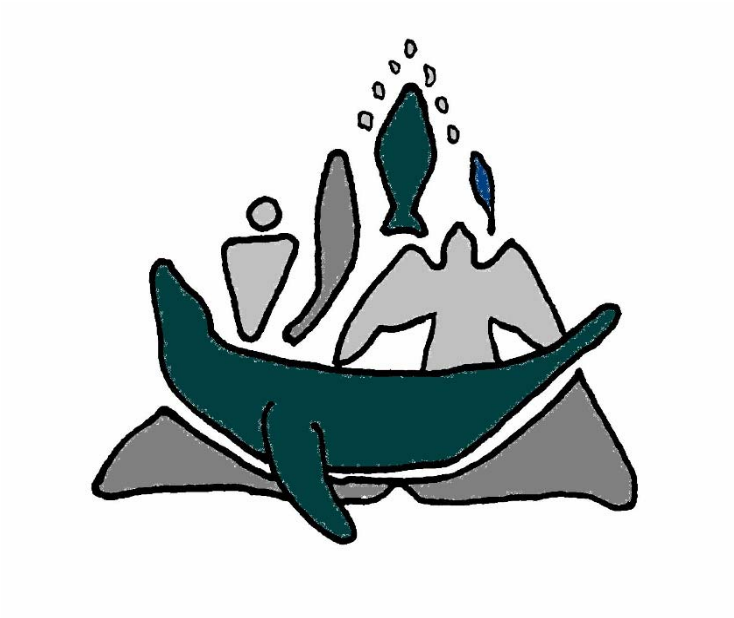
Gulf Apex Predator-prey Study (GAP)

Final Report FY2001-2003
NOAA Grant NA16FX1270



University of Alaska Fairbanks
School of Fisheries and Ocean Sciences
Kodiak, Alaska

30 January 2005

Fishery Industrial Technology Center

Marine Advisory Program
University of Alaska

UAF

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I. EXECUTIVE SUMMARY

The Gulf Apex Predator-prey (GAP) program represents a multidisciplinary effort to assess the status, environment, prey, and potential competitors of Steller sea lions in waters near Kodiak, Alaska. GAP's distinct but interrelated studies broadly assess the diets, distribution, and status of Kodiak's sympatric apex predators while exploring the processes that drive populations of their prey within a dynamic marine environment. These studies were designed to overlap spatially and temporally to allow synchronous collection of predator and prey data and a synoptic assessment of their seasonal interactions. By limiting the geographic breadth of its integrated studies to waters near Kodiak, GAP has been able to collect data with both temporal and taxonomic depth.

Steller sea lion numbers in the Kodiak region declined precipitously through the 1980's and more slowly through the 1990's; counts continued to decline from 2000-2004 despite abatement of the decline elsewhere. We used repeated aerial surveys of haulouts in the Kodiak Archipelago to monitor the seasonal abundance and distribution of Steller sea lion and to explore inter- and intra-annual patterns reflective of changing prey availability and reproductive needs of sea lions. Use of terrestrial habitat peaked in late summer and a negative trend in Steller sea lion numbers was seen in the area over four survey years. Seasonal patterns of use varied on each site, including shifts in overall attendance numbers and use of within-haulout microhabitat.

We assessed the diet of Steller sea lions as a fundamental first step to understanding their potential for competitive interactions with humans and other upper level marine consumers. Preliminary findings indicate that Kodiak's Steller sea lions are currently preying on a diverse diet, including a remarkable nine dominant prey species. Relative use varied both seasonally and regionally but Pacific sandlance (42.0 FOC), arrowtooth flounder (37.0 FOC), walleye pollock (30.1 FOC), Pacific cod (29.2 FOC), and salmon *spp*. (28.5 FOC) were found to be the five dominant prey of Steller sea lion in the samples examined to date.

We conducted a variety of vessel surveys to monitor spatial and temporal patterns in the distribution and abundance of prey species within Kodiak waters. Prey distributions were found to vary spatially and seasonally between 2001 and 2003. Pelagic fish distribution was correlated to the presence of oceanographic features on the northeast side of Kodiak Island and surveys were expanded to accommodate these features. Specifically, horizontal features of the water column off Portlock Bank, Marmot Gully and Chiniak Gully appear to affect the distributions of capelin and walleye pollock. As such, a large amount of variability was found in the energy density of prey available to upper trophic levels. Demersal fish distributions were highly variable among seasons and between years. However, distributions were associated with specific strata, such as distance to shore and depth.

Steller sea lions share Kodiak waters and prey resources with a variety of apex predators, including marine fish, birds, and mammals, whose numbers increased during the Steller sea lion's decline. We documented temporal and spatial patterns in the diets, abundance, distribution, and habitat use of several piscivorous consumers (apex predators) in the Kodiak region as a basis for evaluating interactions among potential competitors and differential response to environmental variables. Kodiak harbor seals prey on the species eaten by sea lions but their numbers have increased steadily in the Kodiak area while Steller sea lion numbers have continued to decline. We examined dive behavior of harbor seals as a first step in assessing potential overlap in marine habitat use between these sympatric and piscivorous pinnipeds.

Large whales are apex predators found in Kodiak waters designated as Steller sea lion Critical Habitat. We documented the year-round presence and distribution of large whales in the Kodiak Archipelago and assessed their abundance, distribution, and habitat use in northeast Kodiak waters. The relative number, diversity, and persistence of whales in the near-coastal community demonstrate their significance as upper level consumers in an area where Steller sea lion numbers continue to decline. We initiated studies to assess the foraging ecology of humpback whales in Kodiak waters, a consumer whose

numbers are rebounding and whose diet includes fish consumed by Steller sea lions and zooplankton that feed those fish species.

We monitored dietary, reproductive, physiological and behavioral parameters of black-legged kittiwakes, glaucous-winged gulls and tufted puffins across their breeding season in 2001-2003. Seabirds exhibited remarkable similarity in the trends of predator-insensitive reproductive parameters thus allowing us to draw some general conclusions about marine foraging conditions in Chiniak Bay from 2001-2003. In 2001 evidence suggests that foraging conditions were consistently good across the entire breeding season for most colonies and species. Energy rich age 1+ sandlance dominated the diets and foraging took place primarily within the confines of the bay. In 2002, although foraging conditions appeared to be excellent early in the season, egg predators severely impacted the reproductive output of approximately 50% of kittiwake breeding colonies within the bay. Impaired nestling growth rates indicated that foraging conditions had declined markedly by the nestling period and were the poorest of any year of the study. Adult kittiwakes responded by devoting more time to foraging and by undertaking longer foraging trips that extended beyond the periphery of Chiniak Bay. Glaucous-winged gulls breed earlier in the season and thus exhibited excellent reproductive performance yet displayed decrease body condition and increase plasma corticosterone levels by late chick rearing suggestive of decreased forage availability in mid-summer. In 2003, egg laying was delayed by cool marine conditions in the spring and egg predation severely impacted most kittiwake colonies within the bay. Rapid nestling growth suggested excellent foraging conditions in 2003 while kittiwake parents provisioned nestlings on a diet of energy-rich capelin and, to a lesser degree, on lipid-poor YOY sandlance.

Key Words:

Steller sea lions, trophic interactions, seabirds, marine mammals, forage fish, predatory fish, ecosystem monitoring, Kodiak, Gulf of Alaska

II. RECOMMENDATIONS

The continued decline of apex predator populations has illustrated the fundamental need to understand ecosystem mechanisms and processes at the organismal and population levels. After years of unprecedented and intensive research on Steller sea lions, there is still no clear evidence that nutritional stress, environmental change, or predation are linked to their continued declines. A primary stumbling block has been in determining what *mechanisms* are expected to control the population's decline/lack of recovery at the ecosystem, population, individual, and cellular levels.

In the first three years of GAP, we began describing the structure of a small marine system east of Kodiak in response to specific Steller sea lion questions. We monitored seasonal abundance and distribution of fish species in relation to oceanographic variability. We identified consumers in the system, including piscivorous fish, birds, marine mammals, and humans that utilize this prey base and monitored their distribution and productivity over time. Then we linked prey availability and dietary overlap among upper level consumers to determine potential competitive interactions between Steller sea lions and other apex predators.

Future effort should focus on exploring the structure of this system and monitor spatial and temporal changes in its biotic and abiotic components. Insights developed in GAP's first three years can be used to explore the *connections* between these components from oceanographic, physiological, and ecological perspectives. While continuing to monitor the structure and variability of the system, future research should explore the physical processes, energetic pathways, and physiological mechanisms that link its components. A multidisciplinary and comprehensive effort should be made to explore the *interfaces* where physical oceanography drives primary productivity, where predators consume their prey, and where captive fish react to controlled environmental change.

Longterm monitoring and hypothesis-driven research on such trophic level interactions will become more critical as managers take an "ecosystem-based approach" to marine resource management relies on understanding both the structural components of the system and the functional mechanisms of their interactions. Future studies should

- continue monitoring the seasonal distribution and abundance of predators and prey
- track oceanographic variability in relationship to zooplankton and fish populations to explore effects of environmental change on primary and secondary production
- develop time-series needed to forecast and predict effect of perturbations
- consider predators and prey in terms of energetic content and their interactions as energetic exchange
- use spatially- and temporally- specific data to develop holistic models of marine ecosystem dynamics

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III. INTRODUCTION

The precipitous and continued decline of the western stock of Steller sea lions *(Eumetopias jubatus*) has been well documented (Calkins and Goodwin 1988, Loughlin et al. 1992, Sease and Loughlin 1999, Hill and DeMaster 1999, NRC 2003). Factors contributing to their decline and preventing recovery remain unclear, although reduced juvenile survival is considered a likely proximate cause (Merrick 1995, Sease and Merrick 1997). One hypothesis is that the western stock of Steller sea lions is nutritionally stressed and their recovery may be limited by the availability, quality, and/or diversity of their prey (ASG 1993, NMFS 1995, Merrick et al. 1997, Sease and Merrick 1997, Calkins, et al. 1998, Trites and Donnelly 2003). Although evidence from the 1970's and 1980's support this hypothesis, studies in the 1990's do not (PSMFC 1997, Millette et al.1999, NRC 2003), suggesting other factors may now be involved. We currently lack adequate understanding of the dynamic ecological processes affecting Steller sea lions to determine or reduce impediments to their recovery.

Since 1999, University of Alaska Fairbanks faculty in Kodiak have been addressing trophic-level questions of immediate biological and economic concern in the western Gulf of Alaska. In 2001, the Gulf Apex Predator-prey program (GAP) received a Congressionally-appropriated NOAA grant to support the program's efforts to document trophic relationships between Steller sea lions, their prey, competitors, and predators in the Kodiak region. Fundamental to the GAP program was the integration of distinct but related hypothesis-driven research projects. Although focused on Steller sea lion concerns, GAP's interrelated studies also broadly assessed the degree of dietary overlap among Kodiak's sympatric apex predators while exploring processes that drive populations of their prey within a dynamic marine environment. These studies overlapped spatially and temporally, allowing synchronous collection of predator and prey data and synoptic assessment of their seasonal interactions. GAP program was planned as a multiyear sampling effort to allow monitoring inter-annual variability against which effects of human intervention may be compared. GAP investigators sought to make synergistic linkages to related studies and efficiently broaden research beyond the scope of individual projects. The Principal Investigators fostered collaboration with fisheries and marine mammal researchers within the National Marine Fisheries Service (NMFS), U.S. Fish and Wildlife Service (USFWS), and the Alaska Department of Fish and Game (ADFG).

Steller sea lions and humans share a position as apex predators in the Gulf of Alaska with a variety of piscivorous fish, birds, and marine mammals. Historically, these apex predators have undergone drastic and potentially interrelated changes (Pitcher 1990, Springer 1992, Merrick 1995, Anderson et al.1997). Yet they have been studied, inventoried, and managed separately without consideration for their multi-species interactions and potentially competitive consumption of common prey resources. Data needed to describe the complex ecological interrelationships among apex predators and to discern effects of natural and anthropogenic change on their prey base are therefore lacking (Boyd 1995). As a result, the potential impact of cumulative commercial fish removals on the endangered Steller sea lion stock remains equivocal (NMFS 2000, pg 182, 227)**.**

Lacking empirical data, the Endangered Species Act mandates a risk-averse approach to the management of human removals of Steller sea lion prey. Although no direct correlations have been made between commercial pollock harvests and continued Steller sea lion declines, restrictions on commercial fishing have been implemented throughout much of the Gulf of Alaska and Bering Sea in an effort to assure adequate prey availability for Steller sea lions within their designated critical habitat. Based on limited data and presumed competition, these actions may be "reasonable and prudent" from an administrative perspective but were not designed to improve our understanding of actual ecological interactions and potential for competition between Steller sea lions, human harvesters, and other apex predators in the system.

Because continued Steller sea lion declines and resulting fishery restrictions bear significant biological, social and economic ramifications, Alaska's congressional delegates rallied federal support for increased research on "all possible factors relating to" declines of Steller sea lions. Funds were appropriated to GAP in support of research that directly addresses research areas Congress identified as necessary for understanding the Steller sea lion's decline and potential recovery. GAP focused on addressing the hypothesis that current Steller sea lion declines are related to *prey limitation* and potential for competition with fisheries or other upper level consumers. Secondarily we addressed the hypotheses that *environmental change* and *predation* could be limiting Steller sea lion recovery in the Gulf of Alaska.

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GAP represents a truly collaborative effort with additional financial, permitting, and/or logistic support provided by personnel from the Alaska Department of Fish and Game (ADFG), NMFS (Alaska Fisheries Science Center (AFSC) and National Marine Mammal Laboratory (NMML)), U.S. Geological Survey National Biological Survey (USGS), and U.S. Fish and Wildllife Service (USFWS). In particular, we appreciate the collaborative efforts and support of Dr. Kathleen O'Reilly (University of Portland), Dr. David Irons (USFWS Migratory Birds), Dr. Tom Loughlin (NMML), and Dr. Gail Blundell (ADFG).

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Finally we extend a special thanks to Al Burch, Jay Stinson, and other members of the community of Kodiak who have supported GAP since its inception, demonstrating their belief that sound resource management must be based on a comprehensive and scientific understanding of interrelated ecosystem components.

GAP research was conducted under the following state permits and authorization:

National Marine Fisheries Service
Fish: LOA# 2001-04, LOA# 2003-01, LOA# 2004-06, LOA# 2002-07
Marine Mammals: NMFS Scientific Permit # 782-1532 Steller sea lion
NMFS Scientific Permit # 358-1585 Harbor seals
NMFS Scientific Permit # 473-1433, # 545-1488, #1049-1718 whales
U.S. Fish and Wildlife Service
Birds: MB088638-0, MB692453-0, MB692453-1
Alaska Dept of Fish and Game
Fish: CF01-001, CF01-027, CF02-033, CF03-024, CF04-031
01A-0109, 01A-0110, 04A-0018, 04A-0017, 04A-0050
Birds: 04-090, 03-057, 02-065, 01-084
Institutional Animal Care and Use Assurance of Care (IACUC)
Fish: # 01-10, # 01-11, # 04-21, # 02-53
Marine mammals: # 01-46, #02-38, #02-48
Birds: # 02-12, # 99-116, # 03-09

V. LIST OF STUDENTS

The following students benefited from financial or logistic support provided by this grant to GAP as they conducted research for their graduate degrees at the University of Alaska Fairbanks:

Baraff, L., MS Marine Biology: “Summer distribution and habitat characteristics of balaenopterid whales off northeast Kodiak Island, Alaska”

Brewer, J.H.,MS Marine Biology: ”Adrenal responsiveness of Black-legged Kittiwake chicks: proximate affects of brood size, status and adult provisioning rate.”

Gamble, J.B., MS Biology: “Ecological and Physiological Factors Contributing to Reproductive Success of Glaucous-winged Gulls (*Larus glaucescens*) in Chiniak Bay, Kodiak Island, Alaska”

Hanna, S. K., MS Marine Biology: “The effect of temperature on swimming speed and metabolic rate of Pacific cod, *Gadus macrocephalus”*

Harper, S., MS Marine Biology: “Dive physiology and behavior of two polar phocid species.”

Knoth, B. MS Fisheries: “Investigating the role of arrowtooth flounders (*Atheresthes stomias*) as a top level consumer in the Gulf of Alaska ecosystem from 2001-2004”

Murra, K. A., MS Marine Biology: “Thesis: Black-legged kittiwake foraging ecology and reproductive performance in Kodiak, AK”

Nash, J., MS Oceanography: “Trophic status of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska”

Wang, X., MS Marine Biology: “Interannual and seasonal zooplankton community composition near Kodiak Island, Alaska”

Williams, C.T., PhD Marine Biology: “Physiological ecology of the Tufted Puffin”

Witteveen, B.H., MS Fisheries: “Abundance and feeding ecology of humpback whales (*Megaptera novaeangiae*) in Kodiak, Alaska.”

VI. PREY AND FISHERIES OCEANOGRAPHY

The prey component of the GAP program includes numerous studies focused on the distribution, ecology and physiology of fish and zooplankton that make up the "prey" of Steller sea lions and their competitors. Interactions among these multiple trophic levels have been assessed to ultimately better understand their influence on apex predators. We have also included a significant focus on oceanography to describe the environment in which these interactions occur. The objectives from 2001-2003 were to:

1. assess the seasonal species composition, distribution, abundance, and quality of prey available to sea lions within 10, 20, and 25 nm of Long Island haulout;
2. monitor oceanographic conditions associated with fish species distribution;
3. determine the feasibility of describing and quantifying prey fields upon which Steller sea lions, whales, and seabirds are observed actively foraging.

The GAP study area was sampled for the first time in the spring of 2000 with funds from the North Pacific Research Board (Wynne et al. 2003). The GAP program was designed to compliment the 2000 research and continue a time series in the same study area. As such, data from 2000 was analyzed as part of the GAP program and included in some of the results in this report. From 2000 to 2003, we assessed prey resources available to Steller sea lions and other apex predators through systematic seasonal surveys on multiple spatial and temporal scales: monthly nearshore (2002), monthly in Marmot Bay-Chiniak Bay (2002), and quarterly Long Island Critical Habitat (2000-2003). From 2000 to 2002, we used waters within 46.3 km (25 nm) of the Long Island Steller sea lion haulout as a core study area in which to document seasonal changes in prey species composition, abundance, and distribution. In 2002, we extended our surveys to include waters surrounding Marmot Island, a site used both as a rookery (seasonally for mating and pupping) and a haulout (year-round for resting). Fish distributions and abundance were related to physical oceanographic features in the region to predict the correlations of environmental parameters to the availability of prey for upper trophic levels. Our final objective was to make preliminary comparisons between data collected on prey resources with data collected on diets and habitats used by Steller sea lions, humpback and fin whales and seabirds.

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Steller sea lion prey availability in the Long Island Critical Habitat (2000-2003)

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Introduction

To assess the seasonal distribution of fish species and to describe the physical environment in Steller sea lion habitat, a series of transect lines were occupied between 2000 and 2003. Other studies have been designed to quantify seasonal availability of pelagic and demersal prey near Steller sea lion haulouts in mid-summer (Byrd et al. 1997, Mueter and Norcross 2000). Our goal was to develop seasonal surveys of a given area to assess intra- and inter-annual changes in sea lion prey availability as has been called for by Pacific States Marine Fisheries Commission (PSMFC 1999). The survey consisted of a 20 nm area around Long Island near Kodiak Island, Alaska. This area is designated as critical Steller sea lion habitat (CFR 50 226.202(a)) and as such provided the initial study area for our program. Waters within a 20 nm radius of Long Island haulout were designated as critical habitat in 1993 but were not closed to fishing at the time. In 1998, waters within a 10 nm radius of this haulout were designated a winter-only Pollock Trawl Exclusion Zone and closed to pollock trawling during pollock A1 and A2 seasons (NMFS 1998).

2000-2002

In 2000, 2001 and 2002 we assessed and compared fish species present within two distance strata (10 nm and 10-20 nm) of the Long Island haulout as a means of comparing prey availability inside and outside of this Pollock Trawl Exclusion Zone. In 2000, the F/V Alaska Beauty was set up with commercial mid water and bottom trawling gear as well as an acoustic echo integration system to conduct surveys in March, May and November 2000. A tow body with a transducer was towed. An acoustic and biological survey was developed based on standard protocol given vessel time available. We conducted two surveys in 2001: 19 – 27 May and 3 –11 November 2001. A March 2001 survey was not possible due to weather and vessel availability constraints. In 2002 the F/V Laura was equipped with a hull mounted 38 kHz transducer. The commercial bottom and midwater trawling gear was the same as that used in 2001.We conducted four surveys in 2002: 1-5 April, 16-28 May, 18-30 July and 11-23 November 2002.

In 2000-2002 the acoustic sampling was on multiple parallel east-west lines equally spaced 5.6 km apart, extending 37 km out from Long Island (Fig.1). The vessel speed during all transecting was 7 knots (1000 rpms). A total of approximately 235 nm was surveyed on each cruise. Information was recorded during the entire transect with respect to noise level, signal acquisition, and weather conditions. Boat noise was found to be minimized around 1500 rpm, which corresponded to approximately 7 knots.

The bottom trawl was deployed at 20 randomly selected locations along the acoustic transect line based on sampling multiple strata including depth and distance from SSL haulouts (Figure 1). The bottom trawl was deployed for 10 min tows beginning when the trawl is “fishing” on the bottom. Upon retrieval, all fishes were separated by species and counted. We randomly subsampled 100 fish of representative sizes of each species and set aside for weight (g) and length (mm) measurements. All subsamples of rare species were weighed whereas only 20 – 30 of common species were weighed from each subsample. Single species with sample sizes totaling more than 500 fish were approximated by counting a single subset. Fish lengths and weights were entered into electronic fish measuring boards (FMB). All large fish were dissected for stomach content analysis.

The midwater trawl was deployed opportunistically as we encountered pelagic fish assemblages to ground-truth the hydroacoustic signals. Tow duration was dependent on the magnitude of acoustic signal, ranging from 10 to 25 minutes. Midwater tows were treating similarly to bottom tows upon retrieval.

A Seabird Conductivity and Temperature at Depth (CTD) instrument was deployed to collect oceanographic data (salinity, temperature, light, productivity) at each station.

2003

In 2003 the objectives of the fish surveys were changed to reflect progress in testing previous hypotheses and to address new hypotheses regarding the trophic and oceanographic linkages in our ecosystem on the east side of Kodiak Island. We continued seasonal monitoring of prey availability within the Long Island Critical Habitat area but reduced the intensity of nearshore sampling in order to expand assessment of prey to shelf waters outside of LICH (see Portlock section). These surveys continued to assess prey availability on a scale being utilized by dependent and recently weaned sea lion pups (NMFS unpublished data).

The previous (2000-2002) survey areas within 46.3 km of Long and Marmot Islands was “monitored” in 2003 such that deviations in trends in fish distribution or relationships to oceanographic conditions established during 2000-2002 could be detected. As such, every other transect line (every 11.12 km) previously occupied throughout the year was surveyed in 2003.

Approximately four days of hydroacoustic and trawl surveying were conducted in each season to assess relative seasonal abundance estimates and distribution of fish within 46.3 km of the Long Island sea lion haulouts. Hydroacoustic sampling included a total of 398.5 km parallel east-west transects spaced 11.12 km apart and to the edge of designated Steller sea lion Critical Habitat around Long Island. Twelve predetermined locations within the survey area were sampled for demersal fish distribution. We conducted three surveys in 2003: 5-9 March, 22 May - 4 June and 1-17 August 2003.

A Seabird Conductivity and Temperature at Depth (CTD) instrument was deployed to collect oceanographic data (salinity, temperature, light, productivity) at each station.

Nearshore surveys

Nearshore waters immediately adjacent to haulouts and rookeries appear to be of particular significance to pre-weaned Steller sea lion pups and may represent biologically critical habitat. Several prey species found in these nearshore waters, including sandlance and other nearshore species, have been found to occur frequently in the scats of Steller sea lions using Chiniak and Long Island haulouts but are rarely caught in our larger scale surveys. Because our other surveys use gear that precludes surveying shallow waters immediately adjacent to haulouts, we explored a number of nearshore survey techniques in 2002 to determine the species composition and relative abundance of fishes present within 1000 m Long Island and Cape Chiniak haulouts (Fig. 2). Techniques for identifying fish prey species present included 1) deployment of beach and purse seines, 2) and examination of seabird diets or stomach contents from sport-caught halibut.

Results, Evaluation and Conclusions

Trawl surveys revealed a significant interannual and seasonal variability in fish biomass (kg/km) on the northeast side of Kodiak from 2000-2002 (Fig. 3). Note that the biomass of fish in the nearshore stations was reduced in 2001 possibly due to warmer temperatures on the shelf. Fluctuations were consistent with what we know about habitat (depth, substrate, distance to shore) preferences of groundfish around Kodiak Island. Sixty-seven species of fish were collected among the seasons and years. These were dominated by arrowtooth flounder, flathead sole, walleye pollock, Pacific cod, rock sole and eulachon making up on average the top 89% of fish caught in the bottom trawls. An average of 130,000 fish was counted each year. It was noted that although arrowtooth flounder dominated most stations, pollock, rock and rex sole biomass increased in 2002 compared to the previous years. Comparing strata among seasons we found a significant pattern for some species between 0-10 and 10-20 nm form the Long Island sea lion haulout (Fig. 4). Walleye pollock biomass was higher in the nearshore region while arrowtooth flounder, flathead sole, rock sole and Pacific halibut all had significantly higher biomasses in the 10-20 nm strata.

Twelve species of fish were caught in the midwater over the 3 seasons from 2000-2003 (Fig. 5). These included, in order of averaged abundance: walleye pollock, capelin, eulachon, arrowtooth flounder, Pacific sandfish, king salmon, sturgeon poacher, unidentified roundfish, steelhead trout, dusky rockfish, prowfish, and spiny dogfish. An average of 19,000 fish was counted each year. Both seasonal and interannual variability was noted in the distribution of pelagic fish species. Spatial differences suggest that both pollock and capelin exhibit strong seasonal variability based on life history stage (Fig. 6). Pelagic biomass was highest in 2001 almost doubling the total biomass of capelin available in the study area.

Comparisons of depth strata of both pelagic and demersal fish revealed a significant species specific pattern (Fig. 6). Walleye pollock, rock sole, and Pacific cod dominated the shallower stations while arrowtooth flounder, flathead sole and Pacific cod dominated the deeper stations. There were noted differences in size class variability among station depths as well.

Temperature and salinity profile data reveal numerous vertical density structures in the water column. Horizontal temperature and salinity structure in Chiniak and marmot Bay also reveal a seasonal variability important for understanding fish distributions (Fig. 7). In March 2002 the surface waters are mostly uniform with slightly warmer water offshore. This coincides with a minimal surface salinity gradient although winter current structure in the area is revealed by a slightly higher saline wedge of water over the deeper gullies at the mouths of Chiniak and Marmot Bays. In May 2002, a stronger temperature gradient is apparent with warmer water over the North Albatross Bank. Surface salinity in May also reveals a stronger gradient of fresher water nearshore and more saline water over the Bank.

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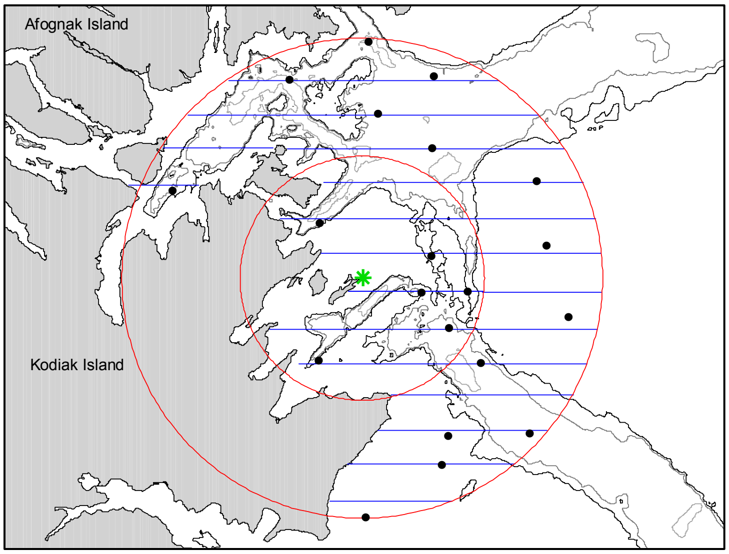


Figure 1. Acoustic transect lines spaced 3 nm apart and occupied in 2001-2002 on the northeast side of Kodiak Island. Dots represent bottom trawl and oceanographic stations occupied during each cruise. Darkest bathymetric line=100 m isobath. Concentric rings represent 10 nm and 20 nm radii around the Steller sea lion haulout (star) at Long Island

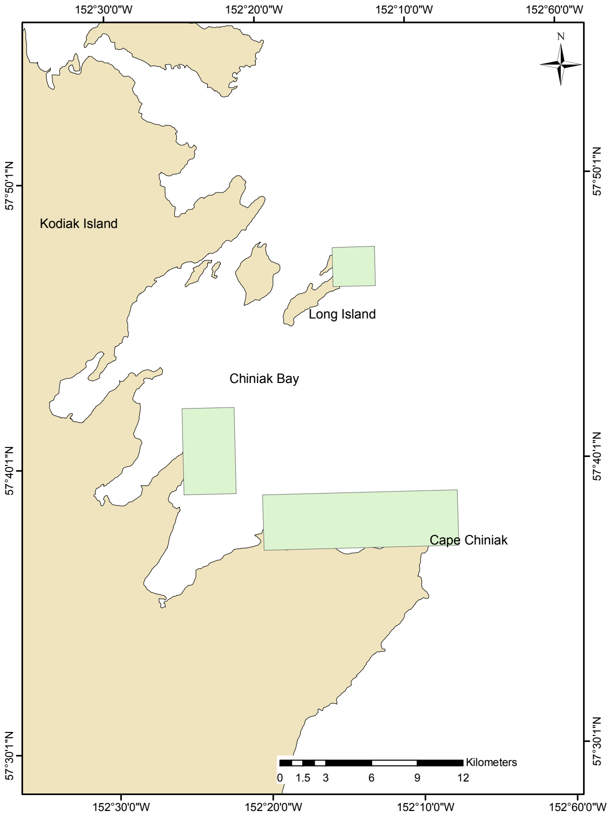


Figure 2. Nearshore areas sampled in the summer of 2002 in Chiniak Bay near Kodiak Island.

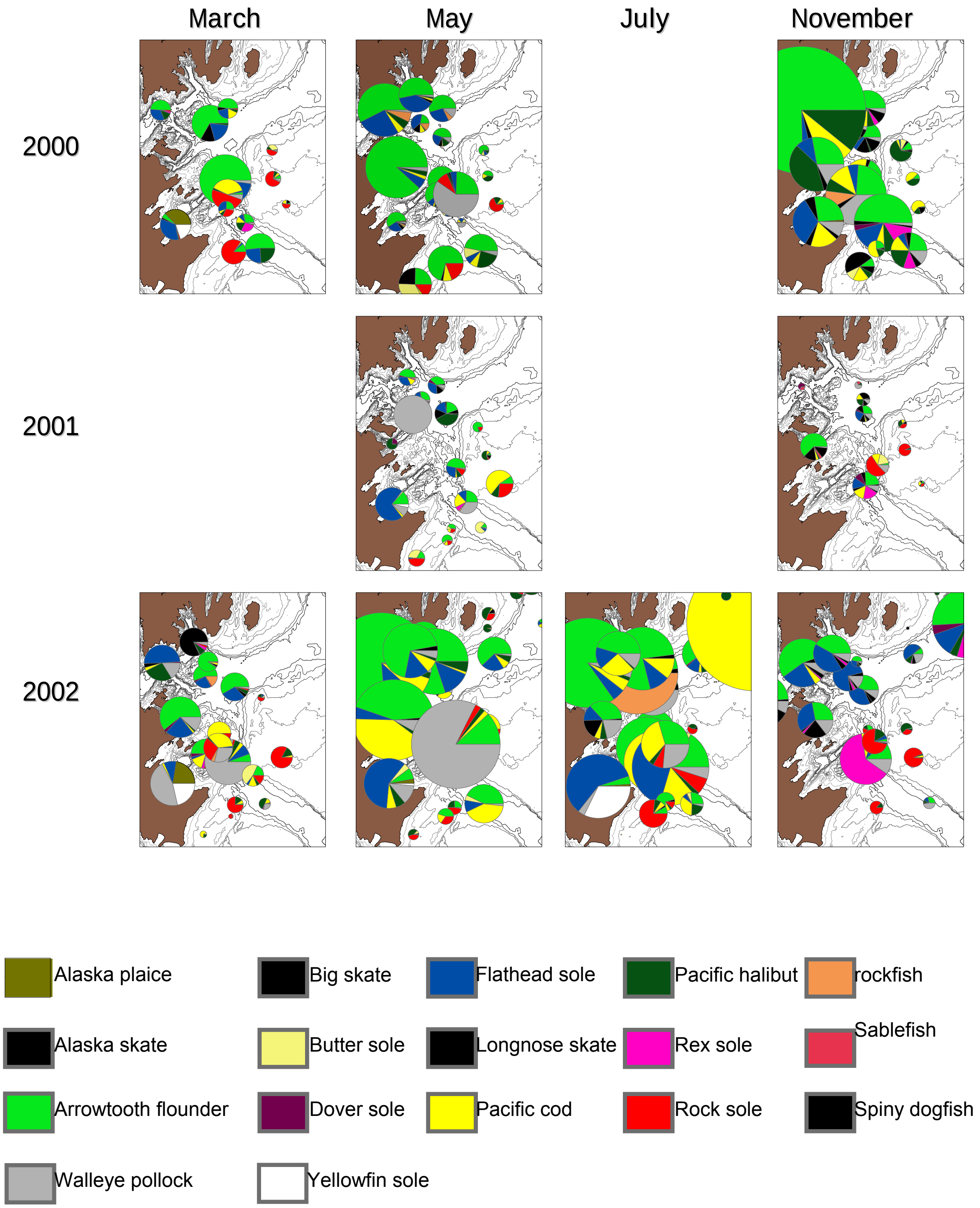


Figure 3. Catch per unit effort (kg/km) of groundfish on the northeast side of Kodiak Island 2000-2002.

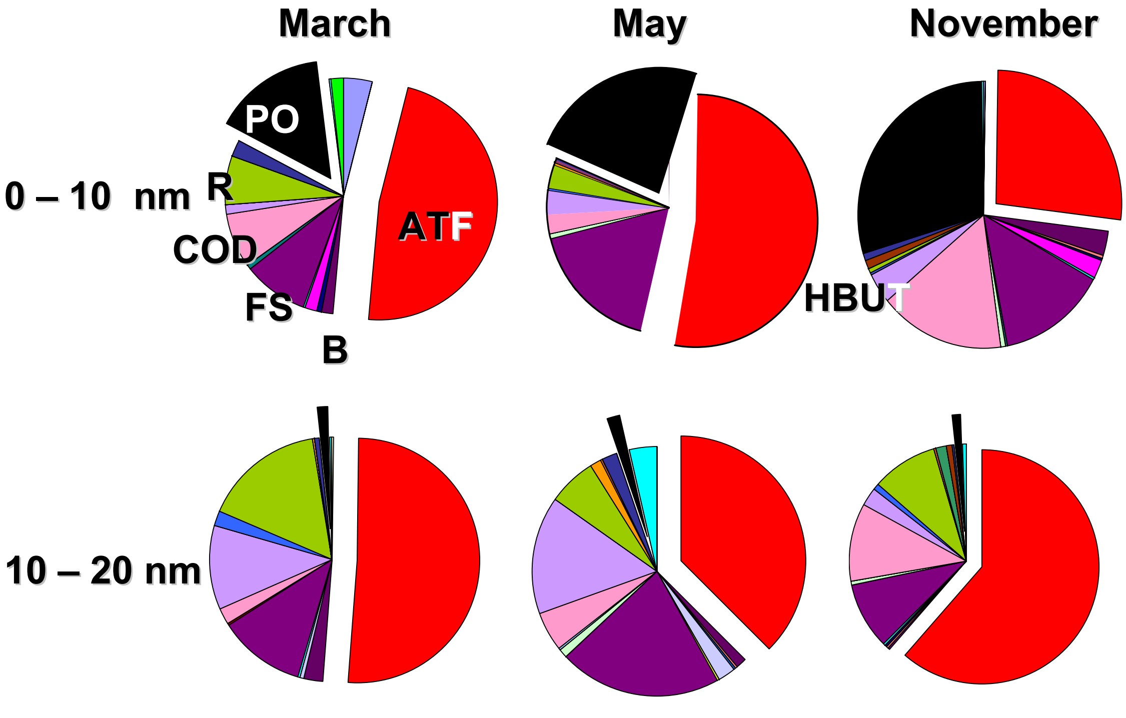


Figure 4. Average biomass of groundfish in two distance-to-shore strata in March, May and November 2000-2003.

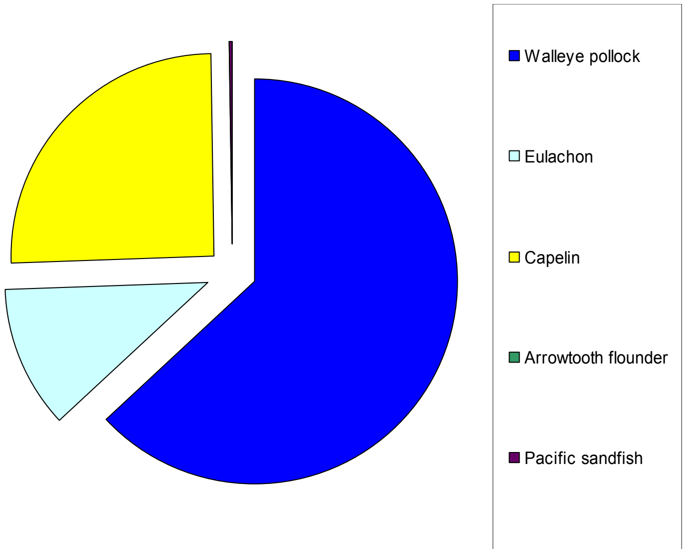


Figure 5. Average species composition of midwater trawls in the Long Island Critical Habitat area.

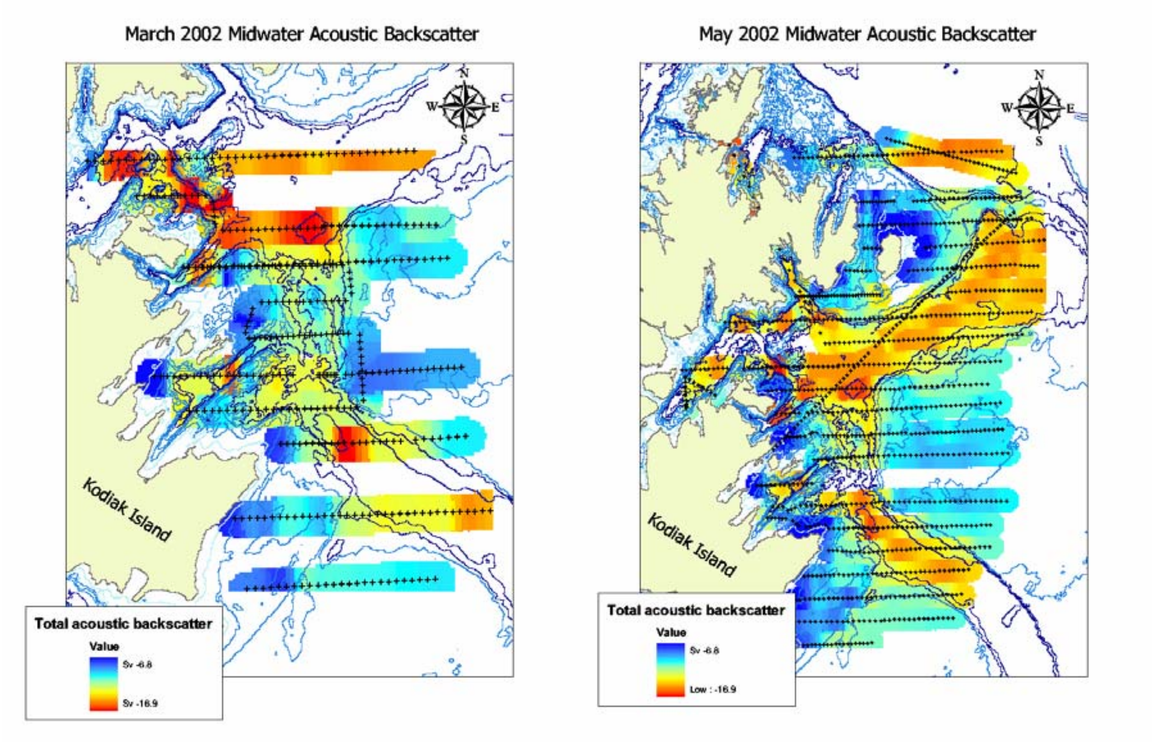


Figure 6. Pelagic fish distribution in March and May 2002 on the Northeast side of Kodiak Island.

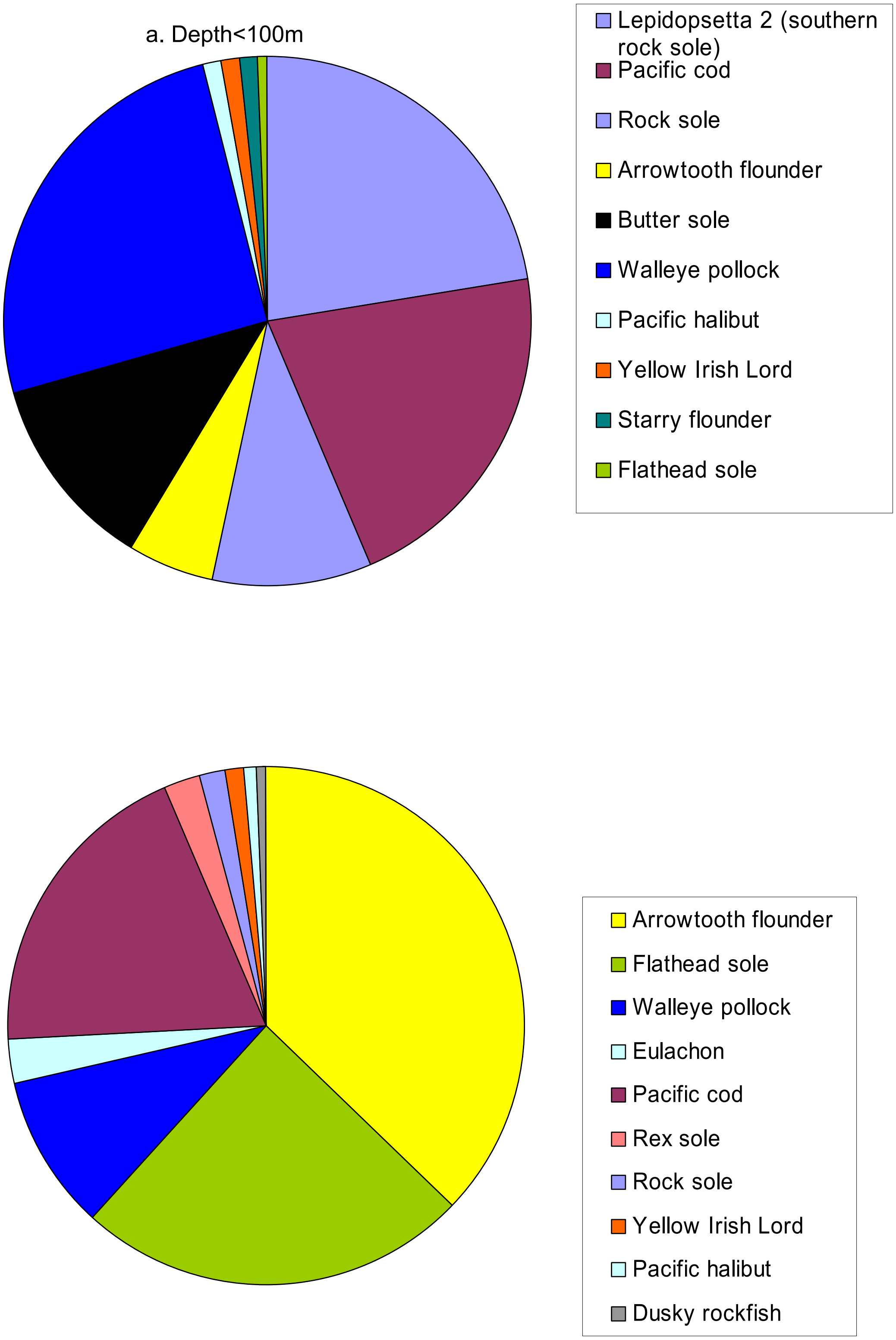
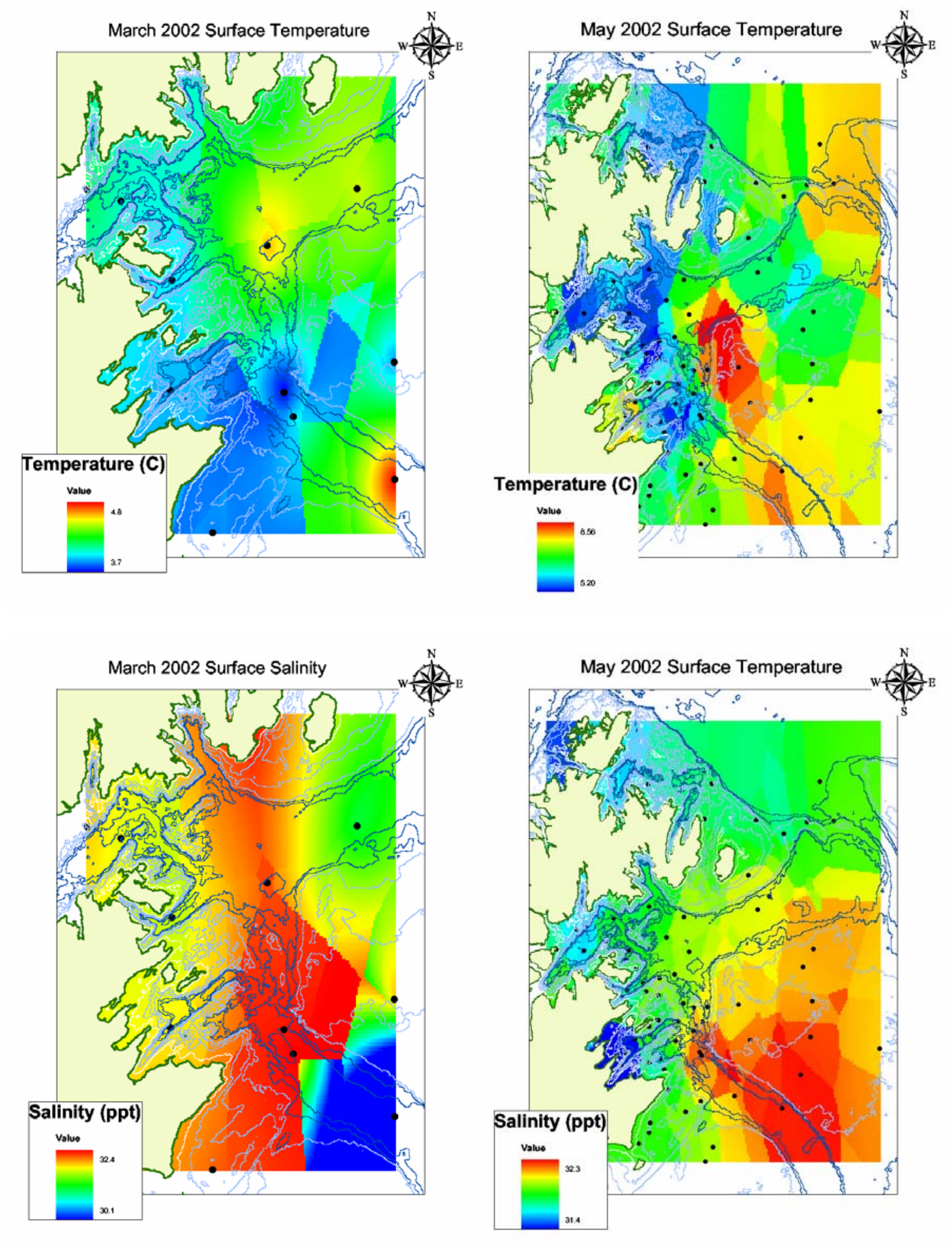


Figure 7. Biomass of fish caught within 25 nm of Long Island by depth strata between 2000 and 2003. a. Fish found shallower than 100 m. b. Fish found deeper than or equal to 100 m.



March 2002 Surface Temperature

May 2002 Surface Temperature

March 2002 Surface Salinity

May 2002 Surface Temperature

Figure 8. Surface temperature and salinity distribution across Chiniak and marmot Bays in March and May 2002.

Preliminary investigations into prey and baleen whale distribution relative to the oceanography on the north and east side of Kodiak Island (ESOK)

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Introduction

In 2001 we conducted a midsummer pelagic prey survey along the north and east side of the Kodiak Archipelago (ESOK) (Fig. 1). The survey was conducted 18-31 July 2001 and served to document pelagic prey availability more broadly than our previous surveys in the Kodiak area at a time when reproductive and energetic demands may be particularly high for local piscivorous predators. The primary goal of the extended ESOK survey was to determine if fish habitat associations found within Long Island Critical Habitat are representative of those found over a broader geographic (north-south and depth) range. Secondarily, these surveys provided a platform for documenting mid-summer associations of marine mammals with prey fields and oceanographic features along the north and east side of Kodiak. This is a preliminary report of our findings; results will be included in a more comprehensive documentation of the distribution of large whales relative to prey within the Kodiak Archipelago being prepared by the authors.

Methods

The ESOK survey utilized both acoustic and midwater trawl methodology to assess prey distribution, abundance, and species composition along the east and north side of the Kodiak Archipelago. Acoustic sampling was conducted along 37 km zigzag transects from Shuyak Island to the Trinity islands, with two lines extending 100 km to the shelf edge off Chiniak Gully (Fig. 1). The midwater trawl was deployed opportunistically as the vessel encountered pelagic fish assemblages to groundtruth hydroacoustic signals.

Throughout the survey period, oceanographic conditions were recorded at multiple locations by deploying a conductivity and temperature at depth (CTD) (Fig.1). Data collected with each CTD cast included salinity, temperature, density, and flourometry at one meter intervals from the surface to the sea floor. Differences between values were calculated for bins of 5, 10, and 15 meters for each of these parameters respectively. The depth at which the maximum change in value for each parameter was then determined.

During the survey, a dedicated marine mammal observer was stationed on top of the wheelhouse to record the species, number, and location of marine mammal observed during transects. Marine mammal observations were made during daylight hours while on transect. Sighting effort was concentrated 90 degrees to the port and starboard from the bow of the boat. For each marine mammal sighting, the vessel location, angle to the sighting, reticle count, and height of the observer off of the water were used to calculate the actual position (latitude and longitude) of animals. Sightings were separated by species for humpback, fin, killer, and gray whales. Sightings of other species or those that could not reliably be identified were binned in a category labeled "other".

Preliminary Results

The distribution of pelagic fish on the east side of Kodiak was found to be highly variable and associated with bathymetry. The highest biomass of fish was found over gullies greater than 100 m. The pelagic composition was dominated by capelin followed by eulachon and pollock (Table 1). A total of 24 species were encountered during this survey. We concluded that the relationship between fish distribution and oceanographic variables was similar on the east side of Kodiak to those encountered in the Long Island Critical Habitat (LICH) survey area. We did, however, find that larger scale physical forcing due to shelf break fronts and off-shore eddies may impact the fish distributions in our study to a large extent. These results led us to establish the Portlock Bank off shore surveys in 2003.

Marine mammal observation effort occurred for a total of nearly 77 hours over 428 nm and resulted in 92 sightings of 223 whales (Table 2, Fig. 2). Humpback whales were the most frequently sighted species, followed by gray whales. Sightings of “other” species were dominated by whales identified as *Balaenoptera spp*. and were most likely fin whales.

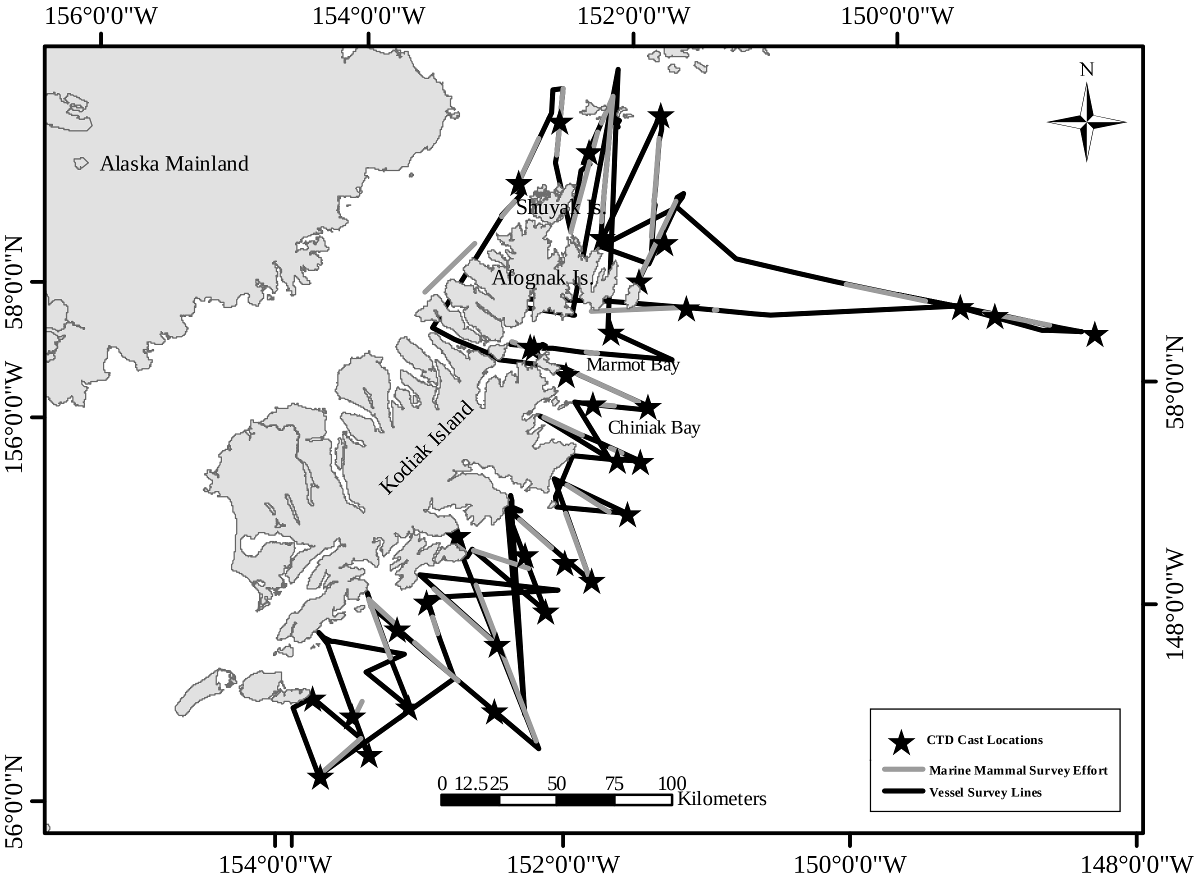
Sightings of fin and humpback whales will undergo further in-depth analysis to characterize their distribution and relative abundance in relation to prey variables and oceanographic conditions (Fig. 3). This will be accomplished by relating whale sightings to oceanographic features determined by CTD casts, including sea-surface temperature (SST), sea-surface chlorophyll concentration, and depth of thermocline, and prey type and distributions as determined by acoustic backscatter at 38 and 200 kHz. We hypothesize that fin and humpback whale sightings will be positively correlated to prey densities and oceanographic features, most strongly to chlorophyll concentration and less so to SST and depth of the thermocline. Previous GAP surveys have found these oceanographic features to influence prey distribution near Kodiak. Secondarily we hypothesize that there is a prey density ‘threshold’ below which foraging by baleen whales is unprofitable and aggregating behavior does not occur. Further, we hypothesize there will be species-specific differences between the correlations of prey and oceanographic features to humpback and fin whale distribution in this area.

Table 1. Species composition and percent abundance of pelagic fish species recorded during the ESOK cruise, July 2001.

Scientific name	Common name	Abundance (%)
Mallotus villosus	Capelin	60.1
Thaleichthys pacificus	Eulachon	25.2
Theragra chalcogramma	Walleye pollock	13.7
Myctophidae	Lanternfishes	0.3
Mysidacea	Mysidacea	0.2
Cnidaria	Jellyfish	0.1
Pandalus borealis	Pink shrimp	0.1
Teuthoidea	Squids	0.1
Oncorhynchus keta	Chum Salmon	<0.1
Oncorhynchus tshawytscha	King salmon	<0.1
Liparididae	Snailfishes	<0.1
Ammodytes hexapterus	Pacific sand lance	<0.1
Salpidae	Salp	<0.1
Atherestes stomias	Arrowtooth flounder	<0.1
Unidentified larval fish	Unidentified larval fish	<0.1
Chauliodus macouni	Pacific viperfish	<0.1
Clupea harengus pallasi	Pacific herring	<0.1
Oncorhynchus kisutch	Silver salmon	<0.1
Gadus macrocephalus	Pacific cod	<0.1
Hemitripterus bolini	Bigmouth sculpin	<0.1
Oncorhynchus gorbuscha	Pink salmon	<0.1
Trichodon trichodon	Pacific sandfish	<0.1
Zaprora sinenus	Prowfish	<0.1
Psychrolutes paradoxus	Tadpole sculpin	<0.1

Table 2. Total sightings and number of whales observed during the ESOK survey, 2001.

Scientific Name	Common Name	No. of Sightings	No.of Whales
Balaenoptera physalus	Fin	6	16
Megaptera novaeangliae	Humpback	50	100
Eschrichtus robustus	Gray	16	21
Orcinus orca	Killer	8	62
-	Other	12	24
Total		**92**	**223**


156°0'0"W
154°0'0"W
152°0'0"W
150°0'0"W
N
Alaska Mainland
Shuyak Is.
Afognak Is.
Marmot Bay
Chiniak Bay
Kodiak Island
58°0'0"N
56°0'0"N
56°0'0"N
58°0'0"N
148°0'0"W
0 12.5 25 50 75 100
Kilometers
CTD Cast Locations
Marine Mammal Survey Effort
Vessel Survey Lines
154°0'0"W
152°0'0"W
150°0'0"W
148°0'0"W

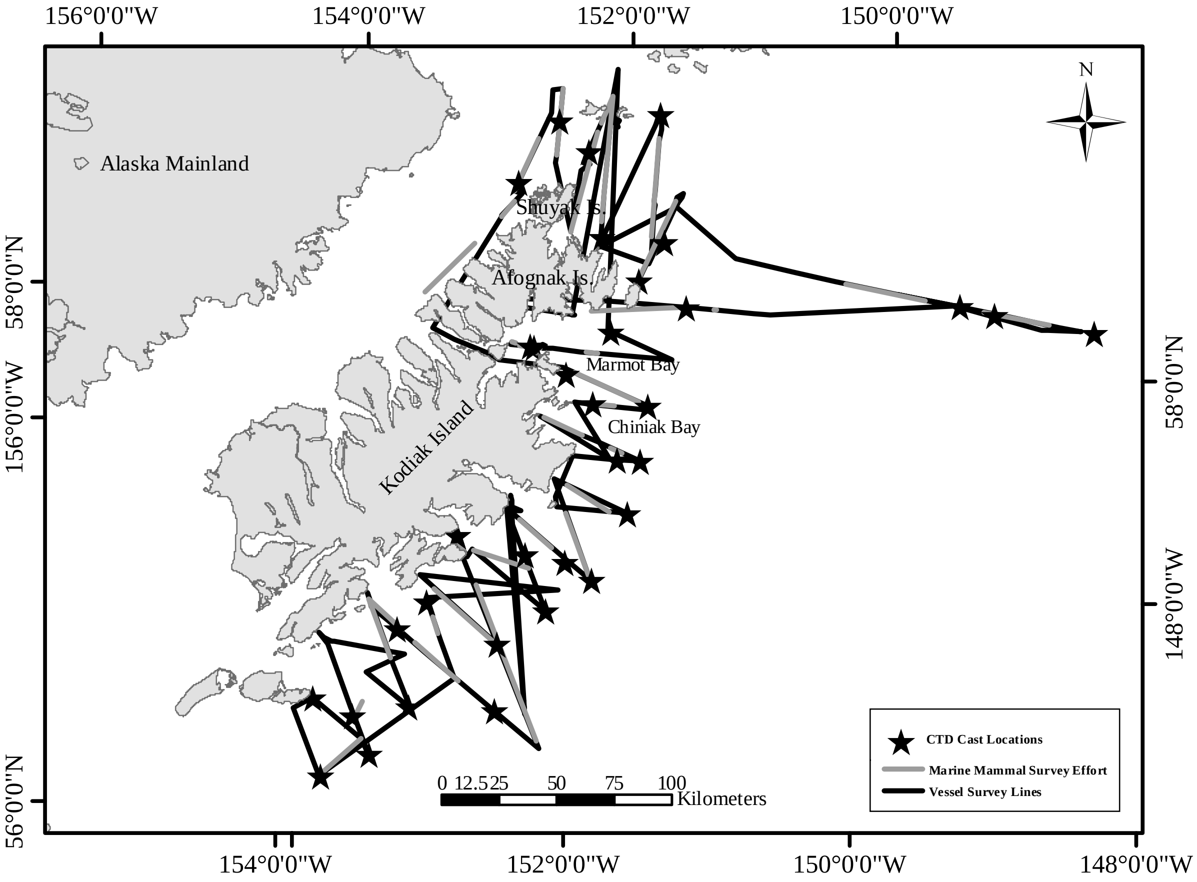


Figure 1. Map of the Kodiak Archipelago showing vessel transect lines for hydroacoustic prey surveys, marine mammal observation effort, and locations of all CTD casts.

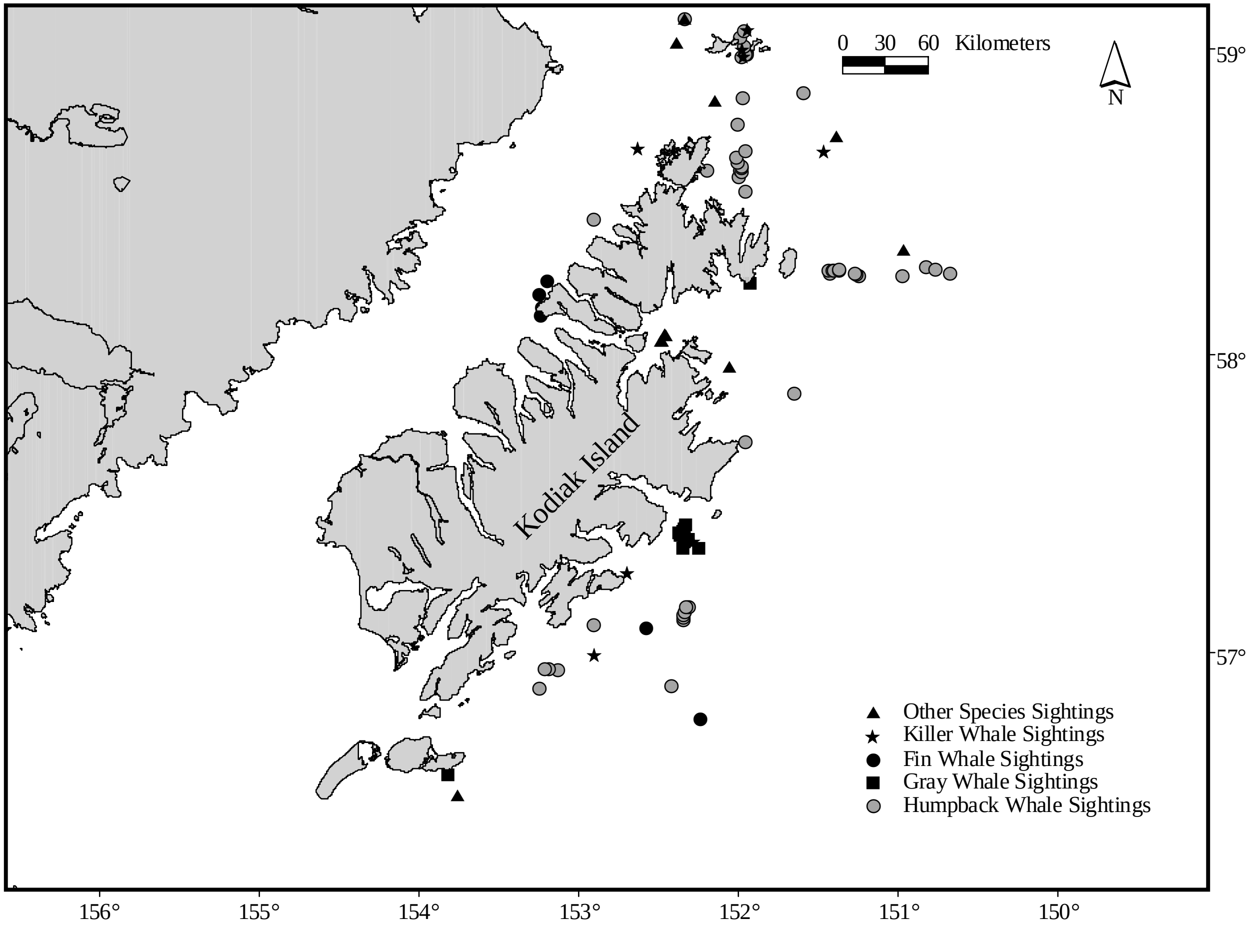


Figure 2. Map of the Kodiak Archipelago showing location of all cetacean sightings recorded during ESOK surveys.

