Sinclair, E.H., Vlietstra, L.S., Johnson, D.S., Zeppelin, T.K., Byrd, G.V., Springer, A.M., Ream, R.R., Hunt Jr., G.L., 2008. Patterns in prey use among fur seals and seabirds in the Pribilof Islands. Deep-Sea Res. II 55, 1897-1918.

Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea Green Belt: Shelf-edge processes and ecosystem production. Fish. Oceanogr. 5, 205-223.

Springer, A.M., Ream, R.R., Iverson, S.J., 2008. Seasonal foraging strategies and consequences for northern fur seals at colonies with opposite population trends - Year2, North Pacific Research Board Final Project Report. North Pacific Research Board Final Project Report, p. 79.

Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temoporal variability of the physical environment over the south-eastern Bering Sea. Fish. Oceanogr. 10, 91-98.

Stabeno, P.J., Hunt Jr., G.L., 2002. Overview of the inner front and southeast Bering Sea carrying capacity programs. Deep-Sea Res. II 49, 6157-6168.

Stabeno, P.J., Kachel, N., Mordy, C., Righi, D., Salo, S., 2008. An examination of the physical variability around the Pribilof Islands in 2004. Deep-Sea Res. II 55, 1701-1716.

Stabeno, P.J., Ladd, C., Reed, R.K., 2009. Observations of the Aleutian North Slope Current, Bering Sea, 1996–2001. J. Geophys. Res. 114, C05015.

Stabeno, P.J., Schumacher, J.D., Ohtani, K., 1999. Physical oceanography of the Bering Sea, in: Loughlin, T.R., Ohtani, K. (Eds.), The Bering Sea: a summary of physical, chemical, and biological characteristics and synopsis of research. North Pacific Marine Science Organization, PICES, Alaska Sea Grant Press, pp. 1-28.

Stabeno, P.J., van Meurs, P., 1999. Evidence of episodic on-shelf flow in the southeastern Bering Sea. J. Geophys. Res. 104, 29715-29720.

Sterling, J.T., 2009. Northern fur seal foraging behaviors, food webs, and interactions with oceanographic features in the eastern Bering sea, School of Aquatic and Fishery Sciences. PhD thesis, University of Washington, Seattle, p. 233.

Sullivan, M.E., Kachel, N.B., Mordy, C.W., Stabeno, P.J., 2008. The Pribilof Islands: Temperature, salinity and nitrate during summer 2004. Deep-Sea Res. II 55, 1729-1737.

Suryan, R.M., Sato, F., Balogh, G.R., David Hyrenbach, K., Sievert, P.R., Ozaki, K., 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: A multi-scale approach using first-passage time analysis. Deep-Sea Res. II 53, 370-386.

Swartzman, G., Napp, J., Brodeur, R., Winter, A., Ciannelli, L., 2002. Spatial patterns of pollock and zooplankton distribution in the Pribilof Islands, Alaska nursery area and their relationship to pollock recruitment. ICES J. Mar. Sci. 59, 1167-1186.

Swartzman, G., Stuetzle, W., Kulman, K., Powojowski, M., 1994. Relating the distribution of pollock schools in the Bering Sea to environmental factors. ICES J. Mar. Sci. 51, 481-492.

Testa, J.W., 2011. Fur seal investigations, 2008-2009, U.S. Dep. Commer., NOAA Tech. Memo., NMFS-AFSC-226, p. 80.

Tew Kai, E., Rossi, V., Sudre, J., Weimerskirch, H., Lopez, C., Hernandez-Garcia, E., Marsac, F., Garcon, V., 2009. Top marine predators track Lagrangian coherent structures. Proc. Natl. Acad. Sci. USA 106, 8245-8250.

Therneau, T.M., 2009. coxme: mixed effects Cox models (R package v. 2.0). http://CRAN.R-project.org/package=coxme.

Therneau, T.M., Lumley, T., 2009. survival: Survival analysis, including penalized likelihood (R package v. 2.35-8). http://CRAN.R-project.org/package=survival.

Towell, R.G., Ream, R.R., York, A.E., 2006. Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. Mar. Mamm. Sci. 22, 486-491.

Trathan, P., Bishop, C., Maclean, G., Brown, P., Fleming, A., Collins, M., 2008. Linear tracks and restricted temperature ranges characterise penguin foraging pathways. Mar. Ecol. Prog. Ser. 370, 285-294.

Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C.-A., Weimerskirch, H., Crocker, D.E., Goebel, M.E., Costa, D.P., 2006. Interpolation of animal tracking data in a fluid environment. J. Exp. Biol. 209, 128.

Trillmich, F., 1990. The behavioral ecology of maternal effort in fur seals and sea lions. Behaviour, 3-20.

Trillmich, F., 1996. Parental investment in pinnipeds. Adv. Stud. Behav. 25, 533-577.

Trites, A.W., 1992. Northern fur seals: why have they declined? Aquat. Mamm. 18, 3-18.

Trites, A.W., Larkin, P.A., 1989. The decline and fall of the Pribilof fur seal (*Callorhinus ursinus*) - a simulation study. Can. J. Fish. Aquat. Sci. 46, 1437-1445.