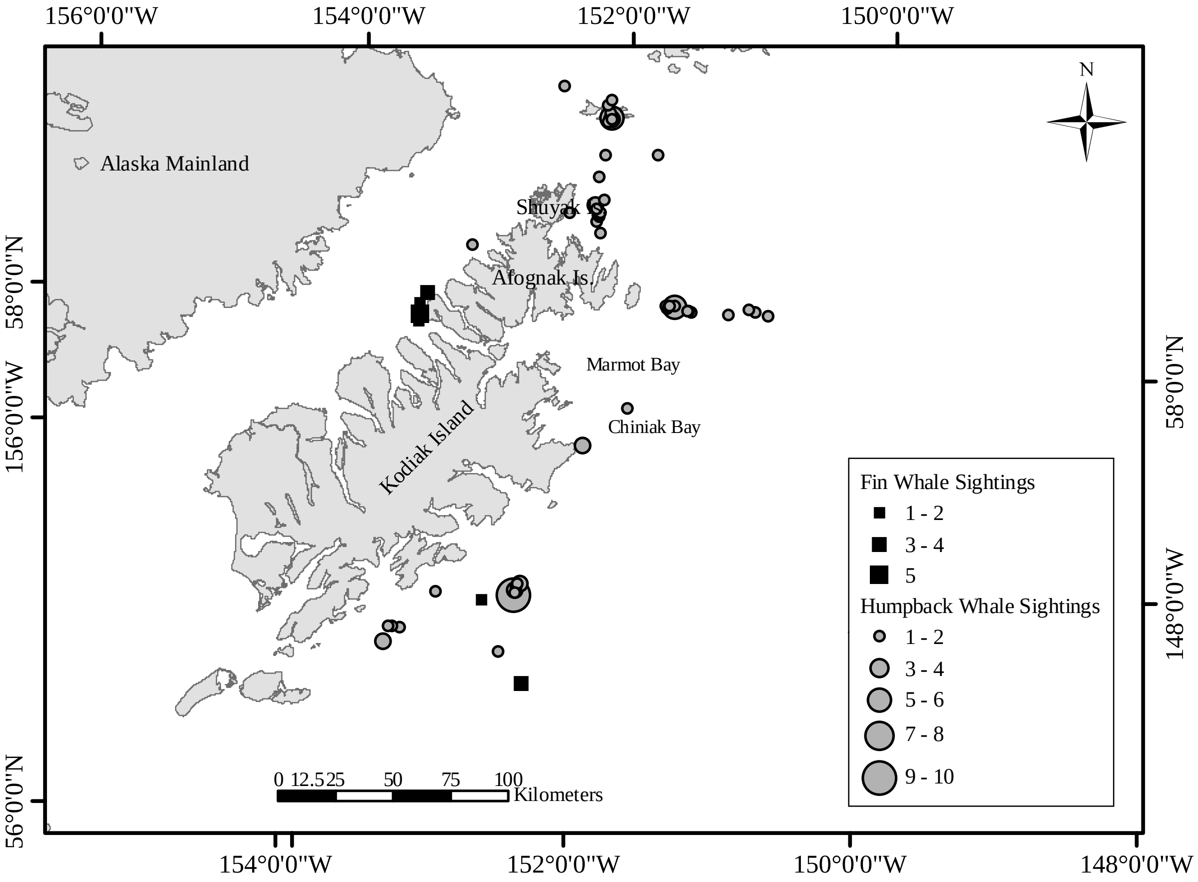


Figure 3. Map of the Kodiak Archipelago showing the location and number of humpback and fin whales sighted.

Monthly variability in fish and zooplankton distributions in Marmot and Chiniak Bays (MaCH) (2002)

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Introduction

In addition to the previous surveys in 2002, we also initiated a monthly pelagic prey survey within Marmot and Chiniak Bays (MaCh) to document pelagic prey available on a finer temporal and spatial scale within our study area (Fig. 1). The MaCh survey was run monthly from May through September 2002. To cover this area in three days, the survey was limited to hydro-acoustic and trawl surveys of mid-water prey (no bottom trawls) on transects. Data collected during this cruise were analyzed as described for the previous surveys (above) with the addition of statistical analyses to account for the multi-colinearity associated with a zigzag survey design.

Results, Evaluation and Conclusions

Seasonal trends were noted in the nearshore Marmot Bay surveys in 2002. In May and September pollock dominated the biomass of fish in this area making up 99 and 96 % of the pelagic fish present, respectively. Eulachon was significantly more abundant in June at 17% than in any other month surveyed. Capelin was most abundant in August, accounting for more than 29% of the total biomass observed along the transect. Formal results regarding the distribution of fish, zooplankton (see Zooplankton chapter) and oceanographic variables are currently being analyzed for publication.

Table 1. Species composition by month in the nearshore areas on the northeast side of Kodiak Island in 2002.

		Month				
Scientific name	Common name	May	June	July	August	September
Theragra chalcogramma	Walleye pollock	99.9	79.1	90.8	68.6	95.7
Mallotus villosus	Capelin	<0.1	1.1	0.7	29.1	0.5
Thaleichthys pacificus	Eulachon	0.1	16.6	3.8	0.4	2.0
Pandalopsis dispar	Sidestripe shrimp		0.7	3.8		
Pandalus borealis	Pink shrimp		1.0	0.3		
Liparididae	Snailfishes		0.4			
Cnidaria	Jellyfish				1.0	0.9
Trichodon trichodon	Pacific sandfish		<0.1	<0.1	0.4	0.5
Hippoglossoides elassodon	Flathead sole		0.3	0.1		
Clupea pallasi	Pacific herring				0.2	0.1
Berryteuthis magister	Majestic squid		0.2	0.1		0.1
Unidentified larval fish	Unidentified larval fish		<0.1		0.2	
Psychrolutes sigalutes	Soft sculpin				0.1	0.1
Gadus macrocephalus	Pacific cod	<0.1	0.2	0.1	<0.1	0.2
Atherestes stomias	Arrowtooth flounder		0.1	0.1		
Mysidacea	Mysidacea	<0.1		0.1		
Lycodes brevipes	Shortfin eelpout		<0.1			
Sebastes aleutianus	Rougheye rockfish		<0.1			
Liparis gibbus	Variagated snailfish				<0.1	
Podothecus acipenserinus	Sturgeon poacher				<0.1	
Lamna ditropis	Salmon shark				<0.1	<0.1
Sebastes alutus	Pacific ocean perch			<0.1		
Aptocyclus ventricosus	Smooth lumpsucker			<0.1		<0.1
Euphausiacea	Euphausiacea		<0.1		<0.1	<0.1

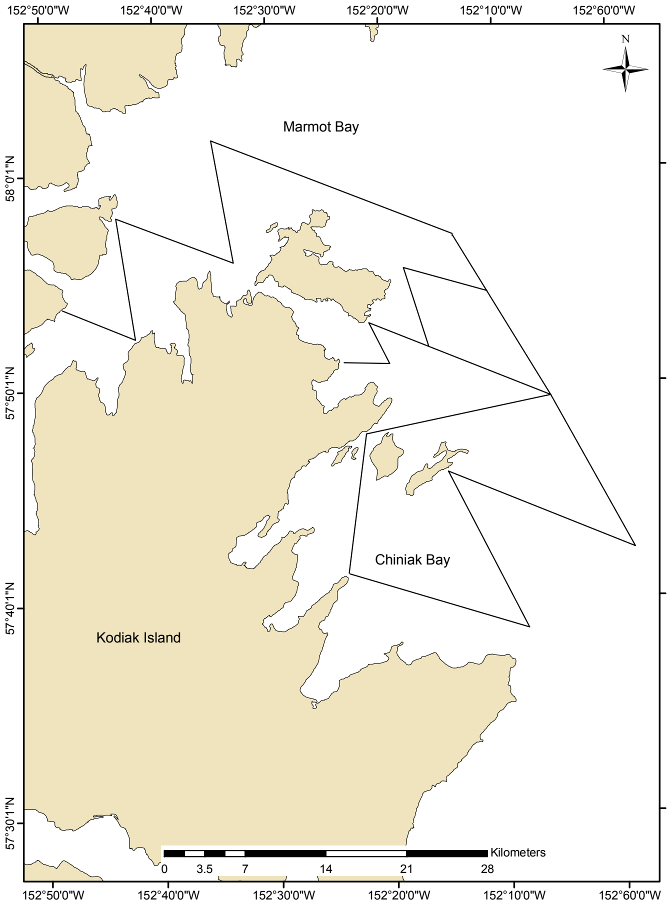

Figure 1. Marmot- Chiniak Bay (MaCh) survey lines occupied monthly in 2002 on the northeast side of Kodiak Island.

Portlock Bank fisheries oceanography (2003)

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Introduction

The productive shelf waters east of Kodiak support intensive foraging by a variety of marine birds, cetaceans, and pinnipeds (Parsons 1987, Waite et al. 1999). Recent telemetry data show that Steller sea lions tagged on haulouts within the GAP study use these waters as weanlings. To assess productivity and prey availability in this area, we modified prey surveys in 2003 to document larger scale fish distribution and related oceanographic features in shelf waters east side of Kodiak Island. In so doing, we produced a unique seasonal view of the physical oceanographic structure affecting the nearshore areas of Kodiak and the resources they support.

In May and August 2003, Portlock Banks (northeast of Kodiak) were surveyed to assess seasonal fish distribution and physical oceanographic conditions (Fig. 1). May represents “spring” conditions where productivity is at its highest and the freshwater driven Alaska coastal current is beginning to gain momentum. Conditions on Portlock Banks drive a source of production and may predict oceanographic influences on the northeast side of Kodiak. In addition, the continental shelf “break” (max depth = 500 m) was surveyed to assess pelagic fish distribution and physical oceanographic conditions in May and July. In both months, we were interested in relating the movement of off-shelf waters into near-coastal fish habitat. We related the oceanographic conditions on the outer shelf to those found closer to shore to determine predictive linkages between the two environments.

The acoustic sampling was conducted on multiple parallel east-west lines equally spaced 18.5 km apart, covering a 12,201 km^2 area over Portlock Bank. The vessel speed during all transecting was 7 knots (1000 rpms) and approximately 741 km were surveyed on each cruise. Midwater fishes were surveyed using a Simrad EK60 echo sounder attached to a 38 kHz, 12-degree split beam transducer. Echo-integration of the acoustic signal was accomplished using Echoview software that, combined with catch length and weight data, yielded estimates of fish biomass. To determine the size and species of target fishes, a small representative sample of prey was collected with a DanTrawl Bering Billionaire midwater net with a modified research cod end. The midwater trawl was deployed opportunistically when we encountered pelagic fish assemblages to ground truth the hydroacoustic signals. Tow duration was dependent on the magnitude of acoustic signal, ranging from 10 to 25 minutes. Fish species caught in the midwater tows included, in order of averaged abundance were walleye pollock, Pacific Ocean perch, capelin, myctophids, eulachon, and king salmon.

From each tow, a random sample of up to 100 fish of each species (per size category) was measured; up to 30 of these were also weighed. A sample of up to 500 fish was collected and frozen for subsequent studies of species-specific quality (proximate analyses). All large fish were dissected to determine reproductive status and stomachs will be preserved for subsequent diet analyses. Specimens that could not be positively identified to species in the field were frozen and returned to the Fisheries Industrial Technology Center in Kodiak for identification.

Results, Evaluation and Conclusions

Results from 2003 acoustic surveys suggested a correlation between areas of high fish biomass (acoustic backscatter) and oceanographic fronts. Data from 2003 and 2004 Portlock surveys are currently being analyzed together to test seasonal and interannual relationships between oceanographic variables and fish distributions.

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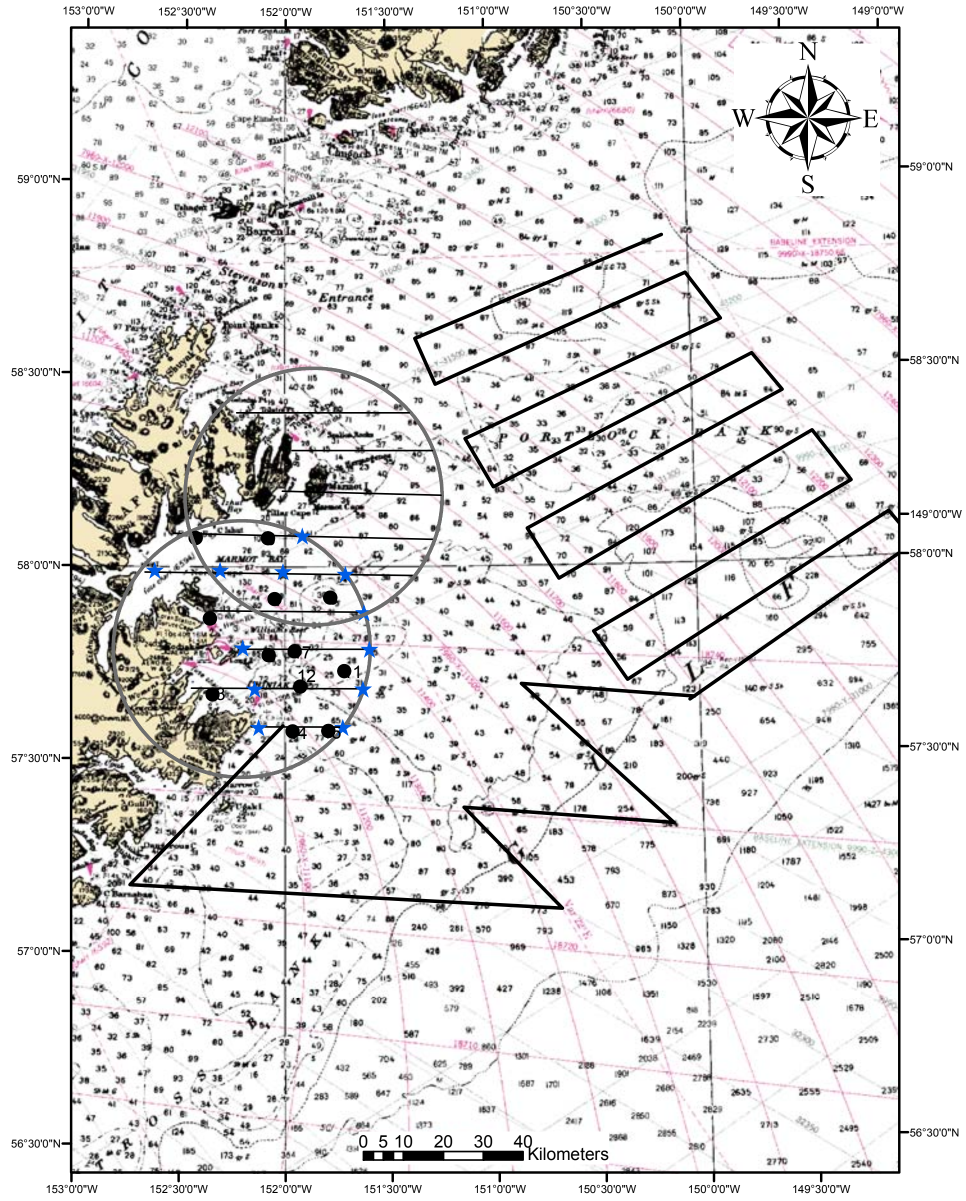

Figure 1. Portlock Bank survey areas occupied in the summer of 2003 on the northeast side of Kodiak Island.

Interannual and seasonal zooplankton community composition near Kodiak Island, Alaska

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This study is part of a M.S. thesis that is currently scheduled to be completed by May 2006. Samples for this project were collected in 2001-2003 as part of the GAP program. Zooplankton samples were collected during most oceanographic station stops from 2001-2004. While not directly linked to Steller sea lion production, data about zooplankton abundance and species composition do contribute to the understanding of the ecosystem production. Steller sea lion prey depend on the zooplankton component of the community which can dictate seasonal biomass and energy density of the prey. Arrowtooth flounder, for instance are prey of Steller sea lions and are strongly dependent on the larger zooplankton community for prey (see Piscivory chapter below). Steller sea lion competitors directly feed on zooplankton suggesting that their role in the ecosystem can not be overlooked in a discussion on Steller sea lion prey availability.

Introduction

Zooplankton are an important component of the marine environment in terms of abundance, biomass and their energy transformation role in the marine food web. They are the most abundant creatures in the ocean and although most zooplankton are small in size, some of them are microscopic. They occupy one of the largest 3-dimensional environments on the planet. Because of zooplankton's special position in the pelagic food web and their world wide distribution and abundance they are considered to be the most significant secondary producers in the ocean (Lenz 2000). Within the zooplankton community, copepods and euphausiids are the most dominant species, especially in boreal and polar regions (Lenz 2000, Irigoien et al. 2002). Key zooplankton taxa include Crustacea, Cnidaria, Chaetognatha, Polychaeta and Tunicata. Calanoid copepods and euphausiids from high latitudes have large amount of lipids, which are significant energy material that transfer from zooplankton to higher trophic levels (Sargent et al. 1981, Ohman 1997).

The ecological role of an organism is largely determined by its position and significance in the food web (Lenz 2000). Zooplankton occupy a key position in the pelagic food web as they transfer the organic energy produced by unicellular algae through photosynthesis to higher trophic levels such as pelagic fish stocks exploitable by humans (Lenz 2000). Because of the short trophic linkage and their intermediate position in the pelagic food web, zooplankton are direct indices of food web structure and carrying capacity for higher trophic level predator species (Mackas 1995). They are also of vital importance in the marine food web because most finfish and shellfish spend critical early parts of their life histories as members of the plankton community (Dunn 1979). Zooplankton are necessary for the maintenance of fish, shellfish and other living resources (Damkaer 1977).

There is positive association between recruitment of certain fish species and copepod abundance (Arnott & Ruxton 2002, Runge et al. 1999). There was a positive association between Sandeel recruitment and Calanus copepod (Stages V and VI) abundance. The seasonal timing and availability of zooplankton prey are important to upper trophic level species, especially larval fish. In Prince William Sound juvenile herring feeding in fall and winter of 1997-1998 decreased following the decline of zooplankton densities in the fall of 1997 (Foy and Norcross 2001). In Resurrection Bay, in the Northern Gulf of Alaska, fish larvae such as pollock, herring, sand lance and flathead sole depended very much on nauplii as their first-feeding food (Paul et al. 1991). To a certain extent, zooplankton species serve as an indicator of important fish habitat (Lee 1980). *Eucalanus bungii* and *Metridia pacifica* were valuable indicator species of the fishing grounds for pollock and yellowfin sole in the south eastern Bering Sea (Lee 1980).

Zooplankton communities change with the fluctuation of the environmental conditions. On large spatial and temporal scale, zooplankton distribution can be governed by water depth and temperature regime (Lenz 2000). Interannual and seasonal variations in climate can influence currents and sea temperature, which in turn impact zooplankton stocks (Coyle 1990). Physical conditions, such as ocean temperature, salinity, wind speed, stratification, thermocline depth, halocline depth, pycnocline depth, light, current, circulation, food availability and predation can all bring changes to zooplankton distribution and abundance (Coyle & Pinchuk 2003). Crustacean growth rates are known to depend strongly on water temperature (Lee et al. 2003, Tittensor et al. 2003). Thus, copepods may be a sensitive early warning of temperature increases or decreases in the ocean in response to climate changes. Because many zooplankton species are relatively short-lived and are capable of high growth rates, they respond quickly to environmental perturbations.

On a local scale, water temperature is one of the major controlling factors of copepod distribution (Lee et al. 1999). Zooplankton abundance and species composition were influenced primarily by mean sea water salinity, and secondarily by the mean water temperature above the thermocline in northern Gulf of Alaska shelf (Coyle & Pinchukn 2003). Zooplankton concentration in the water column and vertical zooplankton appeared to be affected by currents (Roman et al. 2001). Many hydrographic factors such as local wind forcing which may link with upwelling, shelf break pattern, continental shelf and topology of the coast have high correlation with zooplankton biomass, abundance and composition (Cunha 1993, Danielsen et al. 1998). In disturbed or well mixed water, zooplankton biomass tends to be relatively high (Paffenhofer 1980). Whereas, some zooplankton are consistently concentrated along the edge of continental shelf (Sabates et al. 1989). Therefore, hydrographic features may at least partially explain the zooplankton population dynamics.

Zooplankton composition, abundance, distribution and biomass have been studied and described nearly all over the world's oceans, especially in North Pacific, Atlantic Ocean and Indian Ocean (Clark et al. 2001, Bollens et al. 2002, Lindley 2002, Woodd-Walker et al. 2002, Conway et al. 2003). In the North Pacific, studies of zooplankton are mainly concerned with areas that have special physical conditions, such as the California area, Kuroshio Current area, Gulf of Alaska and Bering Sea. Zooplankton studies in these areas investigated seasonal, interannual and interdecadal zooplankton distributions, relationships between zooplankton communities and their oceanographical conditions, zooplankton growth rates and feeding ecology and zooplankton's interaction with higher trophic levels.

Gulf of Alaska environment

Climates are always changing, either on a micro- or on a mega-scale and these changes may affect the biodiversity and production in the ocean. The climate of the North Pacific is known to change sharply over periods of time, compared with climatic processes in other parts of the world. The Gulf of Alaska (GOA) climate is sub-Arctic and is sensitive to climate variations on time scales ranging from the interannual to the interdecadal (http://na.nefsc.noaa.gov/lme/text/lme2.htm). The GOA is a highly productive (>300 $gC^*m^{-2}yr^{-1}$) ecosystem as evidenced by SeaWiFS global primary productivity estimates (http://na.nefsc.noaa.gov/lme/text/lme2.htm). The cold, nutrient-rich waters support a diverse ecosystem. Large-scale atmospheric and oceanographic conditions will affect the productivity of the GOA.

Both long term and short term climate changes, in the GOA, have large influences on resident zooplankton community patterns. Regime shift is a long term shift in ocean climate. During the late 1970's, a regime shift triggered a reorganization of community structure in the GOA ecosystem. The 1977-1978 regime shift was characterized by an ocean temperature increase by 1-3 degrees ^{o}C. This regime shift led to a change in zooplankton composition in the northern North Pacific (Conners et al. 2002). In the Alaskan Gyre, the biomass of zooplankton and nekton doubled after the regime shift during the 1970s (Sugimoto & Tadokoro 1998). These regime shifts have long time effects on the ecosystems which can last 20 years or even more. A possible1990 regime shift was studied by using pacific halibut. The 1977 regime shift may have had a warming effect on the North Pacific Ocean, while a 1990 regime shift had a cooling effect on bottom seawater (Gao & Beamish 2003). The most recent regime shift happened around 1999 when ocean temperature changed from relative warmer to relative cooler (Bond et al. 2003). The effects of this most recent shift are still being investigated. Short term climate and oceanographic fluctuations can also result in zooplankton community structure changes. Ocean conditions and plankton structure vary seasonally. In 1998-2001, there was a temperature decline of the sea water, which caused the zooplankton communities from Alaska to California to yield a trend as follows: boreal calanoid copepod species showed lower abundances in the warm period while subtropical species showed higher abundance and a more northerly distribution (Batten & Welch 2004).

Currents affect nutrient availability, salinity change, and temperature conditions. Currents can also affect zooplankton communities by changing nutrient, salinity, and temperature conditions. Circulation and mixing of different currents provide zooplankton different habitats, which in turn cause zooplankton community structure variability. GOA shelf waters are characterized by two major currents: the Alaska Stream, which flows westward toward the shelf break and contains relatively cold and high saline water and the Alaska Coastal Current (ACC), which is a buoyancy driven current flowing westward within 20–50 km of the shore line (Coyle & Pinchuk 2003). The ACC is the dominant current over the inner shelf. It is forced by both wind and freshwater runoff along the coast (Vaughan 2001) so that it contains relatively warm and dilute water.

The GOA zooplankton community is dominated by a few species which account for most of the biomass and abundance. The GOA is a diverse and rich ecosystem and contains a number of important resources (Coyle & Pinchuk 2003). Over the shelf of northern GOA showed that: the large oceanic copepods such as *Calanus, Eucalanus* and *Neocalanus* are seasonal members of shelf and coastal zooplankton communities. They account for more than 25% of the net zooplankton biomass during the spring and summer months (Cooney 1986). Copepods are the most common taxonomic group. Zooplankton standing stocks vary with season at all oceanic, shelf and coastal locations. The movements of copepods over the GOA shelf have been related to seasonal shifts in vertical distributions and to a persistent pattern of onshore Ekman transport (Cooney 1988). Studies at Station P (at 50°N, 145°W) in the GOA confirmed that zooplankton biomass was highly seasonal; peaking in May and June and decreasing almost an order of magnitude from late fall to early spring (October to March). The annual cycle of zooplankton abundance and biomass on the GOA shelf during 1997–2000 showed a strong seasonal pattern.

Kodiak zooplankton

Zooplankton have not been extensively studied around Kodiak Island, Alaska. The continental shelf waters near Kodiak Island have a diverse plankton assemblage, with complex distribution patterns where the abundance of zooplankton in the fall is higher than in early spring (Dunn 1979). In the summer, cold oceanic zooplankton species were valuable indicators of the fishing grounds for pollock and yellowfin sole (Lee 1980). Zooplankton composition, abundance and disposition were analyzed to compare to higher trophic marine animals in order to assess the significance of the selected holozooplankton to the pelagic food web (Vogel & McMurray 1982). It was found that predation by the higher trophic level species, such as capelin and Atka mackerel, showed a strong relationship with the decrease in zooplankton densities.

Previous studies in the Kodiak Archipelago had addressed small scale relationships between zooplankton composition and environmental variables. No studies have been done to specifically address the seasonal and interannual variability associated with zooplankton community in relation to the dynamic environmental conditions of the region. This relationship must be better understood before variability in production and biomass of upper trophic levels can be understood. Mesoscale zooplankton studies are needed to provide a more solid foundation for high trophic level studies, i.e., fishery studies. These studies will help set up a better understanding and help build up a more sophisticated relationship of the marine food web around Kodiak Island. A broad picture of how zooplankton act under the influence their oceanographic conditions can be achieved by correlating zooplankton distribution and oceanographic conditions. The more we figure out about the relationships between zooplankton distribution and their oceanographic conditions, the better we can predict changes in zooplankton distribution and composition when we only have the oceanographic data available. It is impossible and time consuming to collect zooplankton data everywhere in the study area, while oceanographic data is easier to obtain.

Significance of this study

It is important to study the zooplankton population dynamics around Kodiak Island due to the unique oceanographic conditions of this area. This area is influenced by two major current systems; the Alaska Stream and Alaska Coastal Current. These two currents have distinctive characteristics, specifically differences in temperature, salinity and nutrient availability, which result in different habitats. Under this circumstance, zooplankton have a potential for significant production and biodiversity, which may be responsible for the successful recruitment of numerous commercial fisheries downstream. By getting valuable regional scale zooplankton data and related oceanographic data through survey sampling, we can contribute these mesoscale data to the global scale zooplankton research. We are focusing on a mesoscale zooplankton study that has not been done before: examining the seasonal and annual variations of zooplankton abundance, distribution, and composition in relationship to the oceanographic features. There are gullys, banks and bays within this large coastal area. Different topographies provides different environment for zooplankton, which in turn cause different zooplankton distribution among these topographies. Zooplankton composition and distribution data can also be used to indicate climate change, identify certain water characteristics, and predict fishery community change.

Goals

The overall goal of this project will be to assess the relationship between zooplankton distribution and environmental variables on the northeast side of Kodiak Island.

In order to accomplish the goals above, the objectives are:

1. to describe interannual zooplankton composition, distribution and abundance in Marmot Bay and Chiniak Bay near Kodiak Island from 2001 to 2004.
   H_0: We hypothesize that zooplankton composition, distribution and abundance vary interannually in Marmot Bay and Chiniak Bay near Kodiak Island.
2. to describe seasonal zooplankton composition, distribution and abundance variations in Marmot Bay and Chiniak Bay near Kodiak Island from 2001 to 2004.
   H_0: We hypothesize zooplankton composition, distribution and abundance vary seasonally in Marmot Bay and Chiniak Bay near Kodiak Island. Temperature and salinity changes may at least partly explain the difference. Zooplankton biomass will increase during spring month and decrease during winter month.
3. to assess the across shelf (from shore to the shelf break) distribution of zooplankton in 2003- 2004
   H_0: We hypothesize there are differences in zooplankton composition, distribution and abundance between inshore and offshore areas. Nearshore zooplankton community will be dominated by relatively smaller copepods; offshore zooplankton community will be dominated by relatively larger copepods.
4. to correlate zooplankton distribution with environmental variability using temperature and salinity data.
   H_0: We hypothesize that temperature and salinity changes may at least partly explain the differences in zooplankton composition, distribution and abundance.

Methods

Study time and area

Zooplankton samples from Marmot Bay and Chiniak Bay around Kodiak Island were collected in March, May, August, and November from 2001 to 2004. In March, the ocean temperatures are the coldest and copepods move up towards the surface to release eggs. In May, the ocean is highly productive after the peak of phytoplankton bloom, and certain zooplankton species increase with the adequate food. In August, the water temperatures are the warmest of the year and it has fewer nutrients than in May. Also, the water column is highly stratified due to the lack of mixing by winds. In November, copepods move down in the water column to over winter. Some of the copepods will stay at resting stages in order to stay alive (Baier & Napp 2003, Kobari et al. 2003, Napp et al. 2002).

Zooplankton samples collection

A 1 m diameter, 130 um mesh size ring net was deployed at multiple stations to collect zooplankton specimens. The sampling stations were systematically distributed in the sampling area. The ring net was lowered to a depth of 25 m. This depth was chosen based on the maximum depth of the acoustic scattering layer. In most cases, the thickest layer of zooplankton is from 25 m to the surface. The ring net was lowered 0.5 m*s^{-1} through the water column. A General Oceanics flowmeter will be used with the ring net to calculate the amount of water filtered through the net. The flowmeter is centered in the center of the ring diameter where the flow properties are good. The amount of filtered water (m^3) = flowmeter revolutions* calibration factor*net opening area (m^2) (Sameoto et al. 2000, Coyle & Pinchuk 2003). Zooplankton samples will be preserved on board immediately in 10% buffered formaldehyde. In 2004, we also used rose bengal to dye the zooplankton samples for microscope identification in the laboratory.

Sampling stations

In 2001 and 2002 samples were collected in 24 stations in inshore areas of the Marmot and Chiniak Bays. In 2003 and 2004 samples were collected both in inshore area and offshore stations on the Portlock bank area. All the stations are evenly distributed within the sampling area.

Zooplankton samples analysis

In the microscope laboratory, all the zooplankton samples will be identified to species level. Each sample is poured into a sorting tray and large animals will be counted and removed before splitting the samples. Sub-samples split with a Folsom splitter will be enumerated and identified to the lowest possible taxonomic group and life stage. The number of splits will be determined after approximately 100 individuals of the dominant species remained. After analyzing the smallest fraction of sub-sample, we will go through all other sub-samples from small fraction to large fraction until we get a good description of the whole sample (Coyle & Pinchuk 2003). Zooplankton catches will be standardized to number per 1 m^3 of water after sub-sample analysis.

CTD and TSG

Sea surface temperature and sea surface salinity were collected using a continual data collecting SeaBird 45 thermosalinograph (TSG) attached to the hull of the survey vessel. Temperature and salinity from the entire water column was collected using a SeaBird19 CTD (conductivity and temperature at depth). The CTD was sent down from the surface to bottom at a speed of 0.5 m*s^{-1}. The data series was processed using SBEDataProcessing-Win32 software (Domack et al. 1992). T-S plot will be done using the data collected by CTD in order to determine the thermocline depth. Gray and Kingsford (2003) define the thermocline as a >0.5^{0}C change in temperature in 1 m depth interval. Coyle and Pinchuk (2002) define the depth of the thermocline where dT/dZ was maximum. We will use the latter definition to determine the thermocline because by using the formal method, we might pick up a wrong thermocline if there are more than one temperature changes >0.5^{0}C. T-D and S-D graphs will also be done.

Statistical analysis

To get an overall impression of zooplankton community structure in relation to the environmental variable, multi-dimensional scaling (MDS) will be used. Cluster analysis might be used to analyze the nearshore-offshore zooplankton comparisons (Magadza 1994). The main spirit of this method is to use species as an indicator to group my stations: try to find out similarity and dissimilarity among stations. Statistical software Statistica will be used.

Results, Evaluation and Conclusions

Analyses for this project are continuing with expected publications in the Fall of 2005. The species composition encountered during the study is:

Most dominant small copepods: *Oithona similis*, *Pseudocalanus spp.*, *Acartia longiremis*, copepod nauplii

Most dominant large copepods: *Calanus marshallae*, *Eucalanus bungii*, *Neocalanus spp*.

Other zooplankton: Oikopleura, Fritillaria, Sagitta, crab zoea, euphausiids.

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Proximate composition (energetic value) of important Steller sea lion prey (2000-2002)

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Introduction

The importance of seasonal, spatial and ontogenetic variability in the energetic content of sea lion prey species has been noted but not well studied. In particular, marked species-specific seasonal and size variation in energy density has been observed in fish preyed on by seabirds and marine mammals (Hislop et al. 1991, Martensson et al. 1996). Knowledge of seasonal energetic differences is important to understanding the food requirements of Steller sea lions. It is expected that the energy density of fishes is highest in the fall and lowest prior to increases in spring plankton assemblages. Therefore, fish samples were collected in the fall near the potential maximum energy density and in early March when the accumulated effects of low food availability during the winter could be monitored. It is also expected that increased biomass of zooplankton and variability in production affects fish energy density from May - September.

This study targeted demersal and pelagic fishes within the foraging range of Steller sea lion haulouts. Several demersal fish species are both prey of sea lions and targets of important commercial groundfish fisheries in Alaskan waters (walleye pollock, Pacific cod, flatfishes etc.). Knowledge of the quality of prey around Steller sea lion haulouts will allow us to understand the relative importance of particular prey that are also key commercial fisheries so that the importance of protected Steller sea lion habitat can be evaluated.

The goal of this project was to determine the quality of fish species with the following objectives:

1. Quantify the quality of pelagic and ground fishes around Steller sea lion haulouts.
2. Estimate energetic availability of key Steller sea lion prey species around haulout areas based on biomass and energetic composition of fish species.
3. Compare seasonal quality of multiple commercially important fish species.
4. Make ontogenetic comparisons of the quality of multiple commercially important fish species.
5. Spatial and temporal comparisons of overall energetic densities of the fish community around the eastern side of Kodiak Island.

Pelagic and demersal fish were collected on the east side of Kodiak Island, Alaska. Multiple fish species were collected around the Long Island Steller sea lion haulout on the southeast side of Kodiak Island in March, May, and November 2001 and March, May, June, July, August, September 2002. Fish were collected from the 10 nm closure area and the 10 – 20 nm zone around the Long Island haulout on the northeast side of Kodiak Island. Samples were measured (SL), weighed and frozen whole upon collection and kept until proximate analyses could be done. Temperature data was also collected so that fish quality can be compared to physical attributes of the local environment.

Approximately 1000 samples have been analyzed from an even distribution of species and size classes stratified by depth and distance to shore. Multiple fish were used at once for the smallest fish collected. Each fish was ground in a Butcher Boy commercial grinder with a 1.25 cm grinding plate followed by a Hobart grinder with a 0.4 cm grinding plate. Carbohydrates were not included because of their negligible amounts in fishes.

Lipid was extracted using the Supercritical Fluid Extraction method in a LECO FA-100 Fat Analyzer. One to 3 g aliquots of homogenate were analyzed in triplicate. Total lipid content of the sample will then be used to extrapolate, by direct proportion, the total lipid content of the fish. Water content was determined by isolating two 15 to 30 mg duplicate aliquots of homogenate in separate ceramic crucibles. The crucibles were placed in a 102°C oven, dried until the contents attained constant weight (approximately 24 h), and reweighed. Dry weight was subtracted from wet weight to determine the water content, which was then reported as a percentage of wet weight. Protein content was determined with a Leco FP-2000 Nitrogen Analyzer. Protein was then estimated by multiplying percent nitrogen by a factor of 6.25 (Dowgiallo 1975). Ash content was determined by combusting duplicate 3 g aliquots of each homogenate in a muffle furnace at 510°C until constant weight is attained. Samples were reweighed and ash content reported as a percentage of wet weight.

Results, Evaluation and Conclusions

The proximate composition of fish around the Long Island Steller sea lion haulout differed seasonally and annually. Lipid values ranged from 0.95 to 4.7 percent in May and from 1.9 to 11.6 percent in November over 30 fish species. Moisture ranged from 76.5 to 80.7 percent in May and 69.6 to 79.5 percent in November. Protein ranged from 13.9 to 21.0 percent in May to 14.9 to 17.7 percent in November. Ash ranged from 1.5 to 3.6 percent in both May and November. Data for this report include commercial fish species important to the diet of Steller sea lions (walleye pollock, Pacific cod, arrowtooth flounder, rock sole, and flathead sole). Between 25 and 59 samples of each species were run each season. The mean lengths and weights of fish used for analyses varied among seasons each year (Table 1). Proximate composition values are reported for March, May and November to show seasonal variability in energy density among the most important commercial fish species in the Steller sea lion diets (Table 2). Pacific cod, walleye pollock and rock sole have highest lipid contents in the fall and vary by 2 percent over the season. Arrowtooth flounder and flathead sole have highest lipid content in the spring. These differences may be due to life history variability or due to size class bias in the sampling. The seasonal variability in lipid content of walleye pollock varied significantly among seasons and between years (Fig. 1). Data from 2000 – 2002 show that pollock gain as much as eight percent lipid content between May and November. Average values of lipid content appear to also be greater in 2002 than in similar months in 2000 and 2001.

The seasonal amount of lipid available averaged across all pelagic and demersal species important to the diet of Steller sea lions varies spatially in Marmot and Chiniak Bays. During March 2002, the highest density of lipid was isolated to the area nearest Kodiak City. In both May and in November the area where the highest amount of lipid is available extends to the entire nearshore region. It is interesting to note that in July, the distribution shifted to an area in northern Marmot Bay and a very high amount of lipid was available farther offshore. This was attributed to large biomass of capelin that came closer to shore with increased water temperature in July 2002. July also represents the month with the highest lipid available in most years (Fig. 4). This seasonal phenomenon caused us to increase our sampling efforts in the area of Portlock Banks in 2003 and 2004.

The interannual variability in lipid available in any given month is also large. The amount of lipid available in May of 2001 was larger than in 2000 or 2002 (Fig. 3). Also, the distribution of higher lipid fish species was more spread out over the entire nearshore area in May 2001 and 2002 than in 2000.

While the seasonal and annual variability in lipid content of Steller sea lions is high, the relative lipid content among species remains similar (Fig. 5). Spiny dogfish, eulachon, arrowtooth flounder, starry flounder and capelin continually dominate the highest lipid content diets. It should be noted that sandlance was not adequately sampled in this study and make a large portion of the Sea lion diet and has relatively higher lipid content. Also species such as salmon have a high lipid content and are important in the diet but occur seasonally.

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Table 1. Count, average length and weight of commercial species used for current analyses.

March

	count	mean length (cm)	mean weight (g)
Pacific cod	25	42.00	1131.71
Arrowtooth flounder	25	59.00	1687.50
Flathead sole	25	31.20	270.10
Rock sole	25	38.86	815.71

May

Pacific cod	25	47.14	1215.38
Walleye pollock	25	31.17	374.15
Arrowtooth flounder	25	38.19	657.02
Flathead sole	25	27.68	232.67
Rock sole	25	34.17	278.01

November

Pacific cod	40	61.83	2066.69
Walleye pollock	59	25.11	352.82
Arrowtooth flounder	24	43.99	1024.97
Flathead sole	34	14.51	74.99
Rock sole	15	38.60	770.00

Table 2. Seasonal proximate composition of commercial fish species.

	Lipid		Protein		Water		Ash	
	mean	SD	mean	SD	mean	SD	mean	SD
Pacific cod	1.23	1.8	14.78	3.0	82.09	1.9	1.92	0.3
Arrowtooth flounder	9.18	4.6	14.52	0.9	73.92	5.8	1.77	0.2
Flathead sole	3.38	2.4	13.21	2.0	79.66	1.5	2.45	1.1
Rock sole	1.62	2.1	14.97	1.7	80.27	2.8	2.07	0.2
May								
Pacific cod	1.08	0.9	14.97	1.4	81.10	1.1	1.80	0.3
Walleye pollock	1.86	0.6	14.88	1.5	80.53	1.0	1.80	0.5
Arrowtooth flounder	2.40	1.4	15.67	2.1	79.38	1.5	1.55	0.2
Flathead sole	2.09	1.0	13.75	0.6	79.95	1.8	1.90	0.5
Rock sole	2.49	1.6	16.50	2.3	78.30	2.2	1.90	0.3
November								
Pacific cod	2.56	1.7	15.96	1.1	79.66	2.0	1.72	0.2
Walleye pollock	3.36	1.7	15.62	0.7	78.66	1.8	2.02	0.4
Arrowtooth flounder	5.15	2.3	16.49	1.3	76.06	2.7	1.59	0.2
Flathead sole	1.33	1.6	15.48	0.6	80.28	1.77	2.57	0.5
Rock sole	3.25	1.6	15.92	2.4	78.26	2.1	1.73	0.3

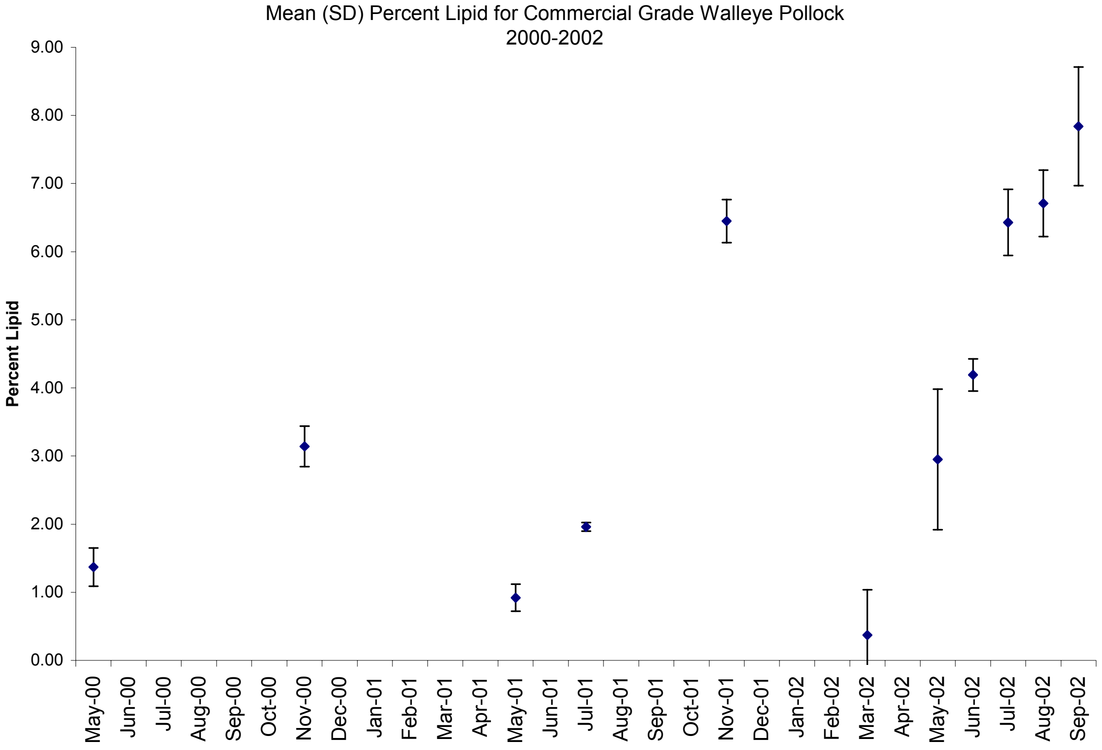
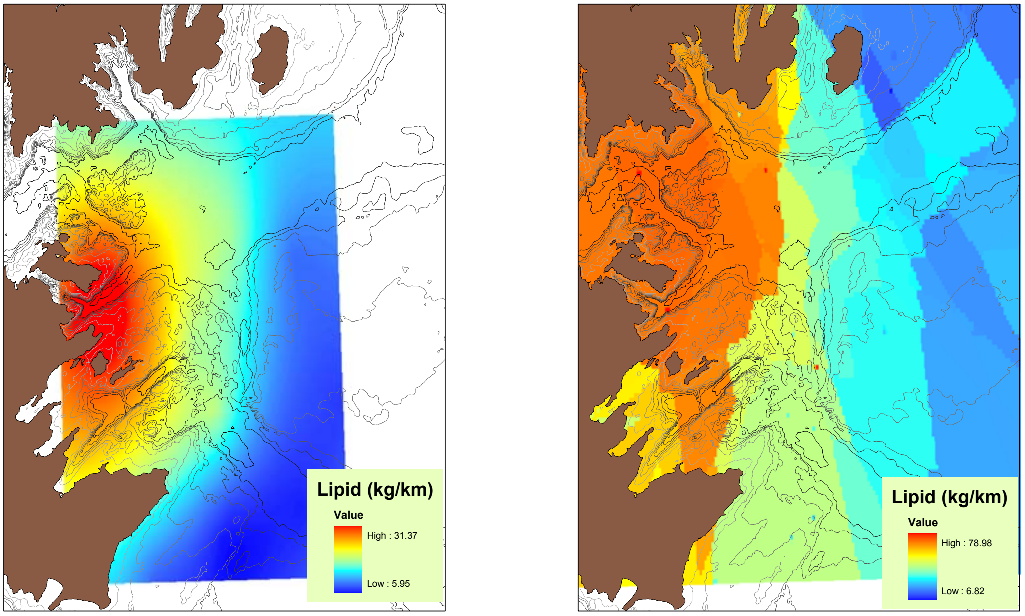
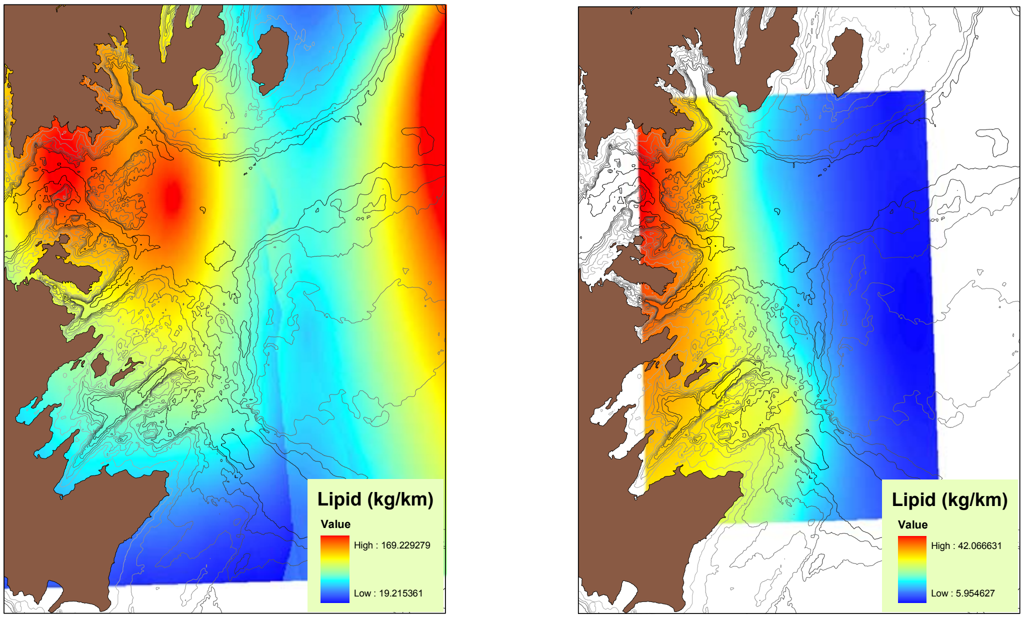


Figure 1. Seasonal and interannual trends in commercial grade walleye pollock lipid content



March

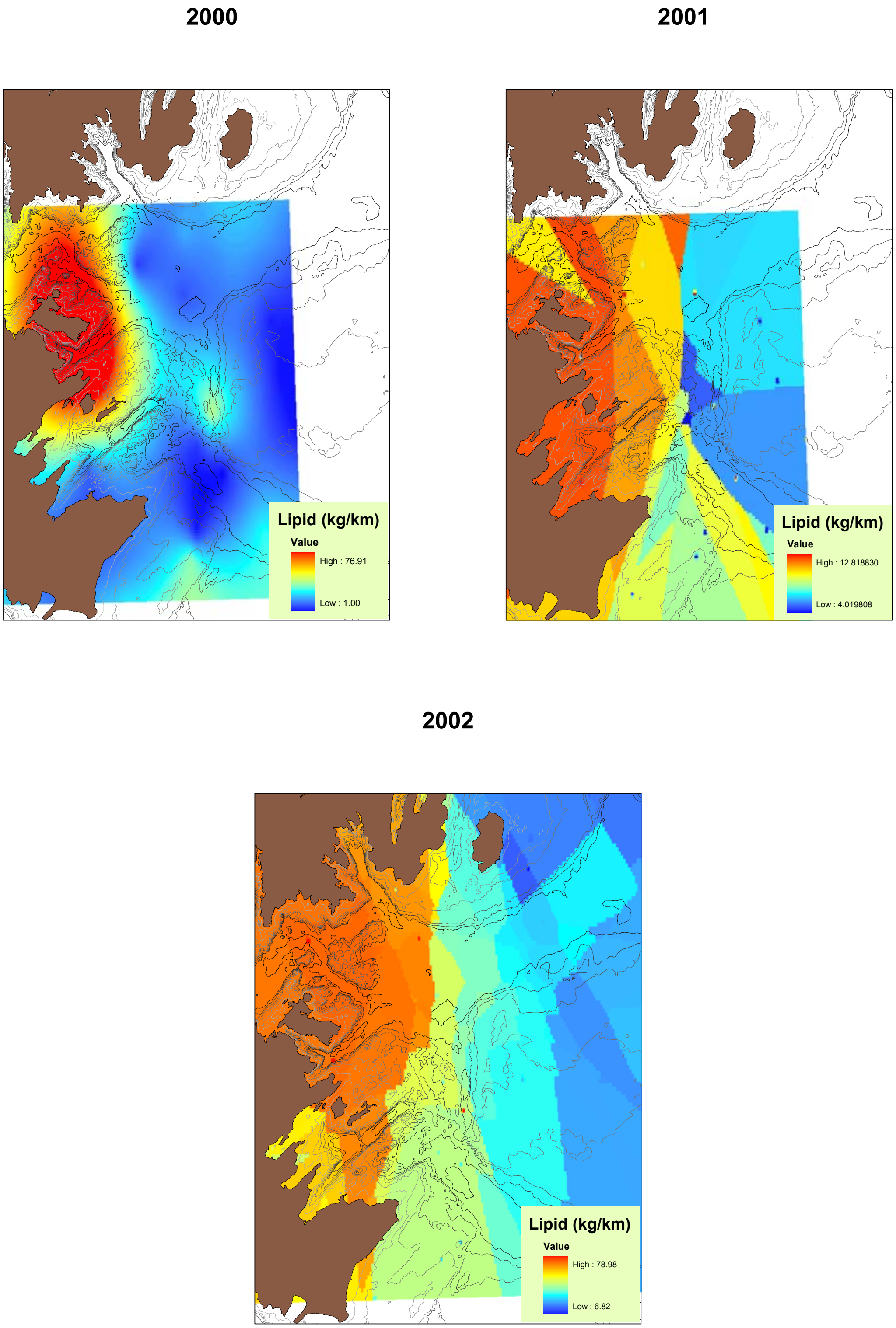
May



July

November

Figure 2. Seasonal distribution of lipid biomass in Chiniak and Marmot Bay in 2002.



2000

2001

2002

Figure 3. Interannual distribution of lipid biomass in Chiniak and Marmot Bay in May 200-2002.

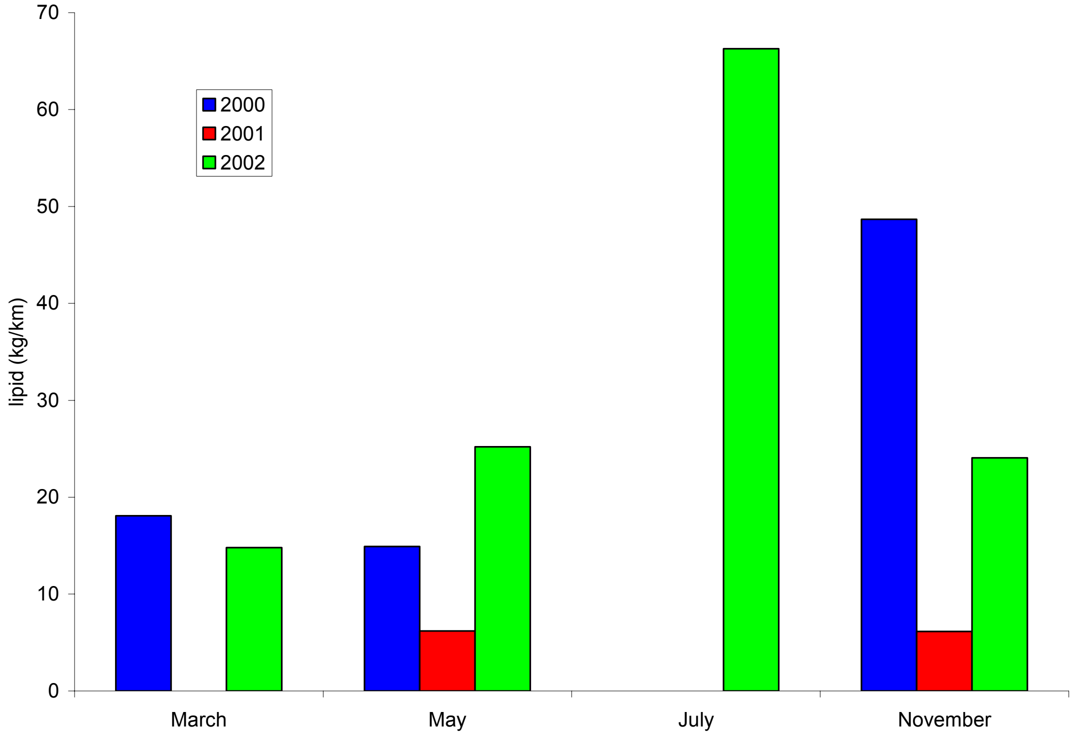


Figure 4. Average lipid content in the demersal fish community on the northeast side of Kodiak Island.

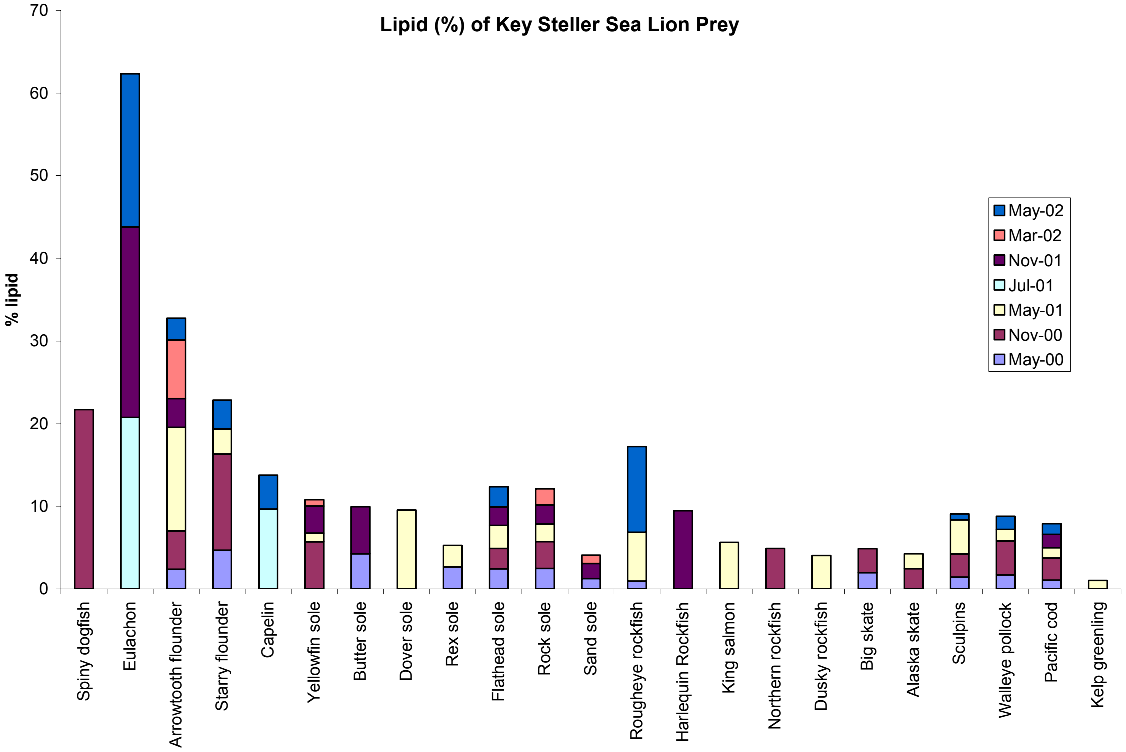


Figure 5. Average lipid content of Steller sea lion prey 2000-2002.

Fatty Acid Analysis of Fish collected within Steller sea Critical Habitat, Kodiak, AK

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Introduction

Much of our knowledge regarding diets of marine birds and mammals comes from fecal (scat) and stomach content analyses. Scat and stomach content analyses are useful for qualitatively assessing most of the diet items but have limitations that may bias the quantification of actual diets of the marine mammal. Limitations include variable digestion of particular prey species hard parts and undetermined species-specific passage rates. Scats also represent prey consumed during an unknown number of foraging bouts to unknown areas. Therefore, alternative methods have been sought to better quantify the diets of marine mammals.

The analysis of fatty acid signatures has been used to identify and quantify the diets of pinnipeds and cetaceans (Aguilar and Borrell 1990, Borabia, et al 1994, Iverson et al 1997). Fatty acids represent a large portion of the lipid component of fish consumed by birds and mammals and are often conserved in fat or blubber following metabolism. Therefore, fatty acid signature analysis represents a tool for determining the origin of ingested food and a quantitative way of assessing prey items important to the diet of marine birds and mammals. In order to analyze fatty acids present in these consumers however, it is first necessary to identify the fatty acid signatures within the prey species they consume.

In 2003, we initiated a project to determine the fatty acid signatures of pelagic and ground fish species collected within the Long, Chiniak, and Marmot Island Steller sea lion critical habitats. From a representative sample of these fish we quantified fatty acid methyl esters using protocols for lipid extraction and fatty acid assessment proven effective in other labs assessing pinniped prey. We will document seasonal and species-specific variability in fatty acids found in fish near Kodiak Island. These data will be critical to subsequent studies involving GAP collections of seabird fat and harbor seal blubber.

The goal of this project was to determine the fatty acid signatures of fish species collected within the Long, Chiniak, and Marmot Island Steller sea lion critical habitats (Table 1) with the following objectives for 2004:

1. Collect pelagic and ground fishes within the Long, Chiniak, and Marmot Island Steller sea lion critical habitats.
2. Determine protocol for lipid extraction and fatty acid assessment
3. Quantify fatty acid methyl esters from a representative sample of fish.

The following methodologies were used for fatty acid extractions:

Methods

Fat Extraction

Lipids were extracted from samples using an accelerated solvent extractor ASE 200 (Dionex). The solvent system used to extract lipids was 2:1 chloroform/methanol (Folch solvent system). Lipids were continuously extracted under nitrogen at 70°C over 15 minutes. After extraction solvents were removed under nitrogen stream on a TurboVap LV ASE Compatible (Zymark).

Fatty acids profile

Fatty acids methyl esters were prepared according to Maxwell and Marmer (1983), and analyzed on a gas chromatographer equipped with a flame ionization detector (FID) GC6850 (Agilent Technologies). Samples were analyzed in duplicate.

Lipid classes

Lipid classes were determined by planar chromatography on an Iatroscan TLC/FID MK-6s (Iatron Laboratories). Calibration curves of the following lipid classes were determined using appropriate standards: wax esters, free fatty acids, triglycerides, sterols, partial glycerides and phospholipids. Lipid classes were quantified after a two-step development system using first a mixture of hexane:diethyl ether:formic acid (99:1:0.1 and) with partial scanning of the rods, and then a mixture of hexane:diethylether (85:15) for elution of the polar lipid classes (Parrish and Ackman, 1983; Parrish, 1987).

Results, Evaluation and Conclusions

Calibration curves for approximately 25 fatty acids were determined and fatty acids quantified (Table 1). Fatty acid signatures from 35 species of pelagic and groundfish have been analyzed (Table 2). Data from 2004 will be added to assess seasonal and interannual variability in the signatures present for each species.

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Table 1. The fatty acids selected for and quantified in 2003 samples

C10:0
C12:0
C13:0
iso-C14:0
C14:0
C14:1n5
iso-C15:0
anteiso-C15:0
C15:0
iso-C16:0
C16:0
C16:1n9
C16:1n7
iso-C17:0
anteiso-C17:0
C16:2n4
C17:0
C16:3n4
C17:1n9
C16:4n3
C16:4n1
C18:0
C18:1n9 c,t
C18:1n7
C18:1n5
C18:2n6 c
C18:2n6 t
C18:3n6
C18:3n4
C18:3n3
C18:4n3
c19:0
C20:0
C20:1n11
C20:1n9
C20:1n7
C20:1n5
C20:2n6
C20:3n6
C20:4n6
C20:3n3
C20:4n3
C20:5n3
C22:0
C22:1n11
C22:1n9
C22:1n7
C22:2n6
C21:5n3
C22:4n6
C22:5n6
C22:3n3
C22:4n3
C24:0
C22:5n3
C22:6n3
C24:1n

Table 2. Species common names and total count used for fatty acid analysis in 2003.