Troupin, C., Machín, F., Ouberdous, M., Sirjacobs, D., Barth, A., Beckers, J.-M., 2010. High-resolution climatology of the northeast Atlantic using data-interpolating variational analysis (DIVA). J. Geophys. Res. 115, C08005.

Van Pelt, T.I., Piatt, J.F., Lance, B.K., Roby, D.D., 1997. Proximate composition and energy density of some north pacific forage fishes. Comp. Biochem. Physiol., A: Mol. Integr. Physiol. 118, 1393-1398.

Vollenweider, J.J., Heintz, R.A., Schaufler, L., Bradshaw, R., 2011. Seasonal cycles in whole-body proximate composition and energy content of forage fish vary with water depth. Mar. Biol. 158, 413-427.

Weimerskirch, H., Pinaud, D., Pawlowski, F., Bost, C.-A., 2007. Does prey capture induce area-restricted search? a fine-scale study using GPS in a marine predator, the wandering albatross. Am. Nat. 170, 734-743.

Weise, M.J., Harvey, J.T., Costa, D.P., 2010. The role of body size in individual-based foraging strategies of a top marine predator. Ecology 91, 1004-1015.

Whitman, L.D., 2010. Variation in the energy density of forage fishes and invertebrates from the southeastern Bering Sea, Fisheries and Wildlife. MSc thesis, Oregon State University, Corvallis, p. 75.

Whitney, F., Robert, M., 2002. Structure of Haida eddies and their transport of nutrient from coastal margins into the NE Pacific Ocean. J. Oceanogr. 58, 715-723.

Winter, A., Swartzman, G., 2006. Interannual changes in distribution of age-0 walleye pollock near the Pribilof Islands, Alaska, with reference to the prediction of pollock year-class strength. ICES J. Mar. Sci. 63, 1118-1135

York, A.E., Hartley, J.R., 1981. Pup production following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38, 84-90.

Zeppelin, T., Orr, A., 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. Mar. Ecol. Prog. Ser. 409, 241-253.

Appendix A: Summary of data collected from northern fur seals

Table A.1 Deployment history and morphometric measures for northern fur seals from St. Paul I. (*n* = 44) and Bogoslof I. (*n* = 43) used in Chapters 2 and 3.

Animal ID *St. Paul seals*	Date Instrumented	Date Recovered	Days Instrumented	Girth$_0$ (cm)	Length$_0$ (cm)	Mass$_0$ (kg)	Mass$_1$ (kg)	Mass Change
Cu09SP-01	11-Jul-09	24-Jul-09	13	77				NA
Cu09SP-02	11-Jul-09	13-Aug-09	33	76			32.6	NA
Cu09SP-03	12-Jul-09	28-Jul-09	16	72				NA
Cu09SP-04	12-Jul-09	20-Aug-09	39	74			33.8	NA
Cu09SP-05	13-Jul-09	11-Aug-09	29	85			42.8	NA
Cu09SP-06	13-Jul-09	26-Jul-09	13	73				NA
Cu09SP-07	15-Jul-09	28-Jul-09	13	84				NA
Cu09SP-09	16-Jul-09	31-Jul-09	15	74				NA
Cu09SP-10	16-Jul-09	15-Aug-09	30	79			36.4	NA
Cu09SP-11	23-Jul-09	20-Aug-09	28	79			29.2	NA
Cu09SP-13	29-Jul-09	15-Aug-09	17	72			30.2	NA
Cu09SP-14	30-Jul-09	11-Aug-09	12	83			34.8	NA
Cu09SP-15	01-Aug-09	13-Aug-09	12	75			30.2	NA
Cu09SP-16	11-Aug-09	18-Aug-09	7	79	114	36.2	32.2	-4.0
Cu09SP-17	11-Aug-09	24-Aug-09	13	73	122	33.2	30.4	-2.8
Cu09SP-18	13-Aug-09	20-Aug-09	7	73	128	34.0	37.4	3.4
Cu09SP-19	13-Aug-09	23-Aug-09	10	76	120	32.0	32.6	0.6
Cu09SP-20	16-Aug-09	25-Aug-09	9	76	114	30.0	29.8	-0.2
Cu09SP-21	16-Aug-09	25-Aug-09	9	75	120	43.0	42.6	-0.4
Cu09SP-22	16-Aug-09	29-Aug-09	13	73	112	30.0	24.4	-5.6
Cu09SP-23	17-Aug-09	27-Aug-09	10	82	130	43.4	41.0	-2.4
Cu09SP-24	17-Aug-09	25-Aug-09	8	89	124	46.2	45.0	-1.2
Cu09SP-25	20-Aug-09	31-Aug-09	11	76	124	30.4	28.2	-2.2
Cu09SP-26	21-Aug-09	31-Aug-09	10	82	125	39.8	40.0	0.2
Cu09SP-27	21-Aug-09	28-Aug-09	7	87	126	42.8	47.0	4.2
Cu09SP-28	23-Aug-09	02-Sep-09	10	79	121	37.6	35.6	-2.0
Cu09SP-29	24-Aug-09	06-Sep-09	13	85	121	41.0	40.0	-1.0
Cu09SP-30	25-Aug-09	02-Sep-09	8	79	125	40.6	38.2	-2.4
Cu09SP-31	25-Aug-09	30-Aug-09	5	82	130	43.0	43.0	0.0
Cu09SP-32	27-Aug-09	05-Sep-09	9	81	128	44.0	39.4	-4.6
Cu09SP-33	27-Aug-09	05-Sep-09	9	82	129	39.2	41.8	2.6
Cu09SP-34	28-Aug-09	07-Sep-09	10	77	128	39.6	37.0	-2.6
Cu09SP-35	29-Aug-09	06-Sep-09	8	85	124	39.6	39.6	0.0
Cu09SP-36	30-Aug-09	09-Sep-09	10	83	130	44.8	47.2	2.4
Cu09SP-37	31-Aug-09	11-Sep-09	11	82	123	38.0	43.0	5.0
Cu09SP-38	31-Aug-09	15-Sep-09	15	82	128	40.2	35.6	-4.6
Cu09SP-39	02-Sep-09	11-Sep-09	9	77	117	34.6	37.6	3.0
Cu09SP-40	02-Sep-09	12-Sep-09	10	75	114	34.6	34.2	-0.4
Cu09SP-41	05-Sep-09	15-Sep-09	10	83	127	47.6	48.0	0.4
Cu09SP-42	05-Sep-09	14-Sep-09	9	91	125	48.4	50.6	2.2
Cu09SP-43	06-Sep-09	19-Sep-09	13	82	126	41.6	42.8	1.2
Cu09SP-44	06-Sep-09	14-Sep-09	8	81	130	40.8	44.2	3.4
Cu09SP-45	07-Sep-09	18-Sep-09	11	82	127	40.6	36.2	-4.4
Cu09SP-46	08-Sep-09	17-Sep-09	9	78	118	34.4	39.2	4.8