Species	Total
AK Plaice	10
Arrowtooth Flounder	25
BigmouthSculpin	5
Buttersole	5
DasycottusSculpin	5
DoverSole	5
EnglishSole	5
Eulachon	25
Flathead Sole	25
Halibut	25
Herring	25
KingSalmon	5
Longnose Skate	5
P. cod	25
PInkShrimp	25
PlainSculpin	5
Pollock	25
RexSole	5
RockSole	25
Rougheye	5
Sablefish	5
Sandsole	5
Shortfin eelpout	5
Shortfineelpout	5
Smooth Lumpsucker	5
Snailfish(liparis)	5
SpinyheadSculpin	5
StarryFlounder	5
SturgeonPoacher	5
Tanner Crab	5
TomCod	5
WhiteSpottedGreenling	5
WryMouth	5
Yelowfin sole	5
Yellow Irish Lords	5

VII. PISCIVOROUS CONSUMERS

Piscivorous fish, seabirds, harbor seals, and whales are among the non-human apex predators that inhabit Kodiak waters, prey on local fish assemblages, and could potentially compete with Steller sea lions for common prey. As a first step in addressing such competitive interactions, we studied the seasonal diets and foraging patterns of these sympatric consumers. In addition, we monitored the health, productivity, and foraging patterns of sympatric predator populations as indicators of relative prey availability to consumers using common prey resources. To assess the roles of these predators and provide input for trophic-level modeling of energy budgets, we collected samples and data to identify seasonal and inter-annual patterns and changes in prey and habitat use by piscivorous birds, seals, whales, and fish in the Kodiak area.

A. PISCIVOROUS FISH

Fish are the dominant consumers of fish in the Bering Sea and other ecosystems. The decline of Steller sea lions in the 1970’s and 1980’s coincided with both declining forage fish abundance and increasing piscivorous groundfish populations. Currently, fish biomass of the Bering Sea and Gulf of Alaska is dominated by piscivorous groundfish, including arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and Pacific halibut (*Hippoglossos stenolepis*). While each have been found in the diet of Steller sea lions in our study area (Wynne, et al *in prep*), these species are also significant or dominant consumers of pollock and capelin in the Bering Sea and Gulf of Alaska and may therefore also *compete* with Steller sea lions for forage fish prey. We initiated several studies intended to assess the seasonal diets and potential for piscivorous fish to compete with Steller sea lions for common prey resource. Overall objectives were to

- examine seasonal diets of arrowtooth flounder, halibut, and spiny dogfish, Pacific cod, and walleye pollock by examining stomachs collected from survey cruises, commercial and sport harvests
- examine stomach contents of sleeper sharks taken as by-catch in commercial fisheries
- determine trophic status of individual spiny dogfish with stable isotope analyses.

Investigating the role of arrowtooth flounder (*Atheresthes stomias*) as a top level consumer in the Gulf of Alaska ecosystem from 2001 – 2004.

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This study is part of a M.S. thesis that is currently scheduled to be completed by December 2005. Arrowtooth flounder represent both a prey item of Steller sea lions in Kodiak as well as an important competitor. As the arrowtooth flounder biomass has increased exponentially in the past decade, the obvious correlation to Steller sea lion declines needs to be addressed. Prior to a direct analysis, the importance of arrowtooth flounder as a consumer in the ecosystem needs to be quantified.

Introduction

The nearshore waters of the Gulf of Alaska (GOA) have undergone a drastic change in the fish species composition since the early 1980's. The community has shifted from one dominated by small forage fish and shrimp to a community dominated by large piscivorous gadid and flatfish species (Anderson et al. 1997; Mueter and Norcross 2000). The species which has shown the most dramatic increase in abundance is arrowtooth flounder (*Atheresthes stomias*). Arrowtooth flounder is a large, piscivorous flatfish found in waters off central California to the Bering Sea (Hart 1973). In the early 1980's arrowtooth flounder abundance was estimated to be around 980,000 metric tons (mt) and the most recent biomass estimates for arrowtooth flounder in the GOA are 2,822,830 mt (Turnock, Wilderbuer, and Brown 2003). In the GOA, arrowtooth flounder are most abundant in waters 76m to 225m deep (Zimmermann and Goddard 1996). Arrowtooth flounder are presently the most plentiful groundfish in the GOA, however, there is little commercial fishing targeting them. In 2003, there were only 23,316 mt harvested in the GOA (Turnock, Wilderbuer, and Brown 2003). Due to their increasingly high abundance and high trophic level in the GOA food web (Trites 2001) it is important to study their feeding behavior and trophic role in structuring the GOA ecosystem.

Predation can play an important role in structuring and regulating prey populations in an ecosystem. Top level consumers may determine the fate of all populations in an ecosystem (Carpenter, Kitchell, and Hodgson 1985). Control of a system, by top level predators, has been illustrated for relatively simple freshwater systems (Carpenter, Kitchell, and Hodgson 1985; McQueen et al. 1989). Such control has been difficult to clearly illustrate in larger, more complex marine ecosystems, however, there are examples where this is occurring. The Georges Bank fish community, off the New England coast, is described as a predator controlled ecosystem (Sissenwine et al. 1984; Tsou and Collie 2001). This system has undergone dramatic changes in community structure due to the over exploitation of valuable, top level fish predators (Fogarty and Murawski 1998). The system is now dominated by elasmobranchs and other lower valued piscivores (Collie and Delong 1999). Predation by these piscivorous species is the most dominant source of mortality on prerecruit fishes in the Georges Bank fish community (Collie and Delong 1999, Overholtz, Link, and Suslowicz 1999, Tsuo and Collie 2001). Predation on the early life stages of marine fish may contribute to the extensive fluctuations seen in some stocks (Bailey and Houde 1989, Bax 1991). In the Grorges Bank ecosystem, the dominance of the piscivorous fish species in the system may be altering the rate of recovery of the valuable groundfish species (Fogarty and Murawski 1998). Understanding how species interact, through competition and predation, is valuable for managers in predicting long term trends in multispecies fisheries (Tsou and Collie 2001).

In the GOA, diet studies have shown that arrowtooth flounder generally feed in the water column and typically feed on commercially important prey. Yang (1993, 1995) found that the majority of prey by weight of arrowtooth flounder >40 cm was walleye pollock (*Theragra chalcogramma*) and fish 20 cm to 39 cm fed mainly on capelin (*Mallotus villosus*) and Pacific herring (*Clupea harengus*) in the GOA. Larger size arrowtooth flounder (> 40 cm) consume mainly age- 0, 1, and 2 walleye pollock (<300 mm) (Yang and Nelson 2000). Like all aquatic species, the main factor limiting prey choice is their body/ gape size (Lundvall et al. 1999). In the GOA, arrowtooth flounder compete with several fish and marine mammals, for food resources, particularly for their main prey walleye pollock. Yang (1993) found that in the GOA that Pacific halibut (*Hippoglossus stenolepis*), sablefish (*Anoplopoma fimbria*), and Pacific cod (*Gadus macrocephalus*) also consume walleye pollock. Diet overlap between these species is highly variable. Yang and Nelson (2000) found that diet overlap varied among years; pacific cod and arrowtooth flounder had a high overlap (>50%) in 1990, arrowtooth flounder and walleye pollock had high overlap 1993, and in 1996 there was low diet overlap between these predators in the GOA. Yang (1995) found that walleye pollock were the most important prey for both arrowtooth flounder and pacific halibut, specifically between arrowtooth flounder >40 cm and pacific halibut >80 cm.

Arrowtooth flounder also compete with Steller sea lions (*Eumetopias jubatus*) for similar food resources. Sinclair and Zeppelin (2002) found that walleye pollock was one of the most common prey items identified in Steller sea lion scat samples in the GOA. Since the decline in the western stock of Steller sea lion may be associated with diet restrictions (National Marine Fisheries Service 2001) understanding the food habits of arrowtooth flounder, a possible competitor, is crucial. Although the food habits of arrowtooth flounder have been documented in the GOA there is a need to take a more detailed look into the temporal (seasonal, inter-annual) variations. Typically, a common assumption is that diet information collected during a few months, i.e. summer months, is representative of predation behavior throughout the year (Hollowed, Ianelli, and Livingston 2000). This does not take into account seasonal changes in a predator's diet. Dwyer, Bailey, and Livingston (1987) found distinct seasonal differences in the prey composition in walleye pollock. This study will attempt to remove this assumption by studying the seasonal and inter-annual variations in the diet of adult arrowtooth flounder in the study area. A better understanding of these variations could lead to more accurate estimates of predation losses.

Presently the GOA is dominated by large piscivorous and gadid species (Mueter and Norcross 2000). Evidence supports the hypothesis that the decline in forage fishes occurred after the increase in large predatory fish, thus supporting the belief that predation was a possible factor contributing to the changes in community structure (Mueter and Norcross 2000). Arrowtooth flounder are the most numerous of all groundfish species in the GOA and being a large flatfish they are considered an apex predator on the same trophic level as marine mammals (Trites 2001). In the GOA, groundfish predation can be a significant source of mortality for important commercial fish species such as walleye pollock (Livingston 1994). Information gained by studying the feeding behavior of arrowtooth flounder and quantifying the consumption of commercially important prey will be useful in the management of the fish stocks in the GOA.

The overall goal of this project is to examine the trophic role of adult arrowtooth flounder, as a top level consumer, in the GOA ecosystem. One objective will be further our understanding of the seasonal and interannual variations in the diet of arrowtooth flounder in the study area. We hypothesize that there will be significant differences in the diet compostition of arrowtooth flounder on a seasonal and interannual scale. The second objective will be to provide an estimate of the consumption of commercially important prey, by adult arrowtooth flounder, in the study area. We hypothesize that consumption estimates will show that adult arrowtooth flounder are consuming significant amounts of commercially important species, i.e. walleye pollock, on a yearly basis. The last objective will be to provide initial estimates on the flow of fish biomass and energy to arrowtooth flounder in the GOA food web. This will help test the hypothesis that a significant portion of the overall fish biomass and energy, in the GOA, is being utilized by adult arrowtooth flounder.

Methods

Study Area

Sampling was conducted in the Gulf of Alaska in the vicinity of Kodiak Island. Specifically, the study area encompasses the water around Marmot and Long Islands. The sampling was in conjunction with ongoing survey cruises that have been operating in the area since May 2001. These cruises are used to survey and monitor fish, seabird, and whale populations around the Long Island and Marmot

Island Steller sea lion haulouts. The survey cruises were conducted four times annually in March, May, August, and November for 2001, 2002, and 2003 and will continue to be conducted in 2004. The cruises follow established, multiple east to west running parallel transect lines that encompass the waters around Marmot and Long Islands. Bottom trawls were conducted at designated stations throughout the study area. Bottom depths of these stations range from 60 m to 215 m deep.

The survey cruises were conducted on the commercial stern trawler F/V Laura. The boat is configured with a main deck reel located directly over the stern ramp which is used to deploy the bottom trawl. The net used is a DanTrawl Fiska Trawl II 380/55 model with a 2.22 cm codend liner with 4.0 meter Nets Fishbuster doors. Each tow is conducted for approximately 10 minutes and the speed of the vessel is maintained at 3 knots (5.5 km/hr) for the duration of the tow. This calculates out to a distance of 0.92 km covered for each tow. The mean width of the net multiplied by the distance traveled results in an area swept by the net for each tow. The effort of each tow is used in conjunction with the data collected from the tows (arrowtooth flounder numbers and sizes) to calculate the catch per unit effort (CPUE) of each tow. CPUE will be calculated for arrowtooth flounder for each tow. Upon retrieval, the catches are were sorted by species and counted. Length measurements (total length (cm)) were taken for subsets of each species in the trawl. Large catches required a subset to be taken and analyzed, with the total catch determined from the composition of the subset. At each station, specimens of arrowtooth flounder were set aside for stomach collection. Depending on the catch size, 5 to 10 specimens were collected at each station. Arrowtooth flounder show size related feeding tendencies, becoming more piscivorous with size. Specifically, arrowtooth flounder > 40 cm tend to be mainly piscivorous (Yang 1995; Yang and Nelson 2000). This size threshold was used to select specimens. Fish that showed evidence of regurgitation or net feeding activities were not included. The following information was collected for each specimen: species, total length (cm), weight (g), sex, and maturity status. Stomachs were removed and placed in individual cloth bags with a corresponding identification tag listing the station code, species, and specimen number. Samples were preserved in a 10% formaldehyde solution in 5 gallon buckets. Stomachs were stored in the buckets until the laboratory analysis can be conducted.

Laboratory Analysis

In the laboratory, stomachs were removed from cloth bags and excess liquid was blotted off with a paper towel. Each stomach was weighed (0.01g). Stomachs were opened with a knife or scissors and contents were placed on a sieve with 300 um mesh. The stomach lining was rinsed off over the sieve, blotted dry, and reweighed on the balance. Stomach content weight was calculated by subtracting the stomach lining weight from the initial stomach weight. A determination of stomach fullness and digestion stage was recorded for each specimen. The following stomach fullness indices were used: 1 - empty, 2 - 25% full, 3 - 50% full, 4 - 75% full, and 5 - 100% full. Indices for digestion stage will be: 0 - pristine, no digestion, 1 - mostly pristine, 2 - mostly digested, 3 - fully digested. The stomach contents were gently rinsed with distilled water over the sieve to rinse off formalin residue. Prey organisms were separated, counted, and identified to the most practical taxonomic level. Emphasis was placed on the identification and measurement of fish, crab, and shrimp prey. Whole fish specimens were measured (1.0 cm) and weighed (0.01g). Crab carapace width was measured for intact crab carapaces. An attempt to identify digested fish prey was made by using otolith and other bony structures. Data from all specimens were recorded and entered into a database.

Data Analysis

The stomach sample information will be divided into four groups according to the season of capture (March, May, August, and November) for each of the study years. The samples will be divided this way to allow for ease of comparison among seasons and years. The prey composition will be described using the following methods: Percent of frequency of occurrence (%FO), percentage of total stomach content weight (%W), and percentage of total prey number (%N). These will be calculated for the major categories of prey items. Consumption of major prey items by arrowtooth flounder, for a certain time, will be calculated by the following equation (Livingston 1993):

$$C = DR \cdot D \cdot B \cdot P$$

Where C = consumption in tons of a prey species, DR = daily ration (expressed as a fraction of body weight consumed daily), D = time period of analysis, B = estimates of predator population biomass, and P = the proportion by weight of given prey species. Daily ration estimates will be obtained from the literature. Predator biomass estimates will be obtained from the bottom trawl data. The consumption estimates of commercially important prey will be analyzed on a seasonal and yearly basis. Comparison to the commercial landings of the particular prey for a given year will be conducted to illustrate the magnitude of the consumption. Additionally, the length of prey items consumed will be calculated and compared with sizes of prey items typically harvested commercially. This will help to determine if the two groups are competing with each other for the same size class of species. Finally, consumption estimates, in terms of biomass, will be converted into energy values by using known energy densities of prey items consumed. Estimates of total energy consumed by adult arrowtooth flounder will expressed seasonally and on a yearly scale. Estimates will be made for the total fish biomass and energy consumed by adult arrowtooth flounder, on a yearly basis, in the GOA.

Results, Evaluation and Conclusions

Stomach samples of adult arrowtooth flounder were collected during surveys in 2001, 2002, and 2003. There are plans to continue the sampling for 2004. During the 2001, 2002, and 2003 surveys, an average of 5 – 10 stomach samples of arrowtooth flounder were collected for each of the tows. In 2004, there are plans to increase the number of stomach samples collected per tow during each of the survey cruises. To date only a small portion (33) of the stomach samples have been initialized analyzed for stomach fullness. Of the 33 samples, 11 of the stomachs were empty. The remaining 22 stomachs averaged 75.11 g and placed averaged ~ 3 on the index of stomach fullness (~ 50% full). No other analysis of the stomach samples has been completed.

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Trophic Status of Spiny Dogfish (*Squalus acanthias*) in the Gulf of Alaska

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This study is part of a M.S. thesis that is currently scheduled to be completed by May 2006. Samples for this project were collected in 2003 as part of the GAP program. Spiny dogfish are both an important prey item as well as competitor with Steller sea lions. As spiny dogfish and other elasmobranch biomass has increased in the Gulf of Alaska in the past decade, the correlation to Steller sea lion declines needs to be addressed. Prior to a direct analysis, the importance of spiny dogfish in the Gulf of Alaska ecosystem needs to be determined.

Introduction

The emphasis of marine research has been increasingly at the ecosystem level. Previously, studies focused on species in isolation. This approach is being supplanted by broader scale investigations of species in relation to both the biotic and abiotic factors that influence their life history strategies. One framework for the study of ecosystems is built around the concept of trophic interactions among species. The significance of these relationships serves as a determinant for the relative success of the populations that comprise a given ecosystem (Pimm 1982).

Trophic interactions, though recognized as being influential on community dynamics, have been a source of controversy among ecologists in terms of the processes that define the structure of a given ecosystem. The bottom-up hypothesis supports the idea that each trophic level is resource-limited. This is countered by the hypothesis of the top-down mediated ecosystem, wherein the upper trophic levels are food-limited while those at the lower end of the spectrum may be defined by either resource availability or predation (Hairston et al. 1960). There is some evidence however, for the presence of a middle ground amidst the controversy: both forcing systems are apt to operate at varying degrees and in different temporal and spatial scales (Roff et al. 1988). In aquatic systems, the top-down controlled system is the preferred paradigm for want of evidence indicating otherwise (Steele 1998). Evolving from the top-down theory, and largely supported by limnological evidence (Strong 1992; Carpenter and Kitchell 1993), is a trophic cascade model. This model is predicated upon the idea that higher trophic levels, by virtue of their presence or absence in a system, will determine the relative amassment of plant biomass at the system's base (Verity and Smetacek 1996), the effects 'cascading' through the various trophic levels. Consequently, alterations to the population structure of a key organism in a system, such as that of a top-level predator, may be extensive and result in considerable changes to the populations of other species within the system, and thus in the nature of the system itself.

Fish at the top of marine food webs tend to be the target and primary harvest of the fishing industry (Pauly et al. 1998). Many shark species are commonly at or near the top of their supporting food webs. Furthermore, it has been suggested that sharks may be fundamental to the maintenance and stability of marine communities, fulfilling the role of keystone predators (Hinman 1998). In addition to their characteristic position within their food webs, sharks exhibit a number of other distinct life history traits that require consideration. Sharks exhibit K-selected life history strategies, defined by slow growth, delayed onset of sexual maturity, low fecundity and natural mortality, and greater longevity than that experienced by their teleost counterparts (Walker 1998). Lately, shark populations the world over have been receiving a great deal of attention in light of their relative trophic position and the effects of fishing on their populations (Kitchell et al. 2002). In 1994, the member countries of the Convention of International Trade in Endangered Species of Wild Flora and Fauna (CITES) mandated a review of the status and trade in sharks (Stevens et al. 2000). This lead to the eventual adoption of the United Nations Food and Agriculture Organization International Plan of Action for Shark Conservation and Management in 1999, which aimed to have national shark fishery management plans in place by 2001. The achievement of this goal remains beyond reach, but continues to be a priority for the organization and many of its member countries (Cavanaugh and Fowler 2004) as the threat faced by many shark species continues to grow in step with the lucrative market for shark products. The growing concern about the impact of fishing on shark population dynamics, and the intention to implement management strategies are justified by the limited information available regarding sharks and what has been observed to happen to shark populations when they are the targets of unmanaged fisheries.

The spiny dogfish (*Squalus acanthias*) has a history of utilization in North America that has been traced back to as early as 5000 B.P. (Ketchen 1986). This species is one of the most plentiful sharks in the world's oceans, distributed in temperate and sub-arctic waters at depths ranging from the surface to 900 meters (NOAA 1999). Spiny dogfish generally seem to prefer a temperature range between 6 and 13 degrees Celsius (Jensen 1966; Shepherd et al. 2002) and have been observed to participate in migratory behavior (McFarlane and King 2002; McRuer and Hurlbut 1996). As with other members of the family Squalidae, the spiny dogfish is ovoviparous, bearing live young after one of the longest gestation periods of any vertebrate: from 22-24 months (Ketchen 1972). In addition to the prolonged reproductive cycle, the species exhibits a remarkably slow growth rate and late onset of maturity. Although age and length at maturity has shown regional variation, in the Northeast Pacific, females have been observed to attain sexual maturity anywhere from 16 to 35 years of age (Ketchen 1975; Saunders and McFarlane 1993). Fecundity tends to increase with length and, while a single reproductive cycle may produce 2-15 pups, the average litter size is 6 pups (Soldat 1979). Offspring measure 20 to 30 centimeters at birth (Jones and Green 1977) and the sexually dimorphic growth exhibited by the species becomes apparent as the individuals mature. Females attain a greater size than males and, in the North Pacific, have been observed to achieve maximum lengths of more than 130 cm. Males, on the other hand, reach maturity at an average age of 14 years and have been observed to attain a maximum length of 107 cm and an age in excess of 40 years (Ketchen 1975).

The spiny dogfish is a gregarious species that tends to school by size and, when mature, by sex (Nammack et al. 1985; Koen Alonso et al. 2002). Juvenile spiny dogfish seem to favor a mid water habitat where their diet has been found to comprise a variety of small invertebrates (Jones and Green 1977). With the onset of maturity however, the species undergoes a shift to demersal habitat utilization where fish become the primary prey (Koen Alonso et al. 2002). The opportunistic feeding habits of spiny dogfish are well documented (Garrison 2000). Numerous and varied food items, predominantly fish, arthropods, and ctenophores, were observed during an extensive study analyzing more than 11000 spiny dogfish stomachs during the Northeast Fisheries Science Center (NEFSC) bottom trawl surveys from 1973-1990 (NMFS 1999). Despite recognition of the opportunistic feeding behavior of the species, any attempt to further generalize regarding the diet of spiny dogfish is confounded by considerations of locality, depth, and seasonality of sampling (Ketchen 1986). Furthermore, the seemingly voracious appetite of packs of spiny dogfish has made the species a target of many a fisherman's animosity.

Those acquainted with the spiny dogfish are familiar with its reputation as a nuisance fish. Its recorded history as a commercially harvested resource, however, dates back to the nineteenth century, when the body and liver oils of the spiny dogfish first became a marketable commodity used in industrial lubrication and lighting (Ketchen 1986). Expansion of the United States (US) east coast fishery on spiny dogfish throughout the 1990s was a result of attempts to ease the pressure on the more valuable collapsed Atlantic groundfish stocks through the creation and promotion of markets for spiny dogfish meat (ASMFC 2002). Consequently, after a decade of fairly stable spiny dogfish landings totaling approximately 6300 metric tons annually, the following decade saw a marked increase in catches. Landings peaked in 1996 at 28, 200 metric tons, followed by a subsequent decline to 22, 000 metric tons in 1998. The US commercial fishery was responsible for more than 95% of these spiny dogfish landings (NEFSC 1999). The spiny dogfish fishery is one that has traditionally targeted females owing to their larger size and greater value; recent stock assessment of spiny dogfish utilizing NMFS data revealed a continued decline in the biomass and numbers of mature females as well as in the overall stock (NMFS 2000). Additionally, pup surveys by NMFS in the northwest Atlantic yielded the lowest numbers on record at the end of the 1990s (ASMFC 2000), indicating a possible failure in recruitment as a result of exploitation. In 1998, the National Marine Fisheries Service declared the species over-fished (ASMFC 2002). Management initiatives were immediately undertaken and a fishery management plan (FMP) was jointly developed by the Mid-Atlantic and New England Fishery Management Councils and implemented in 2000 (NMFS 2000).

The spiny dogfish also has a long history of utilization on the west coast of North America, having been both an abundant and significant component of the Pacific groundfish fishery at various periods throughout history (Ketchen 1986). Though the Atlantic spiny dogfish fishery saw explosive growth followed by a sudden and devastating crash, fishery efforts directed at spiny dogfish in the Pacific have been somewhat more uniform in recent years (NMFS 2001). The average annual landing size in the Washington-Oregon dogfish fishery was approximately 500 mt between 1986 and 2001, which represents a fraction of the catch reported on the eastern seaboard (NMFS 2001). In 2003, however, Rockfish Conservation Areas were established for the protection of rockfish and other valuable groundfish along the west coast (NMFS 2003). Consequently, fishing for spiny dogfish with the traditionally utilized bottom trawls (NMFS 2001) has since been prohibited in these areas.

Although spiny dogfish is not a targeted species in Alaskan waters, increasing abundance of this and other shark species have become apparent to fishermen in the last decade (Wright and Hulbert 2000). Common bycatch in both the pelagic walleye pollock trawl fishery as well as in the longline fisheries for a variety of groundfish species (halibut (), sablefish (), Pacific cod ()), spiny dogfish have experienced a dramatic population increase in the eastern Gulf of Alaska and Prince William Sound. In the six years spanning 1997 to 2002, bycatch of the species ranged from 117 mt to 864 metric tons and was primarily taken between Southeast and Kodiak, Alaska (NPFMC 2003). Catch trends reported by fishermen are supported by the longline survey data obtained by both the National Marine Fisheries Service and the International Pacific Halibut Commission. These data depict an increasing trend in relative abundance of spiny dogfish in the waters along the eastern and central gulf coast of Alaska and the Kodiak Island region during the 1990s (Wright and Hulbert 2000).

The concept of regimes developed with the increasing importance of fisheries management. Regimes were first introduced in the 1970s (Isaacs 1975) to describe both stable conditions in climatic and oceanic data series as well as persistent periods of patterns in fish recruitment (Beamish et al. 1999). McKinnell et al. (2001) describe the low frequency, high amplitude and frequently sudden changes in the biological communities that can transpire simultaneously with physical changes in the climate system as a regime shift. The Gulf of Alaska ecosystem has experienced numerous occurrences of these regime shifts. The first such regime shift to be recognized was that of 1977 when a dramatic alteration in species composition (Anderson et al. 1997) followed a cyclical shift from a predominantly cold regime in the three decades prior to 1977, to a warm regime in the years since (Benson and Trites 2002). The changes observed in the oceanic and climatic conditions during 1977 were not the first such major shift in the oceanic climate. Indications of similar events have been noted to occur prior to the 1977 shift, in 1925 and 1947 (Mantua et al. 1997; Minobe 1997). Additionally, in the years following the 1977 event, there was a shift in 1989 (Beamish et al. 1999) and a potential shift in 1998 (McFarlane et al. 2000). However, it is important to note that a shift does not imply a return to a previous state nor does it imply that a particular regime will be evident in all of the indices that describe the climatic and oceanographic conditions of the Pacific Ocean (Benson and Trites 2002). Where previously the biological community was dominated by small forage fish and crustaceans supporting a vibrant collection of seabirds and marine mammals, by the 1990s the biomass of higher trophic level groundfish had increased by as much as 250% (Anderson and Piatt 1999). This increase in gadoid and flatfish species such as walleye pollock and arrowtooth flounder saw a potentially related decline in the forage fish base and the marine mammals and seabirds that these species support. The cause of the restructuring of the large marine ecosystem of the Gulf of Alaska is unclear. One widely supported hypothesis is that the reorganization of the ecosystem is a result of the ocean climate shift (Orensanz et al. 1998) to an environment favorable to species whose biological characteristics include greater longevity, delayed maturity, and intermittent strong recruitment (Anderson and Piatt 1999). A related hypothesis is that the increasing populations of these species, many of whom prey on forage species, are thought to have further exacerbated the declines in the forage base (Anderson and Piatt 1999; Mueter and Norcross 2000). Evidence supporting this hypothesis demonstrates that predation plays a considerable role in the Gulf of Alaska ecosystem.

The degree to which spiny dogfish affect mortality rates of commercially important species in the Gulf of Alaska is unknown. A better understanding of the trophic role of spiny dogfish in this ecosystem would assist in providing a sound basis from which to make management decisions regarding the potential for a fishery targeting spiny dogfish.

The assessment of diet and trophic position are important aspects in understanding the role of a species in a marine ecosystem. One long-standing practice to accomplish these aims in aquatic food webs has been the use of stomach content analysis (Cortes 1997). This and other indirect methods of dietary evaluation may be misleading unless a wide-ranging sampling schedule is undertaken. Stomach content analysis provides only a snapshot of a species diet and may be biased by discrepancies in rates of digestion (Hansson et al. 1997).

In recent years, stable isotope analysis has been recognized as a useful way to determine trophic position. Predator tissues bear signature δ ^{13}C/δ-^{12}C and δ ^{15}N/δ ^{14}N ratios that are directly related to those of their prey and have been shown to transfer in a predictable manner (Peterson and Fry 1987). δ-^{13}C/δ-^{12}C ratios are often used as a sign of a consumer's primary prey items as enrichment of δ-^{13}C between trophic levels is limited to 0-1% (Peterson and Fry 1987; Hobson and Welch 1992). In contrast, nitrogen stable isotope ratios (δ-^{15}N/δ-^{14}N) are useful as a predictor of actual trophic level as δ-^{15}N shows an increase of 3-4% with increasing trophic level (Peterson and Fry 1987; Post 2002). This disparity in nitrogen isotope fractionation occurs because the consumer's metabolic processes preferentially utilize the lighter isotope (Rau et al. 1983). While the use of stable isotopes does have certain limitations, including a lack of known trophic fractionations as well as the assumptions involved in analysis (Estrada et al. 2003), it also has distinct advantages over traditional diet measures. Stable isotope analysis provides information that represents assimilated and not merely ingested prey, the isotopic ratios present in consumer tissue are indicative of long-term diet (Peterson and Fry 1987) and δ-^{13}C/δ-^{12}C ratios allow conclusions to be drawn regarding inshore versus offshore feeding habits (France 1995). Consequently, stable isotope analysis serves as a complementary method to stomach content surveys.

The goal of this study is to investigate the trophic status of spiny dogfish (*Squalus acanthias*) and to evaluate its role as a top-level predator in the Gulf of Alaska ecosystem.

Objectives

The following objectives pertain to the achievement of the goal stated above:

- Quantify number, biomass, fullness and frequency of occurrence of prey species in the stomach contents of individual spiny dogfish.
- Assess stomach condition of spiny dogfish according to determination of fullness.
- Determine trophic status of individual spiny dogfish with stable isotope analyses.

Hypotheses

- Spiny dogfish occupy a trophic level between 3 and 4 in the Gulf of Alaska.
- There is an ontogenetic shift in the diet of spiny dogfish from pelagic to demersal species.
- There is a seasonal shift in the diet of spiny dogfish due to changes in distribution.
- Spiny dogfish in different areas of the Gulf of Alaska will occupy different trophic levels.

Methods

Sampling will be carried out in the Kodiak Island region of the Gulf of Alaska using bottom trawls at designated stations where depths range from 60 to 215 meters. Sampling for spiny dogfish will be concomitant to studies being carried out by three organizations. During the summer months, when juvenile spiny dogfish and mature females are anticipated to be in nearshore waters, the National Marine Fisheries Service and the International Pacific Halibut Commission conduct surveys in environs of interest. The University of Alaska, on the other hand, conducts surveys at various times throughout the year. Survey and monitoring activities for seabird, whale and fish populations around the stellar sea lion haulouts at Marmot and Long Islands are performed during March, May, August and November and provide opportunities to carry out sampling for spiny dogfish as well.

At each designated station, between 5 and 10 spiny dogfish specimens will be set aside depending on the size of the catch. Any fish that show evidence of regurgitation or net-feeding activities will be excluded from the pool. The 5 to 10 randomly selected spiny dogfish will then be reserved for stomach and tissue collection and the following information for each individual will be recorded:

species, total length (cm), weight (g), sex and stage of maturity. Stomachs will be removed from the specimens and placed in individual cloth bags tagged with a record of the station code, species and specimen number. Samples will then be preserved in 5 gallon buckets containing a 10% formaldehyde solution where they will remain until such time that laboratory analyses can be conducted. A small section of dorsal muscle tissue (2-3 cm) will be excised from each specimen. This tissue sample will be stored frozen with a record of the identifying information corresponding to the specimen until stable isotope analysis can be undertaken.

In the laboratory, stomachs will be extracted from the cloth bags and paper towels will be used to blot excess liquid from each specimen. Individual stomachs will be weighed to the nearest hundredth of a gram using a balance scale. Once the stomach has been incised using a knife or scissors its contents will be placed on a sieve with 300 μm mesh. The lining of the stomach will be rinsed off over the sieve to capture any remaining items, blotted dry and reweighed on the balance. The weight of the stomach contents may then be expressed as the difference between the initial stomach weight and that of the stomach lining. This value, as well as determination of stomach fullness and digestion stage, will be recorded for each specimen. Indices for digestion stages will be: 0 - pristine, no digestion, 1- mostly pristine, 2 – mostly digested and 3 – fully digested. Indices for stomach fullness will be: 1 – empty, 2 – 25% full, 3 – 50% full, 4 – 75% full, and 5 – 100% full. Prior to the sorting, enumeration and identification of prey organisms, the stomach contents will be rinsed of formalin residue over the sieve using distilled water. Identification of prey will be to the most practical taxonomic level with an emphasis on fish, crab and shrimp prey. Whole fish will have length measured to the nearest centimeter and weight determined to the nearest hundredth of a gram. The width of intact crab carapaces will also be measured to the nearest centimeter. Efforts to identify digested fish prey will be made using otoliths and other bony structures.

Lipid has been found to have lighter δ-^{13}C values in comparison to protein and carbohydrate (Parker 1964) and may confound interpretation of diet source data in muscle tissue. Consequently, lipid will be removed from the tissue prior to analysis. The frozen muscle samples will be dried to constant mass at 60 °C and lipid extraction will then be carried out using the method introduced by Bligh and Dyer (1959). The dry, lipid-free tissue will be pulverized. An approximately 1 to 2 mg aliquot of ground, lipid-free spiny dogfish tissue will be used to determine the δ-^{13}C and δ-^{15}N values. Analysis will be carried out using a Europa 20/20 Continuous Flow Isotope Ratio Mass Spectrometry System (CF-IRMS). Stable isotope abundances will be measured by comparing the ratios of δ-^{13}C/δ-^{12}C and δ-^{15}N/δ-^{14}N in the sample to the international standards (Pee Dee Belemnite for carbon and atmospheric nitrogen, respectively). Results will be expressed in parts per thousand (%) deviation from the standard using the equation:

$$\delta X = (\text{Rsample}/\text{Rstandard} - 1) * 1000\%$$

where X is 13C or 15N and R is the isotopic ratio δ-^{13}C/δ-^{12}C or δ-^{15}N/δ-^{14}N (Peterson and Fry 1987). The mass spectrometry facility at the University of Alaska Fairbanks will perform the analysis of δ-^{13}C and δ-^{15}N.

The major categories of prey items present in stomach contents will be described using the following indices: percentage by number (%N), percentage by weight (%W) and percentage frequency of occurrence (%O).

Relative trophic position will be estimated using the equation:

$$\text{Trophic Position (TP)} = \lambda + (\delta\text{-15N spiny dogfish} - \delta\text{-15N base})/\Delta n$$

where λ is the TP of the organism used to estimate δ-^{15}N base, Δn is the enrichment in N-15 per trophic level, and δ-^{15}N spiny dogfish is the direct measurement of δ-15N for spiny dogfish (Post 2002). The species to be used as an estimate for δ-^{15}N base should utilize a habitat similar to that of the spiny dogfish. Additionally, effects of short-term variation should be minimized through the utilization of a base species that will span a large enough time span so as to integrate the isotopic signature of its food web (Post 2002).

A one-factor ANOVA will be used to investigate the possibility of significant dietary differences among maturity stages. This analysis will be applied to stomach content weights with the weight of each food category as a dependent variable and maturity stage (size) as treatment. A one-factor ANOVA will be used to investigate the possibility of significant diet composition differences among seasons. This analysis will be applied to stomach content weights with the weight of each food category as a dependent variable and season as treatment. A one-factor ANOVA will be used to investigate the possibility of significant trophic differences among spiny dogfish in different areas of the Gulf of Alaska. This analysis will be applied spiny dogfish specimens where mean trophic position is a dependent variable and area of the Gulf as treatment.

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A summary of sleeper shark stomach contents collected in the Kodiak Area, Spring 2001

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Introduction

The potential causes for drastic declines in Steller sea lion numbers and their slow recovery are unknown but could involve predation by apex predators (NRC 2003). Pacific sleeper sharks (*Somniosus pacificus*) are among the apex predators living in Kodiak waters whose numbers have increased since the 1980's. Their role as apex consumers in this system is of particular interest as apparent expansions in their populations appear to have coincided with declines in Steller sea lion (*Eumetopias jubatus*) and other marine mammal populations in the Gulf of Alaska.

There is currently no estimate of the abundance of Pacific sleeper sharks in Alaskan waters. The rate at which they are caught incidentally in longline surveys for sablefish and halibut, however, suggest their relative population numbers (RPNs) increased in the 1990's in Alaskan waters with increases in the Gulf of Alaska were focused in Shelikof Trough (Courtney and Sigler, unpubl. data, NMFS Auke Bay Lab).

The diet and tropho-dynamic role of Pacific sleeper sharks in the Gulf of Alaska remain poorly understood. Early interest in the potential role of these sharks as apex predators was generated by the discovery of harbor seal and/or cetacean (harbor porpoise and unknown whale) remains in five of thirty sleeper shark stomachs examined in Prince William Sound (L. Hulbert, NMFS, pers. comm.) and one of three sleeper sharks taken as bycatch from Portlock Banks in 2000 (K. Wynne, unpubl data). Marine mammal remains were recovered from 25 sleeper shark stomachs collected in the Gulf of Alaska in August 2001 and May 2002; 21 contained cetacean remains and the other four were unidentified (Hulbert, Sigler and Lansford, unpubl. data, NMFS Auke Bay Lab). The majority (64%) of these remains was determined to have been scavenged and others were too decomposed for analysis; there was no clear evidence that the sharks actively preyed upon the mammals. No confirmed Steller sea lion remains were recovered (Hulbert, Sigler and Lansford, unpubl. data, NMFS Auke Bay Lab).

Even if not posing a direct predatory threat to Steller sea lion populations, increasing shark populations can potentially compete with Steller sea lions if their diets overlap and prey is limited. Salmon sharks and sleeper sharks are also known to consume prey that are prominent in the diet of Steller sea lions including salmon, walleye pollock, cephalopods, arrowtooth flounder, and other finfish (Bright 1959,Yang and Page1998). Examining the diets of these sharks can provide insight into the degree of dietary overlap and potential for competitive interactions with Steller sea lions in the Gulf of Alaska.

Sharks are species of interest to the University of Alaska's Gulf Apex Predator-prey study (GAP) because they have the potential to be both a Steller sea lion consumer and competitor in the Gulf of Alaska. In 2001, a pilot study was conducted as part of GAP to 1) determine the feasibility of developing an opportunistic shark sampling program, 2) identify dominant prey species in the stomachs of sharks collected in the Kodiak area, and 3) document evidence of consumption of Steller sea lions. This report summarizes efforts in 2001 to assess the diet of sleeper and salmon sharks in Kodiak waters, with collections authorized under Fish Resource Collection Permit number CF01-001 from the Alaska Department of Fish and Game.

Methods

A variety of sharks are caught incidental to Alaskan commercial fisheries but are rarely retained because of their limited marketability. In pilot this study, a small group of fishermen in Kodiak were contacted during one week in Spring 2001 and asked to voluntarily retain for scientific purposes a sample of sharks taken incidentally while trawling for walleye pollock. They were specifically asked to release any live sharks from gear but to retain no more than five sleeper sharks and five salmon sharks from each fishing trip that were recovered dead from fishing gear and return them to Kodiak intact for examination. Some skippers elected to extract the stomachs from sharks while at sea. Upon their return to port, these fishermen notified K. Wynne who met the boats and sampled retained sharks at the dock.

Intact sharks were identified, sexed, and measured (standard fork length). The approximate location of each shark capture was recorded as the latitude/longitude of specific trawls or generic area fished during the trip, as reported by skippers. Stomachs were extracted from intact sharks and their contents removed for examination either on deck or subsequently in the Kodiak Fisheries Research Center lab. Stomachs extracted by fishermen at sea were bagged and frozen separately. Prey remains were extracted from stomachs, identified to the lowest possible taxon, and the length of undigested remains was measured of to the nearest centimeter. Fish otoliths and cephalopod beaks were retained to allow subsequent species identification of partially digested prey. In addition, samples of cartilage, muscle, and liver were collected from sharks to allow assessment of ratios of stable carbon and nitrogen isotopes ($\delta^{13}C$, $\delta^{15}N$) as an indicator of the trophic level at which the sharks were foraging (Hirons 2001, Hobson and Welch 1992).

Results

Sharks sampled in this project were taken incidentally in commercial pollock trawls within 30 miles of Kodiak Island and delivered to processors in Kodiak. Four vessels retained a total of 22 sleeper sharks and three salmon sharks for examination between March and early April 2001 (Table 1). All were collected from Shelikof Strait, off the south or southwest end of Kodiak Island in water approximately 50-150 fathoms deep. Further sampling in other fishing seasons was limited by weather and/or time constraints.

Three salmon sharks were examined, all males that ranged in length from 193-207cm (mean 217cm, SD 7.57). Each contained only traces of prey including fish (capelin, eulachon) and/or cephalopods. Of the 22 sleeper shark stomachs examined, 10 (40%) were from males, five (20%) were from females, and the origin of seven (40%) was not determined. The fork length of these sleeper sharks ranged from 147-348cm (mean 248.7cm, SD 48.72).

Prey remains were found in all but one stomach examined and included walleye pollock, eulachon, arrowtooth flounder, octopus, and squid. Mammalian prey remains were found in only one shark stomach examined, a 348cm female sleeper shark. This stomach contained approximately 10 kg of partially digested whale tissue in chunks that weighed approximately 1-2 kg each and were the diameter of the shark's jaws. Because of the number of chunks and their uniform state of digestion, they most likely represent scavenged chunks from a single whale carcass, possibly a gray whale (*Eschrichtius robustus*).

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Table 1. Summary of sharks taken as bycatch, landed in Kodiak, and sampled in 2001 under provisions of ADFG Fish Resource Permit No. CF-01-001 issued to K. Wynne, UAF.

Species	Date Collected	Specimen Number	Sex	Length (cm)	Approximate Capture Location
Sleeper Sharks					
	03/27/01	032701SLSH01	F	348	mid-lower Shelikof
	03/27/01	032701SLSH02	M	292	mid-lower Shelikof
	03/27/01	032701SLSH03	M	226	mid-lower Shelikof
	03/27/01	032701SLSH04	M	147	mid-lower Shelikof
	03/27/01	032701SLSH05	M	225	mid-lower Shelikof
	03/27/01	032701SLSH06	M	208	mid-lower Shelikof
	03/27/01	032701SLSH07	M	280	mid-lower Shelikof
	03/27/01	032701SLSH08	F	233	mid-lower Shelikof
	03/27/01	032701SLSH09	U	279	mid-lower Shelikof
	03/28/01	032801SLSH01	M	159	Shelikof Strait
	03/28/01	032801SLSH02	M	257	Shelikof Strait
	03/29/01	032901SLSH01	U	320	Shelikof Strait
	03/29/01	032801SLSH02	U	236	Shelikof Strait
	03/29/01	032801SLSH03	U	300	57.08' 155.16'
	03/30/01	033001SLSH01	F	239	Shelikof Strait
	03/30/01	033001SLSH02	M	284	Shelikof Strait
	03/31/01	033101SLSH01	U	231	57.12° 155.20°
	03/31/01	033101SLSH02	U	206	57.12° 155.20°
	03/31/01	033101SLSH03	U	218	57.12° 155.20°
	04/02/01	040201SLSH01	F	225	Shelikof Strait
	04/02/01	040201SLSH02	F	282	Shelikof Strait
	04/02/01	040201SLSH03	M	277	Shelikof Strait
Salmon Sharks					
	03/28/01	032801SaSH01	M	207	east Shelikof
	04/02/01	040201SaSH01	M	193	east Shelikof
	04/02/01	040201SaSH02	M	205	east Shelikof

Table 2. Prey recovered from 22 sleeper shark stomachs taken as bycatch in Shelikof Strait in March and April 2001.

		Walleye Pollock	Eulachon	Arrowtooth Flounder	Squid or Octopus
%FOC in 22 stomachs		90.9%	59.1%	50.0%	36.4%
Number recovered	total	281	86	11	beaks +
	min	0	0	0	95 cm octo
	max	71	13	2	56 cm squid
	mean	13.38	3.91	0.58	whole
	StdDev	15.95	0.92	0.77	
Length (cm)	min	13	14	21	
	max	61	20	65	
	mean	34.36	19.93	42.22	
	StdDev	12.07	2.23	15.30	

B. PISCIVOROUS MAMMALS

Pinnipeds

Harbor seals and Steller sea lions are sympatric pinnipeds that are known to prey on similar fish species and rest on haulouts within 1-5km of each other near Kodiak. Seal numbers have been declining in this area since 1993 while Steller sea lion numbers have continued to decline. In GAP we collected samples needed to document the seasonal prey use and foraging patterns of both pinniped species within Steller sea lion Critical Habitat in Kodiak waters. With these data we can address the potential for competition between harbor seals, Steller sea lions, or other upper level consumers that coexist and share prey resources within Kodiak's coastal waters. Overall objectives were to

- determine prey species consumed by Steller sea lions in the Kodiak region (relative size, diversity, frequency of occurrence, seasonal patterns, inter-annual variability)
- compare diets of Kodiak Steller sea lions to diets of sympatric piscivores and Steller sea lions in southeast Alaska
- monitor the seasonal distribution of Steller sea lions on designated critical haulouts in the Kodiak area
- determine habitat use and prey species consumed by harbor seals
- compare diets and habitat use by Kodiak harbor seals to those of Steller sea lions and other sympatric piscivores in the Kodiak area

Piscivorous whales

Humpback (*Megaptera novaeangliae*) and fin (*Baleanoptera physalus*) whales are known to be significant consumers in many marine ecosystems that may consume large zooplankton and schooling fish. As such, they have the potential to either compete with Steller sea lions *directly* when consuming forage fish species or *indirectly* by consuming zooplankton upon which Steller sea lion prey species feed. We assessed the seasonal abundance, foraging ecology, and habitat use of humpback and fin whales in Kodiak waters as a means of assessing their role as apex predators, degree of prey overlap, and potential for competition with Steller sea lions. Overall objectives were to

- assess the seasonal abundance and diet of humpback whales in Kodiak waters as a means of assessing their role as apex predators, degree of prey overlap and potential for competition with Steller sea lions
- calculate current consumption rates based on seasonal abundance, energy requirements, and feeding rates
- characterize habitats used by piscivorous whales in Kodiak waters

Preliminary assessment of the diet of Steller sea lions in the Kodiak area, 1999-2003

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Introduction

Documenting the diet of Steller sea lions is fundamental to testing the "prey limitation hypothesis", assessing the potential for competition between Steller sea lions and commercial fisheries, and determining the seasonal and regional overlap with other consumers of common prey resources. Despite acknowledged limitations and biases (Olesiuk, et al. 1990, Gales and Cheal 1992, Orr and Harvey 2001, Tollitt et al 2003), fecal samples (scats) represent a "reasonable index of prey field sampled by foraging sea lions" (Merrick, et al. 1997). Identifiable hard parts (bones, eye lenses, teeth, cartilaginous parts, otoliths, cephalopod beaks, and scales) in the scats of piscivorous mammals can be collected and identified by comparison to reference collections (Cottrell, et al. 1996).

Prior to the 1990's, Steller sea lion diets were assessed by examining stomach contents; only 389 stomachs collected throughout western Alaska were examined over a 40+ year period, 1945 – 1986 (Mathiesen et al 1962, Thorsteinson and Lensink 1962, Pitcher 1981, Lowry et al. 1982). Since 1990, researchers have collected and examined fecal samples to assess the relative importance of prey to Alaskan Steller sea lions. From 1990-93, a sample of 338 scats was collected opportunistically in summer months on multiple sites in the Aleutian Islands and the central Gulf of Alaska (Merrick et al 1997). Sinclair and Zeppelin (2002) summarized the contents of over 3700 scats collected opportunistically from 1990 to 1998 throughout western Alaska. Individual site-specific collections were small; samples were grouped into two seasons and four regions to assess seasonal and regional patterns of prey use. A more concerted effort to collect and analyze scat contents since 1999 has improved our understanding of temporal and regional patterns of prey use by Steller sea lions (Wynne et al 2003, Womble and Sigler 2004, Waite and Burkanov 2004).

It has been hypothesized that the catastrophic decline of the western stock of Steller sea lions through the 1980's and 1990's was due, at least in part, to prey limitations (NRC 2003). As a result, focused have been managed to reduce the potential for humans to compete with Steller sea lions for fish that have been identified as important components of their diet. In addition, the degree of Steller sea lion diet diversity has been inversely correlated to rates of population decline (Merrick et al 1997). If so, we would expect decreased diet diversity in Kodiak (where declines continue from 2000-2004 (Sease and Gudmundson 2002, Fritz pers. comm.) than in areas where Steller sea lion numbers are stable or increasing. We would also expect decadal differences as population trends changed. Sinclair and Zeppelin (2002) noted differences in prey use between summer and winter collections which they attributed to changes in availability of prey in these dichotomous season categories. For these reasons, it is important to understand what prey species are important to Steller sea lions, consider regional and seasonal differences in prey use, and to monitor observed changes over time.

Scats were used in this study to monitor the diet diversity and the seasonal and regional importance of prey species to Steller sea lions in the Kodiak region. Specifically, fecal samples were collected on a seasonal basis to a) assess the species, relative diversity, and frequency of occurrence of prey in the diets of Kodiak Steller sea lions, b) compare seasonal prey use to prey availability determined in GAP prey surveys, c) compare seasonal diets of Kodiak Steller sea lions to those diets of sympatric piscivores and Steller sea lions found southeast Alaska and elsewhere, and d) monitor long-term trends in sea lion diets. This report summarizes preliminary analyses of scats processed through 2004 using a subset of samples collected during GAP's 2001-2003 seasons and prior collections (1999-2001) in the same area (Wynne et al 2003).

Methods

Fecal samples (scats) were collected approximately monthly from Steller sea lion haulouts to monitor the seasonal and regional importance of prey species to Steller sea lions throughout the Kodiak region. Collections were more sporadic in 2003 and 2004 due to funding and permit issues. Scats were bagged separately and subsequently rinsed to recover identifiable hard parts (eye lenses, otoliths, vertebrae, cephalopod beaks, and scales) that pass through the digestive tract. These dried remains were sent to Pacific Identifications, Inc (Victoria, BC) for identification to lowest possible taxon and characterization of prey size class. The species, number, and relative size of prey (when possible) contained in each scat were reported. Sample processing and scat content analysis are ongoing. A more comprehensive analysis of the prey identified within scats collected 1999-2004 from Kodiak haulouts will be presented following completion of scat content analyses by Pacific Identifications, Inc.

The relative importance of each prey item was assessed by comparing the frequency at which it occurred in fecal samples. This simple frequency of occurrence (FOC) of identified prey species was calculated for each haulout per collection by determining the percent of scats in which a given prey item was detected (Olesiuk et al. 1990). Some researchers have considered that any prey species found in greater than 5% of scats sampled is of dietary importance to Steller sea lions (Merrick et al 1997, Sinclair and Zeppelin 2002). A higher standard was used in this study: prey items that occurred in >10 % of scats containing identifiable prey were considered important in Steller sea lion diets.

Assessing spatial patterns of prey use requires that regions be defined by reasonable boundaries (natural or contrived). Telemetry studies conducted by NMFS (NMML unpubl data) have shown that tagged individual Steller sea lions may make extended coastal transits to use haulouts throughout the Kodiak Archipelago (NMML unpubl data). Following their move to another haulout, however, these central place foragers tend to forage within 0-20m of the site (NMML, unpubl data). It is therefore reasonable to assume that scats deposited on eastern Kodiak haulouts would not likely represent prey consumed by Steller sea lion foraging greater than 20nm from a haulout. In these analyses, sites considered to represent North Kodiak haulouts (Latax Rks, Sea Otter I, and Marmot I) are located greater than 20nm from the nearest of the East Kodiak haulouts (Long Is, C. Chiniak, Ugak I) or West Kodiak haulout (C. Ugat) (Fig. 1).

Seasonal patterns of prey use were assessed by grouping results from samples collected 1999-2003 during four seasons: winter= December through March, spring= April and May, summer= June through September, and fall= October and November. Months within these seasons share similar oceanographic and environmental patterns with potential biological significance to prey of Steller sea lions. In addition, these seasons may loosely correspond to assumed changes in the energetic demands on Steller sea lions associated with reproduction, lactation, and weaning.

An index of dietary richness was developed by tallying the number of scats within each sample from each site that contained *n* identifiable prey species. The size of most prey species consumed was estimated at the time scat contents were identified; these data will be analyzed following completion of scat analyses.

Results

A total of 2,232 scats were collected from ten Steller sea lion haulouts during GAP's 2001-2003 sampling in the Kodiak Archipelago (Fig. 1). An additional 944 scats collected from the area from 1999-2000 were included in the following analyses to bolster sample sizes and allow longer temporal assessments (Table 1). Of those collected, only 1168 had been analyzed at the time of this report and 37 of those were empty. Therefore, this report summarizes preliminary analyses of dietary patterns observed in the processed subset of 1,131 scats collected in the Kodiak area from 1999-2003 that contained identifiable prey remains (Table 2). Scats collected on Latax Rks, Sea Otter I, and Marmot I are considered to represent North Kodiak haulouts; those collected on Long Is, C. Chiniak, Ugak I are grouped as East Kodiak haulouts. Scats could be collected on only one West Kodiak haulout, Cape Ugat.

Nine prey species (or families) were found in greater than 10% of the scats containing identifiable remains (% frequency of occurrence, FOC) in preliminary analyses (Fig. 2). The five most frequently occurring prey species each occurred in greater than 25% of scats containing identifiable remains: Pacific sandlance[1] (*sandl*: 42.0 FOC), arrowtooth flounder[2] (*arrfl*: 37.0 FOC), walleye pollock[3] (*polck*: 30.1 FOC), Pacific cod[4] (*p.cod* 29.2 FOC), and salmon *spp*. (*salmn*, 28.5 FOC) (Fig.2). Pacific herring[5] (*herng*), capelin[6] (*capln*), and Irish Lord *spp*[7] (*IrLrd*) were found in close to 15% of scats and sole *spp*[8]. in 10% of scats with identifiable remains (Fig. 2). Hexagrammids (*hexgr*), represented primarily by greenling *spp*., were found in >5% of scats examined and would therefore have qualified as a tenth “significant” prey item using standards used in other studies. Only 37 of 1168 (3.7%) scats analyzed to date contained no identifiable remains and were classified as Empty. More ‘Empty’ scats were collected on North Kodiak sites than others (Fig. 3). Cephalopods (primarily octopus spp) and rockfish *spp* were found in >5% of some seasonal samples (Fig. 4) but were not found to be significant prey overall. The spatial, temporal, and overall patterns of diversity in prey use in this area will be analyzed in more detail once identification of prey items in remaining samples is complete.

Scats analyzed to date suggest Steller sea lions on Kodiak haulouts have a “rich” diet, i.e. each scat commonly included remains from multiple prey species (Fig. 3). Scats containing a single identifiable prey species were found in only 20.9, 26.5, and 30.4% of scats analyzed from West, North, and West haulouts, respectively. More than half (53.7%) of scats contained three or more identifiable prey species and more than one-third (35.6%) contained more than four different prey species (Fig. 3).

Several seasonal patterns in use of dominant prey species were found in preliminary analyses of scats sampled throughout the Kodiak Archipelago (Fig. 4). Sandlance, arrowtooth flounder, pollock, and Pacific cod were among dominant prey species in scats collected from October to May. In winter, the relative importance of Irish lords and sole *spp* peaked while that of capelin and salmon was lowest (Fig. 4). In the relatively small spring sample, the FOC of herring was exceeded only by that of sandlance and arrowtooth flounder. Summer scat samples were dominated by capelin and to a lesser degree by arrowtooth flounder and salmon. Use of salmon peaked in October and November, although a broad suite of prey was recovered from fall scat collections (Fig. 4).

Within this sample, seasonal patterns in diet composition were further examined to identify associated spatial patterns of prey use within the Kodiak Archipelago (Fig. 5). In Oct-Nov, Steller sea lions on northern and eastern haulouts used a diversity of prey and dominance was shared by five species. Pollock occurred more frequently in scats from eastern sites and salmon, sandlance, and arrowtooth flounder from northern sites (Fig. 5). During winter months (Dec-Mar), scat samples from C. Ugat suggest herring, pollock, and sandlance are seasonally important to Steller sea lions on the Shelikof Strait.

Shifts in the relative dietary importance of individual prey between sites seen in preliminary analyses could reflect spatial and temporal changes in prey distribution or foraging patterns of Steller sea lions. Sandlance was found to be a key prey item throughout the Kodiak Archipelago but its relative importance decreased in summer samples (Fig 5). Herring and capelin were among the seasonally dominant prey in scats from North and West sites but were rarely found in East Kodiak scat samples (Fig. 5). Arrowtooth flounder were among the dominant prey recovered from April through November scats collected on East and North sites but were of lesser importance to animals using the West Kodiak haulout. Pollock was consistently important in all seasons on East Kodiak sites and of varying seasonal importance in other areas. Salmon *spp* were among dominant prey items in all seasons except winter (Fig. 5). A minor use of hexagrammids (primarily greenling *spp*) was evidenced primarily in fall and winter scats. Cephalopods and rockfish were rarely found in scats sampled to date (Fig. 5)

[1] Pacific sandlance (*Ammodytes hexapterus*)

[2] Arrowtooth flounder (*Atheresthes stomias*)

[3] Walleye pollock (*Theragra chalcogramma*)

[4] Pacific cod (*Gadus macrocephalus*)

[5] Pacific herring (*Clupea pallasii*)

[6] Capelin (*Mallotus villosus*)

[7] Irish Lord spp (*Hemilepidotus* spp)

[8] Soles (*Pleuronectes spp*.)

Discussion

This report summarizes preliminary analysis of approximately one half of the scats collected between1999 and 2004 in the Kodiak Archipelago. Further analyses and final interpretation of results will follow complete processing of remaining scat samples.

Sampling throughout the year on multiple sites in the Kodiak Archipelago has allowed monitoring of seasonal and regional patterns of prey use. Preliminary analyses indicate that Kodiak's Steller sea lions are currently preying on a diverse diet that varies both seasonally and regionally. Nine prey species were found to be important (in >10% of scats) including species of forage fish (sandlance, herring, capelin), flatfish (arrowtooth flounder, soles), groundfish (pollock, Pacific cod), and demersals (Irish lords). Of these, sandlance, arrowtooth flounder, walleye pollock, Pacific cod were dominant and found in greater than 28% of scats examined, with species-specific regional and seasonal shifts in relative importance.

Many of these prey species have been found in Steller sea lion scats examined elsewhere, including walleye pollock, sandlance, arrowtooth flounder, Irish lords, herring, and salmon. The number and diversity of dominant prey species in the GAP sample analyzed to date, however, far exceed those previously reported and with far fewer "empty" scats (i.e. no identifiable remains) than those collected in the central Gulf of Alaska from 1990-1998 (Sinclair and Zeppelin 2002). Whether differences are due to differences in sampling intensity or decadal patterns of prey use will be difficult to assess. The number and diversity of dominant prey species in the GAP sample analyzed to date, however, far exceed those previously reported and with far fewer "empty" scats (i.e. no identifiable remains) than those collected in the central Gulf of Alaska from 1990-1998 (Sinclair and Zeppelin 2002).

Several important (>5% FOC) prey species consumed by Steller sea lions in southeast Alaska in the 1990's were also found to be important in our preliminary analyses reported here. Trites et al (2003) found pollock, herring, sandlance, salmon, arrowtooth flounder, rockfish, skates, squid, and octopus to be important components of Steller sea lion diets in southeast Alaska. Although more thorough comparisons are forthcoming, preliminary results suggest that sea lion scats in southeast Alaska contained a less diverse suite of prey that included more rockfish, skates, and cephalopods than sea lions sampled in this study. The overall, spatial, and temporal patterns of diversity in prey use in this area will be analyzed in more detail once identification of prey items in remaining samples is complete.

Conclusions

Long-term seasonal sampling of Steller sea lion scats in the Kodiak Archipelago has provided a means of identifying important prey and tracking it use spatially and temporally in an area of continuing Steller sea lion decline. Determining the prey species of seasonal importance to Steller sea lions is fundamental to assessing potential prey limitations or competition between Steller sea lions and commercial fisheries. Following completion of all scat analyses, these data will be compared to the seasonal distribution, abundance, and energetic content of key prey species found in GAP prey surveys within the same geographic range and time frame. Spatial and decadal differences between this and other Steller sea lion diet studies will be examined in greater depth upon completion analysis of all 1999-2004 scat samples collected. In addition, these data will be combined with other GAP datasets to examine correlations between the seasonal distribution and diet of Steller sea lions to that of their key prey species and potential competitors within the Kodiak Region.

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Table 1. Summary of Steller sea lion scat samples collected on haulout sites in the Kodiak Archipelago during GAP (2001-2004) and NPMR (1999-2000) studies.

Collection Site	1999	2000	2001	2002	2003	2004	2001-04	Total
LI: Long I.	78	102	162	154	247	0	563	743
CH: C. Chiniak	0	86	0	0	0	0	0	86
UG: Ugak I	0	22	0	0	0	0	0	22
CB: C.Barnabas	0	44	0	32	0	0	32	76
TH: Two-headed I	25	64	24	14	33	0	71	160
CU: C. Ugat	26	45	139	175	134	65	513	584
LA: Latax Rks	27	125	153	85	59	58	355	507
SO: Sea Otter I.	0	197	177	158	56	90	481	678
SL: Sea Lion Rk	0	16	0	0	0	0	0	16
MA: Marmot I.	40	47	83	87	36	61	267	354
	196	748	738	725	495	274	2232	3176

Table 2. Subset of scat samples containing identifiable prey remains used in this preliminary analysis of Steller sea lion prey use in the Kodiak region, 1999-2003.

mo / yr	West	North			East		
Collected	**CU**	**SO**	**LA**	**MA**	**LI**	**CH**	**UG**
Sep 1999	26						
Nov 1999			27		25		
Dec 1999				30	52		
Jan 2000	41	25	23				
Feb 2000		38			34		
Mar 2000						39	
Apr 2000					26		
May 2000	2	18	24				
Jun 2000	6						
Jul 2000							20
Aug 2000		42	32				
Sep 2000				43			
Oct 2000					41		
Dec 2000			46			46	
Mar 2001			12				
Jun 2001							
Jul 2001			47				
Oct 2001			36				
Nov 2001		55		31			
Jan 2002	32				2		
Nov 2002		62					
Aug 2003				36			
Sep 2003		12					
	107	252	247	140	180	85	20

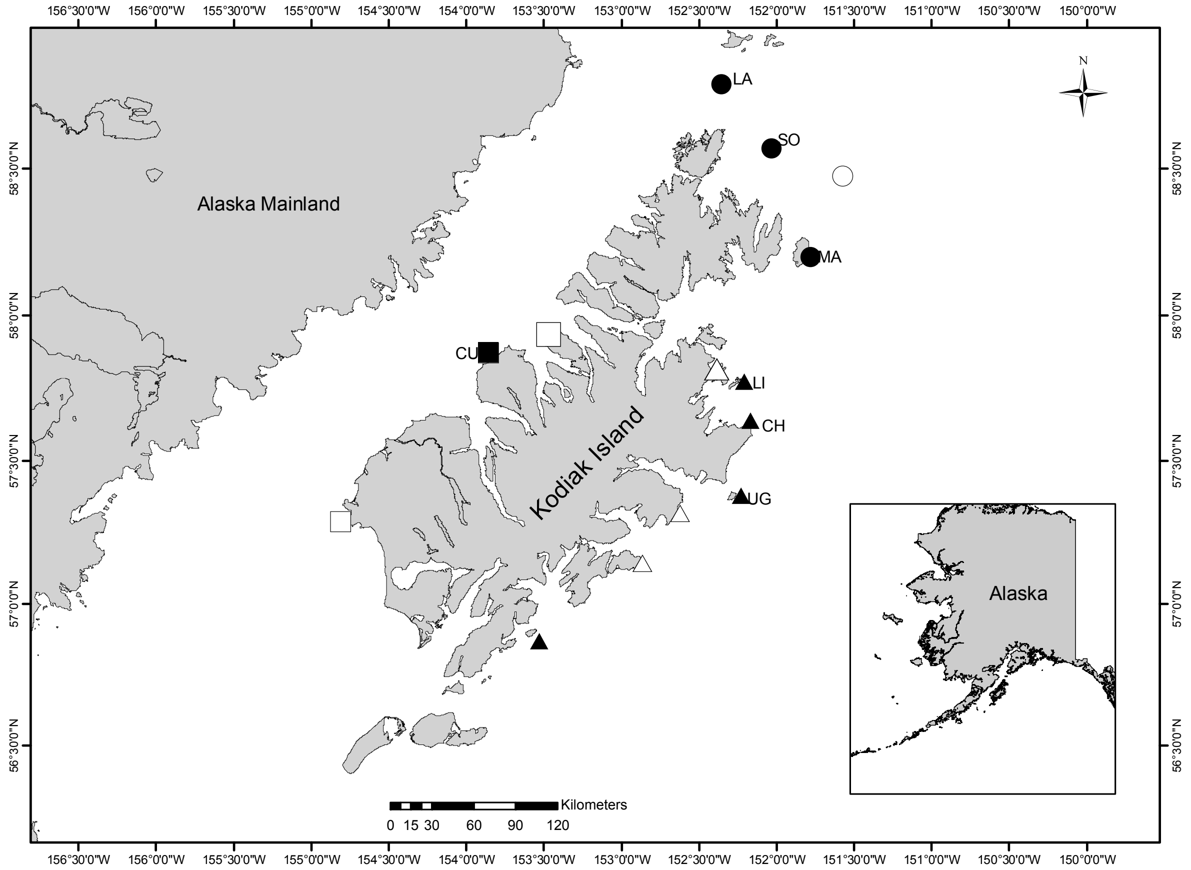

Figure 1. Steller sea lion haulouts of north (○), east (Δ), and west (□) regions of the Kodiak Archipelago. Filled shapes denote scat collection sites included in this preliminary assessment of regional diet patterns.