Animal ID *Bogoslof seals*	Date Instrumented	Date Recovered	Days Instrumented	Girth$_0$ (cm)	Length$_0$ (cm)	Mass$_0$ (kg)	Mass$_1$ (kg)	Mass Change
Cu09BG-01	10-Jul-09	28-Jul-09	18	74	108			NA
Cu09BG-02	10-Jul-09	12-Aug-09	33	76	124		31.0	NA
Cu09BG-03	11-Jul-09	11-Aug-09	31	84	104		44.6	NA
Cu09BG-04	12-Jul-09	22-Jul-09	10	76	111			NA
Cu09BG-05	11-Jul-09	14-Aug-09	34	82	110		33.6	NA
Cu09BG-06	14-Jul-09	23-Jul-09	9	75	92			NA
Cu09BG-07	14-Jul-09	15-Aug-09	32	80	120		28.6	NA
Cu09BG-08	16-Jul-09	24-Jul-09	8		120			NA
Cu09BG-09	15-Jul-09	29-Jul-09	14	74	107			NA
Cu09BG-10	15-Jul-09	17-Aug-09	33	82	112		32.6	NA
Cu09BG-15	24-Jul-09	14-Aug-09	21	88	107		23.8	NA
Cu09BG-16	24-Jul-09	13-Aug-09	20	80	121		34.0	NA
Cu09BG-17	26-Jul-09	13-Aug-09	18	79	124		33.3	NA
Cu09BG-18	27-Jul-09	18-Aug-09	22	94	129		41.0	NA
Cu09BG-19	29-Jul-09	21-Aug-09	23	87	116		38.4	NA
Cu09BG-20	29-Jul-09	16-Aug-09	18	76	117		35.2	NA
Cu09BG-21	30-Jul-09	19-Aug-09	20	84	125		40.2	NA
Cu09BG-22	12-Aug-09	22-Aug-09	10	82	134	35.6	36.4	0.8
Cu09BG-23	13-Aug-09	22-Aug-09	9	87	126	35.2	39.4	4.2
Cu09BG-24	14-Aug-09	31-Aug-09	17	86	121	44.2	47.0	2.8
Cu09BG-25	14-Aug-09	25-Aug-09	11	89	126	41.4		NA
Cu09BG-26	15-Aug-09	25-Aug-09	10	85	118	39.8	39.6	-0.2
Cu09BG-27	16-Aug-09	01-Sep-09	16	86	123	39.4	42.2	2.8
Cu09BG-28	17-Aug-09	08-Sep-09	22	91	139	46.0	44.6	-1.4
Cu09BG-29	20-Aug-09	03-Sep-09	14	82	117	35.0	32.6	-2.4
Cu09BG-30	20-Aug-09	05-Sep-09	16		113	33.2	30.4	-2.8
Cu09BG-31	21-Aug-09	31-Aug-09	10		131	47.2	43.4	-3.8
Cu09BG-32	22-Aug-09	01-Sep-09	10	80	122	39.0	37.4	-1.6
Cu09BG-33	23-Aug-09	02-Sep-09	10	95	131	47.8	49.8	2.0
Cu09BG-34	25-Aug-09	06-Sep-09	12	78	119	40.0	37.0	-3.0
Cu09BG-35	28-Aug-09	08-Sep-09	11	80	124	34.0	35.2	1.2
Cu09BG-36	28-Aug-09	07-Sep-09	10	91	128	43.6	41.8	-1.8
Cu09BG-37	30-Aug-09	08-Sep-09	9	75	114	30.6	29.6	-1.0
Cu09BG-38	01-Sep-09	14-Sep-09	13	85	125	43.0	44.6	1.6
Cu09BG-39	02-Sep-09	15-Sep-09	13	80	117	34.4	34.4	0.0
Cu09BG-40	02-Sep-09	12-Sep-09	10	83	118	34.2	37.6	3.4
Cu09BG-41	03-Sep-09	14-Sep-09	11	86	128	48.6	50.6	2.0
Cu09BG-42	04-Sep-09	13-Sep-09	9	85	121	40.8	45.4	4.6
Cu09BG-43	04-Sep-09	12-Sep-09	8	83	124	35.8	35.0	-0.8
Cu09BG-44	07-Sep-09	11-Sep-09	4	90	133	45.6	44.8	-0.8
Cu09BG-45	07-Sep-09	14-Sep-09	7	82	122	37.6	42.0	4.4
Cu09BG-46	09-Sep-09	16-Sep-09	7	83	116	40.6	48.2	7.6
Cu09BG-47	09-Sep-09	14-Sep-09	5	81	119	30.7	36.6	5.9

Table A.2 Foraging trip metrics for northern fur seals from St. Paul I. (*n* = 54) and Bogoslof I. (*n* = 128). Grayed entries indicate trips without a dive ≥50 m (*n* = 35) and therefore not used in Chapter 2.

Animal / trip code *St. Paul fur seals*	GPS at-sea (*n*)	Trip duration (d)	Trip length (km)	Max. distance from rookery (km)
Cu09SP-01	91	6.6	544.4	211.5
Cu09SP-02A	77	6.5	475.6	202.7
Cu09SP-02B	199	8.0	492.0	195.7
Cu09SP-02C	242	9.9	788.4	289.0
Cu09SP-03	244	13.1	1096.3	348.8
Cu09SP-04A	110	6.2	411.2	78.7
Cu09SP-04B	148	4.9	266.8	93.3
Cu09SP-04C	123	4.2	244.1	96.3
Cu09SP-04D	130	4.5	328.3	134.4
Cu09SP-04E	229	8.1	555.1	159.5
Cu09SP-05A	68	7.1	510.2	200.9
Cu09SP-05B	45	8.3	589.7	271.1
Cu09SP-06	187	10.1	670.1	248.3
Cu09SP-07	229	9.8	822.0	324.4
Cu09SP-09	297	9.4	483.9	103.1
Cu09SP-10A	134	7.1	562.5	217.0
Cu09SP-10B	184	9.3	701.4	270.3
Cu09SP-10C	183	9.3	697.8	305.9
Cu09SP-11A	94	8.3	584.1	231.7
Cu09SP-11B	252	12.3	1047.2	243.3
Cu09SP-13	463	16.9	1267.4	462.4
Cu09SP-14	223	8.2	548.4	214.9
Cu09SP-15	195	8.8	600.3	241.1
Cu09SP-16	132	4.4	243.5	82.3
Cu09SP-17	189	10.1	774.8	265.0
Cu09SP-18	111	6.9	574.3	225.6
Cu09SP-19	96	6.3	386.2	86.8
Cu09SP-20	105	7.2	679.2	286.6
Cu09SP-21	119	6.6	551.2	220.1
Cu09SP-22	95	6.5	486.2	192.3
Cu09SP-23	160	7.4	640.8	208.9
Cu09SP-24	91	6.2	405.6	139.9
Cu09SP-25	165	9.3	653.2	210.2
Cu09SP-26	103	6.8	626.1	232.5
Cu09SP-27	155	6.4	435.5	162.0
Cu09SP-28	164	7.5	703.7	266.3
Cu09SP-29	176	10.2	898.1	359.1
Cu09SP-30	75	5.4	386.6	167.3
Cu09SP-31	79	4.2	365.9	170.8
Cu09SP-32	147	7.0	513.4	181.0
Cu09SP-33	129	6.8	641.2	265.3
Cu09SP-34	101	8.1	901.5	397.7
Cu09SP-35	118	6.8	434.9	155.5
Cu09SP-36	124	7.7	513.5	206.4