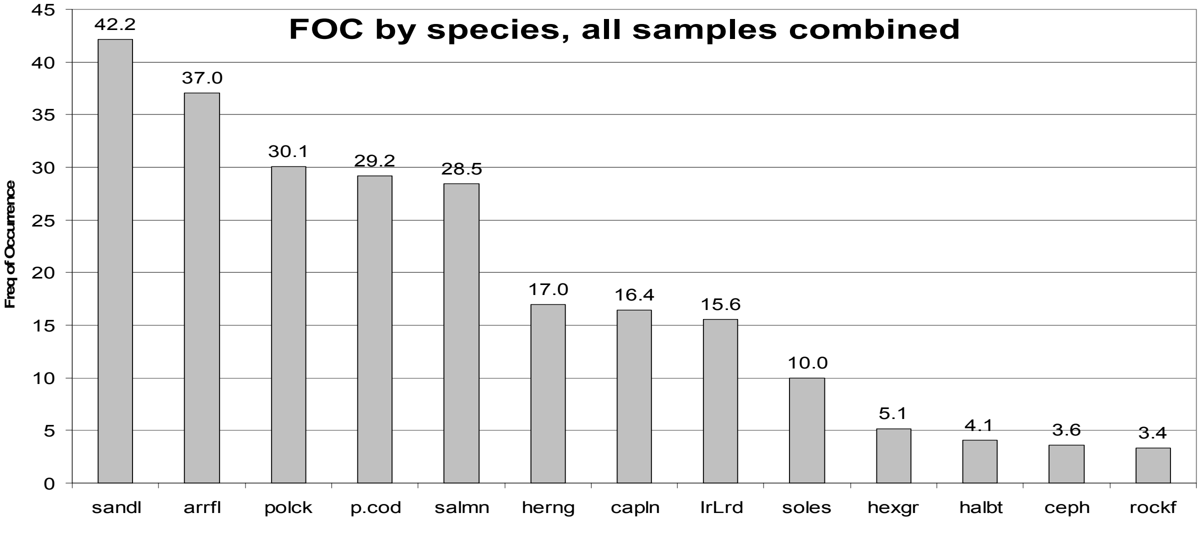

Figure 2. Frequency of occurrence of 13 prey items in a sample of 1131 scats collected on Kodiak Archipelago haulouts, 1999-2003. See text for prey name abbreviations.

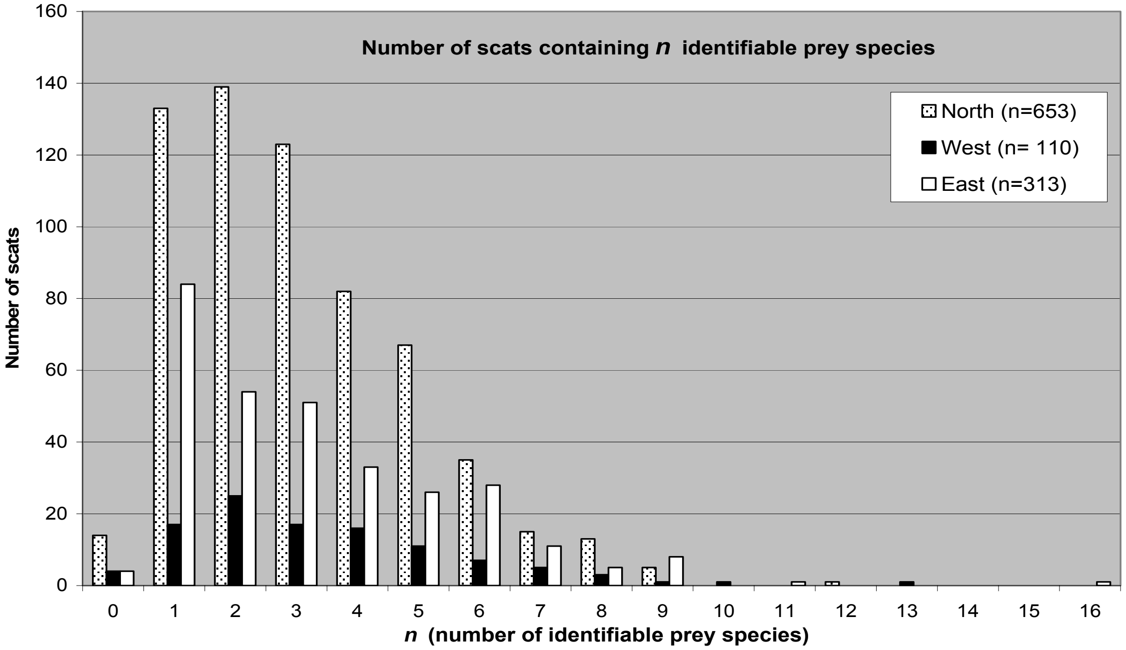

Figure 3. Number of scats containing 0-16 identifiable prey species from a subset of samples collected on Kodiak Steller sea lion haulouts, 1999-2004. North= LA, SO, MA; East= LI, CH, UG; West= CU.

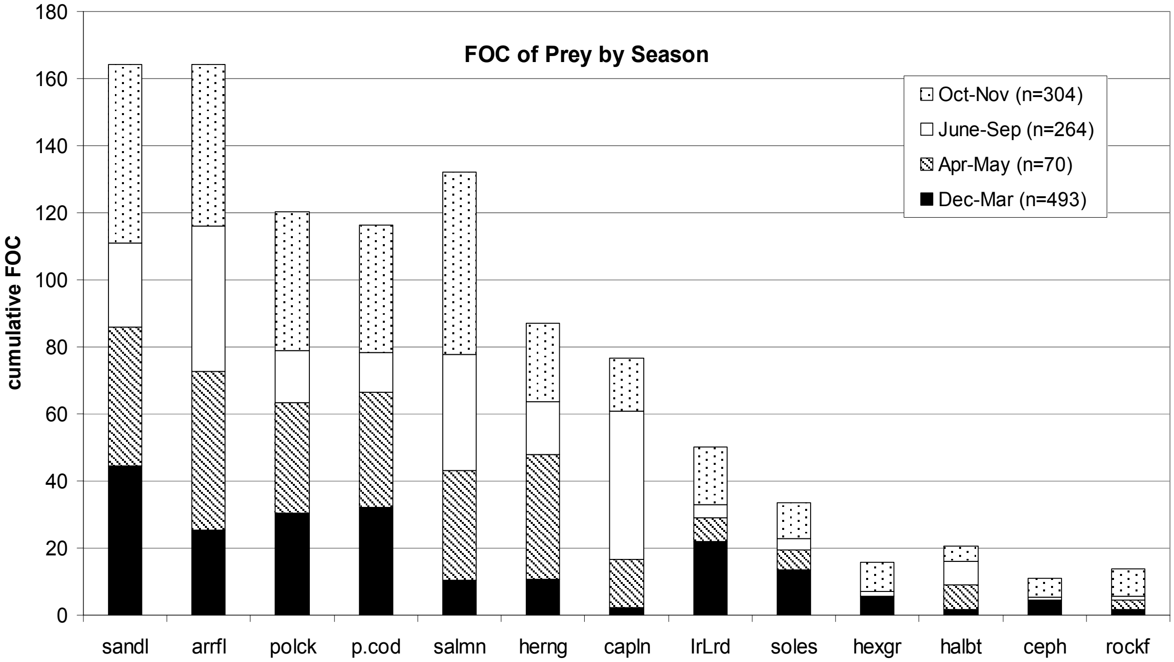

Figure 4. Cumulative and seasonal frequency of occurrence (FOC) of prey species in a sample of 1131 Steller sea lion scats collected in the Kodiak area, 1999-2003. See text for prey abbreviations.

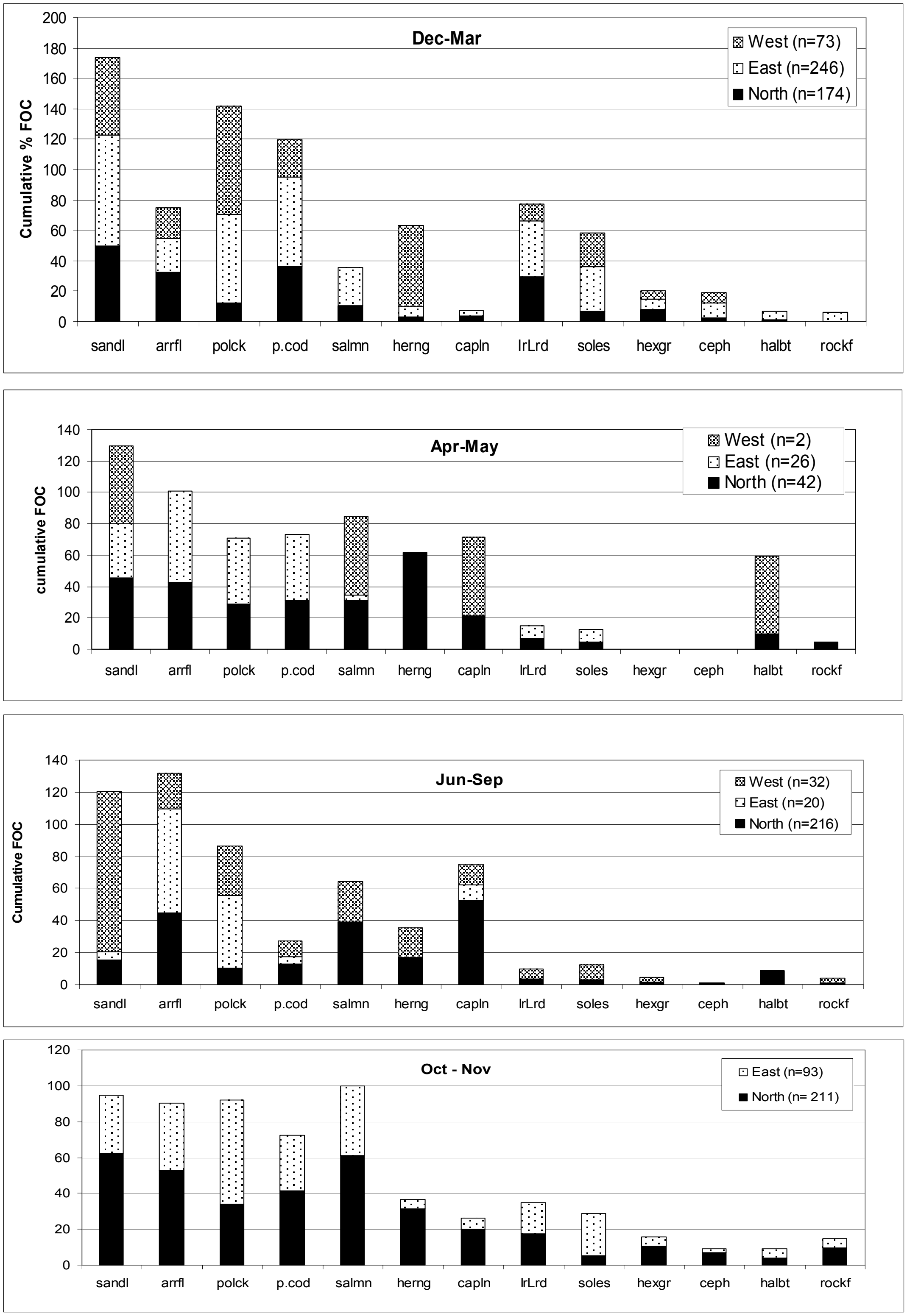

Figure 5. Comparative seasonal importance of prey species identified in 1131 scats collected on Kodiak Steller sea lion haulouts, 1999-2003. North= LA, SO, MA; East= LI, CH, UG; West= CU.

Aerial monitoring of terrestrial habitat use by Steller sea lions in the Kodiak Archipelago, 1999-2003

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Introduction

Steller sea lions are amphibious, foraging at sea but congregating onshore on terrestrial sites between feeding bouts at sea to give birth, breed, rest, and nurse their pups. "Haulouts" are sites used by groups of sea lions for resting; sites used specifically for pup rearing and breeding activities by this polygynous species are called rookeries. Sites used as rookeries during the breeding season may be used as haulouts at other times of the year. The number of individuals that haul out on terrestrial sites and the amount of time they spend ashore varies daily and seasonally in response to temporal variables (time of day and season) weather, energetic demands on individuals, and disturbance among other factors (Gentry 1970, Calkins and Pitcher 1982, Withrow 1982, Milette 1999, Gisiner 1985, Loughlin et al 2003).

Rookeries and most haulouts appear to be traditional sites, with historic use by groups of Steller sea lions being documented for decades (Fiscus et al. 1976). Individual Steller sea lions may use many different haulout sites (NMML unpubl telemetry data) but have been found to exhibit a large degree of site fidelity in their use of rookeries. The majority (67%) of twelve females branded in western Alaska rookeries 1987-88 returned as adults to their natal rookery to breed (Raum-Suryan et al. (2002). Some haulouts are used year-round while others are used only seasonally in response to predictable patterns of prey availability (Womble, et al 2003, Sinclair and Zeppelin 2002). Most traditional haulouts are located on exposed headlands with easy access to waters where bathymetric and oceanographic features support altered. New or transitory haulouts may develop as Steller sea lions find suitable resting sites while opportunistically exploiting a new or sporadic prey source.

When precipitous declines led to the listing of Steller sea lions as threatened under the Endangered Species Act, their Critical Habitat was defined to include major rookeries and their surrounding waters (within a 20nm). In their 1998 Biological Opinion, the National Marine Fisheries Service (NMFS 1998) further defined major seasonal and year-round haulouts within Critical Habitat based on point estimates from counts of Steller sea lions observed on sites from 1976 to 1998. Since then, these designated 'major' haulouts and rookeries have formed the basis for fishing area-closures intended to limit the potential for commercial fishermen to locally deplete Steller sea lion prey resources.

NMFS researchers have counted Steller sea lions on Kodiak area haulouts during sporadic and systematic aerial surveys since 1976 (Loughlin et al 1984). These were developed into systematic biennial aerial surveys of sites from Kenai to Kiska (including Kodiak sites) to monitor the population trend of Steller sea lions in western Alaska (Loughlin et al 1992). Scheduled during June, these surveys have generated point estimates of non-pup Steller sea lion numbers during the breeding season (Sease and Merrick?). Since 2002, use of medium format photography has enabled researchers to more accurately detect and count pups during June surveys (Sease and Gudmundson 2002, Fritz et al. unpubl data).

Biennial June surveys conducted in 2000, 2002, and 2004 showed an abatement of the Steller sea lion decline throughout much of the western stock's range (NMML, unpub data). The exception is the central Gulf of Alaska where counts continued to decline 12.5% from 2000-2004 and 7.4% 2002-2004 (Fritz, unpubl data). Steller sea lion sites within the Kodiak Archipelago are located in the center of this area of continued declining counts. Therefore, long-term year-round monitoring of Steller sea lion counts on terrestrial sites in this area may help identify specific areas of continued decline on which to focus future research efforts. The Kodiak area is also exposed to a variety of human activities that have the potential to directly or indirectly impact Steller sea lions including oil drilling and transport, rocket launches, commercial fishing, tourism, and shipping. For this reason, monitoring Steller sea lion use of terrestrial sites on a fine temporal scale can help managers as they assess and attempt to mitigate the spatial and temporal vulnerability of Steller sea lions to anthropogenic threats. Finally, Steller sea lions are among Kodiak's numerous piscivorous consumers. Monitoring temporal and spatial trends in their abundance and distribution in this area is critical to GAP's ongoing assessment and future modeling of tropho-dynamic interactions in the Kodiak region.

This paper summarizes results of monthly aerial surveys of Steller sea lion haulouts in the Kodiak Archipelago. The objectives were to 1) monitor the number of sea lions using Kodiak area haulouts over time and 2) identify seasonal and annual trends in Steller sea lion use of terrestrial habitat in the Kodiak Archipelago.

Methods

Counts made from fixed-wing aircraft were used to monitor the seasonal use by Steller sea lions of twelve designated critical haulouts in the Kodiak Archipelago (Fig. 1). All sites surveyed were designated by NMFS to be significant sites (NMFS 1998): 10 year-round, one summer-only (Ugak I), and one winter-only site (Long I) (Table 1). When possible, surveys were conducted in the first week of each month but weather delays and charter conflicts prevented rigorous flight scheduling and completion. Surveys were not initiated unless weather conditions favored their likely completion.

Surveys were flown in a Cessna C206 or comparable over-wing aircraft following standard NMML survey methodology regarding timing, equipment, speed, and altitude (Loughlin et al 1992). All sea lions present were photographed (35mm, oblique angle) for subsequent counting off images and a visual estimate was recorded at each site. Pups were included in total counts. Sea lions swimming within 2-3 body lengths of a site were counted as using the site. The specific area on the haulout being occupied (microhabitat) by sea lions was noted.

No effort was made to estimate the percent of sea lions at sea (not hauled out) during surveys or to calculate abundance estimates from counts made. These repetitive counts were used to monitor trends in the distribution and relative use of Kodiak sites by Steller sea lions; results are compared by month and year. In addition, these surveys were used to identify feasible sites for subsequent scat collection (Wynne, this volume). Resulting land-based observations made on those haulouts were used to verify the age/sex composition of Steller sea lion using the site and to record presence of branded individuals.

Results

A total of 47 monthly surveys were made between 25 September 1999 and 9 October 2003 to visually and photographically count Steller sea lions in the Kodiak Archipelago (Table 2). Local weather conditions prevented the aircraft's safe approach (wind sheer) or observation of sea lions (fog or snow) at one or more sites on eight of the surveys attempted. Total counts on haulouts during the 39 surveys completed between 25 September 1999 to 10 October 2003 ranged from 727 to 2544, with a mean of 1688 (+/- 460) sea lions counted. A general negative annual trend in overall numbers throughout the study area was seen over the four survey years (Fig. 2). Negative trends in site-specific monthly counts were most notable on the three northernmost haulouts and the summer-only haulout on Ugak I (Figs. 3, 4). Slight declines were noted on the two haulouts within GAP's LiCh prey survey area (Fig. 4, Long I and C. Chiniak). Counts on other sites showed stable or modest increasing trends (Figs. 3, 4, 5). Two 'new' sites (not previously identified as major haulouts) were added to the survey route as their consistent use was detected during surveys (Fig. 6). Although counts on these sites were not included in the study area trend assessment totals, it is apparent their inclusion would soften the declining trend during the period in which they were surveyed (Fig. 7).

Peak Steller sea lion counts in the study area occurred in late summer while lowest overall counts occurred in midwinter surveys. Seasonal patterns of use varied on each site (Table 2, Figs. 3-5). Cape Barnabas and Long Island were both vacated during summer months while Ugak Island was occupied only during summer months (Fig. 4). All other sites were used year-round by varying numbers of Steller sea lions (Fig.3-5). On most haulouts, sea lions were found to utilize different portions of the haulout (microhabitat) during different seasons.

Counts on Marmot Island, the study area's only major rookery, increased after late May as breeding animals arrived to establish territories and peaked in mid- to late summer when pups were included in total counts. Similarly, counts on Latax Rks (Fig. 8) to the north of the rookery increased in July and peaked in September following the breeding season but land-based observations confirm the increase involved an influx of adult males on the site (Wynne, unpubl data). On sites south of Marmot I (Fig. 9), peak numbers were seen at the onset and immediately following the breeding season on Gull Pt and Ugak I respectively. Land-based observations confirm that animals using Ugak I haulout were large and apparently spent bulls, including one that was seen defending a territory on the Marmot rookery in July by NMML observers (K. Chumbley, pers. comm.). Counts on Long I however show the site vacated during the breeding season and used extensively in the winter. Land-based observations confirm that this site was used extensively by adult females with pups through the winter; females apparently vacate the site in May at the onset of pupping and breeding activities on Marmot I or other rookeries.

Seasonal use of other haulouts appears more associated with temporal fluctuations in prey availability. For instance, the Cape Ugat (CU) haulout on the west side of Kodiak was used fairly consistently with the exception of a drop of attendance in mid-summer and peak in March (Fig.5). The mid-summer drop in counts on the site corresponds to the seasonal arrival of Steller sea lions in Chief Cove (shaded areas Fig. 5) approximately 15 km to the south where sea lions prey on fish caught on salmon gillnets (Wynne unpubl data). March peak counts on this site correspond to spawning of herring and pollock in nearby waters. Variability in counts made on Long Island and Cape Chiniak haulouts coincidental to GAP's in March, May, July, and November prey surveys (Fig. 10) may reflect seasonal and interannual fluctuations in prey biomass within 20nm of Long Island haulout Wynne et al (2003) and Foy (this volume). Detailed analyses of these potential correlations are in progress.

Small-scale shifts in the location where sea lions congregated on given haulouts suggest they exploit seasonally important microhabitat. During relatively warm months, sea lions on many sites (LI, CH, CU, IK, LA, SO) were found to congregate on lower-lying, exposed, north or west-facing areas of the main haulout or adjacent rocks. In winter, sea lions on the same sites hauled out on high, south-facing rock slopes backed by rock faces. A seasonal shift in microhabitat use was also seen on Marmot I, which functions as a rookery from June-September but as a haulout October-May. When Marmot I. functions as a rookery, animals used multiple flat cobble beach sites on the east and south shore of the island, moving progressively southward through the summer and occasionally haul out on a rock beach on the SW tip of the island. In late fall, following the breeding season, use of the southern beaches diminished and remaining animals were concentrated on beaches on the east side of the island. From January to May of each year surveyed, the few sea lions remaining on Marmot I were hauled out on one site, a south-facing cave-like ledge site located approximately midway up the east side of the island. The overhead cave-like structure of this site affords sea lions protection from rocks that fall from cliffs above during freeze-thaw cycles.

Discussion

Combined counts of Steller sea lions on twelve major haulouts in the Kodiak area showed a slight declining annual trend between fall 1999 and 2003. Similarly, NMFS documented continued declines in biennial Steller sea lion counts in the central Gulf of Alaska (CGOA) including the Kodiak Archipelago of 4.3% from 1998 to 2002 and (Sease and Gudmundson 2002) 7.4% from 2002-2004 NMML, unpubl data). During the course of this study, two sites were added to the survey as their repeated or consistent use by large numbers of animals was noted. Animals on both sites apparently exploit prey made seasonally available by human activities. Including these counts in total counts in the years surveyed softens the declining trend within the area. Further assessment is needed to determine if increased use of such new and opportunistic prey sources by Steller sea lions may affect aerial counts made during NMFS' summer trend surveys. Although NMFS has an established set of sites with which to monitor stock trends, those survey routes should be updated periodically with data on newly established haulout sites.

Seasonal patterns of terrestrial habitat use varied by site suggesting the distribution of Steller sea lions within the GAP study area is responsive to the energetic demands on these large consumers. Site-specific seasonal shifts in sea lion numbers correspond to a) specific demands associated with breeding and pup rearing and b) the availability of predictable or readily accessible prey, as seen elsewhere.

Reproductive needs

The demands of breeding, pupping, and pup rearing appear to have an important influence on the use of terrestrial habitat by Steller sea lion. Counts on Marmot Island clearly reflect the seasonal use of multiple beaches on this island for breeding and early pup rearing. Counts on haulouts to the north and south of Marmot Island may reflect distributional changes associated with breeding activities on the rookery. Some sites appear to function as staging and recovery areas for reproductive males while others appear to be particularly important for females rearing pups through their first winter.

The haulout at Long Island forms the center for GAP's seasonal prey availability surveys on the east side of Kodiak. Although considered a 'winter-only' haulout by NMFS (1998), it is more accurately a non-summer site. It is virtually vacated during the breeding season, with only a few subadult animals hauling out on it during summer. In fall, sea lions of all age and sex groups return but usually congregate first on a rocky beach on nearby Long Island. Within a month sea lions start to use the offshore (main) haulout site, which is then used extensively by large numbers of juveniles and females with pups into June. Animals branded as pups on both Sugarloaf and Marmot Island rookeries have been observed on this site as pups and juveniles and are among the animals seen using the site in summer (Wynne, unpubl data).

The physiography and location of the Long Island and nearby Chiniak haulouts make them conducive to rearing young-of-the-year sea lions. Pups captured on one of these sites and branded or tagged with satellite-linked dive recorders were found to haul out on the other site as well (NMML, unpubl data). The structure, slope, and aspect of the haulouts provide pups with thermoregulatory benefits. Both are adjacent to sheltered shallow (<10m) area in which pups can play and gain experience foraging on the areas with greenling, ronquils, sandlance, rockfish and other demersal prey resources (Hegwer 2004). Weanlings and females that nurse then leave their young on these sites do not have to travel far to encounter substantial foraging opportunities. These haulouts are located near a bathymetric trough (northern reach of the Chiniak Gully (see map in Prey section, this volume) that supports substantial volumes of arrowtooth flounder, pollock, and Pacific cod from November to May (Foy this volume). Steller sea lion pups satellite-tagged on these sites spent much of their first winter using very nearshore waters then traveling increasing distances offshore along the Chiniak gulley edges in spring as they assumedly foraged (Loughlin et al. 2003)

Noted shifts in use of specific aspects of these and other haulouts suggest Steller sea lions exploit seasonally important microhabitat. In winter, animals resting on high south-facing sites can exploit and conserve solar energy in these proverbial 'toaster ovens' while being sheltered from northwest winds and increased winter wave action. Such seasonal shifts in microhabitat use have thermoregulatory benefits but also provide young pups access to sheltered waters.

Prey

Seasonal shifts in sea lion numbers on many Kodiak haulout sites appear to be related to Steller sea lions' exploitation of predictable or readily accessible prey, as seen elsewhere. For example, the March peak in counts Cape Ugat are likely related to the abundance of spawning pollock in Shelikof Strait and herring in west Kodiak bays upon which animals using this site feed (Wynne, this volume). Since 2002, midsummer low counts on Cape Ugat have been found to correspond to the seasonal peaks in Steller sea lions presence in Chief Cove. Commercial salmon fishermen in the Chief Cove area have reported for years that Steller sea lions scavenge salmon from their salmon set gillnets, causing extensive damage to their gear and catch (Wynne, unpub data). Salmon taken from these nets provide a predictable seasonal prey source for Steller sea lions on the west side of Kodiak.

Human-enhanced seasonal prey availability may also explain the use of a non-traditional haulout site within Dog Bay boat harbor in Kodiak. The site is a floating platform formerly used as a temporary breakwater and now used as a haulout by an increasing number of Steller sea lions. Initially occupied by older bulls, this site is typically abandoned in midsummer during the breeding season. Since 1998 more females and immature animals have used the site, including some known aged branded or radio-tagged individuals Although a variety of prey are naturally available in the nearby waters of Women's Bay, Steller sea lions are also known to opportunistically scavenge fish and offal from commercial fishing vessels delivering their catch to nearby Kodiak processors.

Conclusions

Many variables affect the number of sea lions hauled out during surveys including weather, temporal considerations, and disturbance factors. No effort has been made to consider these covariates in deriving actual abundance estimates. Actual counts of animals using key sites are used here as an index of abundance and means by which to explore inter- and intra-annual changes in Steller sea lion distribution in Kodiak waters. These shifts in use are likely associated with changes in prey availability and seasonal reproductive needs (breeding and post-breeding adults, young-of-the-year).

Monitoring seasonal patterns of haulout use adds a temporal evaluation of Critical Habitat that may help identify potential exposure of Steller sea lions to disturbance by humans through activities such as commercial fishing, tourism, oil spills, vessel traffic. Identifying terrestrial sites of particular concern during specific seasons may allow compromise in multi-use areas that have minimal potential for affecting Steller sea lion. These data will be combined with other GAP datasets to examine the potential influences of prey field variability of Steller sea lion distribution. Identify areas where greatest physical overlap with other piscivores in the system – ID likelihood of competition with other marine mammals, birds, and fish. Ultimately, having multi-year counts may help ID specific sites or areas that are contributing to continued decline within central Gulf of Alaska.

Acknowledgements

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Table 1. Summary of Steller sea lion aerial survey dates and counts on 12 haulouts in the Kodiak Archipelago, Sept 1999 to Oct 2003.

	Haulout												
Date	**LI**	**CH**	**UG**	**GP**	**CB**	**TH**	**IK**	**CU**	**LA**	**SO**	**SL**	**MA**	**Total**
25-Sep-99	58	139	0	64	28	204	1	172	940	163	72	678	2519
16-Oct-99	72	0	0	10	22	245	56	136	189	212	98	879	1919
16-Nov-99	235	43	0	65	78	370	73	209	162	281	183	674	2373
03-Jan-00	43	67	0	67	27	158	23	95	22	81	48	96	727
15-Feb-00	228	131	0	107	19			209	76	92	133	170	
25-Mar-00	122	175	0	56				302	73	95	78	0	
06-Apr-00	151	147	0	74	40	339	39	491	142	78	133	197	1831
04-May-00	127	147	0	184	26	231	40	215	93	81	156	172	1472
29-May-00	44	95	0	109	0	264	112	221	123	99	137	225	1429
08-Jul-00	14	247	32	69	0	287	58	125	349	149	32	879	2241
04-Aug-00	9	97	103	17	0	263	76	91	357	177	9	1004	2203
02-Sep-00	5	65	128	0	0	240	94	53	631	84	52	773	2125
06-Oct-00	83	85	0	23	71	366	25	154	309	120	42	967	2245
29-Oct-00	246	61	0	37	101	211	49	233	154	217	23	448	1780
30-Nov-00	134	255	0	45	40	322	52	169	28	136	10	287	1478
23-Jan-01	135	129	0	43	0	323	62	223	72	133	21	222	1363
19-Feb-01	158	123	0	89	24	309	112	257	97	119	45	171	1504
19-Mar-01	123	24	0	104	94	335	63	265	81	42	24	136	1291
07-Apr-01	161	130	0	136	20	324	90	269	82	46	43	178	1479
09-May-01	131	168	0	180	195	287	145	154	88	92	108	105	1653
08-Jun-01	72	137	0	161	1	187	116	110	99	150	1	567	1601
08-Jul-01	45	107	0					129	296		1		
10-Aug-01	12	99	0	28	0	166	84	45	203	148	18	854	1657
31-Aug-01	0	67	4	39	10	191	81	86	347	198	3	1242	2268
26-Sep-01	36	75	1	33	29	283	23	193	421	40	2	1408	2544
30-Oct-01	54	38	0	45	74	248		170	88	171	3	913	
06-Dec-01	173	104	0	56	46	185		118	52	108	0	226	
07-Jan-02	240	153	0	67	1	278	89	166	43	103	50	131	1321
05-Feb-02	236	113	0	68	5	376	86	309	91	138	0	205	1627
26-Feb-02	113	86	0	32	7	325	72	334	45	108	20	133	1275
03-Apr-02			0	120	57	307	93	526	87	52	25	203	
12-May-02	95	218	0	192	12	190	106	213	88	69	40	131	1354
31-May-02	145	234	0	132	0	240	96	190	134	75	11	522	1779
12-Jul-02	0	131	5	79	0	348	87	137			3	1300	
09-Aug-02	0	61	44	42	0	297	79	268	385	148	15	971	2310
01-Oct-02	24	78	0	66	78	171	23	122	289	207	6	789	1853
12-Nov-02	218	204	0	131	87	267	54	215	112	143	24	487	1942
13-Dec-02	172	88	0	111	127	273	91	216	55	118	16	209	1476
23-Jan-03	31	67	0	29	0		97	318	49	79	0	59	
19-Feb-03	122	78	0	152	13	201	66	172	51	77	0	218	1150
18-Mar-03	232	132	0	194	72	394	60	574	59	134	0	247	2098
22-Apr-03	150	132	0	163	148	277	51	332	64	37	61	123	1538
20-May-03	135	100	0	119	2	307	92	265	71	44	26	119	1280
16-Jun-03	55	68	0	110	0	204	96	79	115	24	11	682	1444
30-Jul-03	0	97	11	78	0	228	66	21	188	143	6	907	1745
02-Sep-03	0	52	0	28	5	168	41	116	311	55	18	547	1341
09-Oct-03	40	98	0	81	24	330	30	108	164	85	2	906	1868

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[1] LI= Long I, CH= C. Chiniak, UG= Ugak I, GP= Gull Pt, CB= C. Barnabas, TH= Two-headed, IK= C. Ikolik, CU= C. Ugat, LA= Latax Rk, SO= Sea Otter I, sea lion= Sea lion Rk, MA= Marmot I

Table 2. Steller sea lion haulouts monitored during aerial surveys conducted in the Kodiak Archipelago, September 1999- October 2003. Use and season are based on NMFS (1998) designations where H= haulout and R= rookery. Site numbers are found on study area map (Fig.1).

Major Steller sea lion haulouts within the study area

Map #	Site	Abbrev	Use	season
1	Latax Rks	LA	H	year-round
2	Sea Otter Rks	SO	H	year-round
3	Sea Lion Rks	SL	H	year-round
4	Marmot	MA	H, R	year-round
5	Long Is	LI	H	Winter-only
6	C. Chiniak	CH	H	year-round
7	Ugak Is	UG	H	Summer-only
8	Gull Pt	GP	H	year-round
9	C. Barnabas	CB	H	year-round
10	Two-headed	TH	H, R	year-round
11	C. Ikolik	IK	H	year-round
12	C. Ugat	CU	H	year-round

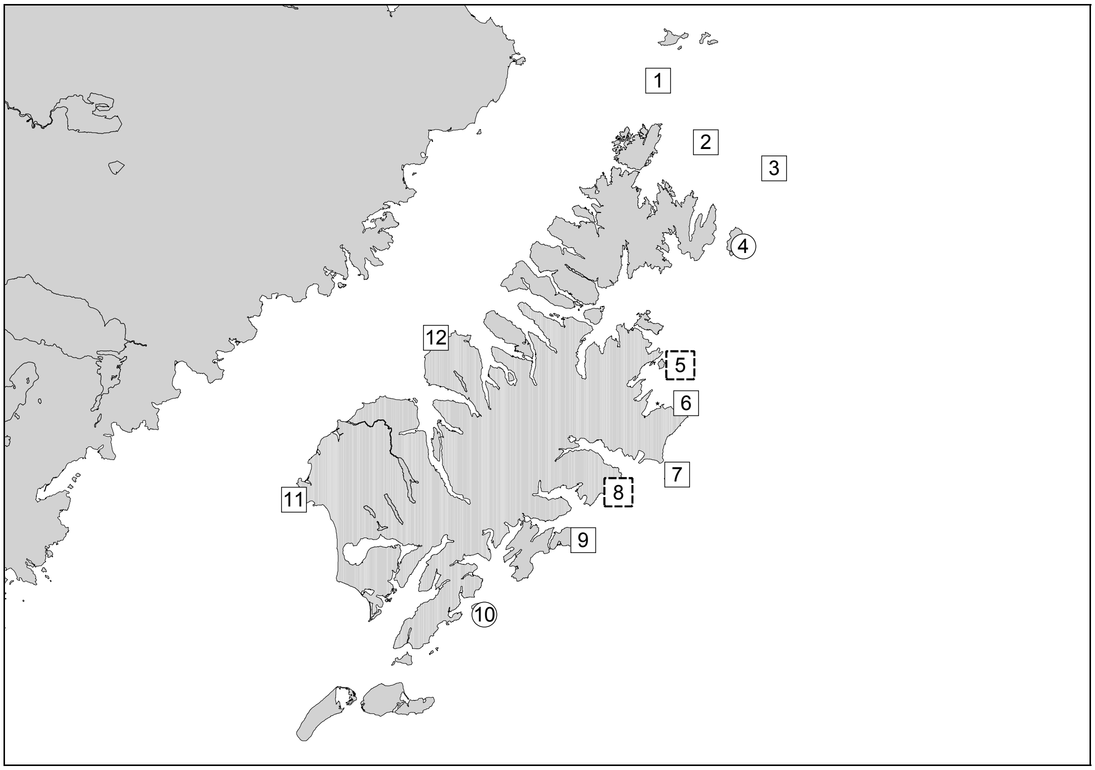

Figure 1. Twelve major Steller sea lion haulouts (□) surveyed in the Kodiak Archipelago, including sites (○) also used as a rookery during the breeding season.

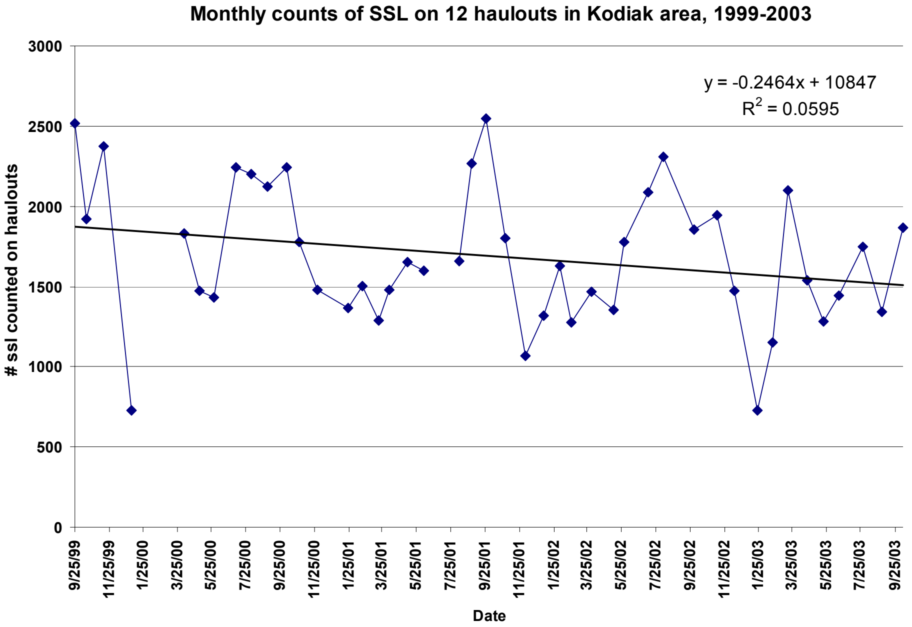

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Figure 2. Counts and trend in number of Steller sea lions using 12 haulout sites in the Kodiak Archipelago during GAP surveys, Sep 1999- Sep 2003.

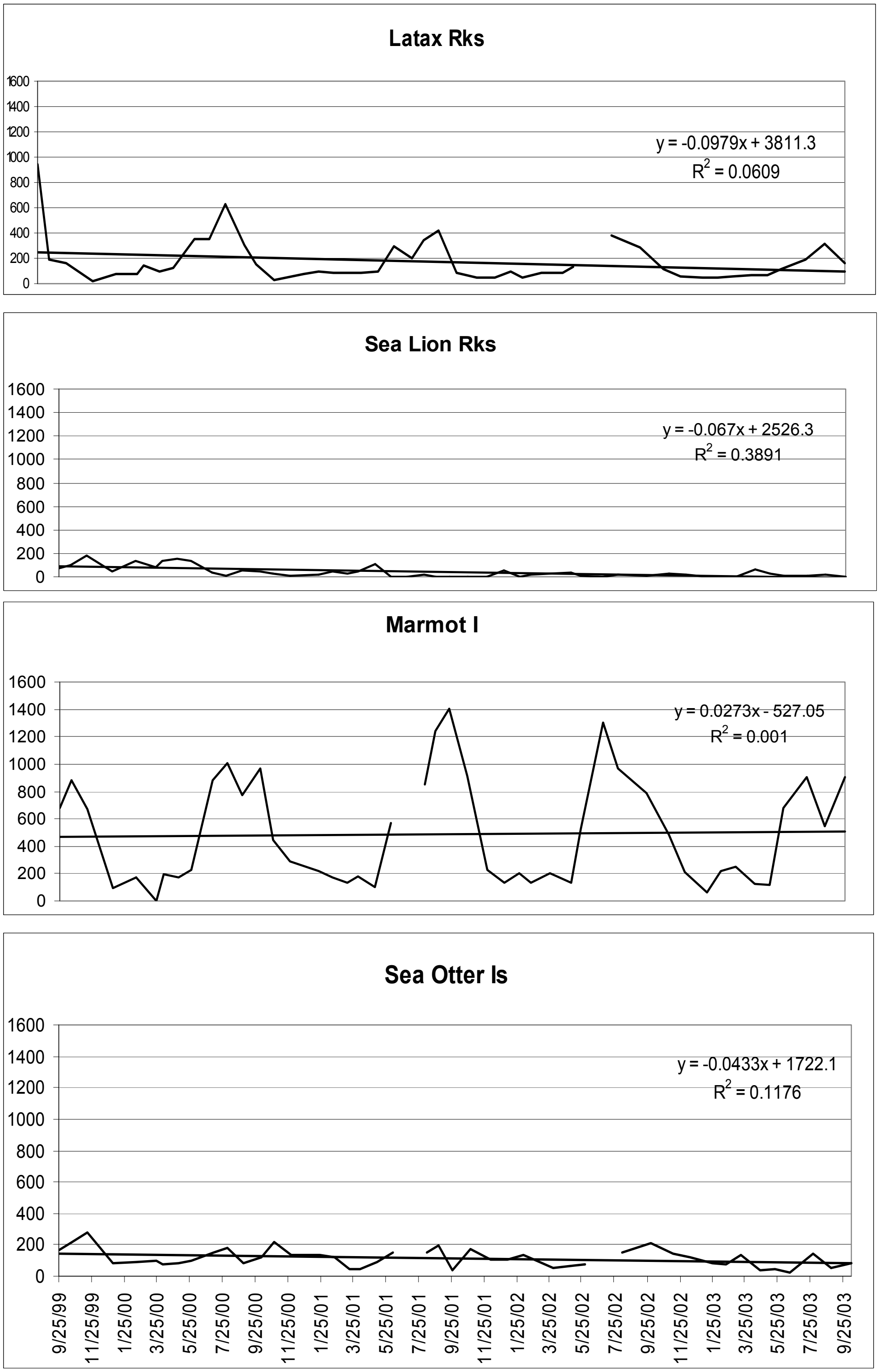
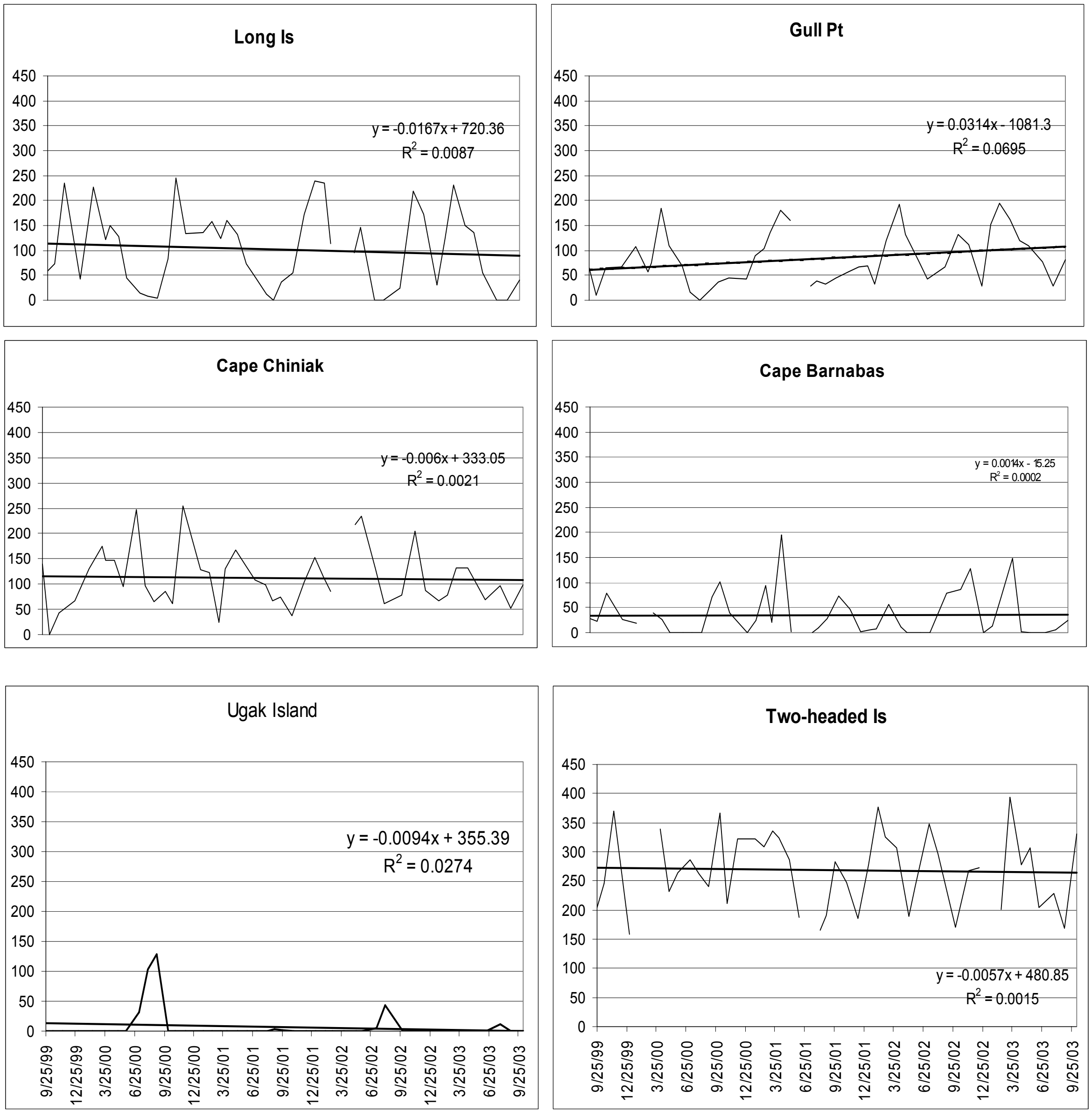


Figure 3. Counts and trends in number of Steller sea lions on north Kodiak haulouts, Sep 1999-Oct 2003.


Long Is

Gull Pt

Cape Chiniak

Cape Barnabas

Ugak Island

Two-headed Is

Figure 4. Counts and trends in numbers of Steller sea lion on eastern Kodiak haulouts, 1999-2003.

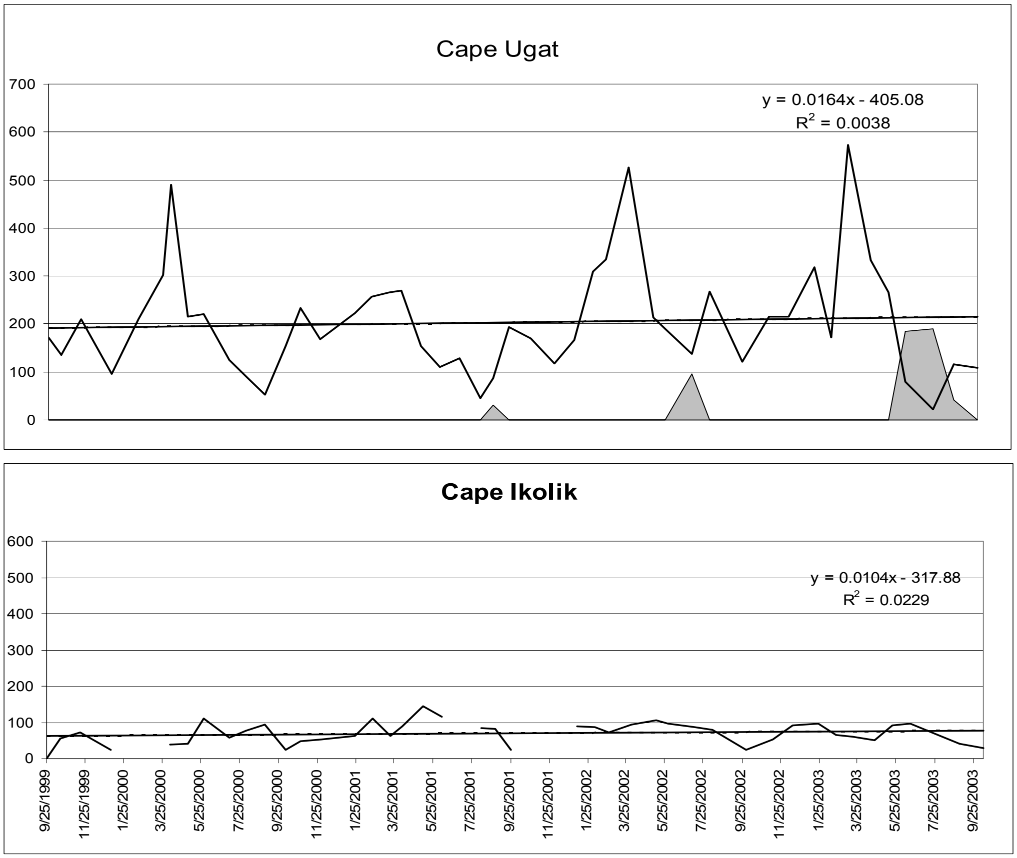


Figure 5. Counts and trends in numbers of Steller sea lion on western Kodiak haulouts, 1999-2003.

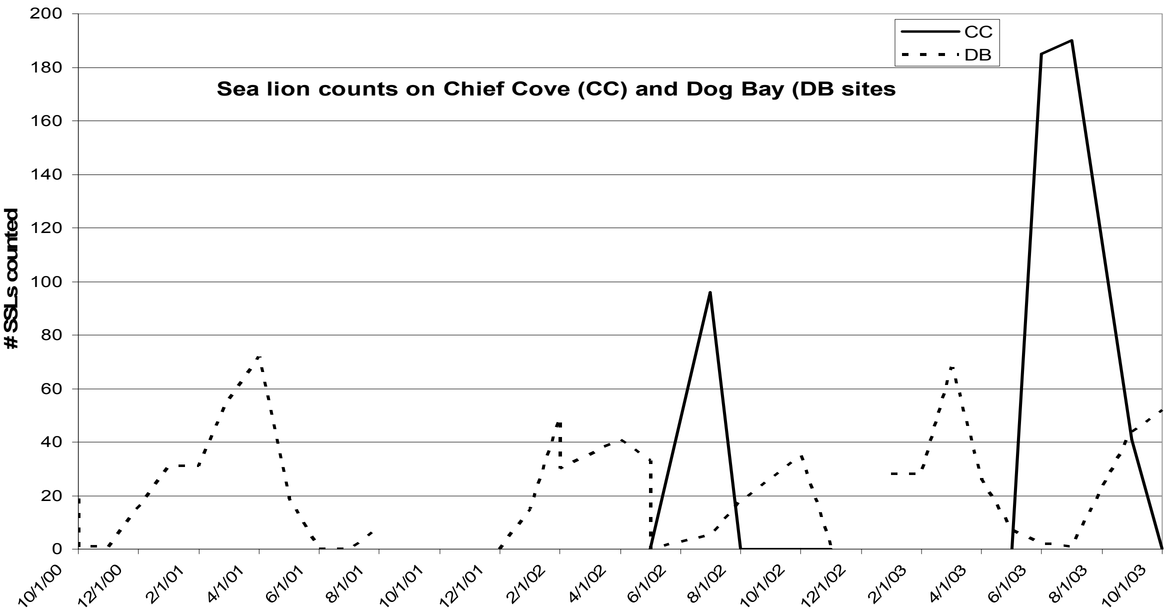


Figure 6. Counts and seasonal trends in numbers of Steller sea lions using two “new” haulout sites, Dog Bay (DB) and Chief Cove (CC). These sites were added to the survey route beginning in October 2000 and May 2002 respectively

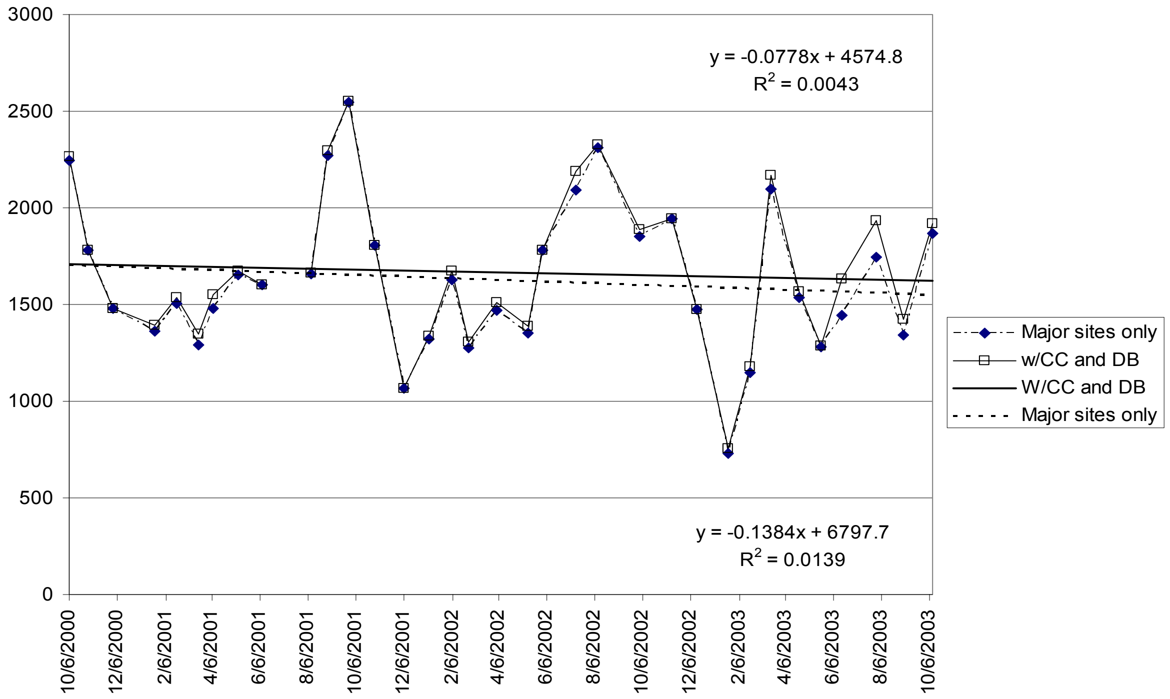


Figure 7. Comparison of totals and trends in number of sea lions using only major sites (__) and with inclusion of counts made on Chief Cove (CC) and Dog Bay (DB) haulouts (- - -), October 2000-2003.

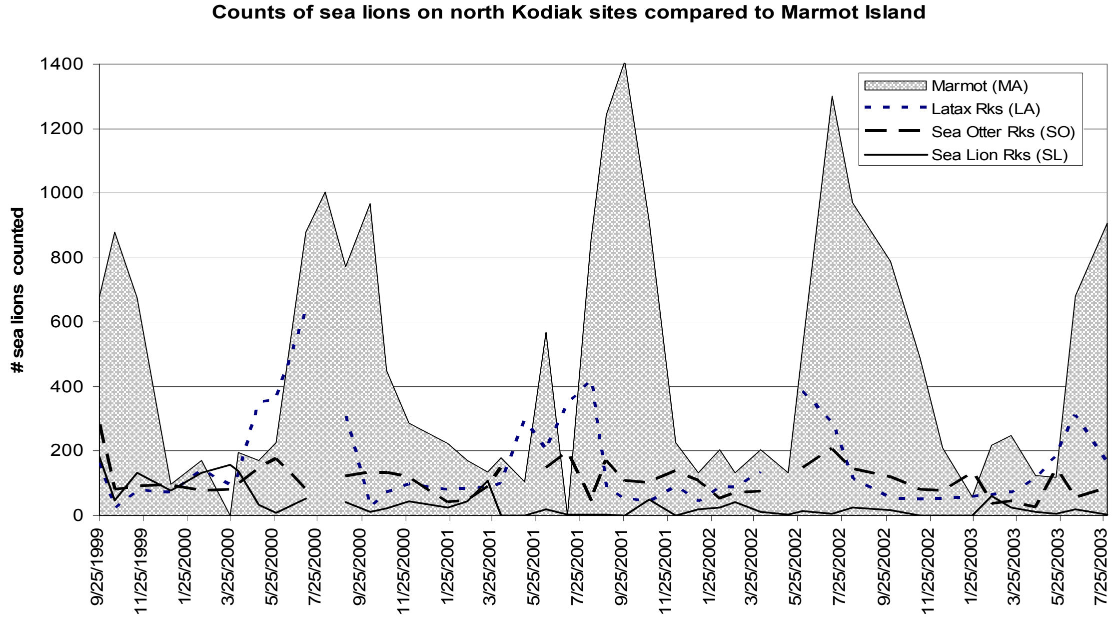


Figure 8. Counts of Steller sea lions on three north Kodiak haulouts compared to counts on Marmot Island (rookery) Sept 1999- Oct 2003.

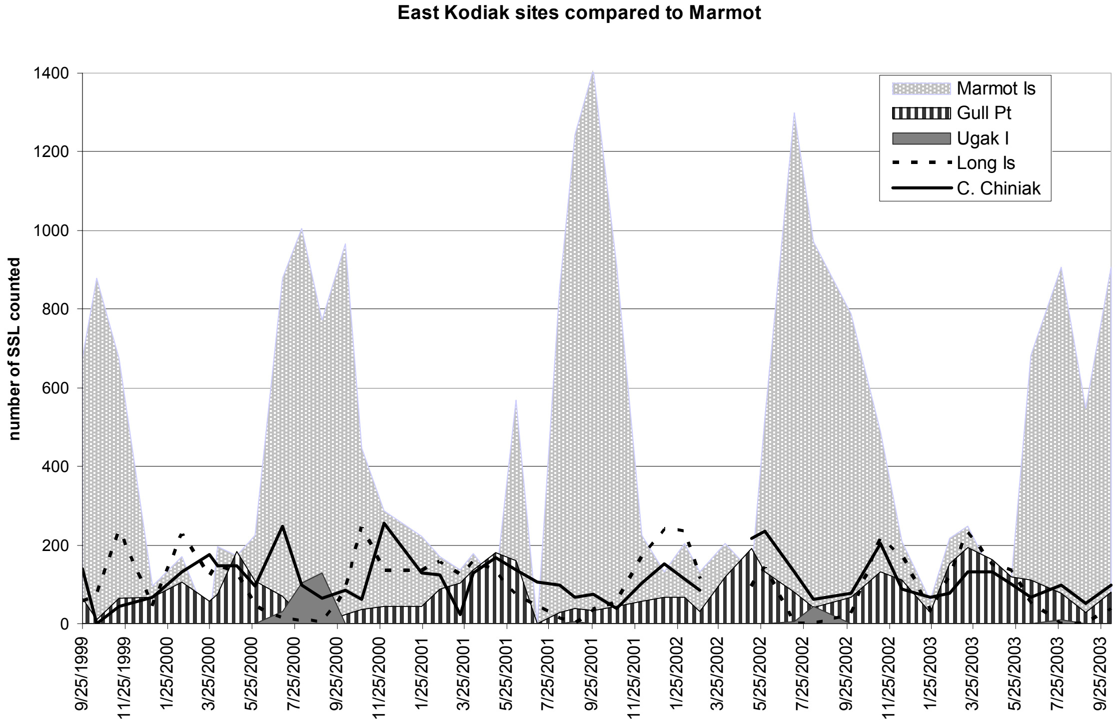


Figure 9. Counts of Steller sea lions on four east Kodiak haulouts compared to counts on Marmot Is (rookery) Sept 1999- Oct 2003.

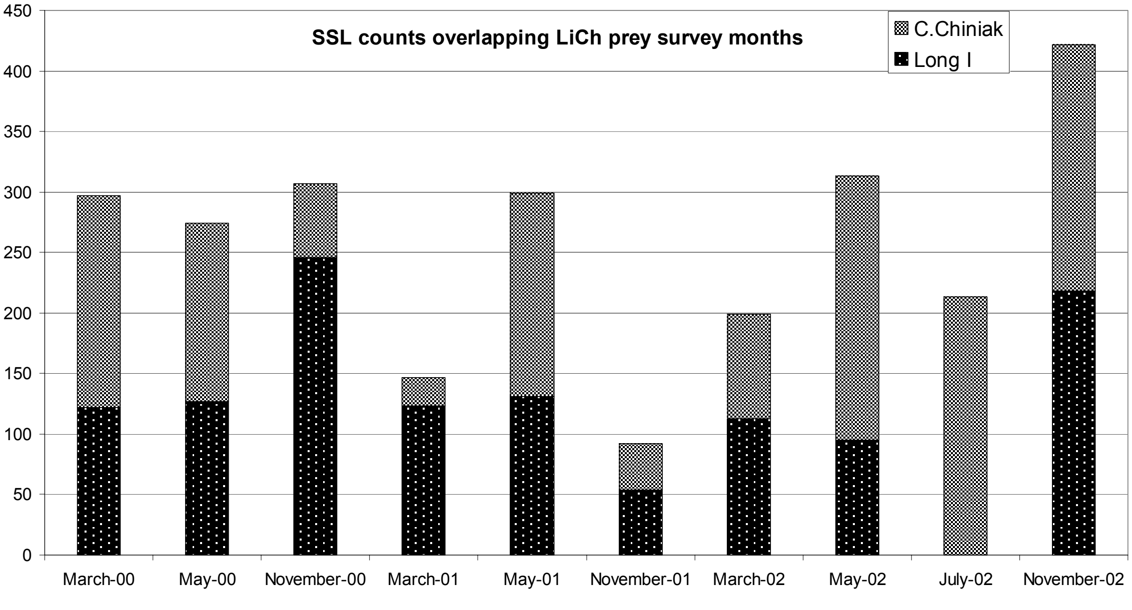


Figure 10. Counts of sea lions on Long Island and Cape Chiniak haulouts in months that overlapped LiCh prey surveys (Foy, this volume).

Dive behavior of harbor seals (*Phoca vitulina richardsi*) within Steller sea lion Critical Habitat on the east side of Kodiak Island, Alaska

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Introduction

Harbor seal (P*hoca vitulina richardsi*) numbers declined more than 80% in western Alaska in the 1970's and 1980's, coinciding with similarly drastic declines in Steller sea lion numbers (Merrick *et al.* 1987, Pitcher 1990). In an effort to monitor the trend in harbor seal population growth, the Alaska Department of Fish and Game (ADFG) initiated a monitoring program at three key "trend routes" in Alaska including one in Kodiak (Small et al. 2001). This route, encompassing 30 haulouts on the east and south coast of the Kodiak Archipelago, was surveyed annually from 1993 to 2003 and showed a 5.6% annual increase in the number of harbor seals counted (Small et al. 2003).