Animal / trip code *St. Paul fur seals*	GPS at-sea (*n*)	Trip duration (d)	Trip length (km)	Max. distance from rookery (km)
Cu09SP-37	248	9.9	786.4	301.4
Cu09SP-38	74	7.7	418.3	163.3
Cu09SP-39	164	7.6	498.7	169.3
Cu09SP-40	150	7.4	624.3	251.3
Cu09SP-41	84	7.6	789.4	345.1
Cu09SP-42	192	7.0	608.6	265.4
Cu09SP-43	127	10.6	1020.9	438.2
Cu09SP-44	77	6.3	499.1	207.0
Cu09SP-45	71	8.2	646.5	273.8
Cu09SP-46	205	8.9	650.8	258.4
Bogoslof fur seals				
Cu09BG-01A	230	4.6	301.5	118.1
Cu09BG-01B	274	6.4	420.3	142.4
Cu09BG-02A	55	4.7	298.3	100.8
Cu09BG-02B	70	5.3	354.5	148.2
Cu09BG-02C	6	0.5	52.6	24.6
Cu09BG-02D	54	4.7	337.3	141.0
Cu09BG-02E	49	3.2	276.4	114.9
Cu09BG-02F	49	2.7	163.3	66.8
Cu09BG-03A	69	5.9	368.4	138.4
Cu09BG-03B	98	4.9	335.9	120.0
Cu09BG-03C	87	5.7	508.5	189.7
Cu09BG-03D	109	4.9	406.1	164.8
Cu09BG-04	12	4.1	280.4	82.4
Cu09BG-05A	38	3.9	280.6	131.4
Cu09BG-05B	101	4.4	339.0	117.6
Cu09BG-05C	80	4.6	306.5	108.9
Cu09BG-05D	43	3.4	252.6	105.5
Cu09BG-05E	54	4.6	303.9	131.1
Cu09BG-06A	41	3.3	189.1	72.1
Cu09BG-06B	54	3.3	160.2	63.2
Cu09BG-07A	27	4.6	304.4	122.6
Cu09BG-07B	36	3.3	128.2	47.7
Cu09BG-07C	56	3.6	183.4	81.7
Cu09BG-07D	12	3.3	162.4	77.3
Cu09BG-07E	2	0.3	2.0	1.0
Cu09BG-07F	7	0.3	21.8	9.3
Cu09BG-07G	26	3.0	184.2	75.3
Cu09BG-08	18	2.8	113.6	32.6
Cu09BG-09	128	7.7	444.2	101.3
Cu09BG-10A	13	3.0	210.8	95.4
Cu09BG-10B	54	3.2	199.6	91.7
Cu09BG-10C	8	0.5	42.8	20.5
Cu09BG-10D	90	4.8	326.2	145.9
Cu09BG-10E	6	0.9	51.3	24.4
Cu09BG-10F	55	1.9	157.3	73.5

Animal / trip code *Bogoslof fur seals*	GPS at-sea (*n*)	Trip duration (d)	Trip length (km)	Max. distance from rookery (km)
Cu09BG-10G	2	0.3	45.3	22.3
Cu09BG-10H	62	2.9	181.7	76.1
Cu09BG-10I	53	2.9	209.5	91.4
Cu09BG-10J	11	0.7	61.2	26.0
Cu09BG-15	62	13.2	519.7	103.9
Cu09BG-16A	69	4.6	236.6	102.7
Cu09BG-16B	73	3.7	176.8	76.0
Cu09BG-16C	91	7.8	440.9	82.3
Cu09BG-17A	24	1.7	87.9	33.6
Cu09BG-17B	81	3.9	308.0	75.8
Cu09BG-17C	53	2.8	176.5	77.5
Cu09BG-17D	57	2.6	146.7	61.7
Cu09BG-18A	23	3.2	207.9	80.0
Cu09BG-18B	56	4.2	245.8	91.3
Cu09BG-18C	49	5.1	348.9	131.1
Cu09BG-19A	52	4.0	223.5	94.4
Cu09BG-19B	87	4.6	269.6	98.6
Cu09BG-19C	46	5.1	251.4	90.9
Cu09BG-19D	53	3.4	259.1	88.4
Cu09BG-20A	156	3.6	207.5	78.5
Cu09BG-20B	217	4.8	295.3	69.6
Cu09BG-20C	218	4.6	357.8	102.0
Cu09BG-21A	32	3.2	197.8	83.8
Cu09BG-21B	15	3.3	180.4	67.2
Cu09BG-21C	24	4.0	255.7	118.4
Cu09BG-21D	2	0.4	45.5	20.4
Cu09BG-21E	38	3.1	138.8	47.7
Cu09BG-22A	5	0.4	20.8	10.4
Cu09BG-22B	67	3.5	161.0	52.8
Cu09BG-22C	6	0.5	25.9	11.4
Cu09BG-22D	5	2.4	107.0	52.0
Cu09BG-23A	80	3.4	221.7	77.1
Cu09BG-23B	79	3.5	239.8	85.6
Cu09BG-24A	68	3.1	194.2	41.8
Cu09BG-24B	9	3.0	155.2	67.9
Cu09BG-24C	13	3.0	141.6	64.2
Cu09BG-24D	20	3.1	198.6	86.7
Cu09BG-25A	49	4.3	205.0	69.7
Cu09BG-25B	49	4.7	239.2	91.4
Cu09BG-26A	19	1.8	112.3	26.5
Cu09BG-26B	29	2.5	108.3	43.0
Cu09BG-26C	15	2.9	136.4	48.6
Cu09BG-27A	19	4.1	288.1	113.7
Cu09BG-27B	3	3.7	87.1	43.1
Cu09BG-27C	14	4.1	252.4	115.1

Animal / trip code *Bogoslof fur seals*	GPS at-sea (*n*)	Trip duration (d)	Trip length (km)	Max. distance from rookery (km)
Cu09BG-28A	41	4.0	242.6	100.4
Cu09BG-28B	41	4.3	273.1	118.4
Cu09BG-28C	71	5.3	309.0	127.4
Cu09BG-29A	11	0.2	15.6	6.0
Cu09BG-29B	25	0.5	36.7	15.1
Cu09BG-29C	15	0.4	44.3	19.8
Cu09BG-29D	15	0.6	26.2	10.5
Cu09BG-29E	15	0.3	17.4	7.7
Cu09BG-29F	207	5.3	374.6	116.9
Cu09BG-30A	25	4.6	255.1	104.4
Cu09BG-30B	26	4.1	205.6	91.4
Cu09BG-31A	34	3.4	187.0	76.0
Cu09BG-31B	64	3.2	202.0	81.8
Cu09BG-32A	24	3.9	237.5	98.8
Cu09BG-32B	37	3.7	200.5	83.5
Cu09BG-33A	7	2.4	131.4	63.0
Cu09BG-33B	14	4.1	205.4	86.3
Cu09BG-34A	16	1.7	107.7	40.4
Cu09BG-34B	74	4.5	300.4	127.9
Cu09BG-34C	6	0.2	14.7	7.3
Cu09BG-35A	43	2.9	179.0	78.5
Cu09BG-35B	68	4.4	247.0	98.7
Cu09BG-35C	2	0.2	14.3	7.1
Cu09BG-36A	4	0.5	27.4	12.5
Cu09BG-36B	7	1.7	76.5	29.8
Cu09BG-36C	90	4.6	260.3	83.9
Cu09BG-37A	5	1.8	107.8	50.6
Cu09BG-37B	36	3.9	200.5	82.0
Cu09BG-38A	2	0.3	7.6	3.8
Cu09BG-38B	8	3.2	205.0	91.4
Cu09BG-38C	19	5.0	289.5	93.8
Cu09BG-39A	44	4.3	245.1	102.0
Cu09BG-39B	69	4.8	198.1	50.3
Cu09BG-40A	43	4.3	243.1	105.9
Cu09BG-40B	28	3.9	254.8	109.7
Cu09BG-41A	6	0.3	4.6	2.1
Cu09BG-41B	32	2.3	162.2	48.1
Cu09BG-41C	7	0.3	23.7	11.5
Cu09BG-41D	86	5.3	355.9	71.0
Cu09BG-42A	43	2.6	139.1	48.8
Cu09BG-42B	2	0.2	0.5	0.2
Cu09BG-42C	45	3.4	151.7	42.9
Cu09BG-43	254	5.3	282.2	56.4
Cu09BG-44	2	2.2	36.5	18.2
Cu09BG-45A	5	0.3	21.6	10.5
Cu09BG-45B	82	4.3	244.9	86.9
Cu09BG-46	40	5.6	213.2	66.4
Cu09BG-47	15	3.7	209.8	92.7

Appendix B: Supplementary statistics for northern fur seal habitat selection models

Table B.1 Models predicting habitat use (time spent within a 12 km radius) by foraging, lactating northern fur seals from the St. Paul I. Nocturnal group as a function of environmental features. Models are ranked by Akaike's information criteria (AIC_C). Model statistics are defined as: AIC_C differences (Δ_i), Akaike weights (w_i), relative model likelihoods (rel. (L)), and coefficients of determination (R^2). The top 25 of 79 models are presented, along with the penalized log-likelihoods (log(L)) and penalized degrees of freedom (df) used to calculate the AIC_C values. Sample size is 1466. Front: distance to nearest front (4 categories: 0–4, >4–10, >10–20, >20 km); Depth: ocean depth (4 categories: 0–100, >100–200, >200–350, >350 m); TC: thermocline depth (3 categories: <25, 25–35, >35 m); TempTC: mean temperature above thermocline; Temp1m: temperature at 1 m depth; Chl: total chlorophyll in upper 100m of water column (2 categories: <350, >350 mg/m^3).