This steady increase in harbor seal numbers in the Kodiak area is in marked contrast to the continued decline of Steller sea lions in this area. Steller sea lion counts on rookeries and haulouts in the central Gulf of Alaska decreased by approximately 6.2% annually between 1991 and 2002 (Sease et al. 2001, Sease and Gudmundson 2002, NMFS unpubl. data 2004). Surveys conducted in 2002 and 2004 suggest Steller sea lion numbers in the central GOA (including Kodiak Archipelago) continue to decline despite noted increases in other regions (NMFS unpubl. data 2004).

Potential causes for the decline of these populations in the 1970's and 1980's remain unclear but are suspected to include limited prey availability or quality and its effects on juvenile survival (Pitcher 1990, Merrick *et al.* 1995, Merrick *et al.* 1997, NRC 2003, Trites and Donnelly 2003). The diets of both species are diverse and often reflect regional and seasonal availability of prey and they often forage on many of the same species. Jemison (2001) found the diet of Kodiak seals in the 1990's to be dominated by Irish lords and sandlance, with Pacific cod, walleye pollock, salmon *spp*, arrowtooth flounder, sole *spp*., greenling, and cephalopods also important (occurring at >10% of 321 scats). Sinclair and Zeppelin (2003) found similar key species in Steller sea lion scats in the Kodiak area in the 1990's, including pollock, salmon, arrowtooth flounder, Pacific cod, Irish lords, snailfish, herring, sandlance, Irish lords and cephalopods (occurring seasonally at >5% of 334 scats). Wynne *et al.*(2003) found pollock, arrowtooth flounder, sandlance, Pacific cod, salmon *spp*., Irish lords, sole *spp*., sandfish, capelin, and snailfish to be seasonally important (occurring seasonally in >10% of 356 scats) in the diet of Steller sea lions in the Kodiak area in 1999-2000.

With this degree of overlap in diet composition and diversity, it would be reasonable to assume that growth in sympatric harbor seal and Steller sea lion populations would have similar direction and trajectories as prey availability changed. The fact that harbor seal numbers have increased since 1993 while Steller sea lion numbers have continued to decline in the Kodiak region suggests 1) the availability of prey is limited for Steller sea lions but not harbor seals or 2) factors other than prey availability are regulating these pinniped populations in the Kodiak area.

Different spatial and/or temporal patterns of habitat use by sympatric consumers could suggest differential availability of certain prey. For instance, physiological constraints on dive ability could limit a mammal's access to some benthic or epibenthic prey resources. The availability of pelagic prey with diurnal migrations could also vary temporally for a mammal with limited dive depths. The prey species found in both harbor seal and Steller sea lion diets utilize habitats ranging from nearshore to shelf break and pelagic to epibenthic. Some have limited diurnal vertical migrations (e.g. Irish lords, sandlance, soles, flounders, and gadids); some have predictable seasonal movements (e.g. salmon concentrate at mouths of natal streams). Examining the dive patterns of sympatric harbor seals and Steller sea lions is one means of assessing their spatial and temporal use of habitat, potential access to shared prey resources, and differential foraging efficiency.

The depth and duration of dives made by Alaskan harbor seals have been found to vary in relation to time of day, season, and location. Frost *et al.* (2001) found that seals in Prince William Sound (PWS) spent most time in the water and diving at night (hours of 2100-0300) and that most dives were in the 20 to 75 m depth range. Gotthardt (2001) suggests that seals in PWS found more prey in shallow water at night where they spent 52% of their time diving to depths <20m, 23% 20-50m, and 25% >50m. Gotthardt also found that adult females dive depths were variable but generally shallower than subadults' (adult female average max. depth (AMD)=39.3m ± 26.4 and subadult AMD=98.2 ± 23.9). Of seals tagged in Kodiak, Swain and Small (1997) found that subadult seals made the deepest mean and maximum dives (33.6m and147m, respectively) while adult females made the shallowest mean and maximum dives (19.1m and 35m).

Steller sea lions in Alaska appear to forage in relatively shallow water depths with a noted increase with age to adulthood (Merrick and Loughlin 1997). Loughlin *et al.* (2003) found that Steller sea lion pups (7-10mos) in Alaska were capable of diving to 252m but that their mean maximum dive depth was 25.7m and their mean dive duration was only 0.8 minutes. Yearlings had a maximum dive depth of 288m but on average they dove for just 1.1min to maximum depths of 63.4m (Loughlin *et al.* 2003). Adult females tracked in summer were found to dive to median and maximum depths of 21m and 150-250m, respectively); those tracked in winter dove deeper and longer (Merrick and Loughlin 1997).

In this report we summarize the depth, time, and duration of dives made by a sample of harbor seals within designated Steller sea lion Critical Habitat in the Kodiak area in 2002 and 2003.Our data will be used in subsequent comparisons to dive data collected from 11 Steller sea lions tagged on Long Island or Cape Chiniak in 2002 and 2003 (NMFS unpub data www.nmml.nmfs.noaa.gov) to elucidate differential use of northeastern Kodiak waters by these sympatric piscivores.

Methods

Project personnel collaborated with Alaska Department of Fish and Game (ADFG) biologists to capture seals within the study area in October 2002 and March 2003. Captures were attempted at five haulouts in the Chiniak Bay area with a variety of techniques; we were only successful using a beach seine at Middle Island in Kalsin Bay (Figure 1). The net was deployed at moderate speed to catch seals as they vacated the haulout, taken ashore at both ends, and hauled in (Frost and Lowry 1994). Seals caught within the seine were removed and held in hoop-nets for subsequent sampling and instrumentation.

Two types of electronic tags were attached to seals to facilitate the assessment of harbor seal dive behavior. A VHF radio (ATS Inc., model MM320; 3.5 cm x 5.6 cm x 2.1 cm, weighing 70g) was attached to the pelt of each seal's head with *Devcon 5-minute Epoxy.* These radios transmitted a signal at 50bpm that was tuned to a unique VHF frequency between 164-166 MHz, allowing identification of individual seals when located. Because VHF signals cannot be detected when the antenna is submerged, the primary use of head-mounted VHFs was to monitor seals at-sea when surfacing between dives, allowing tracking by boat and fine-scale monitoring of movements and location during foraging bouts

Combination VHF/TDR tags were attached with epoxy to the dorso-lumbar pelt on seals to monitor dive behavior. Each tag contained one VHF transmitter (ATS Inc., model MM 190) with distinctive frequency for locating seals (or tags) and one archival time-depth recorder (TDR) (Wildlife Computers Inc., model MK9) for archiving time-linked pressure and temperature data during dives. These instruments were epoxied together with syntactic foam to form a tag 6.6 cm x 14.5 cm x 2.56cm and weighing approx.190g. These VHF/TDR tags were designed to float after being shed during the seals annual molt, allowing location and retrieval of the archival TDR without recapturing the animal. TDRs deployed in October were programmed to record pressure, temperature, light levels, and saltwater resistance every ten seconds, continuously. TDRs deployed in March were programmed to record pressure, temperature, and saltwater resistance every five seconds and light and battery voltage every ten seconds continuously.

Mobile and fixed antenna systems were used to detect VHF transmissions, locate seals, or recover VHF/TDR backpacks after being shed. Automated data-recording systems using mast-mounted Yagi antennas were used to record the presence and absence of tagged seals within Chiniak Bay area. Mobile receivers were used in planes, on boats, and on land to locate and retrieve shed VHF/TDR backpacks.

Once backpacks were recovered, Wildlife Computer's BETA Instrument Helper software (Version 401) was used to access and process data archived in the TDRs. This software generated a graphical representation of two dimensional dive data; recorded dive data were assessed in one hour time blocks. A combination of pressure, salt water resistance, temperature, and light level sensor readings were used to determine when a seal was at the surface. This was also used to derive a correction factor needed to 'zero' the pressure readings to surface pressure equivalence. The Zero Offset Correction (ZOC) command was used to manually correct for erroneous drift that occurred in the pressure recordings; data collected when drift exceeded the programs ability to distinguish individual dive (when reviewing light, seawater resistance, and depth measurements) were excluded from the dive analysis. In the dive analysis, the Minimum Dive Depth was defined as 3 meters, the Allowable Surface Error as 1 meter, and Percent of Maximum Depth for Bottom as 90%. Dive summaries, including start time, duration, max depth, bottom time, number of wiggles, average wiggle distance, average descent rate, and average ascent rate, were saved in an Excel file.

Post-hoc processing in Excel included converting Universal time recorded on the TDRs to local Alaska Standard Time and assignment of dates to TDR deployment week numbers. Data were aggregated in four time blocks (1 = 0300-0859, 2 = 0900-1459, 3 = 1500-2059, and 4 = 2100-0259) and six depth bins (1 = 4-20m, 2 = 21-50m, 3 = 51-100m, 4 = 101-150m, 5 = 150-200m, and 6 = >200), duplicating those used in ADFG's 1993-95 Kodiak harbor seal studies (Hastings et al 2001). Weekly summaries of dive data for each seal were compiled in an Access database to derive query-generated summary statistics.

Results

A total of 19 seals were captured, nine in October 2002 and ten in March 2003 (Table 1). Of these, 15 (8 in October, 7 in March) were measured, tagged, sampled and equipped with a VHF/TDR backpack. Because the tags attached to the pelt were shed during the summer molt, those deployed in October could potentially remain attached for eight to ten months and those deployed in March for four months.

Eight out of the fifteen TDRs were retrieved during summer 2003. Of these, five of the eight TDRs recovered had recorded and collected data and three had suffered catastrophic failure. Of the five functional TDRs, four (one sub-adult and three adult males) collected salvageable data from October 13, 2002 to the middle of February, 2003 before substantial drift and eventual failure of pressure sensors compromised their data. We truncated our data set for these four animals on 15 February at appoint where the data were uncompromised. The other functional TDR, deployed in March on an adult female that was visibly assessed to be pregnant, recorded data through July 2003 (Table 1). Data from these five functioning TDRs provide insights into activity budget (% time submerged below 3m) and dive patterns of individual seals (Table 2).

Adult female (03KOD03)

The adult female, determined visually to be pregnant when captured, made 26,476 dives for a total of 75,573 minutes submerged (or approx 46% of her time deeper than 3m) during the deployment period of 30 March through 26 July 2003 (Table 2). Overall, her dives averaged 2.85 minutes in duration and her maximum dive time was 17.2 minutes. Her overall maximum dive depth was 218m but her average maximum depth within a dive series was only 24m (Table 2). The maximum dive time occurred while she dove within the shallowest depth bin (3-20m) (Table 3). No clear patterns were noted in her diving relative to time of day although she spent more time diving at night and early morning than other time periods (Table 4).

Changes in her dive behavior were evident during the weeks of June 1st through June 15th (relating to week numbers 10 through 12, Figure 2). This time period coincides with the peak period for seal pupping on nearby Tugidak Island (Jemison *et al.* 1998). Total dive counts did not change appreciably during this time but the number of counts within depth bin1 (3-20m) increased while all others fell to zero. The weekly percentage of time spent submerged (below 3m) dropped considerably as most of her time was spent at the surface, either in the water or hauled out.

Adult and subadult males

Four male seals (3 adult:1 subadult) were equipped with functioning TDR packages from 13 October to 15 February 2002 that recorded 113,247 individual dives (Table 1). Mean dive duration was similar for all males, averaging between 2.85 and 3.77 minutes per dive. The percentage of total time spent submerged below 3m varied considerably between individuals, ranging between 44.5 and 66% (Table 2). The maximum individual dive durations ranged from 14.0-22.5 minutes.

A clear dichotomy was noted in the maximum depth of dives recorded by males; two males dove deeper than 200m while two other never dove deeper than 65m (Table 2). The subadult male made consistently deeper dives than the adult males (Table 2), as evidenced by weekly average depth distribution of male dives (Figure 4). No clear temporal patterns were evident in male dive patterns although the three adults spent the least amount of time diving during the mid-day time period (Table 4).

Discussion

Gender-specific trends

Our sample size was too small to assess gender-specific trends. However, a clear shift was noted in the dive behavior of adult female 03KOD03 in early June, coinciding with the period of pupping on nearby Tugidak Island (first pups born mid May, peak numbers in mid-June (Jemison et al. 1998). Female harbor seals nurse their pups for 3-6 weeks (Bishop 1967, Hoover 1983). Our female's time spent diving and average depth of dives dropped precipitously in weeks 10 and 11, presumably associated with post-partum fasting and began to increase by week 12, presumably during late lactation as her pup approached weaning. This female did not dive to depths >10m until 18 June but the next week (25 June) she abruptly began diving to depths >80m and by Week 14 (late June) she had resumed her dive 'routine'. These findings are consistent with those of Bowen *et al.* (2001) who found the onset of diving during lactation varied considerably among female harbor seals, with dive bouts resuming 1-16 days postpartum (range). Others have found that lactating harbor seals may start foraging before the weaning process is completed (Boness *et al.* 1994, Bowen *et al.* 2001, and Baechler *et al.* 2002).

Temporal trends

The five seals in this study spent the greatest amount of their time diving during the 21:00-03:00 time period. Further analyses will seek correlations between time of day and depth of dives made. Gotthardt (2001) observed time of day as having a significant effect on dive frequency and depths to which Prince William Sound harbor seals dove; most dives occurred at night (21:00-03:00) while the deepest dives occurred from 03:00-09:00 and shallowest from 09:00-15:00. Frost *et al.* (2001) also found that Prince William Sound seals spent the greatest percentage of time in water between 21:00-03:00 and the least amount in the water from 03:00-09:00.

Depth trends

Mean dive depths of seals in this study were shallow: both sexes spent most their time and dives in water <50m deep. This finding is consistent with dive depths previously recorded in Kodiak, where 94.7% of dives recorded were <50m (Hastings *et al*. 2001). Frost *et al.* (2001) reported diving by harbor seals in Prince William Sound was focused in the 20 to 100m depth range and more than half of harbor seal dives reported by Gjertz *et al.* (2001) were shallower than 40 m in depth. The three adult males in this study tended to dive deeper during the low light hours of the day but, because the majority of their dives where <20m, this pattern is lost in the depth-binning of our results.

The maximum dive depth recorded by TDRs placed on our seals was 218m for the female and 274m by one of the males. These maximum depths are shallower than those recorded by female (368m) and male (320m) seals tracked with satellite-linked depth recorders (SLDRs) in Kodiak in 1993-96 (Hastings et al 2001). This difference may reflect either bathymetric differences in study areas or shallower foraging by seals relative to the sea bed. Variations seen in dive depths may be a function both of geographic location and prey location (Tollit *et al.* 1998, Frost *et al.* 2001, Gotthardt 2001, Small and Ver Hoef 2001). We cannot address this issue because we lack locational linkages and thus the bathymetric data associated with our dive depths.

Mean dive durations increased with dive depth but the longest dives for both sexes occurred in dives to <50m. Gjertz *et al.* (2001) and Lowry et al. (2001) associated deeper and longer dive durations to seals foraging at or past the shelf break. Problems associated with combining locational and dive data have limited our ability to determine where seals forage relative to the sea bed (Gjertz *et al.* 2001, Tollit 1998).

These preliminary data provide a means of comparing one dimension of harbor seal habitat use to that of other consumers being monitored within the same bays. In particular, we plan to compare seal dive data to data collected from Steller sea lions captured in and near Chiniak Bay by ADFG and NMFS researchers from 2000-2003 (NMML unpub data) as those data become available. In their absence, we compared our seals data to dive patterns of 18 immature Steller sea lions tagged throughout Alaska (Loughlin *et al.* 2003). Young-of-the year Steller sea lions were found to have a mean dive duration of 0.8 min, mean maximum dive depth of 25.7m, and maximum dive depth of 252m. Yearlings had a mean dive duration of 1.1min, mean maximum dive depth of 63.4m, and maximum dive depth of 288m (Loughlin et al. 2003).

On average, the seals we studied made longer but shallower dives than immature Steller sea lions studied in Alaska (Loughlin et al. 2003). Mean seal dives were 2-4 times longer than dives made by these immature Steller sea lions. On average, the immature Steller sea lions dove deeper than the seals in our study (mean max. dive depth) although the maximum depths reached by diving seals and sea lions were similar. Future analysis of dive data from Steller sea lions tagged within our study area in 2002 and 2003 are needed to discern differential use of the marine habitat by these sympatric pinnipeds. Future geo-positional linking of dive data is needed to determine if there is an inshore-offshore segregation of foraging by these sympatric species. Future GAP analyses will seek associations between mean seal dive depths and the species-specific depth of prey fields found during GAP's LICH prey surveys in November 2002, March and May 2003.

Conclusions

In this study we consider spatial and temporal patterns of diving behavior to be indicators of habitat use by harbor seals. Although we lack geographic linkage to dive profiles, we found preliminary evidence suggesting there may be age or gender-specific patterns in habitat use by seals sampled in this study. A larger sample size and longer deployment period are needed to clearly distinguish these patterns from individual variation. There is significant dietary overlap between seals and sea lions in the Kodiak area. A comparison of species-specific dive patterns of tagged animals simultaneously using the same area may illuminate temporal patterns in dive behavior suggestive of differential foraging patterns. Such studies and analyses will further our ability to judge whether prey availability may be differentially affecting these species and contributing to their disparate population trajectories in the Kodiak region.

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Table 1. Summary of time-depth recorder (TDR) deployment history and data recovery for five seals sampled in 2002 and 2003.

Animal				TDR Date			Data recorded		
Seal #	**Age**	**Sex**	**Mass (kg)**	**deployed**	**recovered**	**last usable data**	**# days**	**# dives**	**# minutes**
03KOD03	AD	F	111.6	3/30/03	7/30/03	7/26/03	112	26,476	161,280
02KOD01	SA	M	65.5	10/13/02	8/7/03	2/15/03	126	29,752	181,440
02KOD04	AD	M	101.6	10/13/02	7/14/03	2/15/03	126	24,556	181,440
02KOD07	AD	M	97.5	10/13/02	7/9/03	2/15/03	126	27,158	181,440
02KOD08	AD	M	129	10/13/02	7/11/03	2/15/03	126	31,781	181,440

Table 2. Summary of dive depth, duration, and % time spent diving below 4m for five harbor seals equipped with TDRs in Kodiak, 2002-2003.

Harbor seal			Max Dive depth (m)			Dive duration (minutes)			Diving (>4m)	
Seal #	**Age class**	**Sex**	**Max**	**Mean**	**Std dev**	**max**	**mean**	**Std dev**	**# mins**	**% total time**
03KOD03	AD	F	218	24.1	20.03	17.2	2.85	1.51	75,573	46.9
02KOD01	SA	M	274	43.9	50	16.0	3.63	1.97	107,036	59.5
02KOD04	AD	M	56	15.7	11.1	22.5	3.29	1.96	80,706	44.5
02KOD07	AD	M	215	11.9	9.3	18.5	3.04	1.97	82,484	45.5
02KOD08	AD	M	64	10.7	7.6	14.0	3.77	2.6	119,681	66.0

Table 3. Number, duration, and % of time spent diving in each of six depth bins as recorded by TDRs deployed on one female and four male harbor seals in Chiniak Bay, Alaska.

	Adult female (161,280 minutes total; 75,573 minutes diving)					All Males Combined (725,760 minutes total; 390,808 minutes diving)				
Depth Bins	Dive Count	Mean Dive Duration	Max Dive Duration	Sum Dive Time	% of Total Time	Dive Count	Mean Dive Durat'n	Max Dive Durat'n	Sum Dive Time	% of Total Time
	(n)	(min)	(min)	(min)		(n)	(min)	(min)	(min)	
4-20 m	14623	2.08	17.17	30405	18.8	79010	2.88	15.5	227217	31.3
21-50m	8698	3.85	9.75	33474	20.8	25444	4.56	22.5	116079	16
51-100m	3070	3.65	15.75	11210	6.9	4325	4.9	18.5	21187	2.9
101-150m	73	5.54	7.42	404	0.3	2799	5.76	16	16112	2.2
151-200m	11	6.54	7.33	72	0	1174	5.87	14.5	6892	0.9
> 200m	1	6.83	6.83	7	0	495	6.71	13.5	3321	0.5

Table 4. Number, depth, duration, and % of time spent diving in each of four time blocks as recorded by TDRs deployed on one female and four male harbor seals in Chiniak Bay, Alaska.

	Adult female (161,280 minutes total; 75,573 minutes diving)					All Males Combined (725,760 minutes total; 390,808 minutes diving)				
Time Block	Dive Count	Avg Max Depth	Max Depth Max	Sum Dive Time	% of Total Time	Dive Count	Avg Max Depth	Max Depth Max	Sum Dive Time	% of Total Time
	(n)	(m)	(m)	(min)		(n)	(m)	(m)	(min)	
03:00-08:59	7211	26.5	190	21085	13.1	28494	21.55	261	93166	12.8
09:00-14:59	5642	21.19	186	15612	9.7	24271	21.74	269	83144	11.5
15:00-20:59	6529	25.42	218	18622	11.6	27259	20.25	274	102065	14.1
21:00-02:59	7094	22.77	145	20253	12.6	33223	19.84	245	112433	15.5

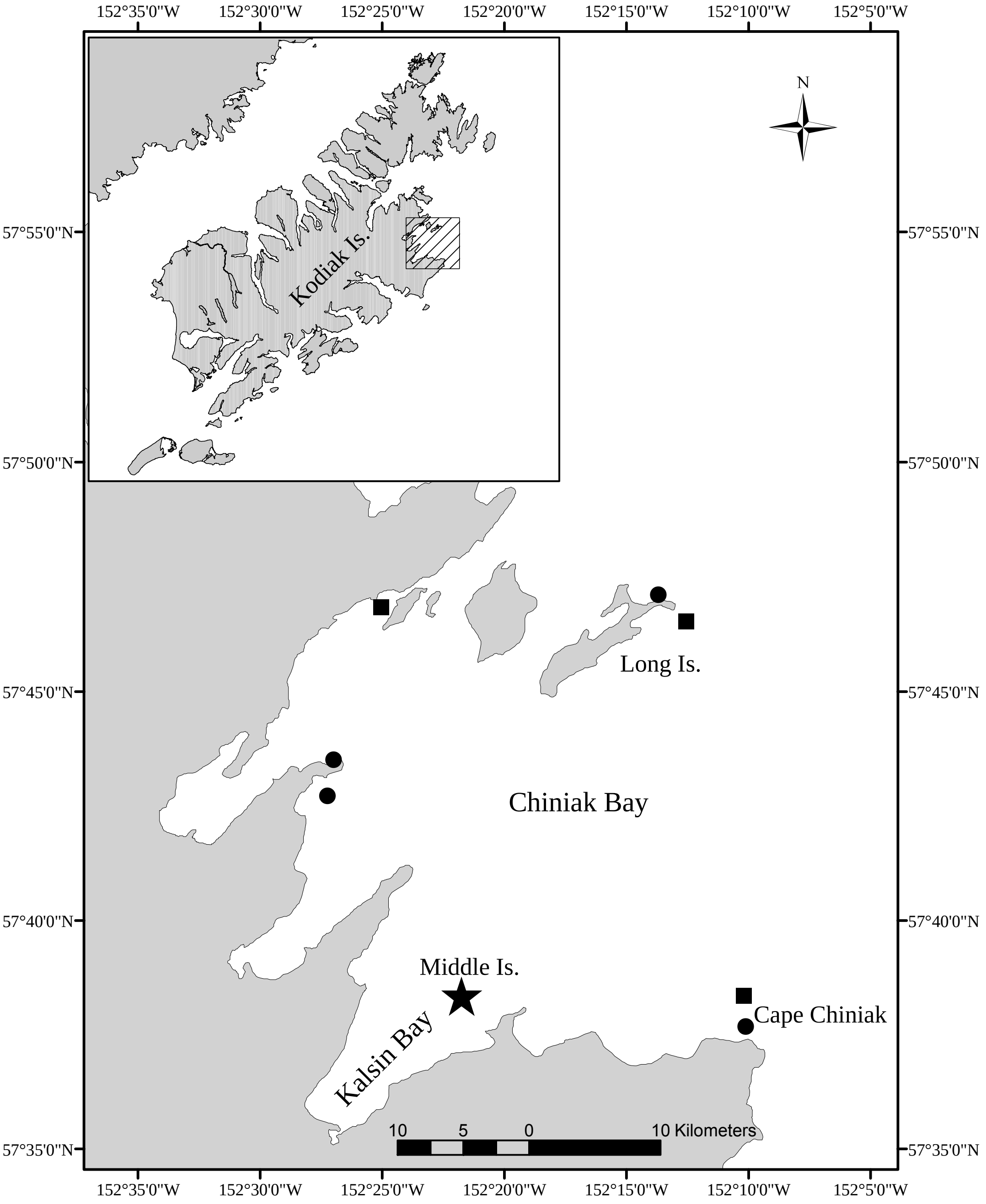

Figure 1. Map of study area in northeastern Kodiak Island, including Steller sea lion haulouts (■), harbor seal haulouts (●), and harbor seal capture location (★) in Chiniak Bay.

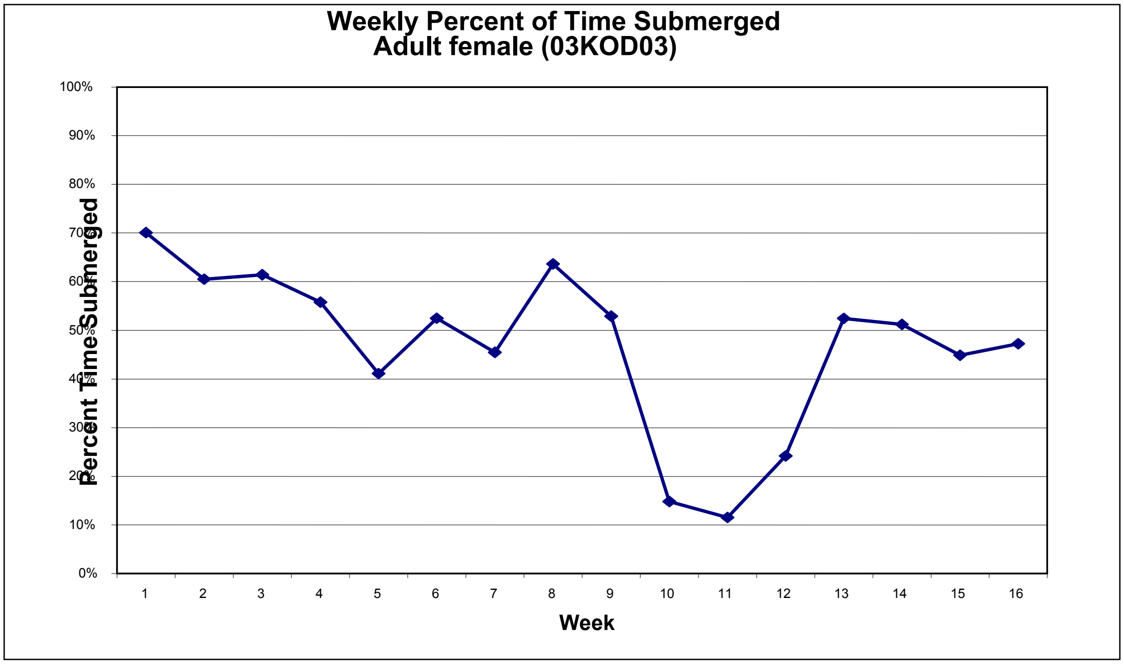

Figure 2. Weekly percentage of time spent diving by an adult female harbor seal (03KOD03) in the northeastern waters off Kodiak Island, Alaska. Weeks 1 through 16 represent the dates March 30, 2003 through July 26, 2003.

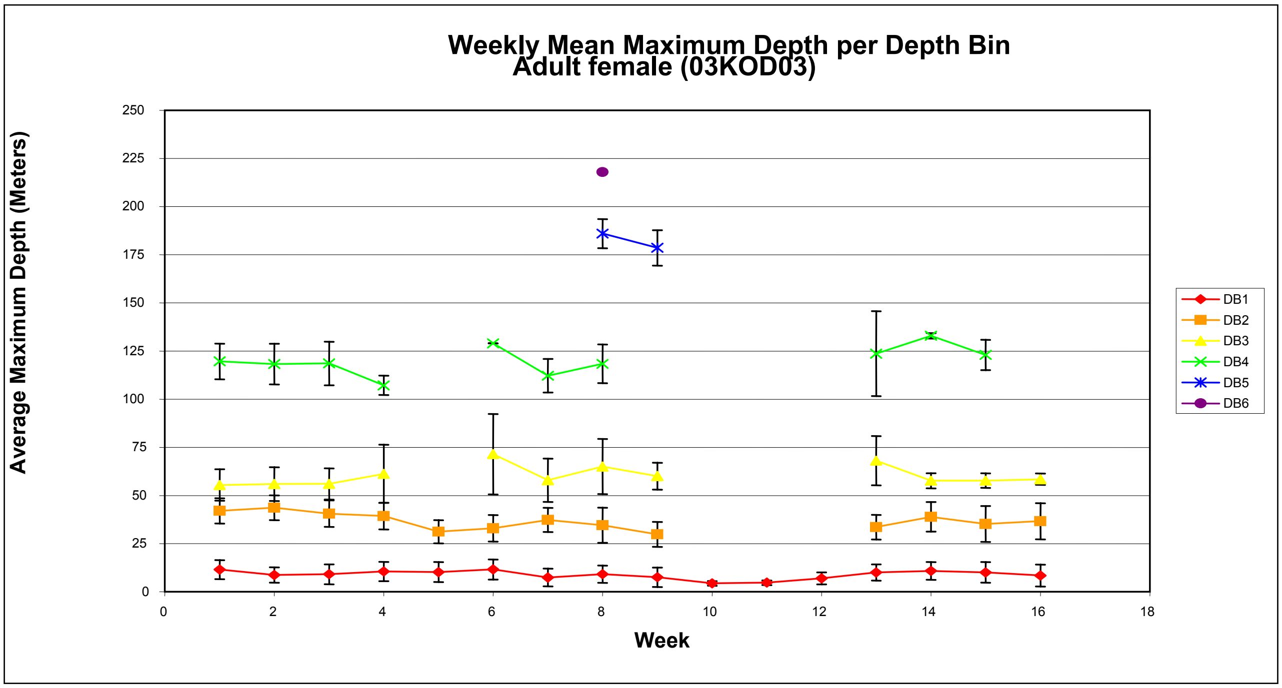

Figure 3. Weekly mean maximum depth values per depth bin (DB1 = 4-20m, DB2 = 21-50m, DB3 = 51-100m, DB4 = 101-150m, DB5 = 150-200m, and DB6 = >200m) with standard deviation bars for an adult female harbor seal (03KOD03) in the northeastern waters off Kodiak Island, Alaska. Weeks 1 through 18 represent the dates March 30, 2003 through July 26, 2003.

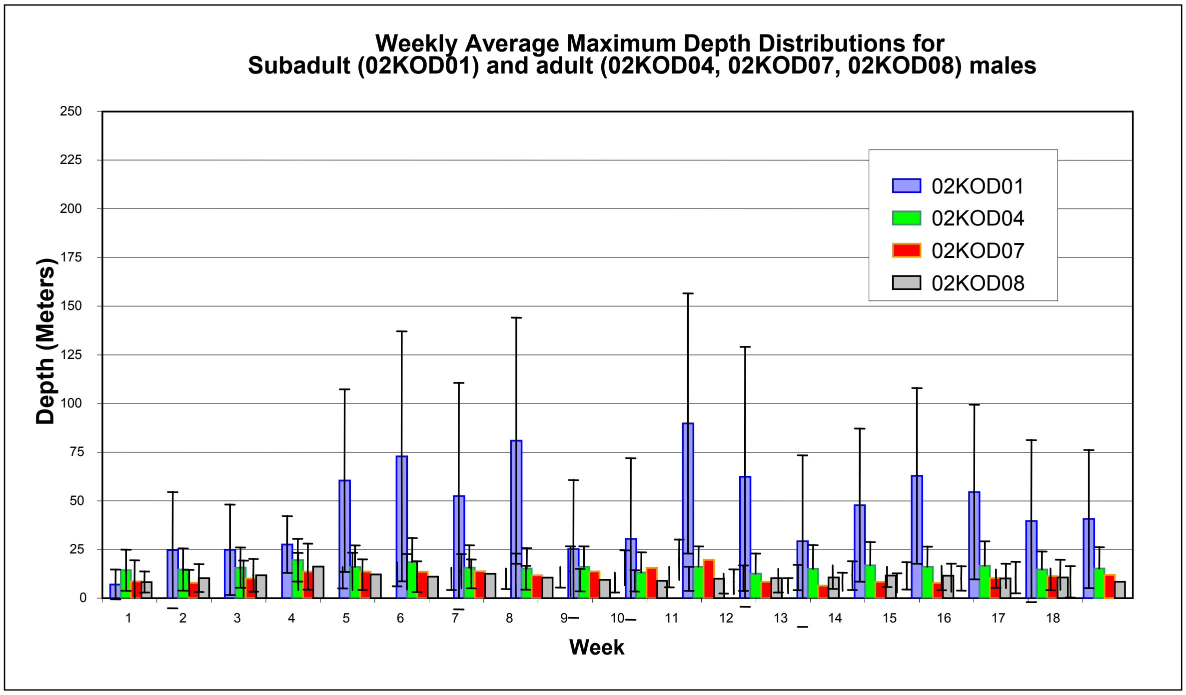

Figure 4. Weekly mean maximum depth values (+/- std dev) for one subadult (02KOD01) and three adult (02KOD04, 02KOD07, 02KOD08) harbor seals monitored in the waters off northeastern Kodiak Island, Alaska. Weeks 1 through 18 represent the dates October 13, 2002 through February 15, 2003.

Opportunistic Aerial Sightings of Large Whales Within Steller Sea Lion Critical Habitat in the Kodiak Archipelago

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Introduction

Kodiak Island waters support both resident and migratory populations of large cetaceans including fin whales (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), gray (*Eschrichtius robustus*), and killer whales (*Orcinus orca*). Several large cetacean species were commercially harvested from Kodiak waters for shore-based and offshore processing as recently as 1937 (Reeves et al 1985) and pelagically in North Pacific waters as recently as 1965 (Mizroch et al 1999). Now protected following centuries of harvest, some of the Pacific whale stocks that feed in Alaskan waters appear to be rebounding (Calambokidis et al 1997, Zerbini in press).

The Kodiak and western Gulf of Alaska waters are known to support substantial seasonal feeding aggregation of humpbacks (Waite et al. 1999, Witteveen 2003), fin (Mizroch et al 1999), and gray whales (Moore et al, in prep). Resident and transient killer whales have been documented feeding on fish and mammals in Kodiak waters (Matkin et al 1996). Fin and humpback whales can be found in Kodiak waters during winter months feeding on nearshore aggregations of herring, capelin, and other schooling fish (Zwiefelhofer, pers.comm.).

Whales that feed in Kodiak waters consume species that are key prey for other consumers in the system, including Steller sea lions (Pitcher 1981,Sinclair and Zeppelin 2002). In the northern hemisphere, humpback diets consist primarily of small schooling fish species including capelin, smelts, herring, juvenile pollock, and other prey commonly found in Steller sea lion diets (Merrick et al 1997, Kenney et al 1997). Fin whales may target euphausiids and large zooplankton as prey (Moore et al. 2000) but are also known to feed extensively on capelin and other schooling fish (Kenney et al. 1997). Gray whales feed primarily on epibenthic zooplankton (Nerini 1984) but have been found feeding pelagically on capelin (N. Black, pers comm.). Killer whales seen in the Archipelago include both mammal-eating ‘transients’ and fish-eating ‘resident’ pods (Matkin et 1999, Hiese et al. 2003). Matkin (pers. comm.)has found that many resident pods are targeting salmon as primary prey in summer months. Many of these prey species are also consumed by Steller sea lion , sea birds, and piscivorous fish in Kodiak waters (this volume). Thus, seasonal and year-round feeding by large whales in Kodiak waters has the potential to directly reduce fish prey available for consumption by Steller sea lions or secondarily reduce the volume of the prey upon which those fish species feed.

Whales are significant marine predators whose consumption of finfish has been estimated to exceed commercial fishery harvests in many ecosystems and which may compete with sea lions, seals, fish, and seabirds for prey (Kenney et al. 1997, Trites et al.1997). Estimating the abundance, distribution, and foraging ecology of these upper level consumers therefore is key to understanding their role as consumers and potential competitors of Steller sea lions in Kodiak waters. To understand the trophic interactions of these apex predators and their common prey source in Kodiak waters, researchers at UAF initiated the Gulf Apex Predator-prey (GAP) program of studies. As part of the GAP program, we monitored the seasonal presence and distribution of large whales in the Kodiak Archipelago through a series of repeated opportunistic aerial surveys.

Methods

Standardized cetacean surveys are typically conducted using fixed wing aircraft or research vessels as platforms following line transect methodology (Carretta and Forney 1993, Barlow 1999, Buckland et al 2001, Waite et al 2002, Zerbini et al in press). Conducting repeated and rigorous shipboard or aerial surveys of the area in this manner would have been cost-prohibitive within scope of GAP. However, GAP conducted as series of pinniped surveys in the area that provided an opportunistic platform from which to monitor seasonal presence/absence of cetaceans. In this report, we summarize the seasonal and annual distribution of large whale species observed during these surveys. Because of their opportunistic nature, no effort was made to use these sightings to derive population estimates.

Whale observations were recorded during two series of pinniped surveys conducted in the Kodiak Archipelago from June 2001 to June 2004. GAP personnel conducted monthly counts of Steller sea lion on 14 sites in the Archipelago from June 2001 to June 2004 (Wynne,this volume). In addition, Wynne collaborated with the Alaska Department of Fish and Game (ADFG) to conduct repetitive counts of harbor seals on 33 haulouts on the east and south side of Kodiak Island during August 2001 and 2002 (Small et al 2001). The area covered by these surveys falls primarily within designated Steller sea lion critical habitat (See Wynne, this volume).

In all surveys, a Cessna 206 on floats was flown at an altitude of 700-1500ft and speed of 90-110kn while transiting between harbor seal or Steller sea lion haulouts. All survey routes began in the City of Kodiak and proceeded south along the east coast of the island, transiting between haulouts on a systematic but not fixed course (FIG. 1). Harbor seal surveys extended to the head of most bays and ended at the south end of Kodiak Island. Steller sea lion surveys circumnavigated the Archipelago and covered waters further offshore. All cetacean sightings (defined here as groups of 1+ animals separated by more than 2-3 km) were noted along with their time and location. When time allowed, the plane diverted off the ‘transect’ to confirm species identification and estimate the number of individual whales present. Whales were often but not always photographed.

Survey timing and observer effort varied among surveys. Harbor seal surveys were scheduled to occur within 2.5 hrs of low tide, often started as early as 08:30 and were completed by 15:00. Steller sea lion surveys were scheduled to occur between 10:00 and 16:00, independent of tide stage. During harbor seal surveys, one observer and the pilot scanned opportunistically for blows and surfacing animals ahead of and on either side of the aircraft. During Steller sea lion surveys, the pilot and up to three observers scanned for whales. An approximate location (latitude/longitude) was recorded for each sighting based on GPS reading near the center of the group. Cetaceans were identified to species when possible or otherwise recorded as “other”; a gross estimate of the number of individuals per group sighted was also recorded.

The number of sightings and individuals recorded were summed by species, season, and year and approximate locations were plotted using ArcInfo. Seasons were defined as Winter (December-March), Spring (April-May), Summer (June-September), and Fall (October-November). This asymmetrical seasonal delineation is used throughout GAP studies and reflects local oceanographic patterns but may or may not affect whale distribution in the region.

Due to variable observer effort and area coverage during each survey, the number of whales observed was not used to calculate density or abundance estimates. A relative measure of survey effort in each survey, ‘survey hours’ (sHr), was determined as the number of hours flown (over water) per survey regardless of the number of observers or whale sighting conditions. This was used to derive a relative index of sighting frequency (# sightings or groups encountered per sHr) and whale density (# animals per sHr) for four identified species (fin, humpback, gray, killer whales) and Other species (unidentified large cetacean) by season and year. The relative density of groups (# animals per sighting) was also calculated for the same species.

Results

Aerial surveys were conducted on 45 days between 1 June 2001 and 1 June 2004 to count pinnipeds in the Kodiak archipelago (Wynne, this volume). On those surveys, approximately 175 hrs were flown over water, 41 hrs while on the harbor seal route and 134 hrs while on the Steller sea lion route (FIG. 1). The replicate harbor seal surveys conducted in August of 2001 and 2002 are responsible for the dominance (39.5%) of total effort in Summer01 and Summer02 (FIG. 2). Survey effort (hr) varied seasonally and annually (FIG. 2) and was used to determine the relative density of sightings per season and year (FIG. 3).

A total of 322 whale sightings involving an estimated 2126 whales were recorded opportunistically during pinniped surveys from 1 June 2001 to 1 June 2004 (Table 1). Whales were distributed throughout the study area (Fig. 4) and a mean of 1.8 groups were seen per hour of survey effort. Although seen in every month and year surveyed, sightings were most frequent during spring and summer surveys (Fig. 5). Group size (# whales per sighting) varied by species (Fig. 6). More than half of the individual whales observed during surveys were gray whales (Table 1A) but fin and humpback whales, combined, accounted for 68.6% of total sightings (Table 1B).

Gray whales

Gray whales were seen most frequently and in greatest density (# animals per sHr) between June and September but were observed in the study area at least once in every month of the year. Mean group size was greatest in summer and ranged annually from approximately 3.4 to 26.6 individuals (Fig. 6). In 2001 and 2002 a large feeding aggregation of 100-200 gray whales was centered in the mouth of Ugak Bay (Fig. 7). Gray whales apparently moved out of this area in 2003 (fewer sightings and animals per sHr). They had returned to the area in early spring 2004 at the end of this reporting period (Fig. 3A) and were seen feeding but in smaller aggregations (Figs. 3B, 6).

Fin whales

Fin whales were observed in every month of the year but were most frequently encountered during spring and summer months (Table 1). Mean group size ranged annually from approximately 2.3 to 4.2 individuals and was greatest during fall surveys (Fig. 6). The greatest number of sightings and individuals were observed along the west coast of Kodiak Island, including Uyak Bay (Fig. 8). Groups in this area often consisted of 12-18 tightly associated individuals. Fin whales were also frequently observed in Kupreanof Straits and throughout Marmot Bay (Fig.8). Fin whales were rarely observed on the tracklines north of Afognak Island or along the eastern shore of Kodiak Island.

Humpback whales

Humpback whale groups were more broadly distributed along the survey routes (Fig. 9). Mean group size ranged annually from approximately 2.7 to 3.8 individuals and was greatest during fall surveys (Fig. 6). Winter feeding aggregations were noted at the head of several area bays where herring and capelin are known to spawn. No humpbacks were observed during February or March surveys. Annual shifts in distribution were noted and may have been associated with shifts in prey upon which whales were feeding. In 2001, large aggregations of humpbacks were seen north of Shuyak Island and southeast of Sitkalidak Island. In 2002, humpback sightings were of smaller groups that were more widely dispersed throughout the survey area (Fig. 9). In 2003, sightings were scarce near Shuyak Island and centered instead off eastern Kodiak. The 2004 results reported here reflect only January through May sightings but again include numerous sightings near Shuyak I (Fig. 9).

Killer whales

Killer whales were rarely encountered during opportunistic aerial surveys; three pods were observed during June 2001-2004 pinniped surveys (Fig.10). One sighting was recorded in each year 2002-04 and group sizes were estimated to consist of 7, 20, and 25 individuals. One sighting (April 2004) was of a tightly associated group in resting formation (Matkin pers.comm.); others were more dispersed and apparently traveling.

Other species

The “Other” whale category was assigned to sightings of large whales when the species could not be determined. Increased effort in later years to stay near whales long enough for identification likely accounts for the reduction of sightings in this category after 2001 (Fig. 3)

Conclusions

Large whales are among the apex predators found in Kodiak waters designated as Steller sea lion Critical Habitat. We documented the year-round presence of large whales in Kodiak waters, many in large feeding aggregations. The relative number, diversity, and persistence of whales in the near-coastal community demonstrate their significance as upper level consumers in an area where Steller sea lion numbers continue to decline. Prey species consumed by these whales elsewhere include fish upon which Steller sea lions feed and zooplankton that feed those fish species. To assess the potential for sympatric dietary overlap, GAP will continue these opportunistic surveys of whale distribution with dedicated and directed studies of prey and habitat use.

We thank pilots Willie Hall (Kodiak Air) and Willie Folsom, Garrett Hosier, and Dean Andrew (Andrew Air) for their safe and skillful flights around the Kodiak Archipelago. We also thank Kathy Hough, Cathy Hegwer, and assorted others for spotting whales during long and arduous survey hours.

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Table 1. Number of animals (A) and number of sightings (B) recorded during opportunistic aerial pinniped surveys. Winter: Dec-Mar, Spring: Apr-May, Summer: June-Sept, and Fall: Oct-Nov.

A. Number of animals

		Species				
		Fin	Humpback	Gray	Orca	Other
Year	2001	100	93	666	0	33
	2002	192	139	536	7	13
	2003	83	103	47	20	0
	2004	21	16	31	25	1
Season	Winter	36	9	90	7	5
	Spring	60	45	115	25	6
	Summer	260	249	995	20	22
	Fall	40	48	80	0	5
Total	2126	396	351	1280	52	47

B. Number of sightings (groups)

		Species				
		Fin	Humpback	Gray	Orca	Other
Year	2001	25	29	25	0	12
	2002	54	51	35	1	6
	2003	20	27	10	1	0
	2004	9	6	9	1	1
Season	Winter	13	8	16	1	6
	Spring	25	19	25	1	3
	Summer	64	79	32	1	8
	Fall	6	7	6	0	2
Total	322	108	113	79	3	19

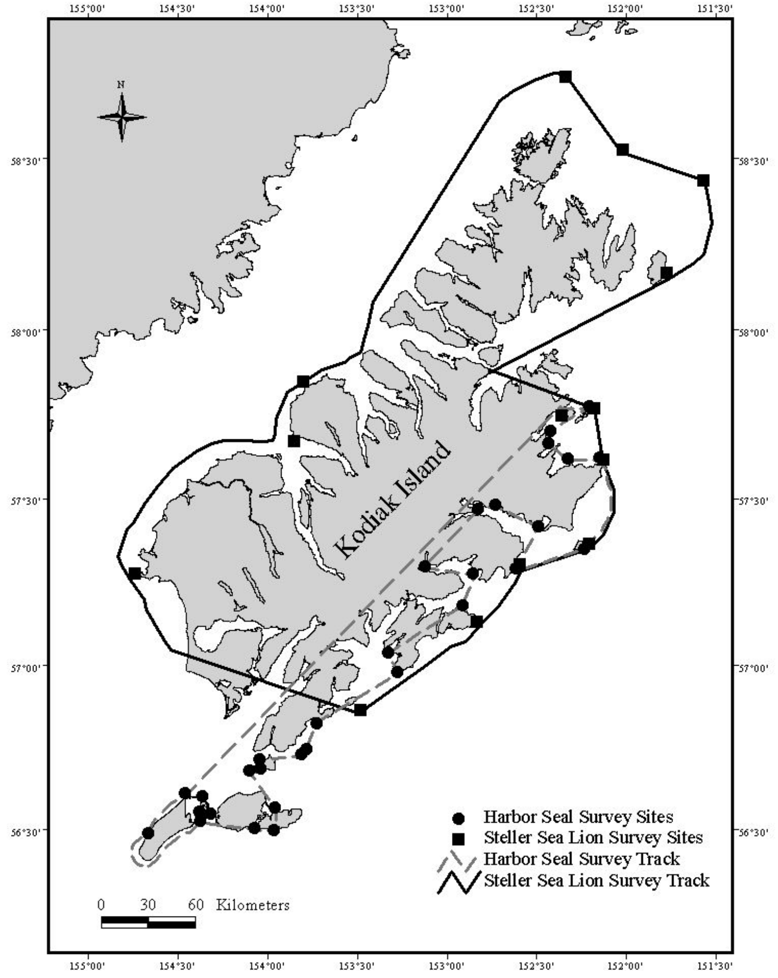


Figure 1. Approximate routes flown during harbor seal and Steller sea lion aerial surveys in the Kodiak area from June 2001-2004.

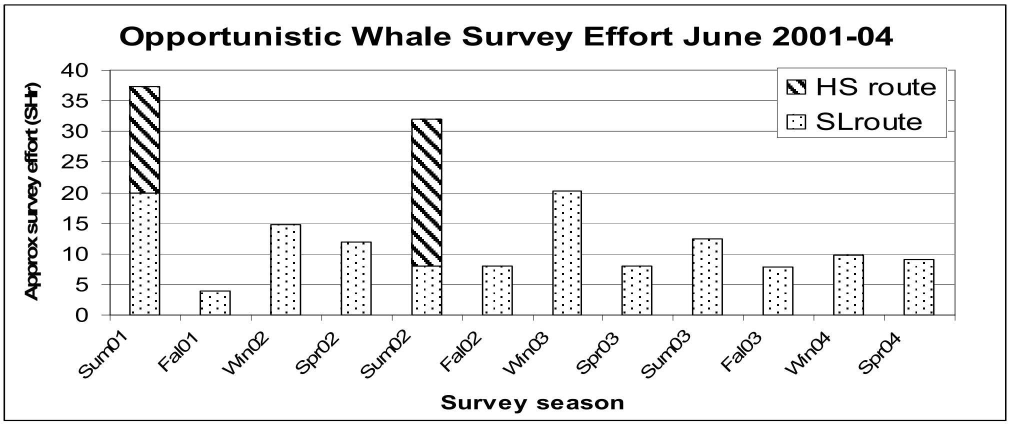
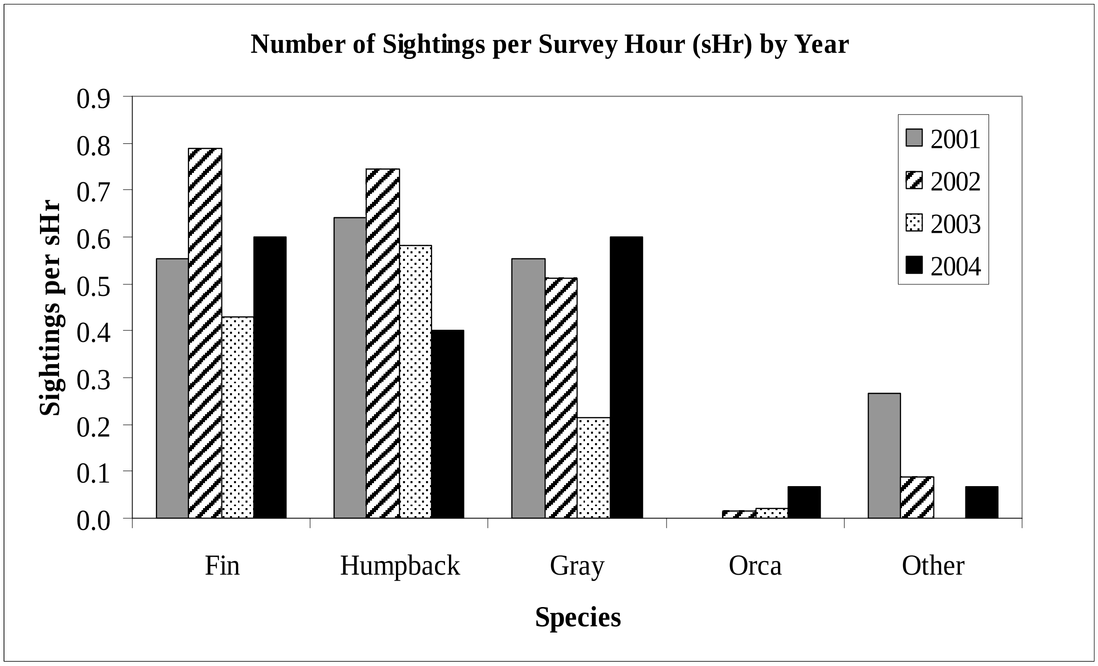


Figure 2. Seasonal distribution of opportunistic whale sighting effort (sHr) during harbor seal (HS) and Steller sea lion (SL) aerial surveys. (Win= Dec-Mar, Spr= Apr-May, Sum= June-Sept, and Fal= Oct-Nov)

A. Sighting (or group) density



B. Whale density

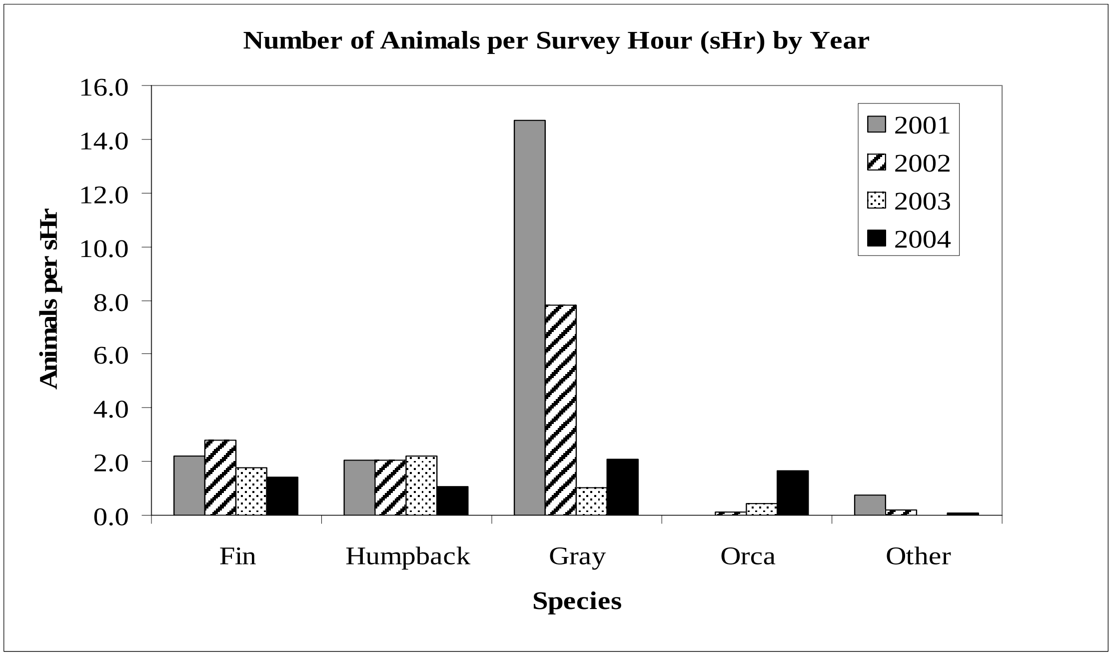


Figure 3. Annual relative density of whale sightings (A) and whale numbers (B) in the study area as determined by number recorded per opportunistic survey hour (sHr).

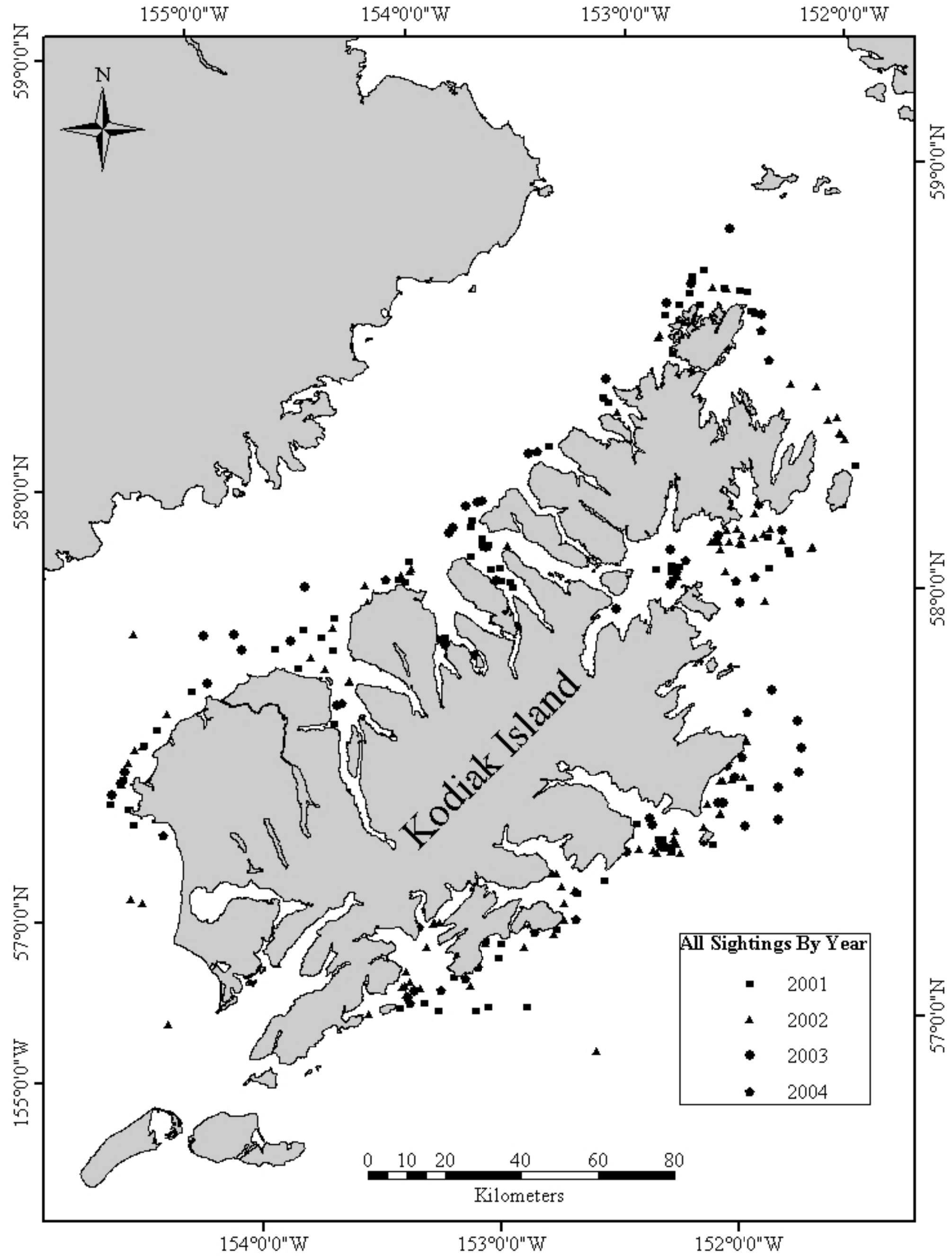
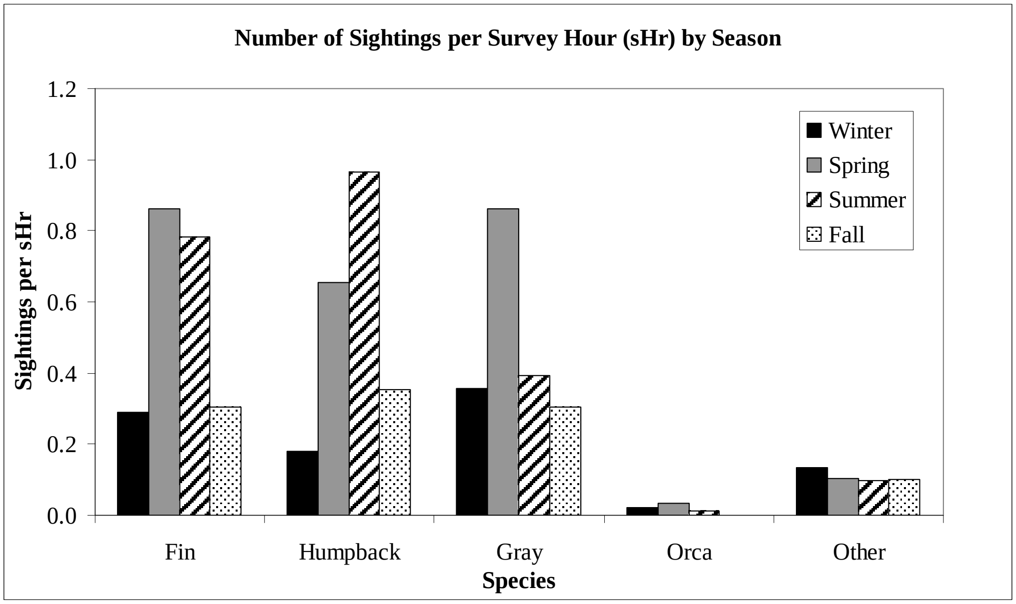


Figure 4. Distribution of all whale sightings recorded opportunistically during pinniped aerial surveys, by year June 2001-2004.

A. Whale sightings



B. Whale numbers

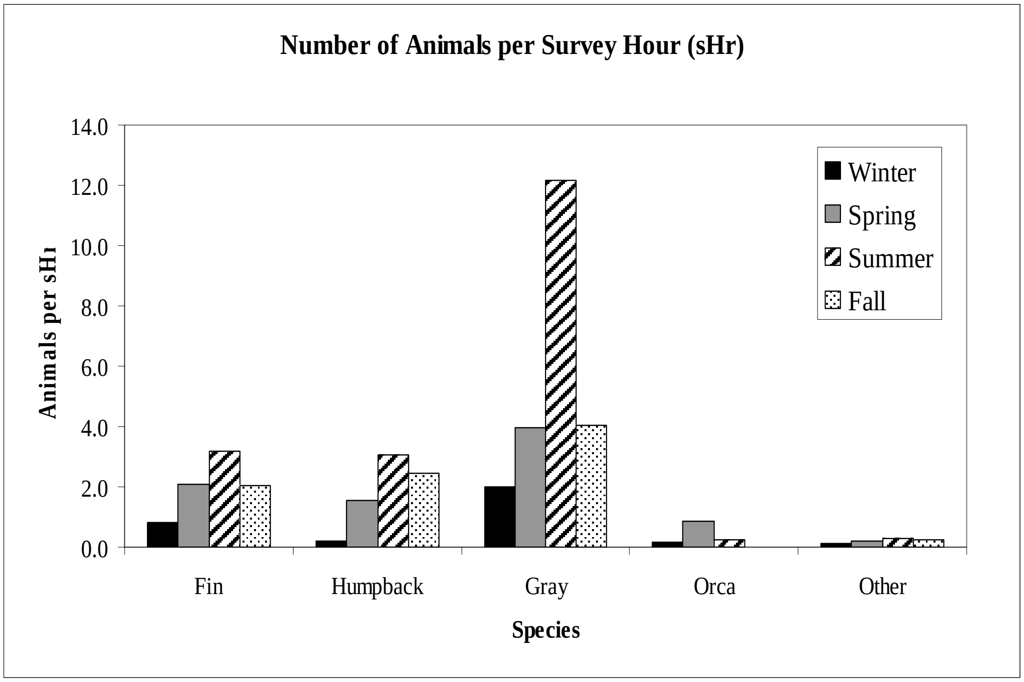
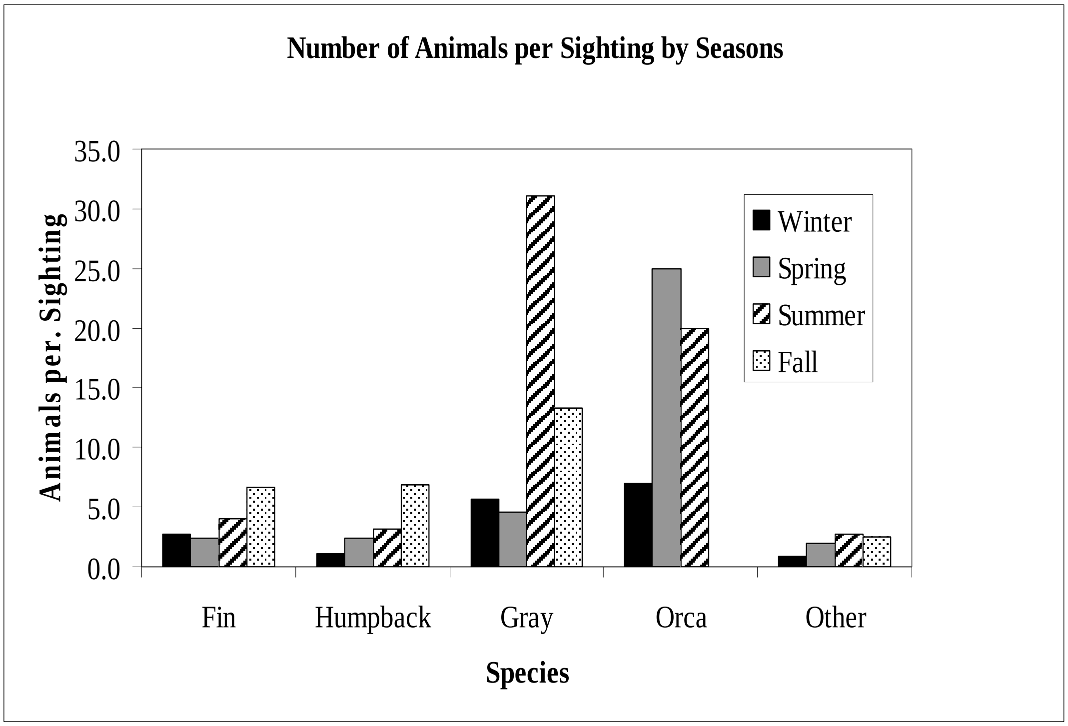


Figure 5. Seasonal relative density of whale sightings (A) and whale numbers (B) in the study area as determined by number recorded per opportunistic survey hour (sHr). Winter: Dec-Mar, Spring: Apr-May, Summer: June-Sept, and Fall: Oct-Nov.