Model variables	AIC_C	Δ_i	w_i	rel. (L)	R^2	log (L)	df
Front + Depth + TC + TempTC + Temp1m	17375.9	0.00	0.56	1.00	0.308	-8651.8	35.26
Front + Depth + TC + TempTC + Temp1m + Chl	17376.8	0.86	0.36	0.65	0.308	-8651.1	36.27
Front + Depth + TC + TempTC	17381.5	5.57	0.03	0.06	0.304	-8655.5	34.41
Front + Depth + TC + Temp1m + Chl + (Front x Chl)	17382.9	6.95	0.02	0.03	0.308	-8651.0	39.25
Front + Depth + TC + Temp1m + Chl	17383.2	7.28	0.01	0.03	0.304	-8655.3	35.40
Front + Depth + TempTC + Temp1m	17384.1	8.23	0.01	0.02	0.302	-8657.9	33.36
Front + Depth + TempTC + Temp1m + Chl	17385.8	9.93	0.00	0.01	0.302	-8657.7	34.35
Front + Depth + TC + Temp1m + Chl + (Front x Chl)	17389.3	13.40	0.00	0.00	0.304	-8655.2	38.38
Front + Depth + Temp1m	17391.0	15.06	0.00	0.00	0.297	-8662.2	32.50
Depth + TC + TempTC + Temp1m	17391.0	15.07	0.00	0.00	0.297	-8662.5	32.20
Front + Depth + TempTC + Temp1m + Chl + (Front x Chl)	17391.7	15.79	0.00	0.00	0.302	-8657.5	37.33
Depth + TC + TempTC + Temp1m + Chl	17392.2	16.28	0.00	0.00	0.297	-8662.1	33.20
Front + Depth + Temp1m + Chl	17393.1	17.21	0.00	0.00	0.297	-8662.3	33.47
Depth + TempTC + Temp1m	17395.8	19.87	0.00	0.00	0.293	-8666.9	30.30
Depth + TempTC + Temp1m + Chl	17397.6	21.67	0.00	0.00	0.293	-8666.8	31.29
Front + Depth + Temp1m + Chl + (Front x Chl)	17399.0	23.08	0.00	0.00	0.297	-8662.1	36.45
Depth + TC + Temp1m	17410.4	34.49	0.00	0.00	0.287	-8673.0	31.45
Depth + TC + Temp1m + Chl	17412.6	36.67	0.00	0.00	0.286	-8673.1	32.40
Depth + Temp1m	17415.9	39.99	0.00	0.00	0.282	-8677.8	29.53
Depth + Temp1m + Chl	17417.9	42.03	0.00	0.00	0.282	-8677.8	30.47
Front + TC + TempTC + Temp1m	17456.3	80.44	0.00	0.00	0.264	-8695.6	31.81
Front + TC + TempTC + Temp1m + Chl	17457.3	81.40	0.00	0.00	0.264	-8695.1	32.79
Front + TC + TempTC + Temp1m + Chl + (Front x Chl)	17460.3	84.39	0.00	0.00	0.266	-8693.4	35.81
Front + TempTC + Temp1m + Chl	17482.0	106.10	0.00	0.00	0.249	-8709.6	30.70
Front + TempTC + Temp1m	17483.9	107.95	0.00	0.00	0.247	-8711.6	29.66

Table B.2 Models predicting habitat use (time spent within a 12 km radius) by foraging, lactating northern fur seals from the St. Paul I. Cathemeral group as a function of environmental features. Models are ranked by Akaike's information criteria (AIC_C). Model statistics are defined as: AIC_C differences (Δ_i), Akaike weights (w_i), relative model likelihoods (rel. (L)), and coefficients of determination (R^2). The top 25 of 79 models are presented, along with the penalized log-likelihoods (log(L)) and penalized degrees of freedom (df) used to calculate the AIC_C values. Sample size is 1152. Front: distance to nearest front (4 categories: 0–4, >4–10, >10–20, >20 km); Depth: ocean depth (4 categories: 0–100, >100–200, >200–350, >350 m); TC: thermocline depth (3 categories: <25, 25–35, >35 m); TempTC: mean temperature above thermocline; Temp1m: temperature at 1 m depth; Chl: total chlorophyll in upper 100m of water column (2 categories: <350, >350 mg/m^3).

Model variables	AIC_C	Δ_i	w_i	rel. (L)	R^2	log (L)	df
Front + Depth + TC + TempTC + Temp1m + Chl + (Front x Chl)	13448.9	0.00	0.62	1.00	0.298	-6686.9	36.34
Front + Depth + TC + TempTC + Temp1m	13452.0	3.14	0.13	0.21	0.291	-6692.7	32.37
Depth + TC + TempTC + Temp1m	13452.2	3.26	0.12	0.20	0.287	-6695.9	29.35
Front + Depth + TC + TempTC + Temp1m + Chl	13453.3	4.39	0.07	0.11	0.291	-6692.3	33.35
Depth + TC + TempTC + Temp1m + Chl	13453.4	4.55	0.06	0.10	0.287	-6695.5	30.33
Front + Depth + TC + Temp1m + Chl + (Front x Chl)	13462.4	13.47	0.00	0.00	0.289	-6694.6	35.42
Front + Depth + TC + Temp1m	13467.1	18.23	0.00	0.00	0.280	-6701.2	31.46
Depth + TC + Temp1m	13468.3	19.43	0.00	0.00	0.275	-6705.0	28.42
Front + Depth + TC + Temp1m + Chl	13468.6	19.65	0.00	0.00	0.281	-6700.9	32.44
Depth + TC + Temp1m + Chl	13469.8	20.87	0.00	0.00	0.276	-6704.7	29.40
Front + TC + TempTC + Temp1m + Chl + (Front x Chl)	13487.0	38.11	0.00	0.00	0.270	-6709.5	33.00
Front + TC + TempTC + Temp1m	13490.7	41.79	0.00	0.00	0.262	-6715.5	29.02
Front + TC + TempTC + Temp1m + Chl	13491.1	42.25	0.00	0.00	0.263	-6714.8	29.98
TC + TempTC + Temp1m + Chl	13506.7	57.76	0.00	0.00	0.248	-6725.9	26.78
TC + TempTC + Temp1m	13508.5	59.64	0.00	0.00	0.246	-6727.8	25.83
Front + TC + Temp1m + Chl + (Front x Chl)	13511.7	62.80	0.00	0.00	0.252	-6722.9	32.01
Front + TC + Temp1m + Chl	13518.2	69.30	0.00	0.00	0.244	-6729.3	29.01
Front + TC + Temp1m	13519.2	70.25	0.00	0.00	0.242	-6730.8	28.04
Front + Depth + TempTC + Temp1m + Chl + (Front x Chl)	13534.5	85.61	0.00	0.00	0.240	-6731.9	34.29
Chl + TC + Temp1m	13538.9	89.97	0.00	0.00	0.225	-6743.2	25.64
Front + Depth + Temp1m + Chl + (Front x Chl)	13540.1	91.16	0.00	0.00	0.235	-6735.7	33.33
Front + Depth + TempTC + Temp1m	13543.1	94.22	0.00	0.00	0.229	-6740.4	30.28
TC + Temp1m	13543.8	94.86	0.00	0.00	0.221	-6746.6	24.67
Front + Depth + TempTC + Temp1m + Chl	13544.0	95.06	0.00	0.00	0.230	-6739.8	31.26
Front + Depth + Temp1m	13549.8	100.92	0.00	0.00	0.223	-6744.8	29.34