A. Seasonal



B. Annual

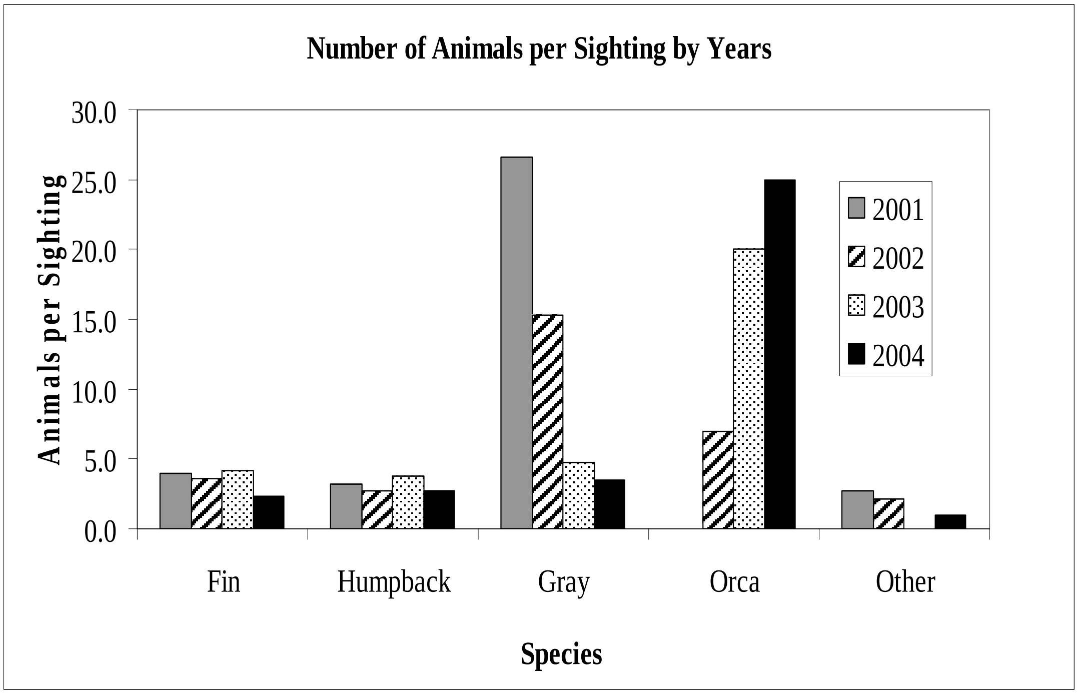


Figure 6. Seasonal and annual patterns in group size (# animals per sighting) by species. Winter: Dec-Mar, Spring: Apr-May, Summer: June-Sept, and Fall: Oct-Nov.

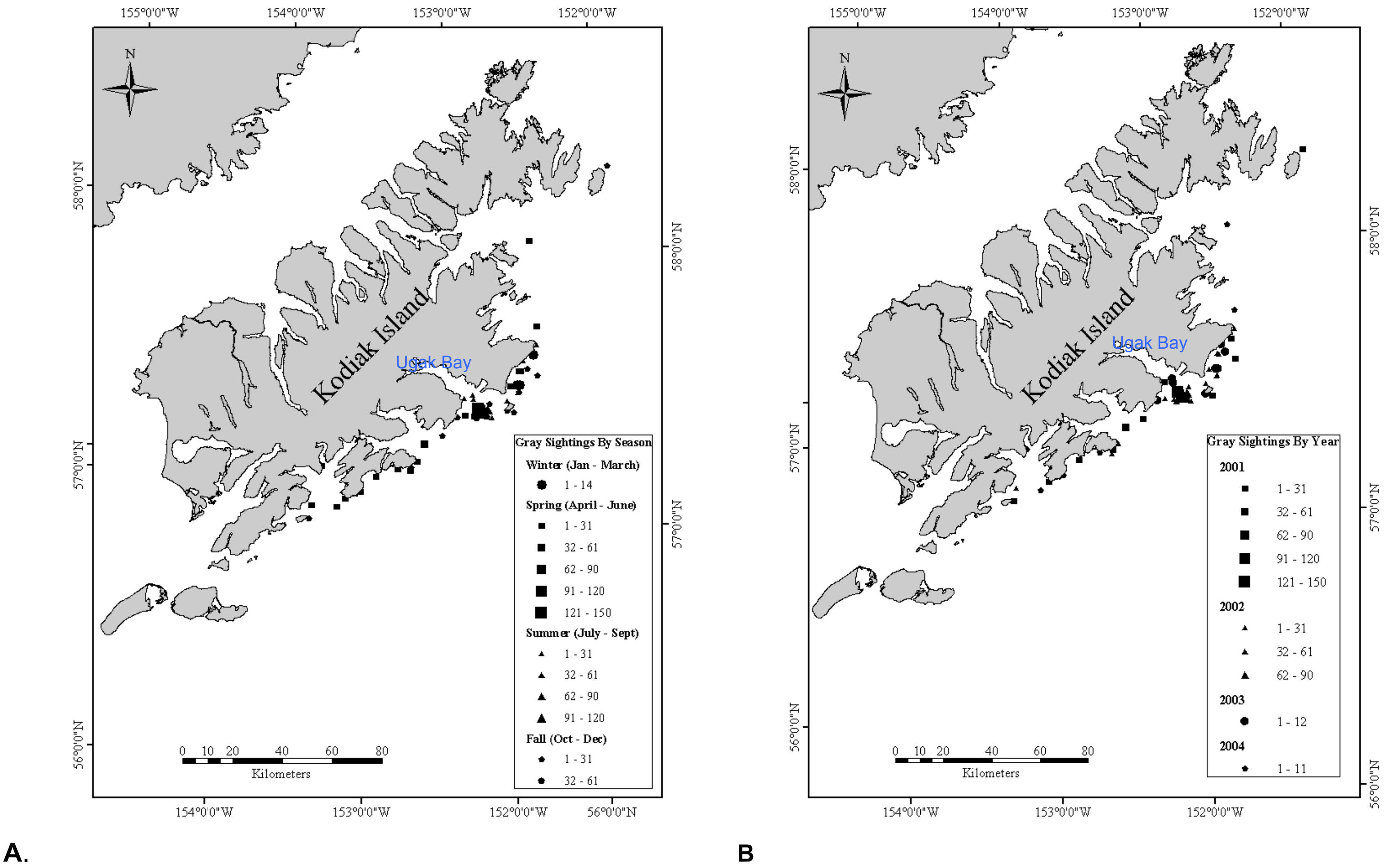
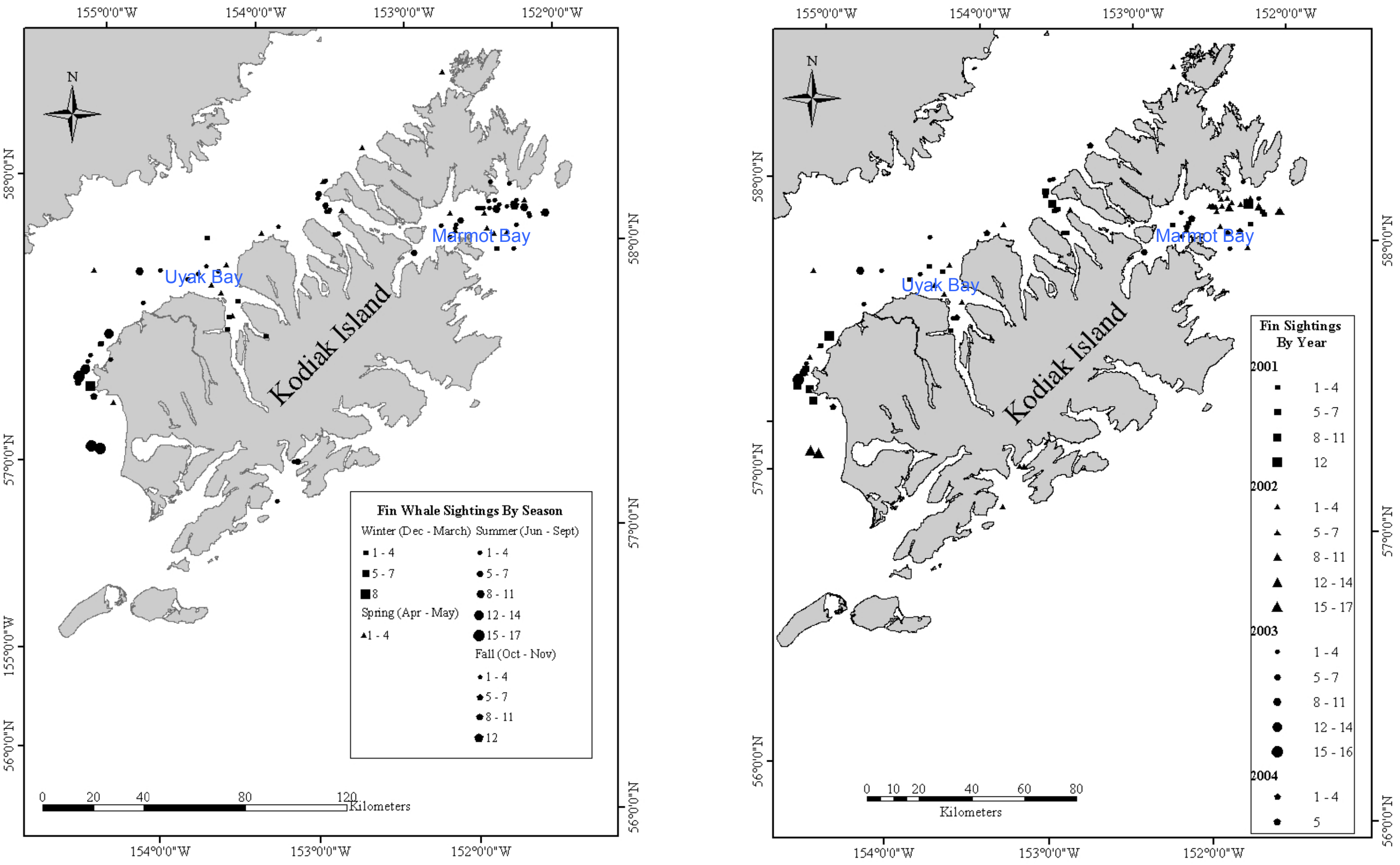


Figure 7. Distribution of gray whale sightings by season (A) and year (B), observed during opportunistic aerial surveys June 2001-04.



A. **B.**

Figure 8. Distribution of fin whale sightings by season (A) and year (B), observed during opportunistic aerial surveys June 2001-2004.

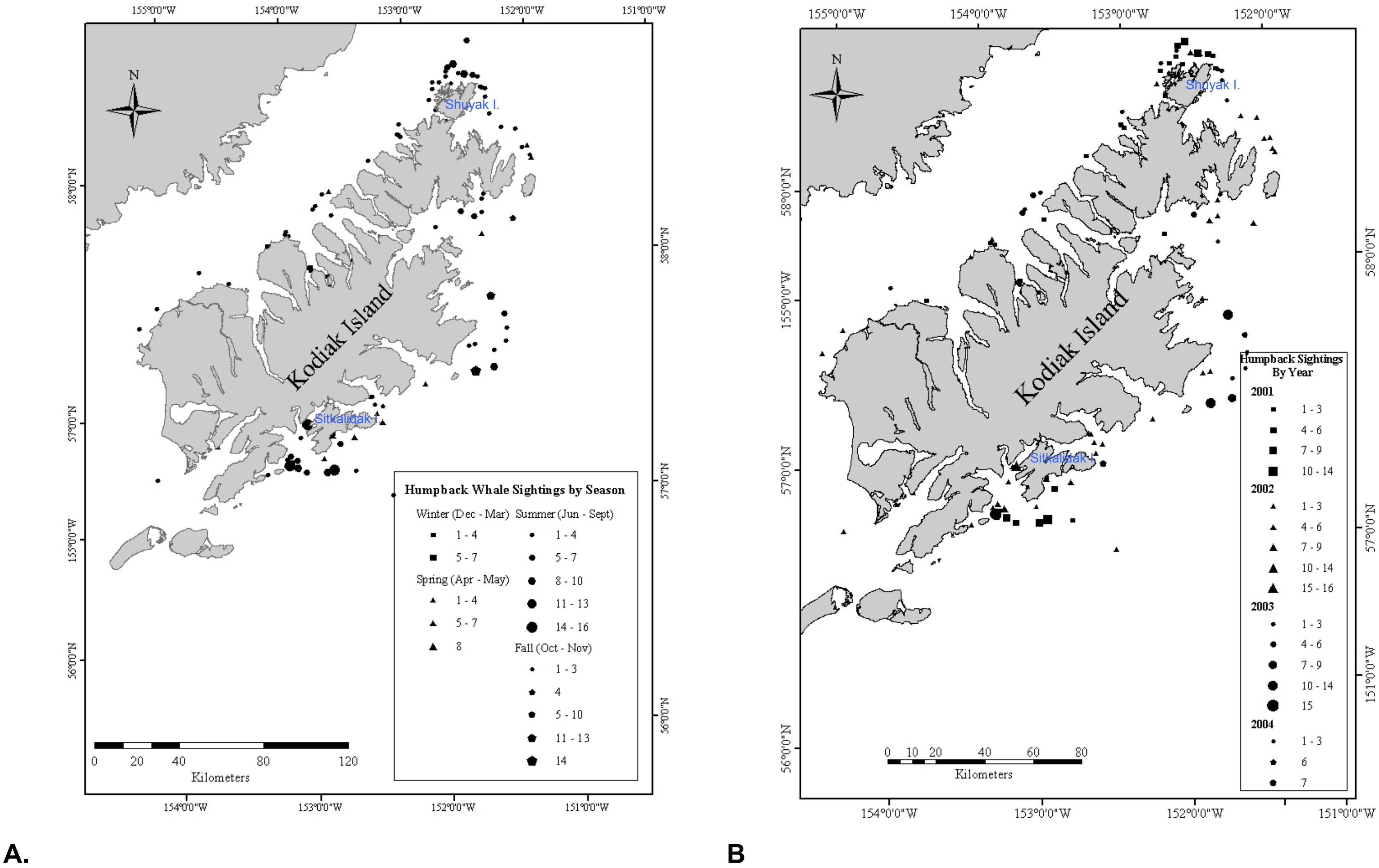
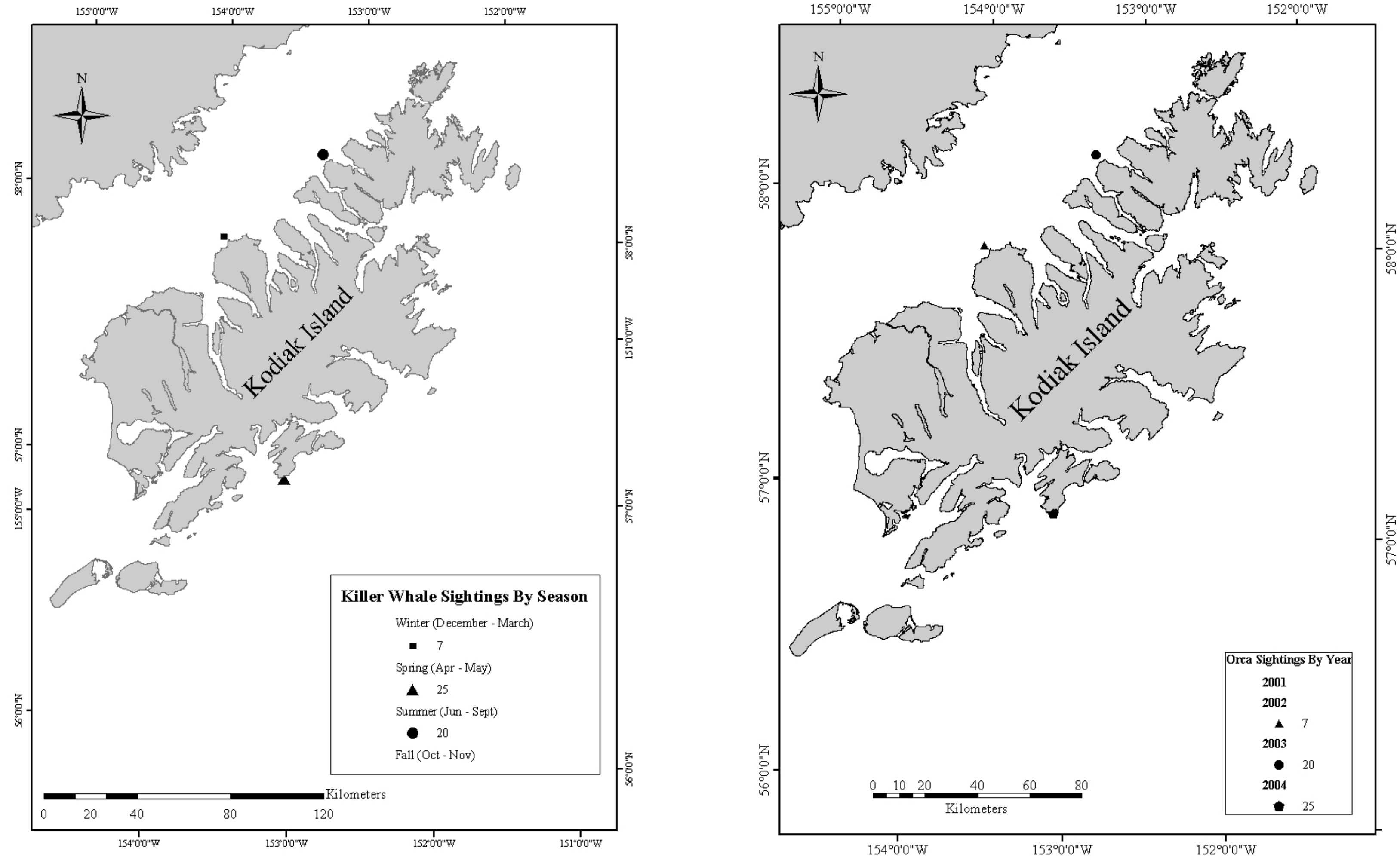


Figure 9. Distribution of humpback whale sightings by season (A) and year (B), observed during opportunistic aerial surveys June 2001-04.



A.

B.

Figure 10. Distribution of killer whale (orca) sightings by season (A) and year (B), observed during opportunistic aerial surveys June 2001-2004.

Summer distribution and habitat characteristics of fin whales and humpback whales in Steller sea lion critical habitat off northeast Kodiak Island, 2002-2003

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Introduction

Large baleen whales are considered significant components of marine ecosystems (Bowen 1997; Katona and Whitehead 1988). Substantial removals of whales through commercial whaling presumably impacted community structure and prey biomass in the Southern Ocean, Bering Sea and northern North Pacific Ocean (Laws 1985; Merrick 1997; Springer et al. 2003). Fin whales (*Balaenoptera physalus*) in northeastern U.S. continental shelf waters were more recently estimated to consume 58,000 mt of herring, sand lance and mackerel annually (Overholtz et al. 1991), with a possible total prey consumption of 646,000 mt (Hain et al. 1992). Estimated annual removal of fishery resources by all cetaceans in this ecosystem was 1/3 to 3 times that of commercial fisheries (Kenney et al. 1997). A paucity of distribution, habitat, and prey data for most cetaceans, however, precludes clearly defining their ecological roles.

Most available distribution, prey, and habitat data are antiquated, having been derived through commercial whaling operations that ended in the North Pacific in 1976 and Kodiak nearshore waters in 1937 (Kawamura 1982; Nasu 1966; Nasu 1972; Nemoto 1959; Nemoto and Kawamura 1977; Uda 1954). Fin whale and humpback whale (*Megaptera novaeangliae*) stocks were heavily exploited and dramatically reduced by whaling in the northern North Pacific, warranting designation as endangered under the U.S. Endangered Species Act of 1973 (Perry et al. 1999). They were the dominant species taken along the Alaska coast (Nemoto 1959) and were primary targets of shore-based whaling out of Port Hobron (off eastern Kodiak Island) between 1926 and 1937 (Reeves et al. 1985).

Few directed surveys for large whales occurred in this region since commercial whaling ended (Brueggeman et al. 1987; Brueggeman et al. 1988; Rice and Wolman 1982; Stewart et al. 1987). Systematic surveys for baleen whales were only recently conducted in the Bering Sea (Moore et al. 2000) and abundance and distribution of baleen whales between the Kenai Peninsula and eastern Aleutian Islands were documented coincident to killer whale (*Orcinus orca*) surveys in 2001 and 2002 (Zerbini et al. 2003). Prior to the study reported here, opportunistic data indicated that Kodiak waters presently support significant numbers of fin and humpback whales (Waite et al. 1999; K. Wynne this volume; D. Zwiefelhofer unpublished data).

The need for whales to forage frequently and efficiently leads to nonrandom distribution and aggregations in areas of high prey concentrations; shifts in whale distribution could indicate ecosystem changes and fluctuations in prey biomass and availability (Hain et al. 1992; Katona and Whitehead 1988; Krieger and Wing 1986; Moore and DeMaster 1998; Moore et al. 2000; Selzer and Payne 1988). Climatic regime shifts occurred in the North Pacific in 1977 and, possibly, 1989 and 1998 (Anderson and Piatt 1999; Hare and Mantua 2000; Hollowed et al. 2001; McFarlane et al. 2000). Forage availability and species composition fluctuated in Kodiak waters during these periods. Shrimp, capelin, and herring abundance declined while gadid and flatfish biomass increased in the 1980s (Anderson and Piatt 1999; Mueter and Norcross 2000). Surveys in Marmot and Chiniak Bays, Kodiak Island, in 2001 and 2002 showed a resurgence of pandalid shrimp and osmerids (eulachon and capelin), with catches reaching levels not seen since the early 1980s (Anderson 2003). Fin and humpback whales killed during North Pacific whaling operations consumed primarily herring, walleye pollock, capelin, smelt, and euphausiids (Nemoto 1959; Nemoto 1963; Nemoto and Kasuya 1965; Nemoto and Kawamura 1977; Thompson 1940); all could be important prey items today. Northeast Kodiak Island baleen whale distribution and habitat use may reflect local fluctuations in prey abundance, type, and availability.

Cetacean distribution is indirectly influenced by physical conditions that concentrate prey (Croll et al. 1998; Davis et al. 2002; Kellogg 1928; Selzer and Payne 1988). Prime whaling grounds (and presumably, feeding areas) in the North Pacific corresponded with oceanic fronts, eddies, and topographic upwelling (Nasu 1966; Nasu 1972; Nemoto 1959; Uda 1954). Recent studies compared distribution to depth and bottom topography (Baumgartner 1997; Davis et al. 1998; Forcada et al. 1996; Hui 1979; Moore and DeMaster 1998; Raum-Suryan and Harvey 1998; Selzer and Payne 1988; Waring et al. 2001; Woodley and Gaskin 1996), sea surface temperature and thermal structure (Baumgartner et al. 2000; Brown and Winn 1989; Davis et al. 2002; Moses and Finn 1997; Woodley and Gaskin 1996) and zooplankton and prey availability (Baumgartner et al. 2000; Fiedler et al. 1998; Foerster and Thompson 1985; Griffen 1997; Murison and Gaskin 1989; Woodley and Gaskin 1996). These studies involved a range of species from the Gulf of Mexico, Gulf of Maine, Mediterranean Sea, Northeast Atlantic, coastal California and Washington State, and the Chukchi and Beaufort Seas. Similar analyses are lacking for the Gulf of Alaska. Environmental parameters that influence cetacean distribution, whether directly or indirectly, are key to defining important feeding habitats for cetaceans.

Proposed recovery actions for humpback and fin whale populations consider the identification and characterization of important habitats primary objectives toward the goal of population recovery (Anonymous 1991; Anonymous 1999). Based on whaling catch locations, Marmot and Chiniak Bays off northeast Kodiak Island were historically important foraging areas (Reeves et al. 1985) and appear to be such today. Most of this area also falls within Steller sea lion (*Eumetopias jubatus*) critical habitat (50 CFR 226.202), including 20 nm buffer zones and seasonal 3 nm - 20 nm federal fishery closure zones around Marmot Island, Long Island, and Cape Chiniak (50 CFR 679.22) (Fig. 1). The region is, therefore, central to the University of Alaska Fairbanks' ecosystem-based Gulf Apex Predator-prey study (GAP), of which this project is a part.

The goals of this study were to describe 2002 and 2003 summer (May-September) distribution of fin whales and humpback whales in Marmot and Chiniak Bays, to measure (or derive) several habitat characteristics that may influence distribution, to assess which (if any) of these characteristics, or suite of characteristics, are significant descriptors or correlates of whale distribution, and to evaluate habitat partitioning among the whale species. Environmental variables included bottom depth and slope, thermocline depth, pycnocline depth, stratification, and zooplankton composition and depth-averaged density. The ecological role of baleen whales in this area can be best evaluated once distribution, physical and biological habitat characteristics and use are defined.

Methods

Data Collection

The study area encompassed roughly 2000 km^2 in Marmot and Chiniak Bays (Fig. 1). Research platforms in 2002 included weekly whale-focused surveys and monthly 3-day hydroacoustic prey surveys. For the weekly surveys, the study area was divided into four comparably sized zones that could be surveyed in one day each.Track lines were not predetermined, but traversed a zone in a manner that afforded full coverage. A zone was considered fully surveyed if the entire area had been within visual range of the 2-3 observers by day's end. Weather frequently prevented full zone coverage; partial coverage was common. Whales were detected visually while cruising at a speed of approximately 18 km/hr. All sighting data were recorded directly at whale locations. Sighting, environmental and navigational data were recorded using a GPS and Nobeltec Navigation Software.

Line transect (passing mode) protocol (Buckland et al. 2001) was used for whale sightings during 2002 hydroacoustic prey surveys. Observations were made by a single observer located on the flying bridge, 4.88 m above the water, and at an average vessel speed of 11 km/hr. Angle to sighting was determined using a fix-mounted angle board. Fujinon 7x50 binoculars, equipped with ocular reticles, were used to determine distance (in nm) to sightings. These data were later used to derive sighting locations. Observations were conducted during all daylight hours, while on transect, except during poor visibility (thick fog, heavy rain), sea states greater than Beaufort 5, or while at prey sampling stations. The vessel did not break effort to approach whales.

In 2003, bi-weekly surveys followed east-west oriented transect lines spaced at 5 km intervals across the study area. Line-transect methods similar to that in 2002 were employed. Observations were made by 2-3 observers in the vessel's wheelhouse, at an eye-height of 3.73 m above the water, and at an average speed of 16 km/hr. A field computer, with GPS interface and WinCruz data entry program (developed by Robert Holland, SWFSC), was used to record sighting and environmental data, and continuous location updates. Sighting effort was "broken" (i.e., closing mode) to approach whales for species confirmation and to sample at whale locations (see below). Watch was maintained, and sighting data recorded while transiting to, from, or between transect lines.

Temperature and salinity profiles were obtained using a Sea-Bird Electronics Sea Cat-19 *Plus* CTD (conductivity-temperature-depth) profiler. The CTD was deployed to approximately 1 m off the bottom at a rate of 1 m/sec. In 2002, sampling occurred only at whale locations. In areas of whale aggregations, sampling occurred central to the aggregation. In 2003, sampling occurred at whale locations, plus at 14-15 predetermined sampling stations during each survey. Station locations were selected using systematic sampling techniques where the start point (station 1) was randomly chosen for each survey and subsequent stations were then spaced at 10 nm increments. This spread sampling effort throughout the study area and will allow for comparison of samples taken directly at whales to those collected at random locations.

Beginning in late July 2002, vertical zooplankton tows were made adjacent to whales presumed to be feeding. Tows were made at individual sightings or in the center of aggregations. Sampling equipment included a 0.75 m diameter ring net of 0.500 mm mesh, with a 5:1 length to mouth ratio and an 11.4 cm collecting bucket, weighted with approximately 11.36 kg. The mesh size was selected to maximize the possibility of capturing euphausiids and copepodite stage V copepods, which were known prey of fin and humpback whales (Horwood 1987; Kawamura 1982; Nemoto 1959; Nemoto 1963; Nemoto 1973; Nemoto and Kasuya 1965; Nemoto and Kawamura 1977; Thompson 1940). Angle of the line during deployment and retrieval was recorded using a protractor and the amount of line deployed adjusted to compensate for angles off vertical. Rate of retrieval was 1 m/sec (Allen 1972). Depth of deployment was to the bottom to maximize the possibility of capturing zooplankton from throughout the water column, especially diel migrating euphausiids (Allen 1972; Brinton 1967; Kendall et al. 1980). Samples were preserved in 1 liter bottles, with 10% formalin buffered with seawater.

In 2003, zooplankton were collected at whale locations and at the pre-determined stations described above. Sampling protocol was otherwise the same as in 2002. Zooplankton were collected throughout the study period (May-September).

Data Processing

Only "on effort" sighting data were included. "Off effort" data, omitted from analyses, were collected when visibility was compromised by fog, rain, darkness, or sea states greater than Beaufort 5, while at sampling stations, or whenever conditions precluded maintaining watch. A sighting refers to a recorded group of whales, not the number of individuals within the group, unless group size = 1. When not recorded directly at whale locations, sighting positions were derived using angle, distance to sighting (based on height of eye and reticle), vessel location, and geofunc.xla Excel functions (Jeff Laake, NMML/NMFS/NOAA). Sighting data were entered into a GIS (ArcView 3.2, ESRI, Redlands, CA) for mapping and analysis. Nearest Neighbor Analysis in the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997) was used to test for spatial randomness of whale distribution. An R value < 1 indicates a clustered pattern tendency, R = 1 indicates random distribution, R > 1 indicates uniformity.

CTD downcast data were processed using SeaBird Data Processing software. These data are being used to derive mean water column temperature, salinity and density, thermocline and pycnocline depths (depth of maximum temperature and density gradients, respectively), and the stratification parameter. The stratification parameter is defined by $\overline{\upsilon} = \frac{1}{h}\int_{-h}^{0}(\rho - \overline{\rho})gzdz; \overline{\rho} = \int_{-h}^{0}\rho dz$, where *h* is depth of the CTD cast, ρ is density, g is gravity (-9.8 m/s^2), z is depth, and dz symbolizes change in depth (Ross and Larson 2003; Simpson et al. 1977). This estimates the energy (Joules/ m^3) needed to redistribute a water mass of depth *h* by complete vertical mixing (Fiedler et al. 1998; Simpson et al. 1977).

Zooplankton samples were being processed to determine taxonomic composition and depth averaged density (organisms/m^3). Samples in 2002 were sub-sampled using 20 ml aliquots until total copepod count equaled 100 individuals. A Folsom splitter was used to divide 2003 samples until roughly 100 copepods remain. Large organisms were removed and enumerated prior to sub-sampling. Identification and enumeration of sub-samples were extrapolated to the entire sample.

Copepods and euphausiids were being identified to at least the genus level. Copepod total length is measured to size class (< 1.0 mm, 1.0-2.5 mm, 2.5-4.0 mm, 4.0-6.0 mm, > 6.0 mm). Euphausiid furcilia were counted, but not identified to species. Mysids, decapod shrimp and crab zoea are identified to at least family level. Other taxa are identified at either family or genus level (e.g., cladocerans, amphipods, gastropods), while some are only grossly identified (e.g., cnidarians, chaetegnaths, barnacle nauplii). For analytical purposes, euphausiids were later categorized as eggs, non-adults, which included furcilia, juveniles, calyptopes and nauplii, and adults, and calanoid copepods were grouped by genus.

Zooplankton data were linked to sampling station information, and total counts, counts by taxonomic groups, and by size class per volume of water sampled were calculated. The volume of water sampled was calculated using a trigonometric function based on angle of net deployment, area of net mouth opening and length of line deployed.

Bathymetric data were obtained from the National Geodetic Data Center (GEODAS) and from the Alaska Earthquake Information Center, University of Alaska Fairbanks. The latter data were compiled by Scientific Fisheries, Inc. using NGDC/NOS combined data, and by TIME/NOAA for use in tsunami predictions. These bathymetric XYZ point files were clipped, compiled and merged using ArcView 3.2 and 3-D and Spatial Analyst extensions. Triangulated Irregular Networks (TINS) were generated then converted to grids (250 m cell size), from which depths and degrees of slope were derived and applied to sighting locations. The slope command in Spatial Analyst estimates the maximum rate of change from each cell to a 3x3 cell neighborhood. Depth classes (50 m increments, 0-300 m) and slope classes (2 degree increments, 0-18 degrees) were created to describe percent of the respective classes available in the study area compared to usage as determined by whale locations. Survey effort per depth and slope class was calculated and sightings (by species) per km effort per class were derived.

Survey area boundaries and depth and slope class availability were based on actual area covered and derived separately for 2002 and 2003. Area was determined by delineating buffers around survey tracklines at a distance within which whales would be sighted and recorded during the respective surveys. Buffers of 2 nm were used for 2002 and 2003 systematic surveys and a 1 nm buffer was used for 2002 whale-focused surveys. Buffers were combined by year; areas of repeated coverage and overlap were only counted once, so that area calculations were inclusive, not cumulative.

Depth and slope data relative to sightings were analyzed for inter-year and inter-species differences using ANOVA (alpha = 0.05). Sightings data from the weekly and monthly 2002 surveys were combined for these analyses. Data for the remaining variables are still being processed, so have not been statistically analyzed.

Results

Table 1 summarizes monthly and total kilometers surveyed on effort in 2002 and 2003. Total coverage was comparable in both years, despite different survey methods, with 2865.638 km surveyed in 2002 and 3061.365 km surveyed in 2003 (Figs. 2 and 3). Line-transect effort was relatively consistent throughout the seven surveys in 2003, ranging from 216.1 km to 266.75 km, out of a total transect length of 266.81 km.

Survey areas are listed in Table 2 and depicted in Figures 4 and 5. Coverage was more consistent in 2003 than in 2002 where the difference between the largest and smallest area surveyed was 125.11 km^2, compared to 468.863 km^2 in 2002. Area surveyed in 2003 was also consistently larger than in 2002, with overall study areas of 2012.994 km^2 and 1732.907 km^2, respectively. Because of variability in area surveyed in 2002, particularly the omission of the northeast segment of the area in May and September, only June-August data were considered in inter-year whale-habitat comparisons. Intra-year analyses include May and September data.

Although fin whales and humpback whales were the focus of this study, all cetaceans encountered were recorded, including Dall's porpoise (*Phocoenoides dalli*), harbor porpoise (*Phocoena phocoena*), killer whales (*Orcinus orca*), gray whales (*Eschrichtius robustus*), and unidentified balaenopterids. The latter were likely either fin whales or humpback whales that could not be identified to species due to distance or weather constraints. Monthly sightings by species and year are summarized in Tables 3 and 4. Total sightings included 170 fin whales and 128 humpbacks in 2002 and 130 fin whales and 79 humpbacks in 2003. In both years, humpback sightings were lowest in May and September and highest July and August, while fin whale sightings were highest in July and remained high in September when humpback sightings diminished. These numbers do not include known re-sightings within a given survey area, but may include individuals re-sighted in different locations of the study area or during different survey periods. Table 5 shows fin whale and humpback sightings corrected for effort. Sighting rates were lower in 2003.

Nearest neighbor analyses, conducted separately by year and species, indicated highly clustered (non-random) distribution in all cases. In 2002, R-values for humpbacks and fin whales were 7.6765E^{-6} and 8.3904E^{-6}, respectively. Values in 2003 were 1.0482E^{-5} and 7.6109E^{-6} for humpbacks and fin whales, respectively. Humpbacks appeared more dispersed in 2003 than in 2002, which may account for the slightly higher R-value that year. Figures 6 and 7 depict 2002 and 2003 sighting locations.

Mean depth distribution of 2002 humpbacks (97.9 m) and fin whales (128.2 m) differed significantly ($p < 0.0001$). Mean depths of 2003 humpbacks (109.6 m) and fin whales (124.4 m) were also significantly different ($p = 0.03$), although by a smaller margin. June – August humpback mean depths in 2002 (96.3 m) and 2003 (115.5 m) were significantly different ($p = 0.025$), but did not differ ($p = 0.146$) when May and September data were included. There was no significant difference between 2002 (129.5 m) and 2003 (125.0 m) fin whale mean depth distribution ($p = 0.454$) (Fig. 8).

There was a significant difference in mean slope distribution for fin whales in 2002 (2.08) and 2003 (3.07) ($p = 0.0008$), for 2002 (1.61) and 2003 (2.45) humpbacks ($p = 0.009$), and for 2002 humpbacks (1.57) and fin whales (2.02) ($p = 0.027$). Slope distribution did not differ significantly ($p = 0.22$) between 2003 humpbacks (2.41) and fin whales (2.86) (Fig. 9).

Percent of sightings in each of the depth classes (e.g., usage) was compared to availability of each class in the respective study areas for June-August (Fig. 10). Percent availability was comparable in 2002 and 2003, but the patterns of usage varied. Whale distribution was not proportional to available depth classes. Fin whales were sighted in the 0-50 m depth class disproportionate to availability (2% of fin whales versus 40% of the study area). Fin whales followed the same general pattern both years, but with a much sharper peak in the 100-150 m depth class in 2003, offset by lower usage in the 50-100 m and 150-200 m classes. In 2002, humpback sightings by depth class approximated that available in the study area. This was not the case in 2003 when far fewer humpbacks were sighted in the 0-50 m depth class and a greater proportion were in the 100-150 m and 150-200 m depth classes.

Figure 11 shows sightings by species and year corrected for km of effort within each depth class. Fin whales generally frequented deeper depth classes, with comparable sighting rates in the 100–150 m depth class in 2002 and 2003. Humpback sightings in this depth class were also consistent across years, as was the difference between fin whale and humpback sighting rates. In 2002, sighting frequency of fin whales in the 150–250 m depth class was 3.6 times greater than in 2003 and twice that of humpbacks in 2002. In 2003, fin whales and humpbacks were seen in this depth class in equal proportions. When corrected for effort, fin whales in 2002 were sighted with the greatest frequency in depths of 50-100 m and 150-200 m. Such corrections did not similarly affect frequency by depth class for 2003. Humpback sighting frequency in the 0–50 m class was 14 times and 5.5 times that of fin whales in 2002 and 2003, respectively. The sighting frequency of humpbacks in this depth class in 2002 was three times that in 2003. Humpback sighting frequency in the 200-250 m depth class was 4.7 times lower in 2003 than in 2002. There were no sightings of either species in depths greater than 250 m.

Approximately 65% of the 2002 and 2003 study areas fall within the 0-2 degree slope class. Usage in both years closely mirrored that available, although there was a shift in usage from shallower to steeper slopes in 2003 (Fig. 12). Whale distribution by slope class, corrected for effort, showed a different pattern (Fig. 13). The most striking difference is between years; both fin whales and humpbacks were sighted in higher slope classes in 2003 than in 2002. Sighting frequency for both species decreased two-fold in the 0-2 degree and 2-4 degree classes while increasing two-fold in the 4-6 degree slope class. In 2002, humpbacks were not sighted in slopes greater than 6-8 degrees, and fin whales in slopes greater than 8-10 degrees. However, in 2003, fin whales and humpbacks were sighted in slopes of 12-14 and 16-18 degrees, respectively. The former was based on only one sighting in a class in which there was little effort.

In 2002, 86 CTD casts were made in the vicinity of whales, 40 with fin whales, 40 with humpbacks and 6 with both species. Sixteen zooplankton tows were made, 8 with fin whales, 7 with humpbacks and 1 with both (Table 6). In 2003, sampling occurred both with and without whales (Tables 7). There were 85 CTDs and 89 zooplankton tows at stations absent of whales and 51 CTDs and 53 zooplankton tows in the vicinity of whales. A breakdown of tows by species is shown in Table 8. There were 29 CTD and 29 zooplankton tows with fin whales, 16 CTDs and 18 zooplankton tows with humpbacks and 4 CTDs and 5 zooplankton tows with both species. These data are currently being analyzed.

Discussion

The overall distribution pattern of fin whales and humpbacks off northeast Kodiak Island in 2002 and 2003 was similar to that seen historically, as well as in more recent surveys of the region (Brueggeman et al. 1989; Reeves et al. 1985; Zerbini et al. 2003). Current locations suggest that this area has either continued as an important summertime foraging area since at least the days of coastal whaling, or has been re-established in more recent years. Catch positions documented by Reeves et al. (1985) for the Port Hobron whale fishery show the majority of fin whales were taken in Marmot and Chiniak Bays between June and August and highest humpback takes there were in July and August. It was not surprising that fin and humpback whales were non-randomly distributed in Marmot and Chiniak Bays since cetaceans are frequently aggregated, presumably in areas of concentrated prey (Katona and Whitehead 1988; Kenney and Winn 1986; Krieger and Wing 1986; Moore et al. 2002; Payne et al. 1990; Piatt et al. 1989; Simard and Lavoie 1999).

Localized distribution within the bays fluctuated from 2002 to 2003 (e.g., absence of inshore humpbacks, more dispersed humpbacks, more humpbacks than fin whales in outer Marmot Bay in 2003). This may account for differences in depth and slope distribution between years. Although some differences could be artifacts of inconsistent levels of effort, it is quite plausible that areas of concentration did change from one year to the next. Zerbini et al. (2003) attributed local differences in humpback and fin whale distribution around Kodiak in 2001 and 2002 to possible shifts in prey concentrations. Changes in spatial distribution relative to prey have been well documented in other areas (Krieger and Wing 1986; Payne et al. 1990).

Bottom topography appears a significant correlate to cetacean distribution (Baumgartner 1997; Baumgartner et al. 2000; Cañadas et al. 2002; Davis et al. 1998; Davis et al. 2002; Woodley and Gaskin 1996). Although analyses are preliminary, data from this study suggest that fin whales and humpback whales may have distinctive depth "preferences". Moore et al. (2002) noted a clear association between fin whales and the 200 m depth contour in the central-eastern Bering Sea. Fin whales were sighted on both the Middle Shelf (0-50 m) and Outer Shelf (>100 m) domains of the central-eastern and southeastern Bering Sea, yet sighting rates were more than two-fold higher in the latter. Humpbacks were more closely associated with the 50 m depth contour. Depth distributions of fin whales off the northeastern U.S. and eastern Canada were comparable to that in Marmot and Chiniak Bays. Woodley and Gaskin (1996) found fin whales in the Grand Manan Basin, Bay of Fundy at mean depths of 128.7 ± 48.2 m, nearly identical to our findings. Those on the northeastern continental shelf were common along the 200 m depth contour, but the mean depth was shallower at 108.4 ± 235 m (Hain et al. 1992). Fin whales are widely distributed throughout the world's oceans and do not strictly inhabit shallow waters. In the Mediterranean Sea, fin whales are frequently off the continental slope in depths from 400 to 2800 m (Forcada et al. 1996). Although there were some differences in distribution relative to slope, the significance in our study is less clear at this time and warrants further investigation and analysis. Variability in bottom topography has been assessed using several different methods, including contour index (Hui 1979), meters of change per kilometer (Baumgartner 1997), as well as slope (Moses and Finn 1997; Raum-Suryan and Harvey 1998). It may be useful to evaluate the data using these different methods.

Fin whales and humpbacks are frequently sympatric, yet often maintain discrete feeding aggregations. Our data suggest some species-specific spatial segregation between areas of concentration (Figures 4 and 5). This was also noted by Brueggeman et al. (1989) and Zerbini et al. (2003) for western Gulf of Alaska and eastern Aleutian Islands humpback whales and fin whales. Thompson (1940) noticed that fin whales and humpback whales killed off eastern Kodiak had different prey preferences despite being taken in relative proximity to one another. Differing feeding strategies could also affect distribution, even when species are feeding on the same prey (Whitehead and Carlson 1988).

The data described here are preliminary and incomplete, so few conclusions regarding correlations between environmental variables and fin whale and humpback whale distribution can be drawn at this time. Completion of zooplankton and oceanographic data processing will allow for more thorough analyses of potentially significant correlates of cetacean distribution in Marmot and Chiniak Bays, including inter-specific differences. Multivariate and logistic regression analyses that simultaneously address the suite of habitat variables – bathymetric, oceanographic and biological – collected and derived during this study should provide a more complete picture of influential habitat characteristics for the largest apex predators in the Marmot and Chiniak Bays study area.

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Table 1. Kilometers surveyed "on-effort" by month and year.

	2002	2003
May	126.79	383.858
June	994.766	448.309
July	911.464	836.524
August	531.242	952.608
September	301.376	440.066
Total km	2865.638	3061.365

Table 2. Survey coverage area (km^2) by sampling period and year.

	2002	2003
May	924.036	1804.952
June	1376.737	1822.769
July	1299.274	1893.048
August	1392.899	1930.363
September	1126.931	1885.284
June-August	1700.434	1974.084
May-September	1732.907	2012.994

Table 3. 2002 "on-effort" sightings by species and month.

2002	Fin Whales	Humpback Whales	Unidentified Balaenopterids	Dall's Porpoise	Harbor Porpoise	Killer Whales	Minke Whales
May	2	0	1	0	0	1	0
June	46	37	2	2	8	1	0
July	59	50	3	3	7	1	1
August	40	35	7	5	4	2	0
September	23	6	3	0	0	0	0
Totals	170	128	16	10	19	5	1

Unidentified balaenopterids were either fin whales or humpbacks, but could not be approached for ID confirmation

Table 4. 2003 "on effort" sightings by species and month.

2003	Fin Whales	Humpback Whales	Unidentified Balaenopterids	Dall's Porpoise	Harbor Porpoise	Gray Whales
May	19	4	15	19	0	0
June	12	3	2	9	4	0
July	54	26	7	50	16	0
August	21	38	13	27	6	0
September	24	8	9	5	0	1
Totals	130	79	46	110	26	1

Unidentified balaenopterids were either fin whales or humpbacks, but could not be approached for ID confirmation

Table 5. Sightings per kilometer of effort by species, month and year.

	Fin whales/km effort		Humpbacks/ km effort	
	2002	2003	2002	2003
May	0.016	0.049	0.000	0.010
June	0.046	0.027	0.037	0.007
July	0.065	0.065	0.055	0.031
August	0.075	0.022	0.066	0.040
September	0.076	0.055	0.020	0.018
Totals	0.059	0.042	0.045	0.026

Table 6. Summary of 2002 sampling stations by month and species.

2002	CTD Stations With Whales				Zooplankton Stations With Whales			
Month	**with Bp**	**with Mn**	**with Bp & Mn**	**Total**	**with Bp**	**with Mn**	**with Bp & Mn**	**Total**
June	10	14	3	27	0	0	0	0
July	15	18	2	35	0	2	0	2
August	10	7	1	18	5	4	1	10
September	5	1	0	6	3	1	0	4
Totals	40	40	6	86	8	7	1	16

* Bp = fin whale (*Balaenoptera physalus*); Mn = humpback whale (*Megaptera novaeangliae*)

* All sampling occurred in the presence of whales

Table 7. Summary of 2003 sampling stations with and without whales present.

2003	CTD Stations			Zooplankton Stations		
Month	**with whales**	**without whales**	**Total**	**with whales**	**without whales**	**Total**
May	10	12	22	8	13	21
June	6	15	21	7	15	22
July	18	25	43	19	26	45
August	11	21	32	13	23	36
September	6	12	18	6	12	18
Totals	51	85	136	53	89	142

* 5 CTD casts failed due to low batteries; 1 was redone

Table 8. Summary of 2003 sampling stations with whales, by month and species.

2003	CTD Stations With Whales			Zooplankton Stations With Whales		
Month	**with Bp**	**with Mn**	**with Bp & Mn**	**with Bp**	**with Mn**	**with Bp & Mn**
May	9	1	0	7	1	0
June	5	1	0	6	1	0
July	10	4	2	10	5	3
August	3	7	2	3	8	2
September	2	3	0	3	3	0
Totals	29	16	4	29	18	5

* 2 CTD stations and 1 zooplankton station listed with whales were with Dall's porpoise only

* Bp = fin whale (*Balaenoptera physalus*); Mn = humpback whale (*Megaptera novaeangliae*)

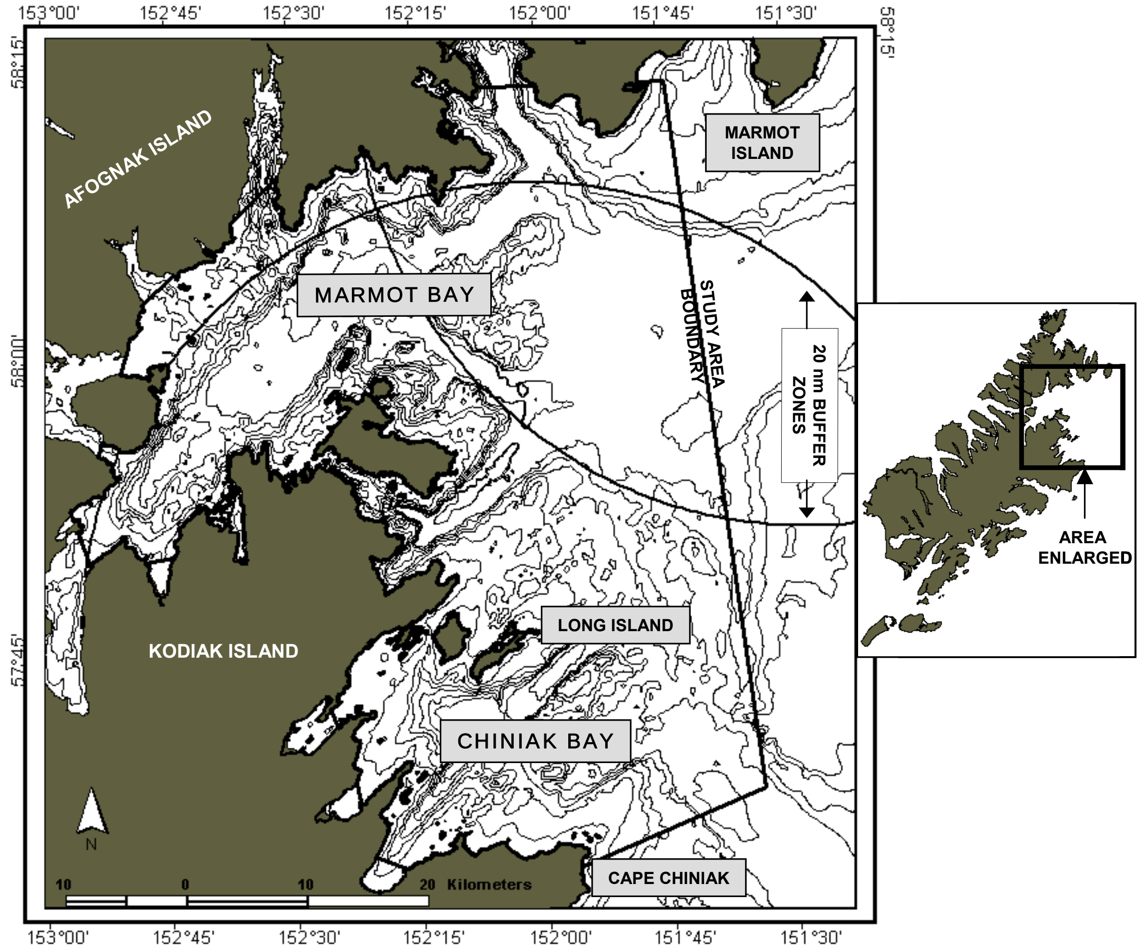
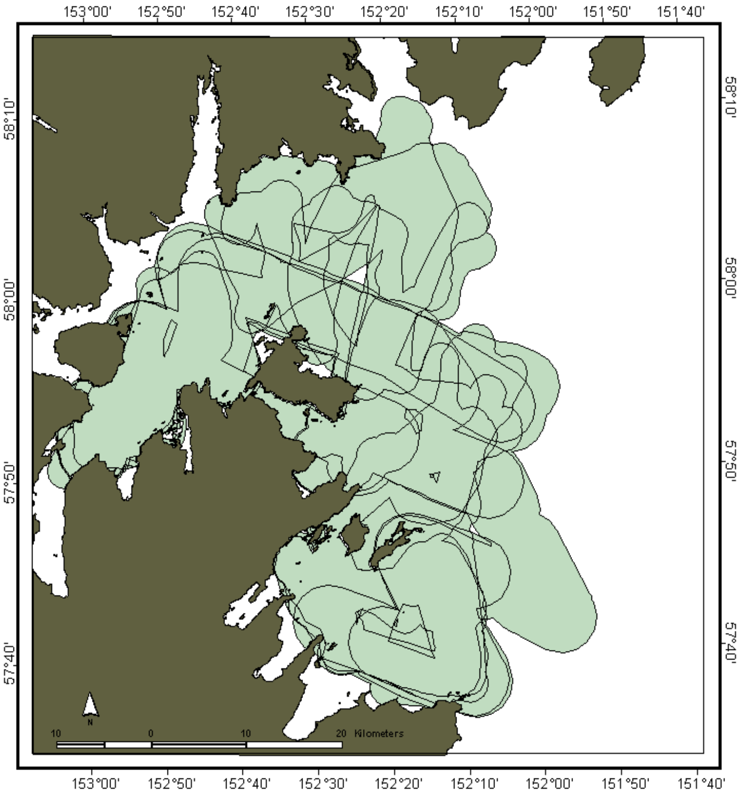
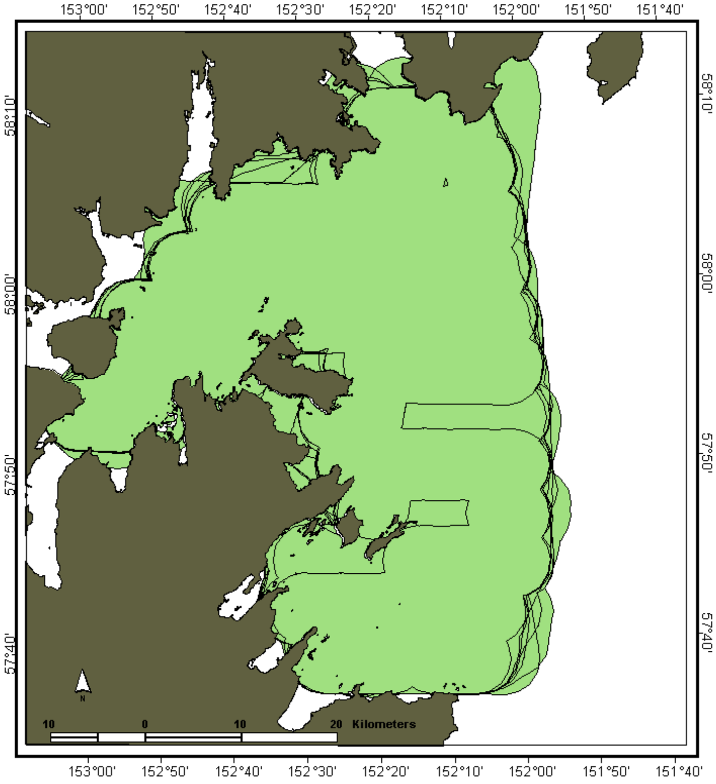


Figure 1. Study area, with 20 nautical mile Steller sea lion buffer zones around the Long Island haulout and Marmot Island rookery. The study area boundary depicted encompasses the cumulative areas included in 2002 and 2003 surveys.



F re h ale- focused survey tracklines.

Figure 4. 2002 survey coverage area.



Fi transect lir o, from, and between transect lines.

Figure 5. 2003 survey coverage area.

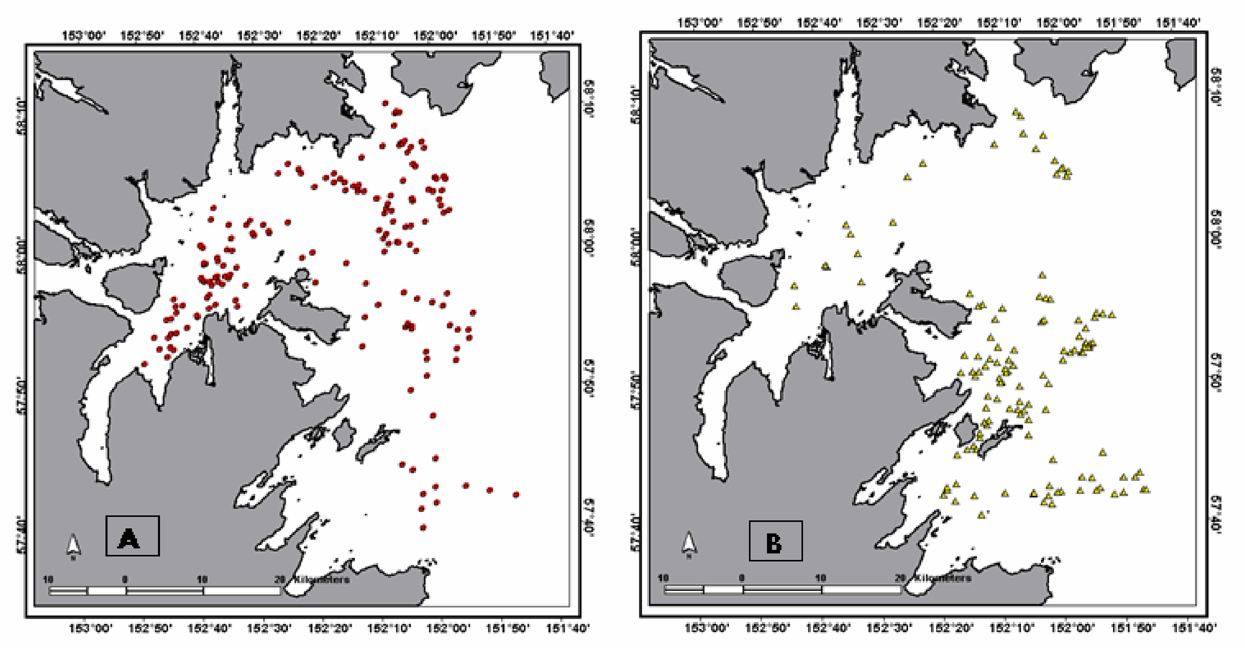


Figure 6. 2002 “on-effort” fin whale (A) and humpback (B) sightings, May-September.

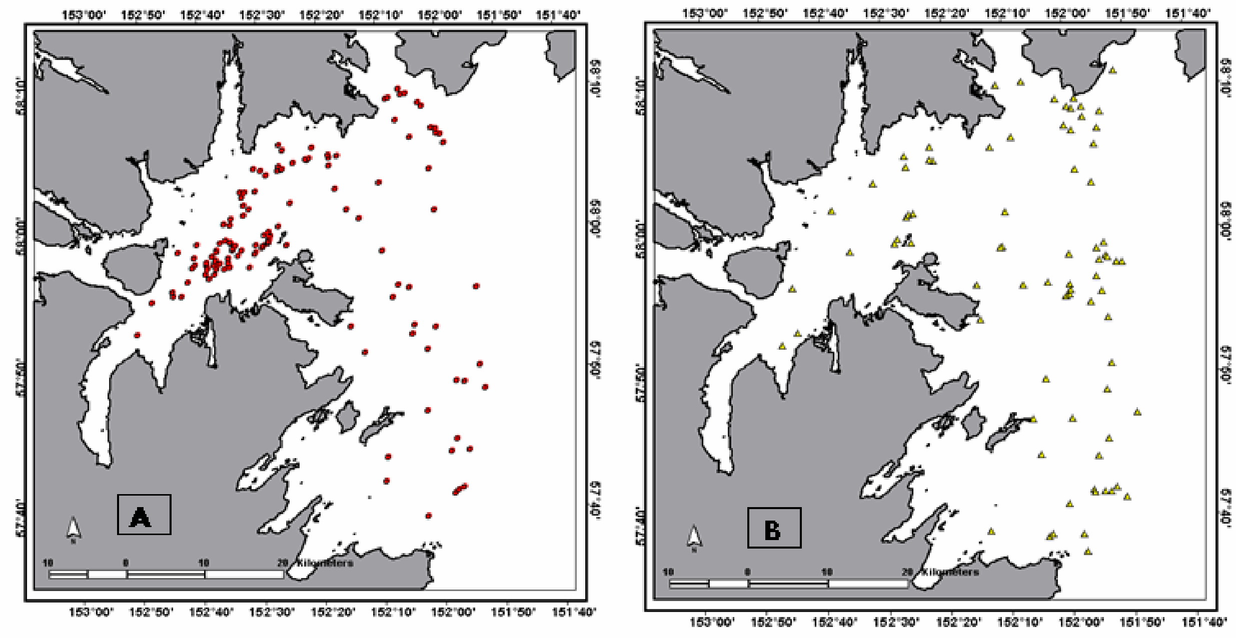


Figure 7. 2003 “on-effort” fin whale (A) and humpback (B) sightings, May-September.

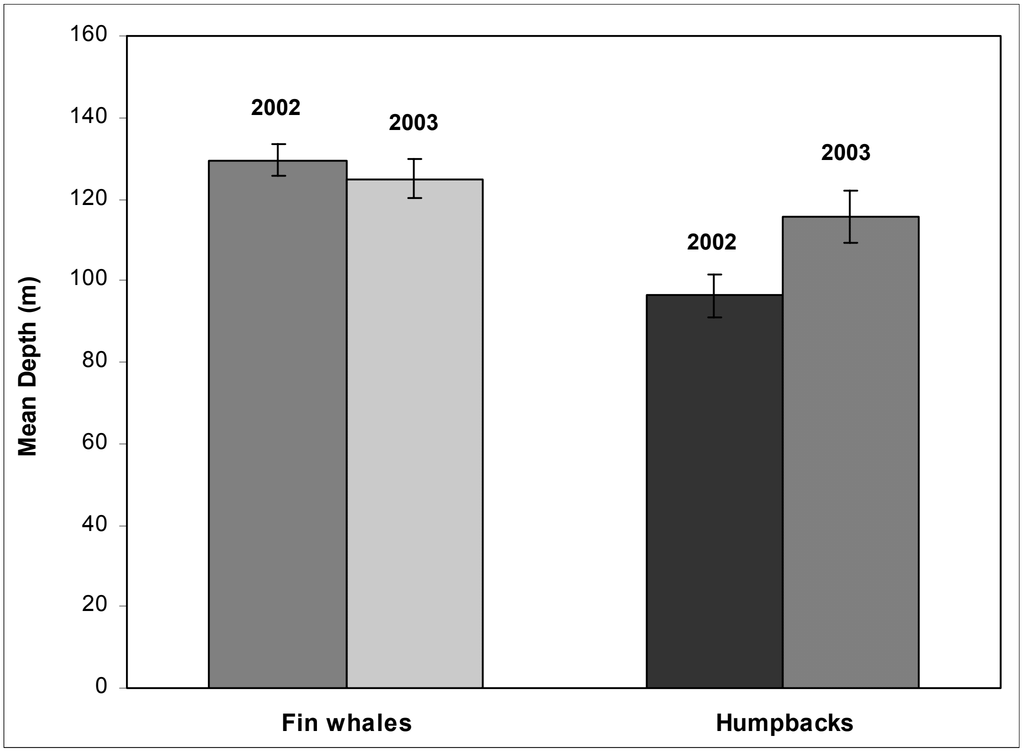


Figure 8. Mean depth distribution (± Standard Error) by species and year (June-August).