Table B.3 Models predicting habitat use (time spent within a 6 km radius) by foraging, lactating northern fur seals from Bogoslof I. as a function of environmental features. Models are ranked by Akaike's information criteria (AIC_C). Model statistics are defined as: AIC_C differences (Δ_i), Akaike weights (w_i), relative model likelihoods (rel. (L)), and coefficients of determination (R^2). The top 25 of 79 models are presented, along with the penalized log-likelihoods (log(L)) and penalized degrees of freedom (df) used to calculate the AIC_C values. Sample size is 3929. Front: distance to nearest front (4 categories: 0–4, >4–10, >10–20, >20 km); Depth: ocean depth; TC: thermocline depth (3 categories: <25, 25–35, >35 m); TempTC: mean temperature above thermocline; Temp1m: temperature at 1 m depth; Chl: total chlorophyll in upper 100m of water column (2 categories: <450, >450 mg/m^3).

Model variables	AIC_C	Δ_i	w_i	rel. (L)	R^2	log (L)	df
Front + Depth + TC + TempTC + Temp1m + Chl + (Front x Chl)	51867.5	0.00	1.00	1.00	0.279	-25825.3	105.33
Front + Depth + TC + TempTC + Temp1m + Chl	51893.0	25.52	0.00	0.00	0.273	-25841.2	102.32
Front + Depth + TC + TempTC + Temp1m	51906.3	38.81	0.00	0.00	0.270	-25848.7	101.53
Front + Depth + TC + Temp1m + Chl + (Front x Chl)	51907.2	39.72	0.00	0.00	0.271	-25845.9	104.59
Front + Depth + TC + Temp1m + Chl	51934.6	67.09	0.00	0.00	0.264	-25862.8	101.58
Front + TC + TempTC + Temp1m + Chl + (Front x Chl)	51949.3	81.79	0.00	0.00	0.263	-25866.3	105.21
Depth + TC + TempTC + Temp1m + Chl	51963.4	95.88	0.00	0.00	0.257	-25879.8	99.09
Front + Depth + TC + Temp1m	51971.3	103.83	0.00	0.00	0.257	-25881.8	101.00
Front + TC + TempTC + Temp1m + Chl	51977.7	110.21	0.00	0.00	0.256	-25883.5	102.40
Depth + TC + TempTC + Temp1m	51984.9	117.35	0.00	0.00	0.253	-25891.4	98.26
Front + TC + TempTC + Temp1m	51993.5	125.97	0.00	0.00	0.252	-25892.1	101.73
Depth + TC + Temp1m + Chl	52007.5	139.97	0.00	0.00	0.248	-25902.7	98.34
Front + TC + Temp1m + Chl + (Front x Chl)	52019.0	151.52	0.00	0.00	0.248	-25903.1	103.43
TC + TempTC + Temp1m + Chl	52044.0	176.52	0.00	0.00	0.241	-25919.8	99.37
Front + TC + Temp1m + Chl	52050.4	182.85	0.00	0.00	0.240	-25921.7	100.62
Depth + TC + Temp1m	52058.3	190.77	0.00	0.00	0.237	-25928.7	97.71
TC + TempTC + Temp1m	52067.8	200.33	0.00	0.00	0.236	-25932.5	98.70
Front + TC + Temp1m	52102.8	235.34	0.00	0.00	0.229	-25948.6	100.03
TC + Temp1m + Chl	52118.8	251.26	0.00	0.00	0.225	-25959.1	97.59
Front + Depth + TempTC + Temp1m + Chl + (Front x Chl)	52182.2	314.71	0.00	0.00	0.210	-25993.0	95.51
TC + Temp1m	52185.5	318.04	0.00	0.00	0.210	-25993.2	96.94
Front + Depth +TempTC + Temp1m + Chl	52222.1	354.60	0.00	0.00	0.200	-26015.9	92.71
Front + Depth +TempTC + Temp1m	52225.3	357.83	0.00	0.00	0.199	-26018.3	91.99
Front + Depth + Temp1m + Chl + (Front x Chl)	52238.0	370.46	0.00	0.00	0.198	-26020.2	96.19
Front + Depth + Temp1m + Chl	52281.2	413.68	0.00	0.00	0.188	-26044.5	93.61