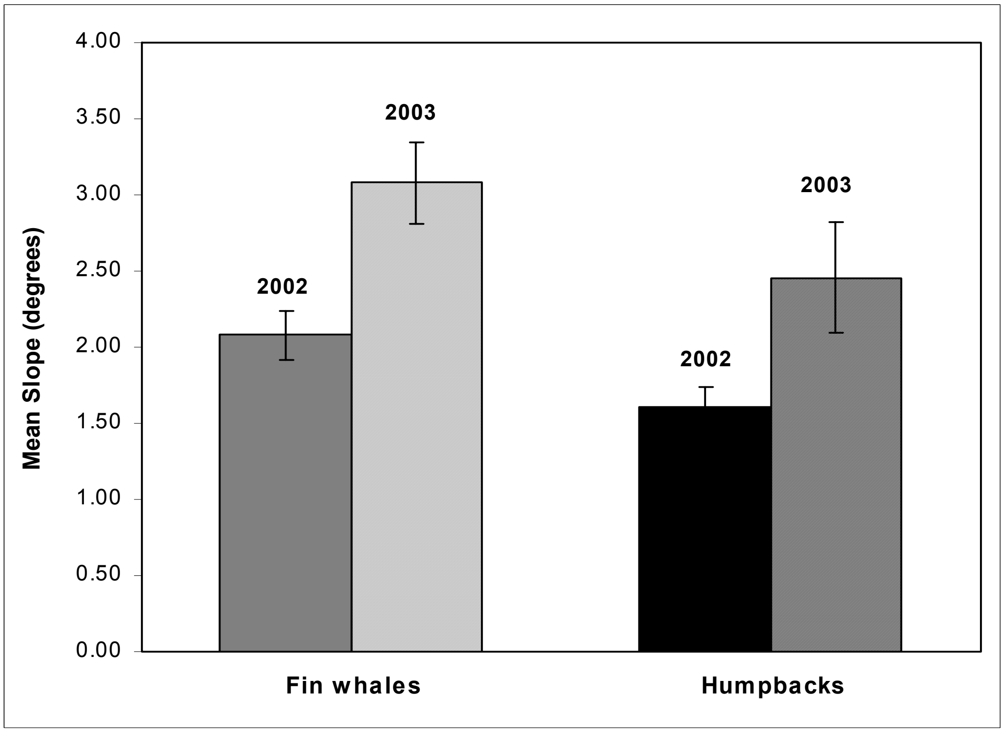


Figure 9. Mean slope distribution (± Standard Error) by species and year (June-August).

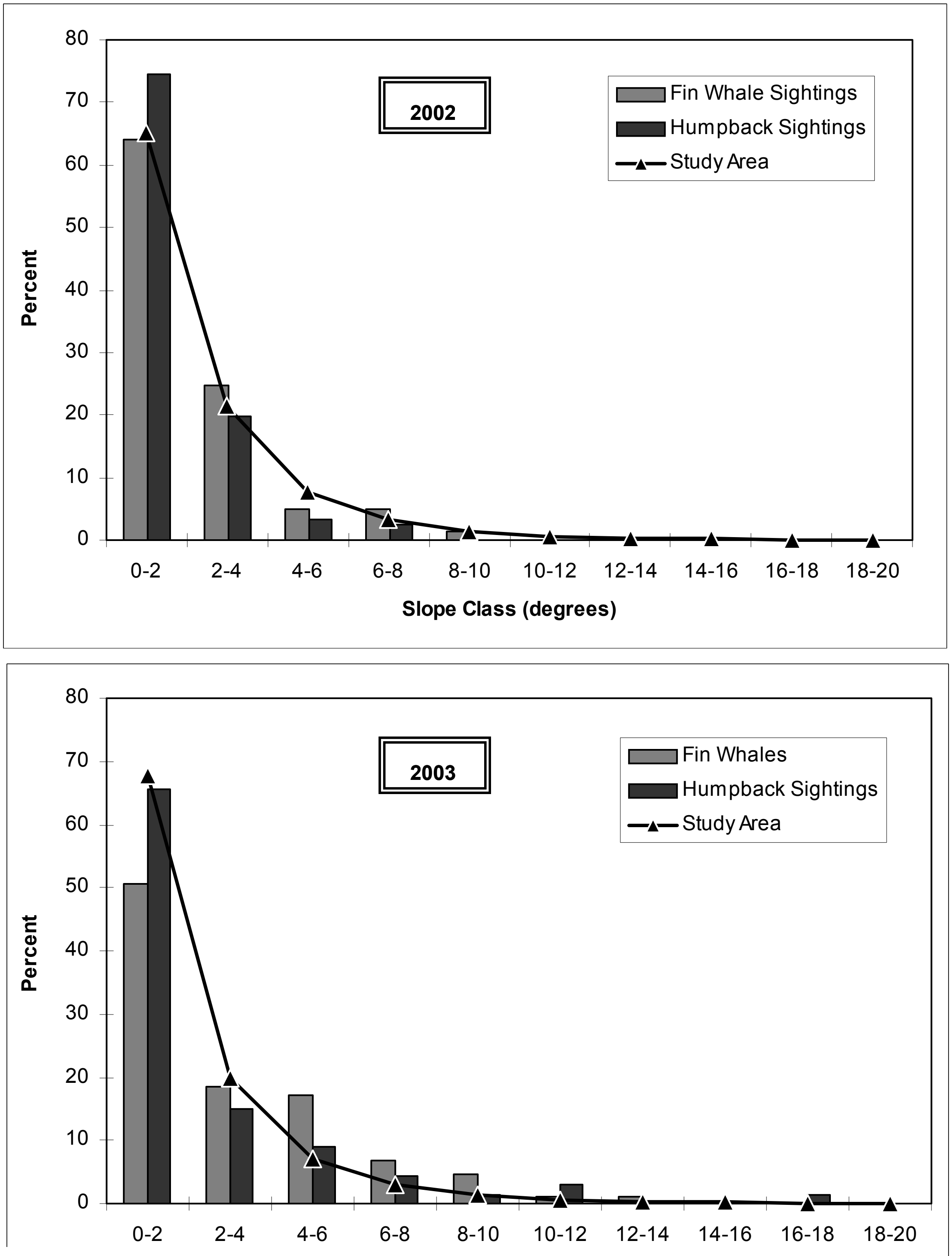


Figure 10. Relative use and availability of depth classes by year (June-August). Shown are percent of fin whale and humpback sightings by depth class and percent composition of the study areas by depth class.

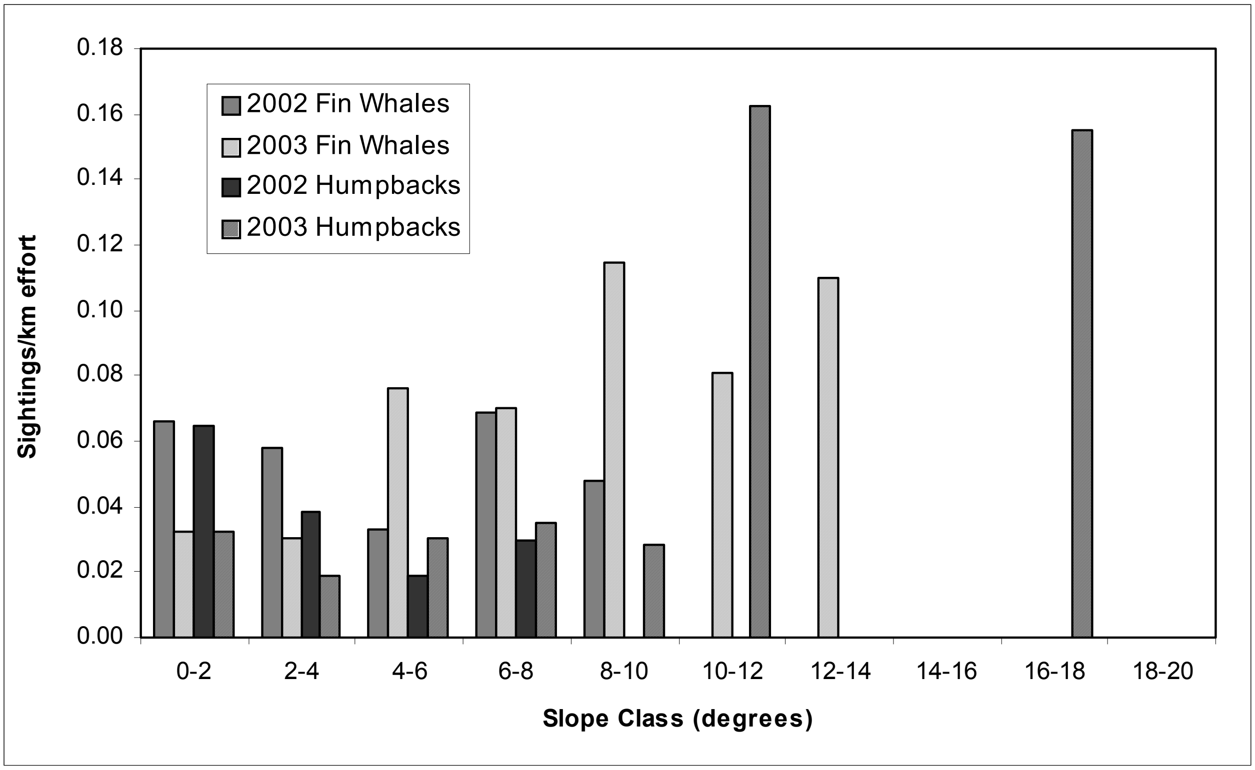
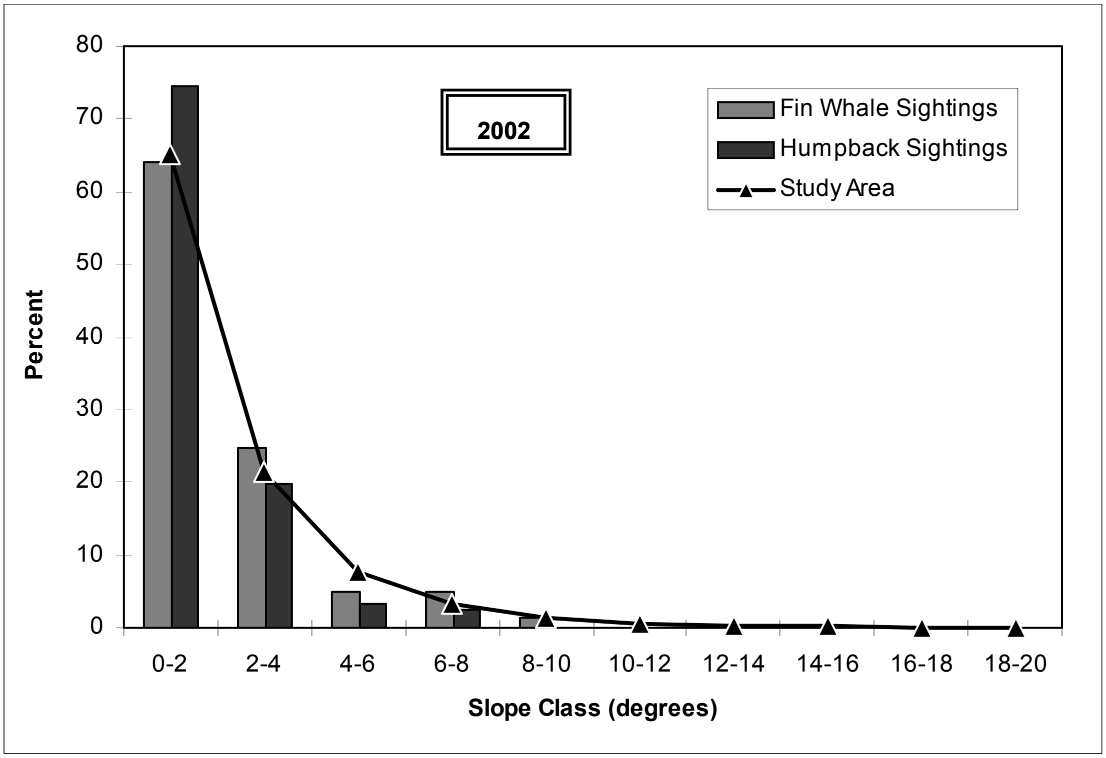


Figure 11. Sightings per kilometer of effort per slope class, by species and year (June-August).



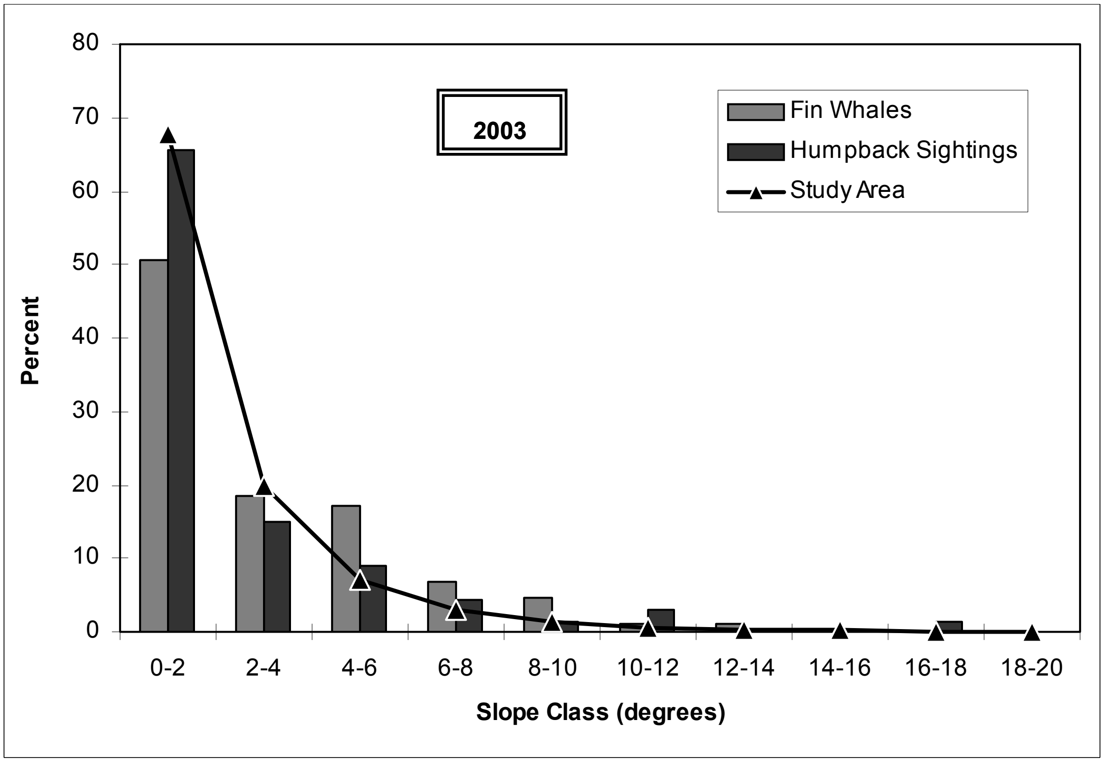


Figure 12. Relative usage and availability of slope classes by year (June-August). Shown are percent of fin whale and humpback sightings by slope class and percent composition of the study areas by slope class.

An Apparent Feeding Aggregation of Humpback Whales (*Megaptera novaeangliae)* Near Kodiak Island, Alaska: Historical and Current Abundance Estimation

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Introduction

Photo-identification has been used for many years as a mark-recapture tool for estimating humpback whale populations and tracking their movements (Baker et al. 1986, 1992; Perry et al. 1990; von Ziegesar 1992; Calambokidis et al. 1993). Photo-identification studies have resulted in moderate understanding of humpback whale stocks in the North Pacific and have proven that, though they may converge on winter breeding grounds, humpback whales are isolated into regional aggregations during feeding seasons with very little exchange between them. Known feeding aggregations in the North Pacific are found along the California/ Oregon/Washington coast and southeastern Alaska (Calambokidis et al. 1993; Straley 1994).

A group of feeding humpback whales (*Megaptera novaeangliae)* is found year-round in the Kodiak Archipelago in the western Gulf of Alaska, with a peak in sightings occurring between June and October (Fig. 1) (Waite et al. 1999; Zwiefelhofer unpub. data). These whales are currently assigned to the Central North Pacific (CNP) stock of humpback whales by the National Marine Fisheries Service (NMFS), though no directed research has been conducted on this population (Angliss et al. 2001). Previous research on humpback whales around Kodiak Island has occurred opportunistically during killer whale (*Orcinus orca)* line transect surveys in the early 1990's (Waite et al. 1999). This research indicated that Kodiak Island humpback whales may be a homogeneous feeding aggregation separate from other known feeding aggregations in Alaskan waters, including southeast Alaska and Prince William Sound. However, until directed research solidifies opportunistic results the understanding of the stock structure of North Pacific humpback whales remains incomplete, making need for directed research efforts in this region critical to management. Stock separation is a concern for managers due to an increase in fisheries interactions, gear entanglement, and a growing whale watching industry in Alaskan waters.

Management concerns in the Kodiak Island area also stem from the need to monitor recovery rates of the population. Large-scale commercial whaling occurred on Kodiak Island between 1926 and 1937, significantly reducing the number of humpback whales in the area (Williams S. Lagen Collection unpub. data, University of Washington). All stocks of humpback whales diminished by commercial whaling are believed to be increasing, but data are inadequate to assess the rate of increase (Angliss et al. 2001).

The purpose of this paper is to give results from a study to assess humpback whale numbers in Kodiak that began in 2001. This study estimated abundance for a portion of eastern Kodiak Island humpback whales based on mark-recapture, photo-identification studies conducted in 2001 and 2002. Estimates of pre-whaling and immediate post-whaling populations within the study area are also constructed using a delay-difference population model (Quinn and Deriso 1999).

Methods

Study area

For logistic reasons, the study area was limited to the waters of eastern Kodiak Island, including Chiniak and Marmot Bays (Fig.1). Kodiak Island is part of the Kodiak Archipelago and is located approximately 30 miles from the Alaskan mainland in the Gulf of Alaska.

Vessel surveys and field data

Individual whales were identified from photographs of the black and white pigment patterns and other natural markings on the ventral surface of their tail flukes (Katona et al.1979). Photographs were taken during vessel surveys with a 35 mm camera with 300 mm lens and black and white 3200 ASA speed film exposed at 800 ASA. Photographs of calves were not used in the analysis, due to the tendency of the pattern on the flukes of some calves to change prior to maturity.

In addition to photographs, data collected included the date, time, latitude and longitude, nearest headland, and general behavior of the whale. Information about the number of whales in the group and the role (mother, calf, adult) of each whale was documented for each encounter.

Study and sample periods

Vessel surveys were conducted during study periods in June through September of 2001 and 2002 from the R/V Soundwave, an 8.2 m bowpicker. For each year, the study periods were divided into seven-day sample periods with the exception of the final sample periods in both years, which were shorter (Table 1). The 2001 study period consisted of 10 total sample periods beginning June 13th and ending September 14th (Table 1). Surveys took place for 18 days and a total of about 74 hours. Effort in 2002 consisted of 15 sample periods beginning June 4th and ending September 17th. Surveys took place on 38 days for a total of about 224 hours (Table 1). Survey effort was increased in 2002 primarily due to vessel availability. Inclement weather conditions such as fog and high winds limited survey effort in both years.

Current abundance estimation

An estimate of current humpback whale abundance within the study area was made using the Schnabel maximum likelihood estimator (MLE) (Seber 1982). Two critical assumptions of the Schnabel MLE are that the population is closed and that all whales have equal capture probabilities at each sample period. The Schnabel MLE was only applied to 14 sample periods in 2002 because no whales were seen in the shortened 15th sample period. Table 2 summarizes model input. Small sample sizes in 2001 prevented estimation of abundance. A parametric bootstrap was performed to 1000 replicates to obtain 95% confidence intervals for estimated abundance $\hat{N}_{2002}$.

Alternatives to the closed population Schnabel MLE were also explored. A Jolly-Seber estimate was calculated for the 2002 data. This method of estimation assumes an open population and allows for recruitment and mortality to occur within the study period. In addition, robust estimators from program MARK, including the Pollock robust model that combined results from 2001 and 2002, were also explored (White and Burnham 1999).

Historical abundance estimation

Estimates of eastern Kodiak Island humpback whales within the study area were calculated for pre-whaling (pristine) and immediate post-whaling populations following an Allen-Clark delay-difference model (Quinn and Deriso 1999). The following equation, adapted from Breiwick et al. (1981), was used to calculate historical abundances, which were dependent upon the current abundance estimate and historical catch:

$$N_{t+1} = (N_t - C_t)(1 - M) + R_t \quad (1)$$

where $N_t =$ population size at the beginning of year *t*

C_t = catch in year *t*

M = natural mortality rate

$R_t = r_t N_{t-\tau}$ is the gross recruitment between the beginning of year *t* and *t* +1

. $\tau =$ lag time assumed for population response.

The recruitment rate was assumed to be a density-dependent function, according to the equation:

$$r_t = M + (1 - \frac{N_{t-\tau}}{N_o})(r - M) \qquad (2)$$

where r_t = recruitment rate in year *t*

N_0 = initial population size (pristine population size prior to commercial exploitation)

(r-M) = net recruitment rate.

Currently, there are no estimates of net recruitment for humpback whale populations in the North Pacific. Therefore, the value of net recruitment was set equal to 0.04, which is equal to the general cetacean maximum productivity rate defined by Wade and Angliss (1997). The value of *M* was taken as one minus survival rate. A survival rate of 0.96 came from the estimated survival rate for humpback whales in the North Pacific (Mizroch et al. in press). The values of *r* followed from the fact that the net recruitment rate is equal to *r* minus *M.* The value of *r* was thus set equal to 0.08 in order to achieve a net recruitment rate of 0.04 given an *M* of 0.04. The value of τ was set equal to five years, as per the age of average sexual maturity in humpback whales (Chittleborough 1958, 1959; Clapham and Mayo 1990).

The values for C_t were taken from the William S. Lagen collection at the University of Washington. The collection contains catch history, including date, year, and number of kills for humpback whales harvested out of the Port Hobron whaling station in Kodiak, Alaska (Fig. 2). Locations of most kills are given in the collection, but are very general and typically only account for approximate bearing and distance offshore in which the whale was harvested. The whaling grounds encompassed most of eastern Kodiak Island; an area approximately four times that of the study area (Fig. 2). As a result, values of C_t were divided by four to account for the size difference between whaling grounds and the study area, assuming random harvest throughout the grounds.

Initial population size, $\hat{N}_0$, was estimated by first entering a trial value for $\hat{N}_0$ into equation 2 and projecting the population forward to 2002. The estimate for $\hat{N}_0$ was the value that resulted in $\hat{N}_{2002}$ corresponding to the MLE, given values of C_t, R_t, and *M.* The initial population size applies to the years 1920 through 1925 and is assumed to represent the carrying capacity prior to commercial exploitation. Once a value of $\hat{N}_0$ was found, population size at any subsequent time period could be estimated. Thus, immediate post-exploitation abundance, $\hat{N}_{1938}$, was easily found by use of this method. The values of $\hat{N}_0$ and $\hat{N}_{1938}$ were dependent on $\hat{N}_{2002}$, therefore confidence intervals for each followed from a parametric bootstrap in which $\hat{N}_0$ and $\hat{N}_{1938}$ were estimated based on the $\hat{N}_{2002}$ values from the previous 1,000 bootstrap replicates

Sensitivity study of historical estimation to model parameters

A sensitivity study of the *r* and *M* parameters in the delay-difference model was performed in order to determine which parameter was the most influential in the final estimation of historical population sizes. Changing the value of each of the parameters and re-running the model tested the sensitivity of the model to each parameter. New values of *M* and *r* were used to reflect both higher and lower values than the baseline model. The two parameters were tested independently from one another. Values of M used came from the 95% confidence intervals of survival from Mizroch et al. (in press), which equaled 0.94 and 0.98. Therefore values of M were 0.02 and 0.06. No confidence intervals were available for r, so values were set at 0.06 and 0.10 to reflect both lower and higher rates of recruitment. An additional scenario was examined in which r and M were both set equal to 0.04 to represent a situation in which net recruitment was zero. A final scenario set net recruitment equal to 0.10 between 1980 and 1990 inclusively to reflect a period of increased productivity (Baker and Herman 1987; Calambokidis et al. 1997).

Sensitivity study of historical estimation to catch numbers

A sensitivity study of the historical catch (C_t) in the delay-difference model was performed in order to determine how influential catch was in the final estimation of historical abundance. To test the sensitivity of the model to catch, catch numbers were left as given values as well as divided by two to represent scenarios in which catch within the study area comprised either all or one half of the total number of humpback whale kills. Results were compared to the base model in which catch numbers were divided by four.

Results

Vessel surveys

Vessel surveys in 2001 resulted in 68 sightings of humpback whales. The 68 sightings produced fluke photographs of 31 unique adult whales that were used in the estimation of abundance (Table 3). Excluded from analysis were sightings of calves or animals for which no fluke photograph was obtained. Adult whales were sighted in all months surveyed in 2001.

Vessel surveys in 2002 resulted in 148 sightings of humpback whales (Table 3). As in 2001, some sighted whales were calves or animals with no associated fluke photograph. Thus, 2002 vessel survey data resulted in fluke photographs of 71 individual whales that were used in analysis. Adult whales were sighted in all months surveyed in 2002.

Current abundance estimation

The Schnabel MLE of abundance, N_{2002}, was 157 animals (CV 18%) with a 95% confidence interval of (114, 241) (Fig. 3). Estimated parameters in the Jolly-Seber method, such as capture probability and survival, were not biologically realistic (i.e. survival over 100%). Thus estimates of abundance from the Jolly-Seber method are not reported. Robust models produced highly unreasonable results, including negative estimates of abundance and capture probability, due to low sample sizes. Therefore, estimates from robust models are also not reported.

Program CAPTURE was used to evaluate the degree of heterogeneity in the 2002 sighting data (Rexstad and Burnham 1992). CAPTURE extends the Schnabel experimental design by applying sighting histories to increasingly complicated models in which the probability of capture varies with time, behavior, and heterogeneity. The program then recommends models that best represent the input data. Two of the top four models suggested by CAPTURE included heterogeneity as a factor in estimation, though the top recommended model did not. Thus, program output suggested that heterogeneity may be present to some extent.

Historical abundance estimation

The delay difference model estimated the pre-whaling humpback whale abundance at 343 (CV 3%) animals within the study area given the value of $\hat{N}_{2002}$ equal to 157 (Fig.3). The 95% confidence interval was (331, 376). The model estimated post-whaling abundance, $\hat{N}_{1938}$, as 27 (CV 42%) animals, with a confidence interval of (14, 61).

Sensitivity study of historical estimation to model parameters

Pristine abundance was estimated at 341 and 373 when M was equal to 0.02 and 0.06 respectively. $\hat{N}_{1938}$ equaled 5 and 72 under the same parameterization (Figure 4). Pristine abundance was estimated at 392 and 371 when r was set equal to 0.06 and 0.10, respectively. $\hat{N}_{1938}$ was equal to 67 and 8 under the same parameterization. During the "1980" scenario pristine abundance was estimated at 332 and $\hat{N}_{1938}$ was equal to 16 (Figure 4). Similar patterns of population growth and decay were seen for all values of both M and r.

Sensitivity study of historical estimation to catch numbers

When historical catch numbers were divided in half, representing a scenario in which one half of humpback whale kills occurred within the study area, pristine abundance was estimated at 645 and abundance in 1938 was estimated at 11. When catch numbers were not altered and 100% of the historical catch was assumed to occur within the study area, N_0 was estimated at 1258, while N_{1938} was estimated at -11 (Fig. 4).

Discussion

Current abundance estimation

Estimated abundance for the Kodiak Island humpback whale population, within the study area, 157 animals, had a precise CV of about 18%. However, the model may have not met at least two of its assumptions; closure and equal probability of capture.

A violation to the closure assumption stemmed from the limitation of the study area. The study area was defined based on historical accounts of humpback whale occurrence and vessel accessibility from the city of Kodiak and did not incorporate all areas around Kodiak Island in which humpback whales may feed. Thus, this study estimated only a proportion of the whales that may be part of a much larger feeding aggregation. The whales in the study area may belong to a feeding aggregation that utilizes waters not only around Kodiak Island, but waters throughout the western Gulf of Alaska as well. Whales may have migrated into and out of the study area throughout the study period, as humpback whales have been previously observed throughout the Kodiak Archipelago.

The amount of movement that may have occurred into and out of the study area cannot be estimated without photo-identification effort in other high use areas around the island. One survey of the entire east coast of Kodiak Island in September 2002 sighted 67 individual whales outside of the study area, of which only two whales had been previously sighted in the study area within the study period (B. Witteveen, unpubl. data). This would suggest some very limited movement between the whales within the study area and other feeding whales around Kodiak Island, but data were too few to draw conclusions about the degree of violation to the closure assumption within the study area.

Despite other areas of high use by humpback whales and slight evidence for movement out of the study area, the assumption of closure was probably justified due to the fact that only a single year of sighting histories was examined. However, if the closure assumption was violated to a high degree, abundance could be overestimated (Seber 1982).

The assumption of equal probability of capture within each sampling period may not be satisfied. The Schnabel MLE allows for time-varying capture probabilities, meaning capture probability was equal for all animals at each time period, but not, necessarily, over all time periods. An equal capture probability for all whales at each sample period is highly unlikely.

Problems with model assumptions such as these may be rectified in the future as effort continues and sample size is increased. Additional research will further clarify habitat usage by humpback whales within the Kodiak Island study area and the degree of exchange between these whales and feeding humpback whales in other regions of western Alaska. This would allow for more advanced models that examine closure assumptions and heterogeneity in *p* to be utilized (Pollock et al. 1990; White and Burnham 1999).

Historical abundance estimation

The estimation of the historical populations of humpback whales was dependent on the estimate of current abundance. A negative bias associated with the current estimate would lead to underestimation of the historical estimates. However, the estimated carrying capacity was affected more by the whaling removals and choice of parameters *r* and *M*.

Sensitivity study results show the delay-difference model was highly dependent on the values of *M* and *r*. Changing each value by a few percent causes changes in estimates of abundance throughout the time scale by means of changes in net recruitment to the population. In cases when $r > M$, the population will continue to increase until carrying capacity is reached. When $r < M$, the population will decrease. The mortality parameter seems to exert more influence on the model, causing larger variations in estimates from the baseline (Fig. 4).

In most scenarios examined here, parameters were kept constant throughout the time period. In reality, recruitment and mortality rates have significant annual variation and are not likely to remain constant throughout the time period. The delay-difference model is deterministic and does not allow for variations in these parameters over time when, in reality, variations over a long time period, such as the one represented here, are likely to occur. Notably, the scenario that does allow for some variation in the parameters over time, the 1980 scenario, estimates abundances that are the most similar to the base model.

The values for *M* and net recruitment used in this model were taken from large-scale humpback whale research projects and are not specific to the Kodiak region. Using new values of *M* and *r* based on the Kodiak Island population would result in an improved assessment of historical population size and growth, but no data currently exist for such values to be estimated. Therefore the values of *M*, *r*, net recruitment, and subsequently estimates of the historical population, are provisional.

Historical abundance here was estimated only within the study area though humpback whale kills occurred throughout the east side of Kodiak. It is likely that historical abundance within the study area would be overestimated if catch had not been altered to account for the size of the study area in relation to the whaling grounds because results show that the delay difference model is highly sensitive to changes in catch numbers (Figure 4). Applying all of the humpback whale kills to the study area results in a negative abundance in 1938 indicating a complete depletion of the population and showing the impracticality of not adjusting catch numbers. Specific information about kill location would allow for a more accurate proportion of catch to be applied and would result in a more realistic account of historical abundance within the study area. Reeves et al. (1985) gives a rough distribution of Port Hobron humpback whale kills based on the general locations given in the William S. Lagen collection. Examination of this distribution supports a one-quarter proportioned catch within the study area. The most conservative estimate of local abundance within the study area assumed that the study area comprises one quarter of the whaling grounds. Applying that same proportion to the historical catch numbers resulted in 343 (CV 3%) whales as the best estimate of historical abundance within the study area given the current level of data.

The total population utilizing the entire Kodiak area is clearly greater than that of the study area. Depending on the annual utilization of the study area, the population could be just slightly larger than that in the study area to several times the estimated population. The whales in the study area may belong to a feeding aggregation that utilizes waters not only around Kodiak Island, but waters throughout the western Gulf of Alaska as well. Further research is needed to accurately define the boundaries of feeding humpback whales in the Kodiak Island study area and in western Alaska in general.

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Table 1. Start and end dates and effort for the 2001 and 2002 sample periods for humpback whale photo-identification vessel surveys.

	Year							
	2001				2002			
Sample Period	Period Start Date	Period End Date	# of days sampled	# of hours sampled	Period Start Date	Period End Date	# of days sampled	# of hours sampled
1	11-Jun	17-Jun	2	4.9	3-Jun	9-Jun	4	27.9
2	18-Jun	24-Jun	3	14.4	10-Jun	16-Jun	4	29.1
3	25-Jun	1-Jul	2	8.6	17-Jun	23-Jun	3	17.9
4	2-Jul	8-Jul	1	8.3	1-Jul	7-Jul	5	28.8
5	9-Jul	15-Jul	3	14.6	8-Jul	14-Jul	3	17.8
6	16-Jul	22-Jul	1	4.6	15-Jul	21-Jul	2	10.7
7	23-Jul	29-Jul	1	2.1	22-Jul	28-Jul	2	10.5
8	30-Jul	5-Aug	3	9.1	29-Jul	4-Aug	4	23.7
9	3-Sep	9-Sep	1	3	5-Aug	11-Aug	2	10.3
10	10-Sep	14-Sep	1	4	12-Aug	18-Aug	1	5.3
11					19-Aug	25-Aug	3	13.9
12					26-Aug	1-Sep	1	4.9
13					2-Sep	8-Sep	1	7
14					9-Sep	15-Sep	1	8.8
15					16-Sep	17-Sep	2	7.7
Total			18	73.6			38	224.1

Table 2. Schnabel unconditional MLE model input and results of abundance estimate. Schnabel MLE was applied to 2002 Kodiak Island humpback whale sightings only.

i	n	m	M
1	3	0	0
2	6	1	3
3	11	2	8
4	10	2	17
5	28	2	25
6	1	0	51
7	5	3	52
8	7	3	54
9	0	0	58
10	0	0	58
11	2	2	58
12	4	1	58
13	2	0	61
14	11	3	63
Sum:	90	19	71
s:	14		
r:	71		

n = the size of the ith sample

m = the number of marked animals in the ith sample

M = the number of marked animals just prior to the ith sample

s = the total number of samples

r = the total number of marked animals at the end of the experiement.

Table 3. Number of sightings and the number of flukes photographed by study period. Photographs were collected during humpback whale vessel surveys conducted in 2001 and 2002.

	Year			
	2001		2002	
Sample Period	# of sightings (adults only)[*]	# of flukes photographed	# of sightings (adults only)	# of flukes photographed
1	3	2	4	3
2	7	7	8	6
3	5	5	13	11
4	4	4	11	10
5	5	5	29	28
6	2	1	1	1
7	2	2	7	5
8	12	11	9	7
9	5	3	1	0
10	0	0	0	0
11			3	2
12			4	4
13			2	2
14			11	11
15			0	0
Total	45	40	103	90

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[*] Number of sightings columns include all adult whales sighted.

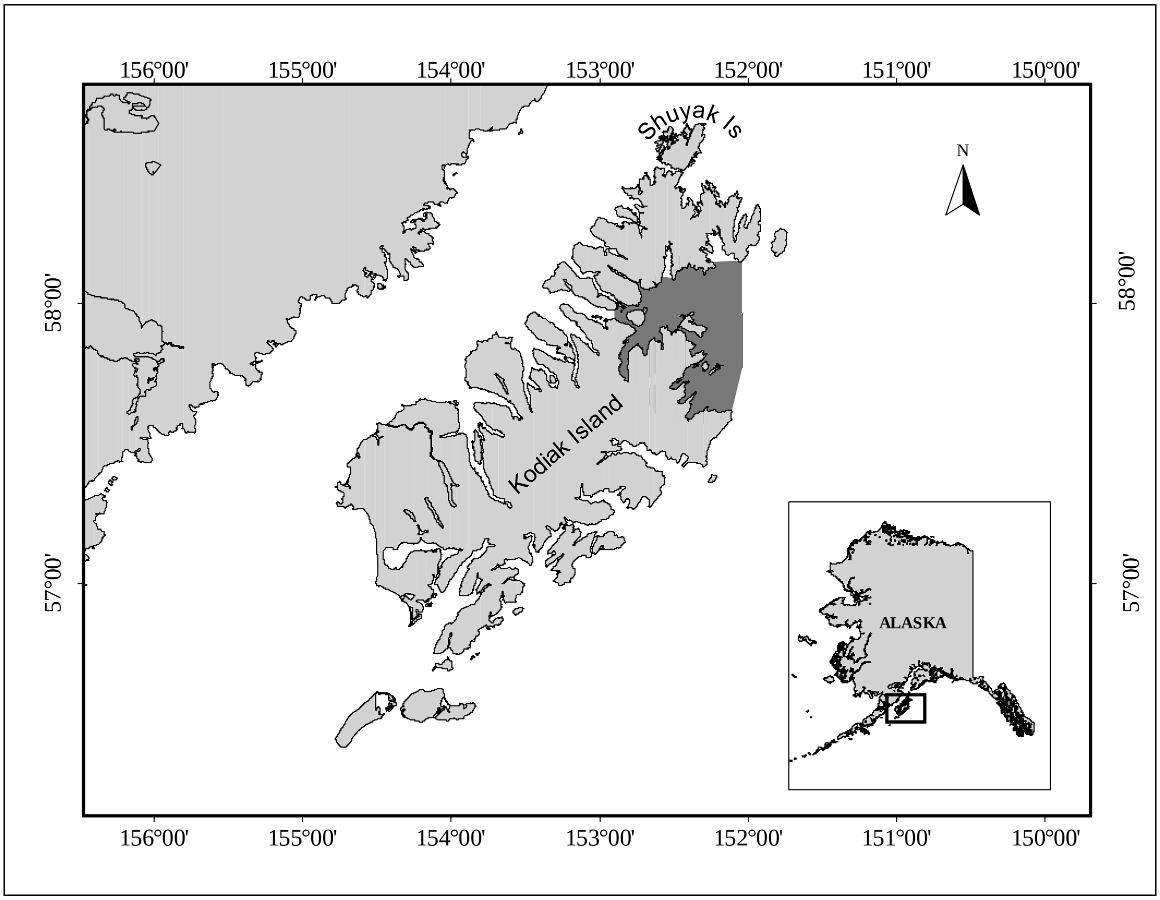

Figure 1. Map of the Kodiak archipelago showing Kodiak and Shuyak Islands. The study area is shown in shade.

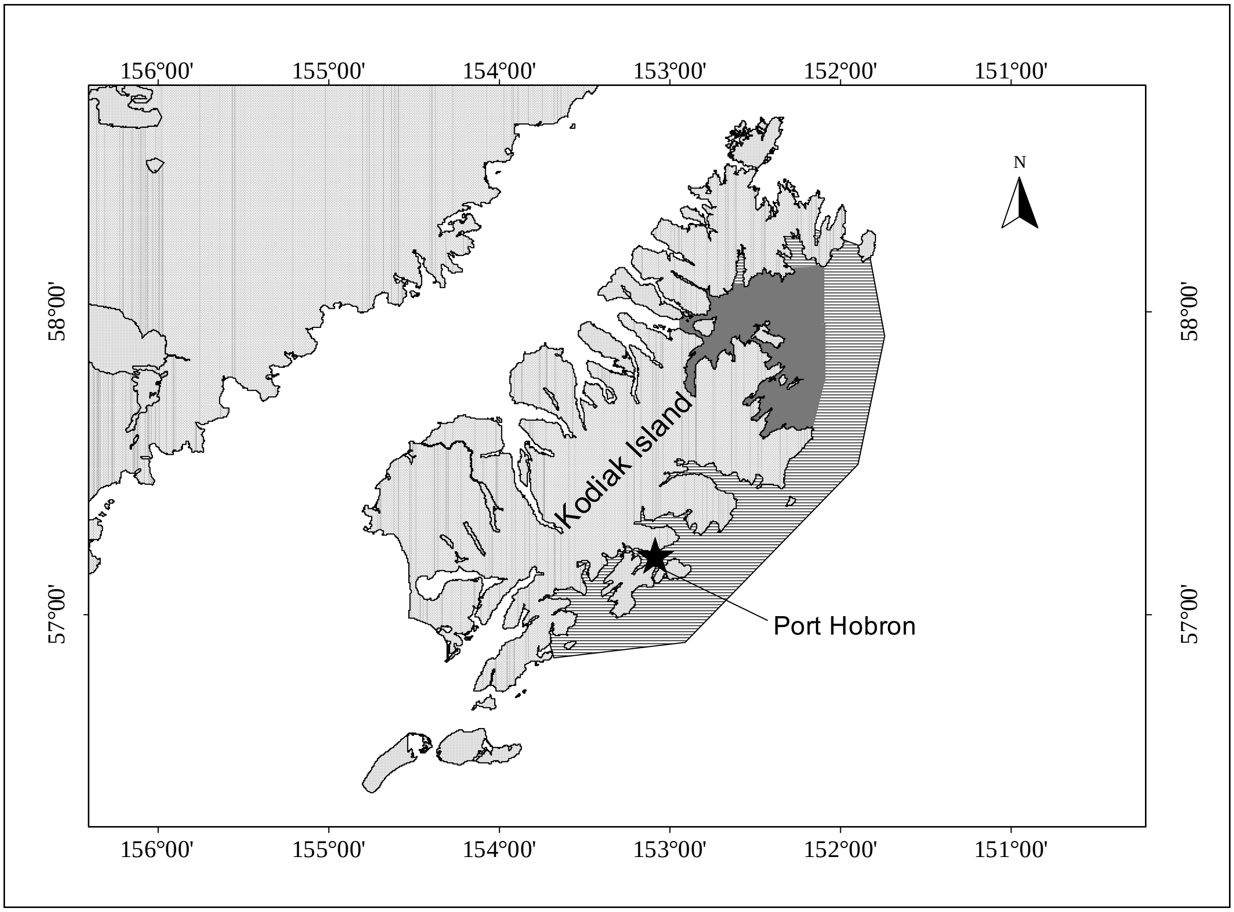

Figure 2. Location of the Port Hobron whaling station. The approximate coverage area of commercial whaling operations is shown in stripes and the study area is shown in shade.

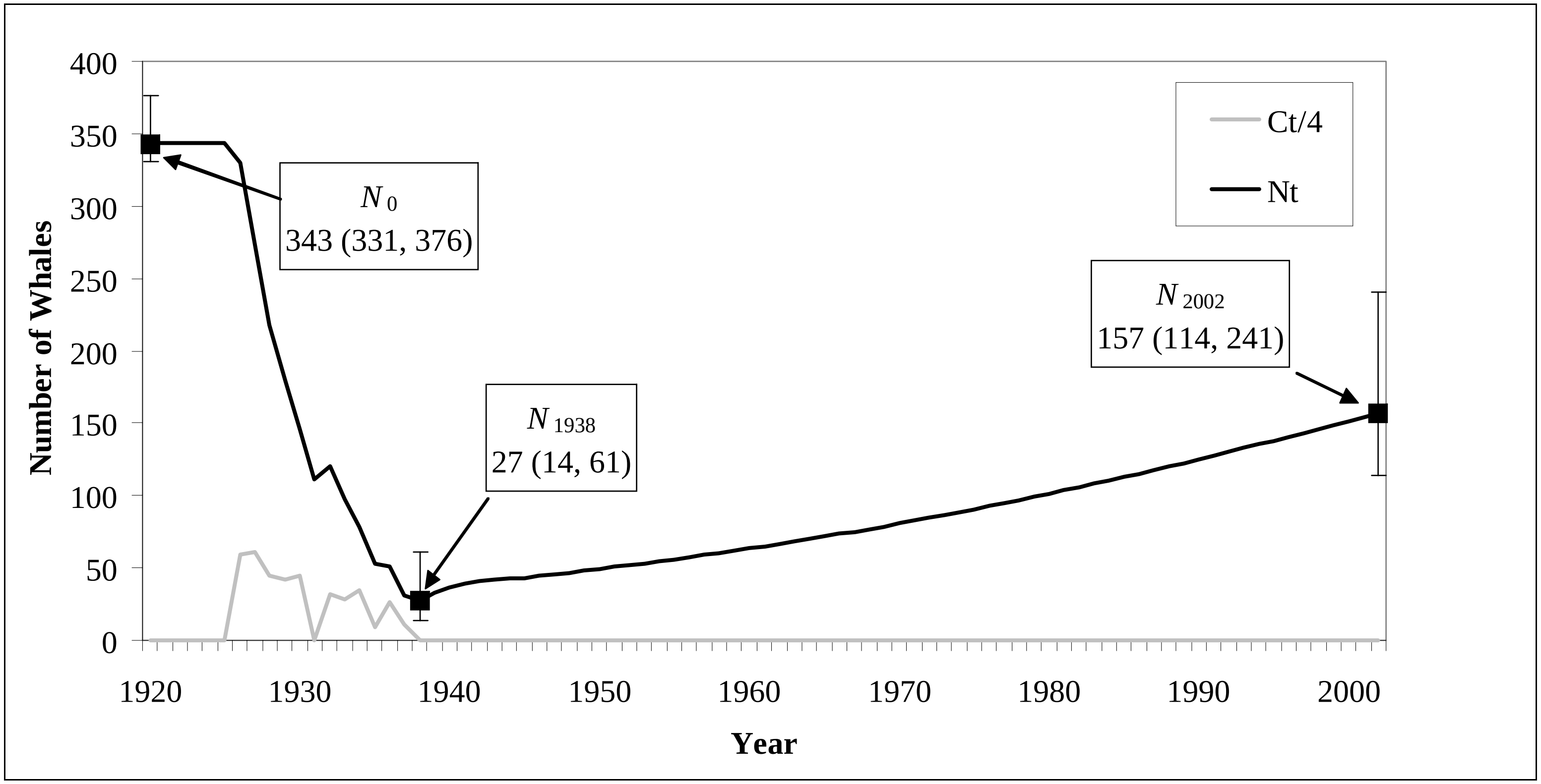

Figure 3. Comparison of adjusted commercial catch ($C_t/4$) and estimated abundance (N_t) between 1920 and 2002. Abundance estimates (± 95% CI) from delay-difference model for N_0, N_{1938}, and N_{2002} are shown.

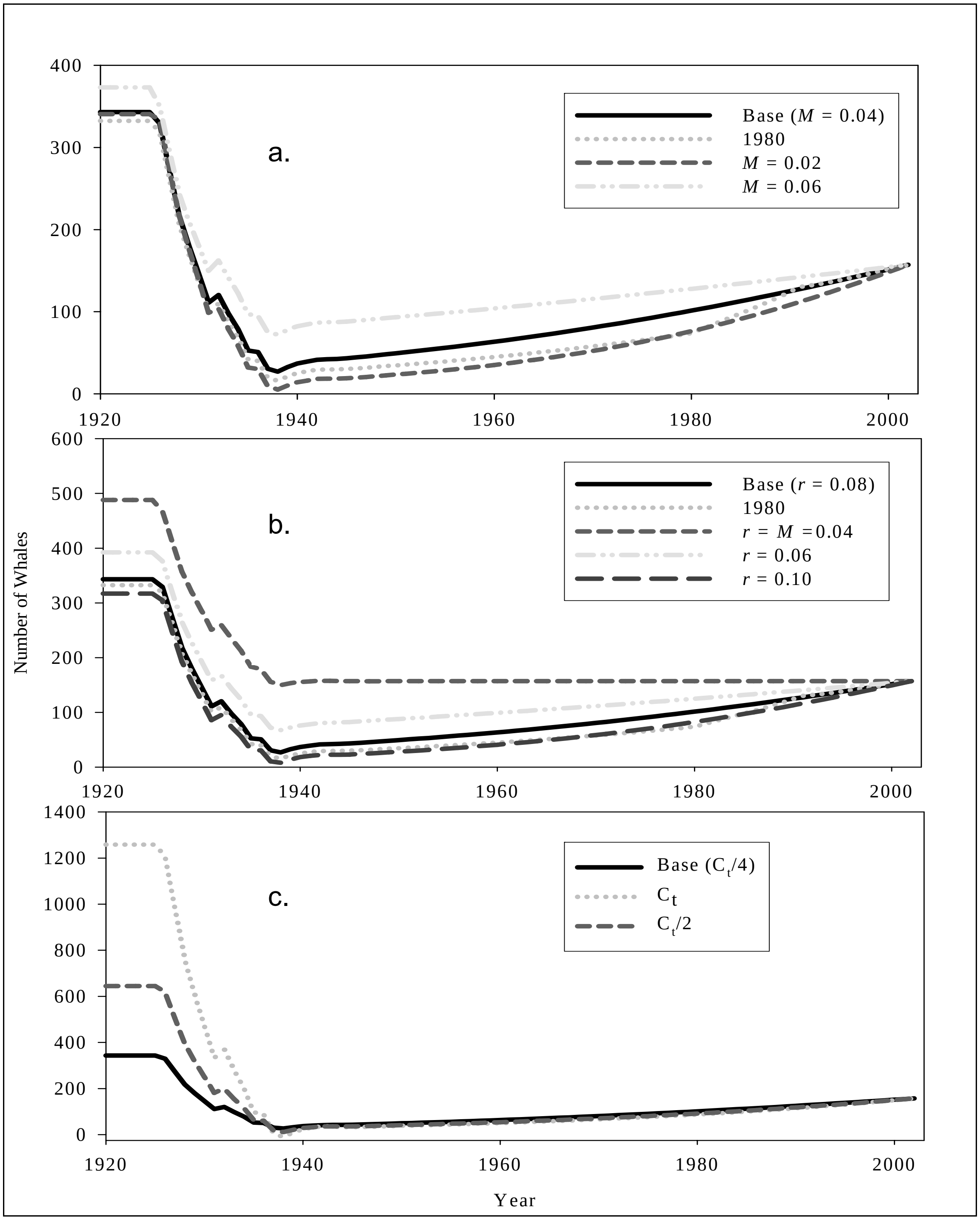

Figure 4. Comparison of estimated abundance showing sensitivity of the delay-difference model to a) the *M* parameter, b) the *r* parameter, and c) historic catch values (C_t). In the "1980" scenario, (r-M) was fixed at 0.10 between 1980 and 1990.

Potential current and historic prey removal due to consumption by humpback whales (*Megaptera novaeangliae)* near Kodiak Island, Alaska[*]

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Introduction

Numerous studies have revealed that an increased awareness of trophic-level interactions is essential in assessing the status of complex marine ecosystems (Overholtz et al. 1991; Pascual et al.1993; Hairston and Hairston 1993; Estes 1994; Kenney et al. 1997; Trites et al. 1997). Such studies have shown that predator-prey linkages in marine systems can have direct and indirect effects on all ecosystem members, but predictions of their effects cannot be made without multi-species models.

Cetaceans are top predators in marine ecosystems and consume significant amounts of prey. Knowledge of the distribution, abundance, and foraging habits of cetaceans is, therefore, an essential element of any pelagic ecosystem study (van Franeker 1992). Many species preyed upon by cetacean populations are targeted by other marine predators and commercial fisheries or are linked to fisheries through complex food webs. Previous studies have reported that prey removal due to cetacean consumption approach or exceed removals due to commercial fishing (Laws 1977; Laevastu and Larkins 1981; Bax1991, Markussen et al. 1992; Nordøy et al. 1995; Kenney et al. 1997). Such high levels of consumption can have significant effects on the distribution and abundance of prey species and the structure of marine communities (Perez and McAlister 1993; Kenney et al. 1997; Croll et al. 1998). Therefore, examining consumption by cetaceans contributes information about complex ecosystem linkages and the long-term sustainability of marine resources (Perez and McAlister 1993; Kenney et al. 1997; Tamura and Ohsumi 2000).

Humpback whales (*Megaptera novaeangliae)* feed in the waters off Kodiak Island and, because they are considered apex predators, may influence the structure of the Kodiak Island marine ecosystem (Figure 1) (Trites et. al. 1997; Croll et. al. 1998). Modeling the amount of prey consumed by feeding humpback whales is, therefore, a useful tool for evaluating their role as marine predators.

Cetaceans, in general, are described as opportunistic in their food selection, though species tend to select broad categories of prey such as cephalopods, fish, or zooplankton (Tomilin 1954; Nemoto 1959; Klumov 1966; Sigurjónsson and Víkingsson 1998). Humpback whales are classified as generalists and target a wide variety of prey species (Nemoto 1970; Perry et al. 1999). They have been shown to be seasonal feeders on euphausiids (*Thysanoessa* spp*.)* and schooling fish species up to 30 cm in length, including capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasi),* walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius),* cod (*Gadus* spp.), sardines (*Sardinops* spp.), and sandlance (*Ammodytes* spp.) (Nemoto 1957, 1959; Mitchell 1973; Payne et al. 1990). The variety, as well as the amount, of prey removed from Kodiak waters may therefore be significant. Resource removal from Kodiak waters is of particular importance when considering the high value of Kodiak Island commercial fisheries, which totaled 63.3 million dollars in ex-vessel value in 2002 (NMFS 2002a).

Modeling consumption by humpback whales as they recover from severe population declines could shed light on patterns of change seen in prey and sympatric consumer populations, such as marine birds and pinnipeds (Merrick 1997; Anderson and Piatt 1999). Commercial whaling in the 1900's significantly reduced the number of humpback whales, both within coastal Kodiak waters, and throughout the North Pacific (Rice 1978). Following their protection in 1965, however, humpback whale numbers in

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[*] Manuscript currently in review for publication in Fishery Bulletin

the central North Pacific increased, possibly by as much as 10%, between the early 1980's and early 1990's for some North Pacific stocks (Baker and Herman 1987; Calambokidis et al. 1997). Removal and subsequent recovery of a marine predator of this magnitude may cause large variations in the biomass removal of prey in the ecosystem, as has been hypothesized in other studies (Laws 1985; Springer et al. 2003). However, no empirical evidence exists to demonstrate such trophic interactions in the Gulf of Alaska. In this paper, we model the historic and current consumption by humpback whales within waters of northeastern Kodiak Island in order to assess the impact these whales have as predators on local prey populations.

Materials and methods

Study area

The study area encompassed waters of northeastern Kodiak Island, including Chiniak and Marmot Bays (Figure 1). The study area was divided into four subareas of approximately equal size in order to equalize sampling effort and maximize coverage of the study area. Subareas were also used to separate sightings of humpback whales for the purpose of weighting diet composition in relation to prey availability. An additional subarea, including the waters near Woody and Long Islands, was not considered a survey subarea but was designated in the post-study period for calculating diet composition ("nearshore," Figure 1).

Sightings and abundance of humpback whales

Data on humpback whale sightings was collected during vessel surveys conducted between June and September 2001 and 2002. Individual whales were identified from photographs of the black and white pigment patterns and other natural markings on the ventral surface of their tail flukes (Katona et al. 1979). A humpback whale sighting was defined as a sighting of an individual whale on a single day. Therefore, no whale was counted twice on one day, but may have been counted multiple times during the study period. Humpback whale sightings were summed by month and then by subarea for calculation of whale diet (see Methods: Composition of simulated diets).

An associated study used these sightings and fluke photographs to estimate current humpback whale abundance within the study area (Witteveen et al. this volume). This estimate was used in conjunction with historic catch data from the Port Hobron whaling station to estimate historic humpback whale abundance. The whaling grounds of Port Hobron encompassed most of eastern Kodiak waters; an area approximately four times that of the study area. To account for the size difference between whaling grounds and the study area, catch values were divided by four assuming random harvest throughout the grounds. The pre-whaling and current estimates of N in the study area are 343 (95% C.I. 331, 376) and 157 (95% C.I. 114, 241), respectively (Witteveen et al. this volume).

Composition of simulated diets

Two diets were simulated to reflect both a historic and current suite of possible humpback whale prey species. The diets were simulated because direct observation of humpback whale feeding behavior is rare and, even when observed, cannot produce a concrete determination of the prey species being eaten.

Diet A simulated historic target species and was based on the stomach contents of 39 humpback whales harvested at the Port Hobron whaling station on southeast Kodiak waters between May 30 and August 9, 1937 as analyzed by Thompson (1940).

Diet B simulated current target species and assumes no prey selectivity. It was based on the assumption that humpback whales will eat suitably sized prey (<30cm) in proportion to its relative occurrence in areas used by humpback whales. Euphausiid proportions in the diet were based on historic stomach contents and assumed to be constant over time, since no current euphausiid abundance estimate is available.

Information on seasonal prey availability was collected from mid-water trawl surveys that were conducted within eastern Kodiak waters in July 2001 and June through September 2002. Multiple passes with a commercial mid-water trawl net with a 22-mm mesh cod-end liner were made through acoustic scattering layers, ensuring an accurate representation of mid-water fish composition and occurrence. Species composition, species counts, and fish size were determined for each tow and grouped within the study subareas. Only data from tows conducted during the study period in 2001 and 2002 in areas utilized by humpback whales were included in this analysis. Therefore, prey surveys overlapped humpback whale sightings both temporally and spatially. A separate series of acoustic and purse seine (center panel with a 3.2-mm mesh net) surveys was used to determine prey availability within the near-shore subarea in June through September 2002 (Foy unpubl. data). Prey composition determined by these surveys was assumed to be homogeneous throughout the near-shore habitat within the study area.

To calculate diet B, the occurrence of fish smaller than 30 cm was determined from the mid-water trawl surveys within each subarea and month for both 2001 and 2002. Tow data was first separated by subarea and month. Percent composition of prey species in each tow was calculated by dividing the total number of fish of each species caught by the total number of all fish caught in each tow, excluding species larger than 30 cm (Nemoto, 1959) and species that were not previously documented as prey, such as flatfish and other non-schooling fishes (Nemoto 1957 1959; Klumov 1963; Kreiger and Wing 1984 1986; Perry et al. 1999).

To calculate diet B for the entire study area, prey proportions were weighted by the number of whales in each subarea. The weighted proportions were then summed across all months and subareas and multiplied by one minus the percentage of assumed euphausiid occurrence within the diet. Thus, diet B simulates a weighted availability of prey species based on temporal and spatial overlap between prey surveys and humpback whale sightings within the study period (Figure 2).

Consumption and biomass removal

Seasonal consumption was estimated for both the current humpback whale population and the pre-whaling humpback whale population. Pre-whaling consumption was estimated using diet A only. Diet B was used to estimate consumption by the current humpback whale population and to project consumption by a humpback whale population at the pre-whaling abundance estimate.

The active metabolic rate (kcal/day) of feeding humpback whales was estimated in this study as $E = 192M^{0.75}$, where Kleiber's (1961) model for basal metabolic rate (BMR; $E = 70M^{0.75}$) was modified using average oxygen consumption estimates for feeding baleen whales and *M* is average body weight (kg) (Wahrenbrock et al. 1974: Sumich 1983; Perez and McAlister 1993).

Daily prey consumption was then estimated as:

$$I = \frac{E}{K}\frac{1}{1{,}000}$$

where $I =$ total prey consumption (kg/day), $E =$ estimated daily energy requirements (kcal/day) and, $K =$ the estimated energy density (kcal/gram wet weight) of presumed prey. The average body mass for humpback whales (*M)* was set equal to 30,408 kg (Trites and Pauly 1998). The total energy density (*K)* of each diet was calculated by multiplying the average seasonal energy density of each prey species sampled in the study area by the percentage of that species within each diet and summing across all species. Values of *K* for individual prey species came from proximate compositions that were determined from prey collected during 2002 trawl surveys for all months within the study period (Foy unpubl. data). For each month, energy density was calculated by multiplying percent lipid by 9.4 kcal/g and percent protein by 4.3 kcal/g, which are conversion factors based on heat produced during metabolism of foodstuffs (Schmidt-Nielson 1997). Carbohydrates were considered to be bound and not available for nutrition (Gaskin 1982). The average seasonal energy density of each prey species was calculated by summing all values of energy density and dividing by the number of months in the study period. Previously published proximate composition values for surf smelt (*Hypomesus pretious)* and energy density data for euphausiids (*Thysanoessa* spp*.)* were used (Davis et al. 1997; Payne et al. 1999).

Seasonal prey consumption for the population was estimated by multiplying I by estimates of abundance (N) and the total number of days in the humpback whale feeding season. Consumption estimates were calculated for both the upper and lower 95% confidence limits on the abundance estimates to show a possible range of consumption. The length of the feeding season was presumed to be 152 days (Perez and McAllister 1993).

Results

Analysis of sightings showed that humpback whales were not uniformly distributed within the study area (Table 1). Occurrence of humpback whales within subareas was variable, indicating within-season shifts of habitat use. Peak humpback whale sightings occurred in subarea 2 in July of 2001 and 2002. No humpback whales were sighted in the near-shore area after the month of July in either year.

Only two prey items were identified in the 27 stomachs that contained appreciable quantities of prey of 39 stomachs analyzed by Thompson (1940). Surf smelt occurred in 21 of 27 (78%) stomachs and euphausiids occurred in 6 of 27 (22%) stomachs (Table 2). These percentages comprise diet A.). Energy densities of these two species combined to give a total energy density of 1.31 kcal/gram (Table 3).

The fish species found in areas used by humpback whales in 2001 and 2002 were pollock (36.96%), capelin (28.89%), eulachon (7.60%), Pacific sandlance (4.44%), Pacific sandfish (0.08%), and Pacific herring (0.03%) (Table 2). Diet B is comprised of these percentages. Calculated energy densities of prey species ranged from a high (eulachon) of 2.52 kcal/gram to a low of 1.12 kcal/gram (juvenile pollock). The total energy density for diet B was 1.19 kcal/gram (Table 3).

Based on energetic content of the above diets, the model suggests each humpback whale in the study area would consume 338 kg/day on diet A and 370 kg/day on diet B. Using a pre-whaling estimate of 343 (95% C.I. 331 - 376) animals in the study area, humpback whales feeding on diet A prior to 1927 would have removed an estimated 1.76 x 10^{7} kg of prey annually (95% C.I.1.70 x 10^{7} – 1.93 x 10^{7}), including nearly 3.87 x 10^{6} (3.74 x 10^{6} – 4.24 x 10^{6}) kg of euphausiids and approximately 1.37 x 10^{7} (1.32 x 10^{7} – 1.50 x 10^{7}) kg of surf smelt (Table 4). Assuming diet B accurately reflects prey use by the estimated 157 (95% C.I. 114-241) humpback whales currently feeding in the study area, these whales would be removing nearly 8.83 x 10^{6} (6.41 x 10^{6} – 1.36 x 10^{7}) kg annually, including 3.26 x 10^{6} (2.37 x 10^{6} – 5.01 x 10^{6}) kg of pollock, nearly 2.55 x 10^{6} (1.85 x 10^{6} – 3.92 x 10^{6}) kg of capelin, and 6.71 x 10^{5} (4.88 x 10^{5} – 1.03 x 10^{6}) kg of eulachon. If the same diet was consumed by a population of humpback whales allowed to return to pre-whaling abundance the projected population would remove 1.9 x 10^{7} (1.86 x 10^{7} – 2.12 x 10^{7}) kg of prey annually, including approximately 7.13 x 10^{6} (6.88 x 10^{6} – 7.82 x 10^{6}) kg of pollock, 5.57 x 10^{6} (5.38 x 10^{6} – 6.11 x 10^{6}) kg of capelin, and 4.25 x 10^{6} (4.10 x 10^{6} – 4.65 x 10^{6}) kg of euphausiids (Table 4).

Discussion

Consumption

Estimating the energy requirements of large cetaceans is inherently difficult and values presented here may be subject to substantial uncertainty. Previous studies in which consumption rates for cetaceans are estimated have used a range of values to adjust BMR ($E = 70M^{0.75}$) for active metabolism. These values generally range from approximately 1.5 to 3 times BMR (Hinga 1979; Lockyer 1981; Sigurjónsson and Víkingsson 1998). Our value of 192 is 2.7 times larger than 70 and is, therefore, a reasonable estimate, as it fits within this range and is based on observed oxygen consumption of baleen whales. However, the consumption estimates are highly sensitive to perturbations of model input; a 5% error in this value would cause deviation of that same percent in final consumption values. Further, all input values in our consumption model are assumed to be constant when body mass, physiological status and assimilation efficiency are likely subject to large seasonal fluctuations (Innes et al. 1987; Perez and McAlister 1993; Kenney et al. 1997; Trites et al. 1997; Sigurjónsson and Víkingsson 1998). Our model, however, did account for seasonal changes in the energy density of local prey sources, a limitation of previous models (Perez and McAlister 1993). Further research is necessary to obtain reliable field estimates of metabolic rates if model uncertainty is to be reduced.

The historic prevalence of surf smelt in diet A could imply a dramatic change in surf smelt availability, misidentification or an overestimation of smelt found in stomachs. Thompson's (1940) analysis resulted from "samples of stomach contents" obtained from catcher vessels; therefore, these samples may have completely missed less prevalent species. Further, stomach samples may have only reflected the most recent meal of the whale and therefore be biased toward a single species. This potential bias, however, may have been minimized by sampling stomachs throughout the season (May 30 – August 09) (Thompson 1940). Diet B is dominated by walleye pollock, a species not present in historic diet A. The increased importance of juvenile pollock in contemporary humpback whale diet B could reflect changes in prey species availability and use, foraging selectivity, or our diet reconstruction methodology.

Modeled diet B is considered provisional for two reasons. First, it assumes humpback whales eat prey species in proportion to their availability within foraging areas. Humpback whales may have preferred prey species and consumption may be disproportional to availability. That is, they may be selectively foraging from all available prey sources. Previous foraging studies have described humpback whale distribution as being correlated with areas of capelin (Whitehead and Carscadden 1985; Piatt et al. 1989) and sandlance abundance (Payne et al. 1986; Kenney et al. 1996) indicating a possible preference for small forage fish species. Given that in the decades since whaling, the Gulf of Alaska shifted from a system dominated by forage fish to one dominated by pollock and other groundfish (Merrick 1997; Anderson and Piatt 1999; Benson and Trites 2002), a shift in prevalence from surf smelt in the historic diet to pollock in the current diet is not unexpected. Pollock has been shown to be a dominant prey source of humpback whales harvested in Russia (Klumov, 1963). Additionally, humpback whales in southeastern Alaska have been observed near schools of juvenile pollock and are believed to eat pollock to an unknown, but potentially large, extent in some years (C. Gabriele pers. comm.).

The second source of uncertainty in diet B stems from the assumption that our mid-water trawl surveys are unbiased samples of all available prey. Because these surveys were not designed to sample zooplankton, they may have produced a biased estimate of euphausiid availability. This bias may not be significant, however, as the 22% value we used in diet B was based on historic usage and falls within the range of euphausiid consumption (5 -30% of the total diet) estimated in other humpback whale studies (Perez and McAlister 1993; Kenney et al. 1997).

Further, diet B was constructed based on results of mid-water trawl surveys that may underestimate the availability of some forage fishes, particularly Pacific sandlance. Pacific sandlance are often small enough to swim through the meshes in the net or are found in benthic habitats and cannot be captured by mid-water trawl methods. To minimize this potential sampling bias, we supplemented our trawl surveys with purse seine sampling in the nearshore subarea. Despite this effort we may have underestimated the prevalence of Pacific sandlance in the area, as it was found to dominate the diets of other coastal piscivores; the contents of 34 coho salmon (*Oncorhynchus kisutch*) and Pacific halibut (*Hippoglossus stenolepis*) stomachs in 2002 (Witteveen unpubl. data); and regurgitants from blacklegged kittiwakes in 2001 (n = 96) and 2002 (n = 147) were dominated by Pacific sandlance (Murra et al. 2003).

Potential Ecological Effects of Humpback Whale Consumption

Though estimates of consumption are highly dependent on estimates of population abundance and metabolic rates, these values indicate that humpback whales were, and still are, significant predators within the Kodiak Island ecosystem.

Historic commercial whaling reduced the population in our study area to an estimated low of 27 animals by 1938 (Witteveen et al. this volume). The removal of so many large consumers likely had significant impacts on the surrounding ecosystem. As modeled, reducing historic consumption to that of current levels would release nearly 10,000 tons of prey within the study area in a single feeding season. Such a release could have invoked a trophic cascade effect.

Cetacean removals in the Southern Ocean have demonstrated how trophic cascades can affect marine ecosystems through removal of large marine predators, including whales (Laws 1985). It has been hypothesized that a similar reorganization of the marine community may have occurred in the Bering Sea and Gulf of Alaska, although the mechanisms of such a cascade are not well understood (Merrick 1997; Trites 1997; Springer et al. 2003). Removal of whales during commercial harvest reduced predation on certain fish, cephalopod, and zooplankton species, which were then available to other consumers. This large release of prey, when coupled with environmental factors such as the 1977 regime shift, may have contributed to the growth of sympatric marine predator populations from the late 1940's to late 1970's. It is hypothesized that whale stock resurgence, coupled with the 1977 regime shift that favored the proliferation of groundfish species, may have reduced prey availability to other piscivores in the system and led to declines seen in harbor seal (*Phoca vitulina)*, Steller sea lion, Northern fur seal (*Callorhinus ursinus),* common murre (*Uria aalge*), thick-billed murre (*U. lomvia*), and red-legged kittiwake (*Rissa brevirostris*) populations (Merrick 1995, 1997; NRC 1996; Trites 1997). The Gulf of Alaska and Bering Sea ecosystems may still be seeing changes caused by baleen whale removals and recovery (NRC 1996).

Assuming the Kodiak Island study area was similarly affected by this trophic reorganization, estimating current consumption by humpback whales would help elucidate the role their recovery is playing in ecosystem dynamics. If our diet composition and subsequent consumption estimates are accurate, our results suggest the diet of humpback whales in Kodiak waters directly overlap those of sympatric piscivores and the biomass removed may be substantial.

The top species modeled in the humpback whale diet represent an important source of energy for multiple higher-trophic-level species and are known to be significant dietary components for Steller sea lions (Wynne), harbor seals (Jemison 2001), tufted puffins (*Fratercula cirrhata)* (Piatt et al. 1997), blacklegged kittiwakes (Murra et al. 2003), adult pollock, Pacific halibut, and arrowtooth flounder (Livingston et al. 1993; Yang 1995; Merrick 1997; Best and St. Pierre 1986).

Our model suggests humpback whales within the study area may currently be consuming a significant amount of fish, including over 3.26×10^6 kg of juvenile pollock and nearly 3.62×10^6 kg of small forage fish, such as capelin, eulachon and Pacific sandlance, during a 152-day feeding season. In comparison, tufted puffins consume only 6.40×10^4 kg of juvenile pollock between mid-July and mid-September, but this accounts for as much as one-tenth of the age zero pollock stock in the GOA during early July (Hatch and Sanger 1992). In addition, gadid removal by Steller sea lions in 1998 was estimated to be 1.79×10^8 kg, or 12% of total gadid biomass removed commercial fisheries for that year (Winship and Trites 2003). Though nearly 55 times the pollock removal due to consumption by humpback whales, this figure includes all gadid (not only pollock) species removals in all Alaskan waters. More importantly, these fish are likely larger ($\geq$60 cm vs. $\leq$30 cm) than fish targeted by humpback whales.

Although humpback whales generally feed on smaller age classes than are targeted by commercial fisheries or Steller sea lions (Perez and McAlister 1993; Kenney et al. 1997), consumption of younger age classes may affect future recruitment into the fishery. Barrett et al. (1990) stated that consumption of young cod (*Gadus morhua)* and saite (*Pollachius virens)* by shags (*Phalacrocorax aristotelis)* and cormorants *(P. carbo)* in the Northeast Atlantic could be a limiting factor in recruitment in years of low stock size, even if consumption of these species was overestimated by an order of magnitude. Thus, it is noteworthy that the humpback whales' removal of an estimated 3.26×10^6 kg of pollock (age 0-2) equal 30% of the 2002 commercial pollock harvest of 1.09×10^7 kg (ages 3 to 8) for the entire Kodiak Island management area and 2.1% of the 2002 spawning biomass of pollock for the entire Gulf of Alaska, which was estimated at 1.58 x 10^8 kg (NMFS 2002b; NPFMC 2002, 2003).

These comparisons are based on mean estimates of prey removal and do not take into account model uncertainty. When uncertainty is considered, however, comparison to even the lower end of estimates of prey removal are still of note. For example, assuming removal of juvenile pollock is equal to the lower estimate, or 2.37 x 10^6 kg, the humpback whale's removal of pollock still equals 21.7% of the 2002 commercial pollock catch and 1.5% of 2002 spawning biomass. Thus, it follows that if true consumption is actually closer to the upper estimates, that impact of prey removal by humpback whales would likely increase.

The humpback whale represents only one of a myriad of marine consumers within the Kodiak Island ecosystem whose ecological role cannot be determined without sophisticated multi-species models and analysis of ecosystem interactions. This study was designed to provide essential baseline data and a model for estimating prey removal by foraging humpback whales. Our results show that the potential for biomass removal due to consumption by humpback whales is significant and that the foraging strategies of these whales warrant further investigation. Continued research efforts can improve estimates of biomass removal by identifying target prey, determining the degree of prey selectivity, and assessing variable foraging efficiency.

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Table 1 Combined 2001 and 2002 sightings of humpback whales by subarea and month in the Kodiak Island study area.

	2001 and 2002				
Area	June	July	August	September	Total
1	10	7	10	3	30
2	29	89	22	3	143
3	20	8	0	12	40
4	0	3	0	7	10
Near Shore	5	14	0	0	19
Total	64	121	32	25	242

Table 2 Composition and relative occurrence of prey species represented in simulated humpback whale diets A and B.

Diet	Prey Species	Common Name	Percent of Diet
A	*Hypomesus pretious*	Surf smelt	78.00%
	Thysanoessa spp.	Euphausiids spp.	22.00%
		Total	100%
B	*Theragra chalcogramma*	Walleye pollock	36.96%
	Mallotus villosus	Capelin	28.88%
	Thysanoessa spp.	Euphausiids spp.	22.00%
	Thaleichthys pacificus	Eulachon	7.60%
	Ammodytes hexapterus	Pacific sandlance	4.44%
	Trichodon trichodon	Pacific sandfish	0.08%
	Clupea harengus pallasi	Pacific herring	0.03%
		Total	100%

Table 3 Monthly and average energy densities (kcal/gram) of prey species represented in simulated humpback whale diets A and B based on lipid and protein composition. Energy densities were used to estimate consumption by humpback whales. Average values in parentheses have been adjusted to reflect standard deviations of lipid and protein composition.

	Energy Densities (kcal/gram)				
Species	June	July	August	September	Average
capelin	1.1285	1.2632	1.1956	1.4298	1.2542 (1.1665, 1.3755)
Pacific sandlance	1.4179	1.4179	1.4179	1.4179	1.4179 (1.3211, 1.5590)
Pacific sandfish	0.8661	1.2126	1.1165	1.1165	1.0779 (1.0449, 1.1300)
eulachon	2.1582	2.5218	2.6758	2.7424	2.5245 (2.3761, 2.6860)
herring	2.0999	2.0999	1.9454	2.1205	2.0664 (1.9432, 2.2942)
juv. pollock	1.0144	1.0657	1.1380	1.2461	1.1160 (0.9730, 1.2994)
euphausiids	N/A	N/A	N/A	N/A	0.7430
surf smelt	N/A	N/A	N/A	N/A	1.4698

Table 4 Daily and annual (over a 152-day feeding season) consumption of prey from two different diets off northeastern Kodiak Island by humpback whales at two levels of population abundance: the current population of 157 and the historic population of 343 (also presumed to be the carrying capacity to which the current population will recover). Diet A is the historic diet; Diet B is based on currently available prey.

		Prey Species	Daily removal (kg)	Annual Removal (kg)		
				Mean	Lower Limit	Upper Limit
Historic Population	Diet A	Surf smelt	90,300.75	13,725,714.57	13,245,514.65	15,046,264.37
		Euphausiids	25,469.44	3,871,355.39	3,735,914.39	4,243,818.16
			115,770.20	17,597,069.97	16,981,429.03	19,290,082.53
	Diet B	Euphausiids	27,934.25	4,246,006.15	4,097,457.83	4,654,514.03
		Walleye pollock	46,923.73	7,132,406.25	6,882,876.01	7,818,614.44
		Capelin	36,670.67	5,573,942.52	5,378,935.79	6,110,211.05
		Eulachon	9651.69	1,467,056.65	1,415,731.06	1,608,202.05
		Pacific sandlance	5634.70	856,474.64	826,510.51	938,875.99
		Pacific sandfish	98.08	14,907.49	14,385.94	16,341.74
		Pacific herring	33.15	5038.20	4861.94	5522.93
			126,973.87	19,300,027.95	18,624,808.32	21,156,881.95
Current Population		Euphausiids	12,786.23	1,943,507.19	1,411,209.04	2,983,345.43
		Walleye pollock	21,478.21	3,264,687.41	2,370,537.36	5,011,399.15
		Capelin	16,785.12	2,551,338.12	1,852,563.99	3,916,385.27
		Eulachon	4417.83	671,509.90	487,593.17	1,030,789.08
		Pacific sandlance	2579.15	392,030.67	284,659.21	601,779.56
		Pacific sandfish	44.89	6823.54	4954.68	10,474.36
		Pacific herring	15.17	2306.12	1674.51	3539.96
			58,119.23	8,834,123.58	6,414,586.55	13,560,661.04

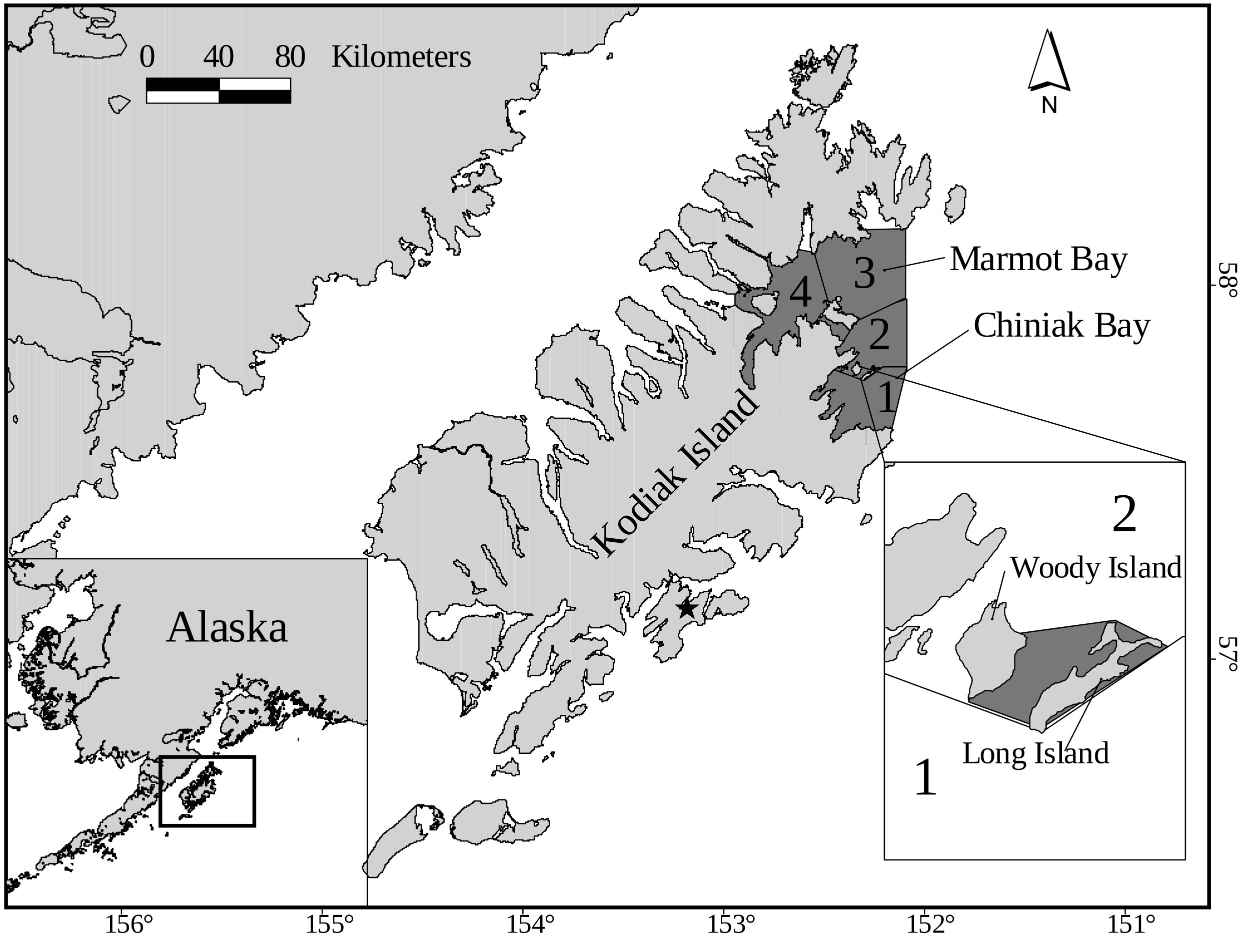

Figure 1 Map of Kodiak Island study area. Study area is shown in shade with subareas outlined and numbered. In detail is the near-shore subarea between Woody Island and Long Island.

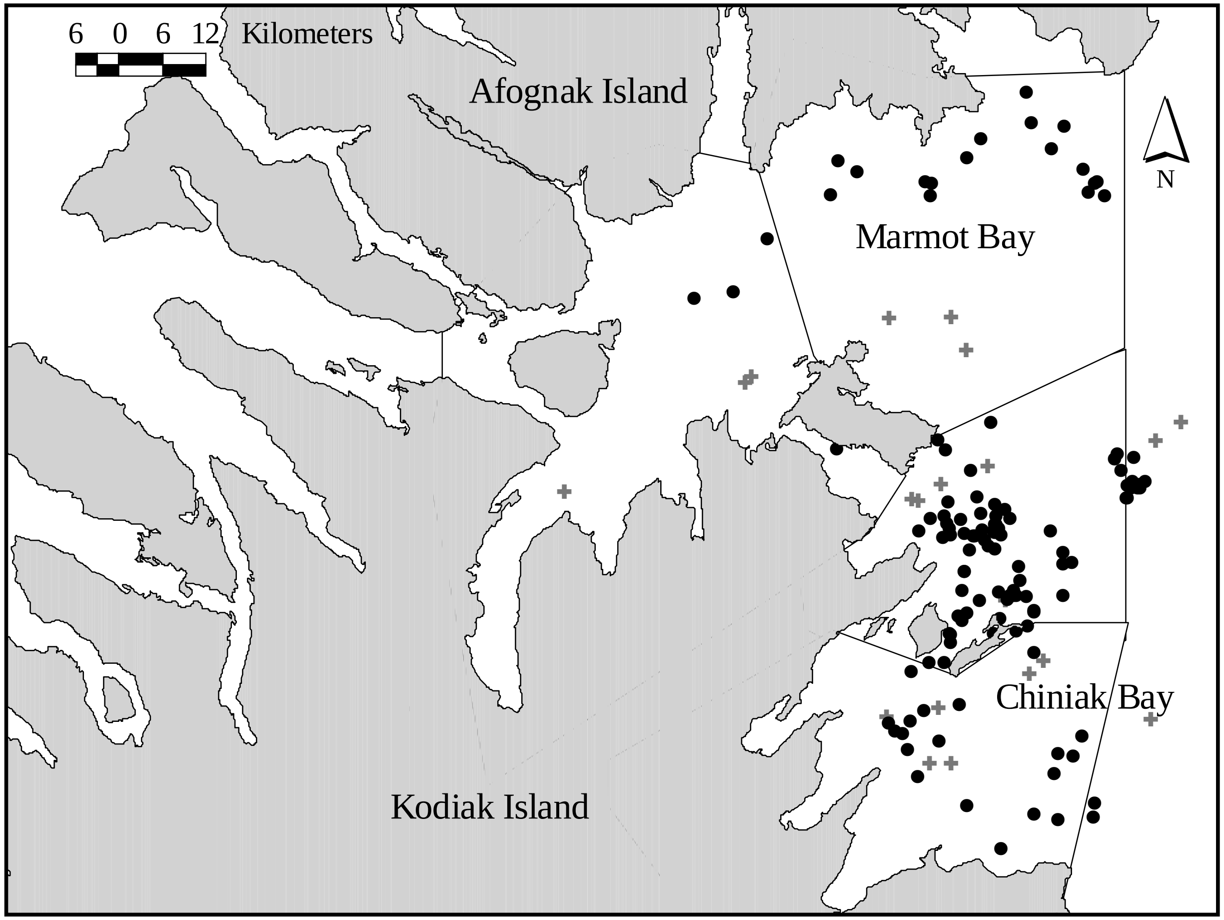

Figure 2 A close-up of the study area showing locations of humpback whale sightings (N) and prey tows (+) for 2001 and 2002. Only prey tows utilized in diet simulation are shown.

C. PISCIVOROUS BIRDS

Seabirds may serve as sensitive indicators of marine conditions that impact Steller sea lions because their diet overlaps that of sea lions and other apex predators in the Gulf of Alaska and because seabird reproductive parameters are both easily monitored and responsive to food availability (Cairns 1987). In particular, seabirds are useful indicators of relative abundance and demographics of intermediate trophic levels because they eat small, young-of-year fishes which are ecologically important links in the food web but difficult to quantify in trawl and hydro-acoustic surveys. Therefore, we used seabirds as bio-indicators to monitor the relative abundance and distribution of forage fishes and other trophic intermediates of the Gulf of Alaska food web. Overall objectives were to

- determine seasonal diets and foraging areas of black-legged kittiwakes, glaucous-winged gulls and tufted puffins during breeding season
- monitor the numbers and breeding performance of offshore divers (tufted puffins, common murres), surface feeders (black-legged kittiwakes, glaucous-winged gulls), and nearshore divers (pigeon guillemots, cormorants).
- determine nestling diets and growth rates of tufted puffins, black-legged kittiwakes, glaucous-winged gulls, and pigeon guillemots.

Black-legged kittiwakes as bio-indicators of marine conditions in the western Gulf Of Alaska

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Introduction

Changes in the structure and function of marine ecosystems in the North Pacific Ocean are hypothesized to have been driven by a gradual decline in primary production over the past century (Schell 2000), decadal-scale climatic oscillations in the northern hemisphere (Hare and Mantua 2000), or commercial exploitation of keystone species (Springer et al. 2003). A "regime shift " from lower than average sea surface temperatures to higher than average temperatures in the late 1970's (Hare and Mantua 2000) was concomitant with the replacement of energy-rich forage fishes (capelin *Mallotus villosus*, and herring *Clupea pallasi*) in the western Gulf of Alaska by energy-poor Gadid fishes (Anderson and Piatt 1999), and was associated with population declines of Steller sea lions *(Eumetopias jubatus*), seabirds and other apex predators in the Gulf of Alaska and Bering Sea (Springer 1998; Agler et al. 1999). Our lack of understanding about how and why marine ecosystems respond to climatic and anthropogenic perturbations limits our ability to develop effective management strategies to halt the precipitous decline of the endangered Steller sea lions in western Alaska.

In an effort to better understand linkages between ecosystem change and apex predator populations in the Gulf of Alaska, researchers from the University of Alaska established the Gulf Apex Predator-Prey (GAP) project as an interdisciplinary program of integrated ecosystem research. The seabird component of the GAP program is an important facet because seabirds forage at intermediate trophic levels and their reproductive performance is highly responsive to changes in forage availability. Therefore, seabirds can contribute to our understanding of ecosystem structure and function by serving as bio-indicators of marine conditions (Aebischer et al. 1990; Kitaysky and Golubova 2000; Durant et al. 2003).

Black-legged kittiwakes are small, pelagic gulls with a holarctic distribution (Baird 1994). During summer they nest on shear cliff faces and may travel <75 km from their nesting sites (Daunt et al. 2002) to feed on invertebrates and surface schooling fishes (Baird 1994). Kittiwakes in the Gulf of Alaska feed on forage fishes such as sandlance (*Ammodytes hexapterus*), capelin, herring and juvenile gadids (Baird 1994; Suryan and Irons 2001) and exhibit dietary overlap with Steller sea lions and other apex predators. Kittiwakes are particularly useful as bio-indicators of marine foraging conditions because they are a conspicuous, widely distributed and readily monitored. And, like other seabirds, aspects of their breeding biology, foraging ecology and physiology are highly sensitive to food availability (Hamer et al. 1993; Rindorf et al. 2000; Barrett 2002; Gill et al. 2002; Suryan et al. 2002).

Predation may be additive or compensatory to effects of food supply on many breeding parameters that are traditionally monitored by seabird biologists. Adult kittiwakes and their nest contents are at risk to bald eagles (*Haliaeetus leucocephalus*), peregrine falcons (*Falco peregrinus*) and ravens (*Corvus corax*) throughout the breeding season but the potential impact of these predators on kittiwake populations or productivity is limited by numeric swamping. Disturbance of kittiwakes by aerial predators potentially has a far greater indirect impact on kittiwake reproductive performance by facilitating egg predation by abundant magpies (*Pica pica*) and northwestern crows (*Corvus caurinus*).

Breeding parameters of kittiwakes can be divided into two groups; those affected only by forage availability and those that are potentially confounded by the effects of predation. Laying success, egg volume and clutch size, chick growth rate, regurgitation rates of chicks, foraging behavior, diets, timing of breeding and body condition are primarily, if not exclusively, dependent upon foraging conditions either prior to or during the reproductive season. Hatching success, fledging success, brood size at fledge and plasma corticosterone levels, however, can be driven by either foraging conditions or predation or some combination of the two. In addition, we anticipated that "floor" and "ceiling" effects would limit the sensitivity and utility of each monitored parameter to a small portion of the potential range of prey abundance and to a specific stage of the breeding season (Cairns 1987). Therefore, we monitored multiple parameters in an effort to collectively canvas a broad range of prey abundance across the entire breeding season.

Although the intent of this report is to summarize data collected between 2001-2003 on the abundance, reproductive performance, diet, foraging behavior, and physiology of kittiwakes breeding in Chiniak Bay, on Kodiak Island, in the western Gulf of Alaska, we also assess historical patterns of abundance and productivity of kittiwakes over the past 3 decades for the sake of comparison. We feel that this context is important for interpretation of our results given the dramatic regime shifts witnessed over that time period.

Methods

Study Area

We studied kittiwakes breeding at colonies located on numerous sea stacks and islets within Chiniak Bay (57 43' N, 152 20' W) in the northeastern corner of Kodiak Island, Alaska (Figure 1). Kodiak Island is located in the Western Gulf of Alaska in a marine region that experienced "regime shifts" - dramatic changes in oceanographic conditions and food web structure - in 1977, 1989, and possibly 1998 (Anderson and Piatt 1999; Hare and Mantua 2000) that potentially effected seabirds and other apex predators in the region. Fieldwork was conducted May–August in 2001, 2002, and 2003 on colonies that ranged in size from < 10 to approximately 2000 nests. Personnel were housed in the City of Kodiak and colonies were accessed via daily excursions in open skiffs.

We monitored black-legged kittiwakes at 3 levels of precision. We conducted "colony surveys' of all kittiwake colonies within Chiniak Bay to obtain information on population size and gross chick production. We also established multiple ‘visual monitoring plots’ at several colonies and visited these on a 5-day cycle to obtain more detailed information on breeding chronology and reproductive performance. Lastly, we used ladders and climbing ropes to reach kittiwake nests on a small number of ‘access plots’ on a 5-day cycle and, in addition to detailed chronology and productivity data, we obtained weights and measurements of eggs and chicks. Detailed methods for each of these 3 types data collection are presented below.

Colony Surveys

We conducted annual surveys (n=3 years) of nests and chicks at 21 kittiwake colonies within Chiniak Bay to determine indices of population size and chick production and to estimate brood size at fledging. Chicks were counted in the second week of August, just before the oldest were due to fledge. Nests were counted during the second week of August in 2001 and 2002 and during mid-incubation (end of June) in 2003.

We counted kittiwake nests and chicks from an open skiff at a distance of approximately 40-150m using 8x or 10x binoculars and tally counters. Each colony was divided into readily identifiable subsections and duplicate counts were made of nests and chicks within each section. Nests were defined as any site where a hand-sized "patty" of nesting material was present regardless of the presence of an adult. Nest counts were repeated if they differed by more than 10 percent and the two closest counts were then averaged.

We made separate tallies of 1-, 2-, or 3-chick broods and of broods with large vs. small chicks. Chicks were considered large if black-tipped tail feathers were visible (approx 18-20 day old) or lacked down on their backs. We also recorded newly fledged chicks observed roosting on the cliff face or on water near the colony and that otherwise could not be associated with a particular nest. Chick counts are minimum estimates only and can differ markedly between observers depending on experience, visibility, and sea conditions, therefore, we used the highest chick count of the two observers and did not repeat counts if the observer with the highest count was comfortable with their census total.

Visual Monitoring Plots

We quantified a suite of reproductive parameters that are potentially useful as indicators of marine conditions by following the breeding status of individual kittiwake nests on 48 visual-monitoring plots over the course of the breeding season. Plots each contained approximately 30 nests and were established at 12 accessible kittiwake colonies within Chiniak Bay (Fig 1). The location of every nest was marked directly onto a laminated photo of each plot and then each nest was uniquely numbered. Plots were observed from cliff-top vantage points and the contents of each nest was determined every 5 days, weather permitting, from late May (pre-laying) to late August (post fledging).

Reproductive events (laying, hatching, disappearance of eggs or chicks) were assumed to have occurred on the mid-point of a time "window" between visits for which nest contents were confirmed; however, we refined these initial estimates in two ways:

(a) if a clutch was completed over two nest visits or if more than one egg appeared in the nest between two visits, we assumed that eggs were laid 2.5 days apart (Gill et al. 2002) and adjusted the ‘lay window’, and lay date for each egg accordingly.
(b) we refined the ‘hatch window’, and hatch date, by extrapolating from visit dates before and after laying using minimum (25.5 days) and maximum (29.5 days) estimates for incubation duration (Gill et al. 2002).

We assumed chicks had fledged if their computed age was a minimum of 36 days at the time of their disappearance, or a minimum of 25 days if they were still present in the nest on the last visit of the season (chick mortality is quite low in the later half of the nestling period). We observed an abnormal spike in chick loss as their age approached the fledging cutoff of 36 days and attributed this to uncertainty in our estimation of chick age at the time of disappearance rather than to a sudden increase in the death rate of chicks. We corrected for this bias in two ways:

(a) we added 6 days to the minimum observed age of chicks that had a combined uncertainty in the timing of hatch and disappearance of 14+ days, and added 12 days to the minimum age of chicks with combined uncertainty of 24+ days.
(b) we assumed that a chick fledged, rather than failed, if the difference between its estimated age at disappearance and the fledging cutoff of 36 days was less than 1/4 of the combined uncertainty in the timing of hatch and disappearance for that chick..

Access plots

We reached kittiwake nests on six access plots from the beach or by using a ladder or climbing rope. Access plots were established and monitored using the same procedures outlined for visual monitoring plots but facilitated the collection of three additional types of data:

(a) Egg measurements: we numbered all newly discovered eggs (n=1768 in all years) on each end with a permanent marker and measured the maximum length and diameter of each egg to the nearest 0.1 mm using dial calipers. We inspected each egg during the visit prior to hatch and recorded evidence of impending hatch (star pips, hole pip) and used this info to refine our estimates of hatch date. Egg volume was computed using the formula: volume = 0.487 x length x width^2 (Coulson 1963).
(b) Chick measurements: we measure the mass of all chicks (n=913 in all years) on every visit using a Pesola spring scale with an accuracy of ± 1-5g (depending on the scale’s capacity), and measured the wing chord (± 2mm) of all chicks that had erupted primary feathers. To minimize premature fledging, we stopped handing chicks when their wing cord exceeded 220mm at approximately 30-32 days of age. We estimated the growth rate of each chick by fitting a linear regression through mass measurements collected between 3 and 22 days of age, a period for which the mass trajectory of even the most rapidly growing chicks was approximately linear.
(c) Regurgitation rate of chicks: we recorded whether each chick spontaneously regurgitated during handling as an index of chick provisioning rates (n=4255 total chick handlings in all years). No effort was made to stimulate regurgitation by nestlings. We determined the regurgitation rate for each colony visit (n=171 total visits) by dividing the number of nests from which at least one chick

regurgitated by the total number of nests with chicks that were handled on each visit (n=2837 total nests with handled chicks). We use colony visits as our sampling unit because chicks within nests and nests within colony visits are not statistically independent.

Diet Samples

We obtained diet samples from kittiwakes by collecting regurgitations volunteered by adults and nestlings that were captured and handed for other purposes. Diet samples (n=801) were collected from 6 colonies primarily during the nestling period between mid-July and mid August in each year of the study (n=3 years). Samples were grouped by colony and date of visit and five samples with a minimum mass of 5g were randomly selected from each group for processing and identification of prey. Samples varied considerably in their state of digestion so fish and invertebrate prey items were identified from hard parts recovered by picking though samples with the aid of a dissecting scope. Maximum lengths of fish otoliths were measured to the nearest 0.01mm using a calibrated ocular micrometer built into the eyepiece of the dissecting scope. We estimated the fresh-mass of individual fish from otolith measurements using mass-otolith regression equations derived from voucher samples of fish collected within the study area, and estimated the fresh mass of invertebrate prey items from voucher specimens collected in the Gulf of Alaska and Bering Sea. For each diet sample, we determined the total estimated mass of all prey items and the proportion of the mass of each sample comprised by each prey species. Lastly, the total length of each capelin and sandlance was determined from otolith measurements (via otolith-fish length regressions determined for voucher specimens) and was used to classify individuals as either young of year (YOY) or age 1+ (Hatch and Sanger 1992). For each sample we then determined the proportion of each species that were YOY individuals.

Blood Samples and Stress Hormones

Over the three years of the study, we collected blood samples from 136 adult kittiwakes captured at their nests with noose poles or foot snares and determined the concentration of corticosterone in blood plasma as a physiological indicator of stress. Samples were obtained within three minutes of capture, before circulating levels of corticosterone became elevated in response to handling-induced stress (Kitaysky et al. 1999). A 0.05ml sample of blood was collected into heparinized capillary or Nettleson tubes from the alar vein (located on the underside of the wing) following puncture with a 25 gauge needle. Blood samples were immediately transferred to 1.5 ml snap-cap vials and stored on ice for several hours until centrifuged and separated. Plasma fractions were drawn off using long-stemmed Pasteur pipettes and were held at -70°C until assayed for corticosterone concentration via a direct radioimmunoassay as detailed in Wingfield and Farner, (1975). Briefly, aliquots of plasma (10 - 25 µl) were measured into centrifuge tubes and allowed to equilibrate overnight with 2000 cpm tritiated corticosterone. Corticosterone was extracted in 4 ml re-distilled dichloromethane added to each sample. Extracts were aspirated with pasteur pipettes and evaporated under nitrogen in a warm water bath. After evaporation of dichloromethane, samples were resuspended in 550 µl phosphate-buffered saline with gelatin and allowed to equilibrate overnight at 4° C. Aliquots of samples were transferred to duplicate test tubes (200 µl each) for radioimmunoassay. In addition, a 100 µl aliquot was placed in a vial for determination of percentage recovery of the initial 2000 cpm. This recovery value is used to adjust final assayed concentrations of corticosterone. Standard curves were set up over the range of 2 - 500 pg. Samples were refrigerated overnight after addition of equal (100 µl) amounts of labeled corticosterone and antiserum. Dextran-coated charcoal (0.5 ml) was added 12 min prior to centrifugation to separate bound and free fractions. Supernatants were decanted into scintillation vials and counted after addition of 4.5 ml Ultima Gold® scintillation fluid.

Patterns of Colony Attendance

We determined the proportion of time that adult kittiwakes spent at the colony and the duration of their foraging trips by outfitting individuals with radio transmitters (*n* = 29 birds in 2001; *n* = 39 birds in 2002) and monitoring colony attendance using automated receiving stations that consisted of an ATS (Advanced Telemetry Systems, Isanti MN) model R4000 VHF radio receiver, data collection computer (ATS model D5241), 12v battery (30 amp hour), solar panel (45 watt), and charge regulator (5 amp). We captured adult kittiwakes at their nest sites via noose pole or foot snare and glued 9g radio transmitters (ATS model 3PN) directly to the shafts of three central tail feathers using "superglue" adhesive (Locktite 422) and accelerant (Locktite 712) to reduce setup time. All radio-tagged kittiwakes returned to their nests after capture and resumed parental duties. Furthermore, reproductive performance (chicks fledged per nest attempt) of kittiwakes with radio-transmitters was similar to that of kittiwakes without transmitters in both years (2001: 0.68 vs. 0.67, 2002: 0.46 vs. 0.43) suggesting that transmitters had, at most, a limited impact on breeding individuals (Wanless 1992). Receiving stations had a reception range of only a few hundred meters and cycled through all frequencies every 5-10 minutes; therefore, we assumed that birds not detected by the receiving station were absent the colony and were potentially foraging. We validated the proper functioning of automated receiving stations by placing a reference transmitter at each colony to assess false negatives and by including "dummy" frequencies in the list of scanned frequencies to assess false positives. We only used data from time periods during which the receiving station at a given colony functioned correctly.

We divided the breeding season into 3 stages that were based on the timing of hatch of the first-chick (*a*-chick): Incubation (pre-hatch), Early Chick (chicks 0-20 days old), and Late Chick (chicks 20-40 days old). Kittiwakes with nests containing eggs or chicks were defined as active 'breeders', and those with empty nests as 'failed breeders'. Thus, an individual kittiwake could contribute data to the analysis as both a 'breeder' and a 'failed breeder' within the same stage of the breeding season. Kittiwakes generally have at least one member of the pair at the nest at all times (Hatch and Hatch 1988), and the attendance behavior of breeding kittiwakes is directly affected by the behavior of their mates. Therefore, we captured only one adult per breeding pair for all nests, except for one nest in 2001 in which we inadvertently captured both adults. We excluded the second bird from this nest from data analysis to not violate the assumption of independence of samples.

We continuously collected data of presence at the colony from radio-tagged kittiwakes from July 3rd to August 30th (total 59 days) in 2001 and from June 22nd to August 27th (total 67 days) in 2002. Absences from the colony were calculated as the inverse of presence at the colony. We required a minimum of four bouts of absence and four bouts of presence to include a nest in data analysis. To exclude short absences from the colony for the purpose of roosting, bathing or group "panic flights" (Coulson and Johnson 1993; Hamer et al. 1993), we considered only absences from the colony of longer than 40 minutes to be potential foraging bouts. Black-legged kittiwakes feed mainly during daylight hours and spend much of the night roosting offshore (Coulson and Whooller 1984; Coulson and Johnson 1993). To eliminate the time spent roosting at night from analysis of attendance patterns, we determined "Day" (5:23am to 11:02pm, total time 17 h 39 min.) and "Night" (>11:02pm to <5:23am, total time 6 h 21 min.) periods based on mean times of dawn and dusk in the Kodiak region during the month of June. We determined for each individual, within each year and stage of the breeding season, the proportion of the daylight period present at the colony and the average duration of colony absences (foraging bouts) that occurred entirely during the daylight period as indicators of foraging effort.

At-Sea Distribution

We erected triangulation stations on Pillar Mountain (305m ASL) and Heitman Mountain (260m ASL) to determine the at-sea distribution of kittiwakes. Each station consisted of two 6-element Yagi antennas (Maxrad, Hanover Park, Illinois) "stacked" parallel to one another and attached to a swiveling mast pole. Simultaneous bearings, adjusted to true north, were determined for each transmitter frequency using a null-peak switch box and an R4000 radio receiver (ATS). Triangulation activities at both stations were coordinated via two-way radio. Although we could only detect birds resting on the water over a distance of a few kilometers, we determined that the reception range of a transmitter mounted 3 m above the surface of the water on the rigging of a boat, and that emulated a flying kittiwake, was at least 45km. We determined locations (latitude and longitude) of birds and reference transmitters via triangulation and plotted locations from black-legged kittiwakes in 2001 and 2002.

In 2003 we switched from land-based triangulation to aerial telemetry to determine the foraging distribution of blacklegged kittiwakes. We determined the location of radio-tagged kittiwakes by flying aerial transects along a fixed grid (10km or 15km) on six occasions between 22 July and 18 August. Aerial transects were flown at 2000-3000 meters using a Cessna 206 equipped with paired four-element Yagi antennas mounted on the wing struts. The initial survey covered an area that extended 40 km in all directions (excluding land) from Chiniak and Cliff Islands. The area flown on subsequent flights was expanded in the direction of signals that were detected outside of the original survey coverage area.

Aerial coverage for all flights combined is shown in Figure 2. We scanned each frequency for 2 seconds using an R4000 VHF receiver (ATS) and a left/right switchbox to determine a subjective measure of signal strength (on a scale of 1-5) and the direction (right or left) of the loudest signal. We estimated bird locations by plotting the location of all signals detected for each individual in ArcView 3.2 (ESRI Inc.) and calculating its weighted mid-point location. We estimate the precision of locations by comparing estimated and actual locations of reference transmitters placed on anchored buoys at known locations. At this time we have not yet completed analysis of aerial telemetry data.

Data Analyses

General considerations

Statistical analyses were performed using Statistical Analysis Software (SAS, Version 8.2), or Sigma Plot (version 3.2). The objective of most statistical analyses was to test for differences among years in reproductive, foraging, and physiological measures of kittiwakes. We included additional pertinent variables (e.g. colony, chick category) as "blocking" factors in ANOVA analyses to statistically control for masking effects these factors could potentially have on difference among years (Neter et al. 1996). We could not and did not test for three-way interactions in these analyses and dropped all two-way interactions where $P>0.10$ from final models. Where significant two-way interactions were encountered, we examined interaction plots and sub-divided each analysis. We used Tukey's multiple comparisons to compare factor-level means of all significant main effects with α set at 0.05. Because many ANOVA models were unbalanced, we present least-square means and pooled standard error bars in all figures. Least-square means weight all levels of all factors equally, independent of sample size.

Historical Patterns of Abundance and Productivity

We used counts of nests and chicks from colony surveys in Chiniak Bay as indices of kittiwake abundance and reproductive performance and used data from surveys initiated in 1975 and conducted annually since the mid 1980's to evaluate historic patterns in these parameters. We performed separate population trend analyses on kittiwake colonies located within "inner" and "outer" regions of Chiniak Bay (Fig. 1) because population trends appeared to differ between regions (Fig. 3a) and because, prior to 1998, complete surveys of outer bay colonies were rare. We determined population trends by fitting regression lines through annual nest-count totals of inner and outer bay colonies and compared trends between regions by testing for differences between slopes of the two regression equations.

Kittiwake productivity was determined for each colony in each survey year (n=294 total data points) by dividing total chicks by total nests. We compared productivity between three "regimes" (1978-1989, 1990-1998, and 1999-2003) that represent periods of relative ecosystem stasis in the North Pacific Ocean bounded by abrupt transitions in climate and ecosystem structure (Anderson and Piatt 1999; Hare and Mantua 2000). We controlled for effects of colony location (inner vs. outer) and colony "age" (old vs. new) on kittiwake productivity by incorporating these variables as blocking factors in a three-way ANOVA model. "Old" colonies were present during the initial surveys in 1975 while "new" colonies formed in subsequent years but mainly between 1984 and 1990. If age and location are not included in the ANOVA model, variability associated with greater productivity of new (n=13) vs. old (n=9) and of inner bay (n=11) vs. outer bay (n=10) colonies masks effects of regime on productivity.

Reproductive Parameters

We computed the following reproductive parameters for each visual and nest-access plot in every year of the study:

Laying Success = nests with eggs / total nests constructed
Hatching Success = total chicks / total eggs (first and re-layed clutches combined)
Fledging Success = fledged chicks / total chicks
Productivity = fledged chicks / total nests constructed
Clutch Size = total eggs (first clutches only) / nests with eggs
Lay Date= mean date of lay of "A" eggs in first clutches

We compared reproductive parameters among years using ANOVAs that incorporated colony and year x colony interaction as blocking factors. For these analyses we used data from 24 plots in 7 colonies and were observed in all three years of the study.

Egg volume

We compared egg volume among years using an ANOVA that included as blocking factors colony, “egg category”, and interactions between year, colony and egg category. Interaction terms with p > 0.10 were excluded from the final model. Egg category has three levels that are a combination of clutch size and lay order: (a) lone egg from a single egg clutch, (b) first egg of 2-egg clutch, and (c) second egg of 2-egg clutch. We restricted the analysis of egg volume to data from 5 colonies that provided data on first clutches of 1 and 2 eggs (n= 1389 eggs) in all three years of the study.

Nestling growth

We compared the growth rate of nestlings among years using a blocked ANOVA that incorporated as blocking factors, colony, “chick category” and interactions between year and these variables. Chick category has three levels that represent a combination of brood size and hatch order: (a) singleton chick, (b) α chick from a brood of two, (c) β chick from a brood of two. We reclassified α chicks as singletons if the β chick in their nests disappeared before age 12. We restricted the analysis of chick growth to data from 541 chicks from 4 colonies that provided data in all three years of the study. We excluded from this analysis, chicks with fewer than three mass measurements between 3 and 22 days of age.

Regurgitation Rate of Nestlings

We determined regurgitation rates for each colony visit and separated visits into 3 time periods: (a) July 10-20, (b) July 21-30, and (c) July 31 - August 15. Time periods correspond roughly to early (1-10 days old), mid (11-20 days old), and late (20+ days old) stages of chick rearing and included a minimum of two plot visits per period for each colony (n=4 colonies) that was observed in all three years of the study (n= 89 colony visits in total). We compared regurgitation rates between years with an ANOVA that included as blocking factors, colony, time period and interactions between year and these two variables.

Diet Composition

Sandlance and Capelin comprised the bulk (90%+) of the diet of kittiwakes; therefore, we pooled sample-proportions from all other species into an "other" prey category. To account for potential effects of season on diet, samples were pooled into 4 time periods within each year of the study: (a) July 10-20, (b) July 21-30, (c) July 31 - August 9, and 4) August 10+. These time periods correspond roughly to early (1-10 days old), mid (11-20 days old), late (21-30 days old) and fledging (31+ day) stages of the chick-rearing period. Mean proportions of each prey type were computed for diet samples pooled by colony and time period within each year. These period means were used in statistical analyses because diet samples collected on a given day from a given colony are not independent. We compared kittiwake diet among years with a separate ANOVA for each prey type that included as blocking factors, colony, time period and interactions between year and these two variables.

We computed means for the proportion of YOY capelin and sandlance in the kittiwake diet by pooling samples by colony and time period within each year. The resulting period means were used in statistical analyses because diet samples collected on a given day from a given colony are not independent. We compared the proportion of YOY capelin and sandlance among years using an ANOVA model that incorporated as blocking factors colony, time period and interactions between year and these two factors.

Blood Samples and Stress Hormones

We compared the baseline corticosterone concentration in blood plasma of adult kittiwakes between years using one-way ANOVAs for incubation and brood rearing periods separately.

Patterns of Colony Attendance

For each stage of the breeding season (Incubation, Early Chick, and Late Chick), we compared the proportion of time present at the colony (colony attendance) and the average duration of forging bouts between years (2001, 2002) using a two-factor ANOVA that included breeding status (active or failed) as a blocking factor.

Results

Historical Patterns of Abundance and Productivity

Overall, the kittiwake population in Chiniak Bay increased by 43% in the 19 years since it was first surveyed in 1975 and has increased 84% from a population low in 1997 (Fig. 3a). Trends in nest counts have been largely driven by a significant increase in abundance of nests built within the inner region of Chiniak Bay (slope= 172 nests/year, r^2=0.74, t_{22}= 0.89, P<0.0001). In contrast, outer bay colonies exhibited a declining trend over the past 19 years that borders on significance (slope= -122 nests/year, r^2=0.35, t_9= -2.22, P=0.053). Differing trends of inner and outer populations (t_{31}=6.07, P<0.0001) can be explained largely by changes in nest counts that occurred between 1984 and 1990 colony surveys: population trends are remarkably concordant between the two regions both before and after this time interval (Fig. 3a). Abrupt declines of nest counts in 1983 and 1997 coincided with extremely intense El Nino events that occurred in 1982-1983 and 1997-1998 (Fig. 3a). The striking decline in nest-count in 1983 was likely due to reduced nesting propensity rather than real change in kittiwake abundance because it was associated with utter reproductive failure in1983 (Fig. 3b) and was reversed in 1984 (Fig. 4a). For this reason, we excluded data from 1983 from regression analyses of population trends. In contrast to El Nino events, the kittiwake population of Chiniak Bay apparently was not strongly or immediately affected by changing marine conditions associated with regime shifts in 1977, 1989, or 1998 (Fig. 3a).

Despite marked inter-annual variability (Fig. 3b), kittiwake productivity in Chiniak Bay differed among regimes ($F_{2,289}$= 14.9, P<0.0001), and was significantly greater for young vs. old colonies ($F_{1,289}$= 21.9, P<0.0001) and for inner vs. outer colonies ($F_{1,289}$= 6.94, P=0.0089). Interactions between regime and age and location blocking factors were not significant (P>0.10) and were dropped from the final model. Post-hoc comparisons revealed that productivity in the current regime of the 2000's was significantly greater (P<0.05) than during the 1980's or 1990's (Fig. 4). Intense El Nino events of 1982-1983 and 1997-1998 were associated with 2 years of reproductive failure that occurred, in each instance, during the second year of the warm-water event. In contrast, there were only six years of reproductive failure (productivity <0.05) for the 22-year time series on the whole.

General Reproductive Parameters

Reproductive parameters common to all visual and nest access plots within all colonies monitored in every year of the study are summarized in Tables 1 and 2. ANOVA results described below were based on a subset of 24 reproductive plots within 7 colonies that were observed in all three years of the study.

The initial ANOVA performed on kittiwake laying success indicated a significant year x colony interaction ($F_{12,51}$= 1.96, P=0.048). We examined the interaction plot (Fig. 5) and concluded that this interaction was driven by reduced laying success of the KU colony in 2002 and of KU and MA colonies in 2003. We neutralized the interaction by separating MA and KU from 5 other colonies and ran separate ANOVA analyses on the two groups. The 5-colony analysis found that laying success did not vary across years ($F_{2,27}$= 0.08, P=0.92, Fig. 6). In contrast, the second analysis of only KU and MA colonies revealed a significant decline in laying success across years ($F_{2,24}$= 4.54, P=0.02, Fig. 6). Post-hoc comparisons indicated that laying success was greater in 2001 vs. 2003 for these colonies.

The initial ANOVA performed on hatching success found a significant year x colony interaction ($F_{12,51}$= 3.98, P=0.0002) that was driven by reduced hatching success of KU and MA colonies in 2002 and of KU, MA, and PU in 2003 (Fig.7). We subdivided this interaction by separating KU, MA and PU from the remaining 4 colonies and performing separate analysis on both groups. In the 4-colony analysis, hatching success did not differ among years ($F_{2,24}$= 0.93, P=0.41, Fig. 8), however, the analysis of KU, MA and PU revealed a year effect ($F_{2,27}$= 17.7, P<0.0001) and post-hoc comparisons indicated progressively reduced hatching success from 2001 through 2003 (Fig. 8).

Analysis of fledging success revealed a significant year x colony interaction ($F_{12,46}$= 2.37, P=0.02) that was driven by reduced fledging success of the KU colony in 2003 (Fig. 9). We removed the interaction by separated KU from the remaining colonies and found no difference in fledging success among years ($F_{2,36}$= 1.18, P=0.32, Fig. 10). We then performed a one-way ANOVA on KU alone and found a significant decline in fledging success declined across years ($F_{2,15}$= 4.91, P=0.03) and a significant difference between 2001 and 2003 (Fig.10).

The initial ANOVA on kittiwake productivity indicated a significant year x colony interaction ($F_{12,51}$= 4.31, P=0.0001) that was driven by reduced productivity of KU, MA and PU in 2002 and 2003 (Fig. 11). We neutralized this interaction by separating KU, MA and PU from the remaining 4 colonies and performing two analyses. Results of the 4-colony ANOVA indicated a trend among years towards higher productivity in 2003 that bordered on significance ($F_{2,24}$= 2.84, P=0.08, Fig. 12). A separate analysis of KU, MA and PU colonies found a significant year effect ($F_{2,27}$= 25.1, P<0.0001) while post-hoc comparisons indicated that productivity declined in a stepwise fashion between 2001 and 2003 (Fig. 12) for those colonies.

Analysis of clutch size found a significant year x colony interaction ($F_{12,51}$= 2.40, P=0.02) that was largely driven by low clutch sizes for KU and MA colonies in 2003 (Fig. 13). Excluding KU and MA from the analysis produced no year effect ($F_{2,27}$= 1.36, P=0.27) while a separate ANOVA performed on KU and MA found that clutch size differed among years ($F_{2,24}$= 16.8, P<0.0001, Fig. 14). Post-hoc comparisons for this second analysis revealed that clutch size was significantly smaller in 2003 than in either 2001 or 2002 (Figure 14).

Lay date of first clutches differed significantly among years ($F_{2,63}$= 1.46, P=0.25, Figure 15) with no year x colony interaction. Post-hoc comparisons revealed that laying was delayed by 3 days in 2003 relative to 2001 and 2002 (Fig. 15).

Additional Reproductive Parameters

Reproductive parameters only available from nest access plots (egg volume, chick growth, regurgitation propensity, and diet composition) are presented in Tables 2 and 3. ANOVA results for egg volume and chick growth are based on data for 5 reproductive plots from 5 colonies that were sampled in all 3 years of the study. Analyses of regurgitation propensity and diet composition were based on data from 4 colonies with samples from all time periods.

Egg volume significantly differed among years ($F_{2,1380}$= 3.10, P=0.05, Fig. 16) and displayed no interaction between year and either colony or egg category. Post-hoc comparisons revealed that eggs were larger in 2002 than 2003 (Fig.16).

Analysis of chick growth rates revealed a significant year x colony interaction ($F_{6,535}$= 2.58, P<0.02) that was driven by decreased growth rates for the KA colony in 2002 (Fig. 17). When we excluded KA and repeated the analysis, we found a significant effect of year ($F_{2,443}$= 5.83, P<0.003) and post-hoc comparisons indicated a higher growth rate in 2003 than in either 2001 or 2002 (Fig. 18). Analysis of KA alone also found a significant affect of year on growth rate ($F_{2,90}$= 9.15, P<0.0002) while post-hoc comparisons indicated lower growth rates in 2002 vs. either 2001 or 2003 (Fig.18).

Propensity of nestling kittiwakes to regurgitate did not differ among years ($F_{2,81}$= 0.67, P<0.51; Fig. 19). All two-way interactions were not significant and were dropped from the final ANOVA model.

Diet Composition

We preformed separate analyses of diets of kittiwake chicks on each of three prey categories: capelin, sandlance, and a catch-all "other" category. Note, however, results of the analyses of capelin and sandlance in the diets are not independent because roughly 90% of the kittiwake diet was comprised of these two prey types and their relative abundance in a diet sample is highly buy inversely related.

The proportion of capelin and sandlance in kittiwake diets varied among years (capelin, $F_{2,32}$= 6.73, P=0.004; sandlance, $F_{2,32}$= 13.14, P<0.0001; Fig. 20). Significant year x time period interactions for capelin ($F_{6,32}$= 2.72, P=0.03) and sandlance ($F_{6,32}$= 2.39, P=0.05) were driven by a high proportion of capelin and low proportion of sandlance within the 3rd time period of 2001 (Fig. 21). Excluding the 3rd time-period from these analyses to neutralize this interaction did not affect the results substantively. Post-hoc comparisons indicated an increased contribution of capelin (and reduced sandlance) to the diet of kittiwakes across years, with 2003 significantly greater than either 2001 or 2002.

The proportion of YOY sandlance in the diet of kittiwakes increased across years ($F_{2,38}$= 9.96, P=0.0003; Fig. 22). All interactions were not significant and were dropped from the final model. Post-hoc comparisons indicated that the abundance of YOY sandlance was greater in 2003 than either 2001 or 2002.

Corticosterone

Baseline levels of plasma corticosterone significantly differed among years during the brood rearing period ($F_{2,78}$= 5.74, P=0.005; Fig. 23) but not during incubation ($F_{2,80}$= 1.67, P=0.20; Fig. 23). Post-hoc comparisons indicated significantly elevated levels of corticosterone in 2003 vs. 2001 during the brood rearing period.

Patterns of Colony Attendance

The proportion of daylight hours that actively breeding kittiwakes were away from the colony foraging was significantly greater in 2002 vs. 2001 during the early chick and late chick stages of the breeding season, but did not differ between years during the incubation period.

The duration of foraging trips undertaken by actively breeding kittiwakes during the daylight hours was significantly longer during the incubation period in 2001 vs. 2002, was significantly shorter during the late nestling period in 2001 vs. 2002 and did not differ between years during the early chick period.

At-Sea Distribution

We determined 70 locations for black-legged kittiwakes during 6 triangulation sessions in 2001 and 137 locations during 11 triangulation sessions in 2002. In 2001, black-legged kittiwakes were concentrated inside Chiniak Bay, with many found along the Cape Chiniak coastline (Fig. 26a). In 2002, a number of locations were documented well beyond the confines of Chiniak Bay to the north and east (Fig. 26b).

Discussion

Historical Trends in Abundance and Productivity

Opposite trends in kittiwake populations between outer vs. and inner regions of Chiniak Bay were driven by a substantial decline in the outer bay population between 1984 and 1990 (Fig. 2a) that resulted from a 50% decline (3100 nests) from the large colony at Cape Chiniak. Between 1984 and 1990, kittiwakes in Chiniak Bay experienced generally poor productivity (Fig. 2b). Despite this, 10 new breeding colonies (4 outer bay, 6 inner bay) formed and grew rapidly. These observations suggest that regional population trends within Chiniak Bay may have been driven by the mass emigration of adult birds from the Cape Chiniak colony; however, declines in the outer bay far exceeded gains in the inner bay (Fig 2a) and the kittiwake's high fidelity to nest sites and mates (Baird 1994) suggest that other factors are responsible.

Depressed nest counts of kittiwakes in 1983 and 1997-8 were associated with extreme El-Nino events and low breeding success of kittiwakes in Chiniak Bay (Fig. 2a) and the western Gulf of Alaska (Hatch 1987). The recovery of nest counts one year after the 1982-3 El Nino and within two years of the 1997-8 event, suggest that low nest counts were likely caused by reduced nesting propensity rather than actual population declines. El Nino events can have "bottom up" effects on breeding seabirds by altering ocean temperature, nutrient availability, and phytoplankton production in the Gulf of Alaska kittiwakes typically exhibit (Goes et al. 2001; Whitney and Welch 2002), but warmer water temperature can also affect seabirds more directly by affecting the abundance (Harding et al. 2003) and distribution (Stergiou 1991) of forage fishes such as capelin and sandlance. In contrast to El-Nino events, regime shifts in ocean climate did not appear to affect kittiwake nest counts.

Differences in kittiwake productivity across regimes were likely due to differences in ecosystem structure that characterized each time period (Anderson and Piatt 1999). Poor kittiwake productivity recorded during the mid-late 1980's was associated with a "warm" regime and the absence of energy rich capelin from trawl surveys (Anderson and Piatt 1999) and seabird diets (Francis et al. 1998) in the region. Increased productivity of kittiwakes in the 1990's followed a "minor" regime shift that was characterized by ecosystem reorganization rather that climatic change (Hare and Mantua 2000), and that was associated with reduced zooplankton and increased groundfish (cod, pollock, flatfish) in the Gulf of Alaska (Anderson and Piatt 1999). Higher kittiwake productivity in the recent years has been associated with cooler ocean temperatures that have prevailed since a candidate regime shift back to a "cold" state in late 1998 (Hare and Mantua 2000).

Kittiwakes as Bio-Indicators of Forage Fish Abundance

We monitored a suit of dietary, reproductive, physiological and behavioral parameters of kittiwakes as indicators of the abundance and distribution of forage fishes within Chiniak Bay. Each monitored parameter is specific to a particular stage of the breeding season and may be more or less sensitive to food abundance. We will first consider the implications of each parameter separately then will then attempt to integrate these diverse indicators to arrive at a generalized view what kittiwakes tell us about how foraging conditions in Chiniak Bay have changed over the three years of our study.

Diet - Kittiwakes are generalist foragers who's diet reflects the abundance of surface schooling forage fishes within foraging range (60-100 km, ref.) of their breeding colonies (Suryan et al. 2002). An increased abundance of capelin in the kittiwake diet between 2001 and 2003 and a reduced abundance and average size of sandlance, suggests that kittiwakes responded to reduced availability larger size classes of sandlance in the near shore environment by foraging farther offshore where they encountered more abundant capelin.

Reproductive Performance - Kittiwakes are long-lived seabirds and that face a life history tradeoff between survival and reproduction (Golet et al. 2004). Breeding kittiwakes will curtail or abandon reproductive investment when faced with food limitation that exceeds their behavioral buffering capability (Hamer et al. 1993). As a result, overall productivity and several of its component measures of reproductive success (clutch size, laying success, hatching success, and fledging success) are sensitive to food availability (Hamer et al. 1993; Gill et al. 2002). Interpreting trends in measures of reproductive performance of kittiwakes across years is complicated by interactions between effects of year and colony for a number of parameters. Our results indicated two discrete patterns of reproductive performance: some colonies displayed no trend in productivity among years while others exhibited a stepwise decline in productivity across years that was inline with a the more general bay wide pattern (Fig. 4b). Productivity declines were mainly a consequence of reduced hatching success and to a lesser degree, reduced clutch size and laying success. In contrast, fledging success did not differ among years and did not contribute to differing trends in productivity among colonies. Access to food resources is not responsible for differing productivity trends among colonies because they are located near to one another and, in principal have overlapping foraging ranges and share common food resources.

Measures of reproductive performance are unique relative to all other monitored parameters because they may be influenced by predation in addition to food abundance. Predation affect hatching and fledging success directly through loss of eggs and nestling but can also indirectly lead to underestimation of clutch size and laying success because eggs can be laid and lost to predators before they are documented. We propose that predation may be responsible for differing trends in reproductive performance of kittiwakes observed among colonies. Northwestern crows and black-billed magpies are abundant within Chiniak Bay and are facultative predators of kittiwake eggs that are dependant on the disturbance of nesting kittiwakes by less abundant peregrine falcons, bald eagles, common ravens and, on occasion, humans. Peregrine falcons are the least common of the larger aerial predators but target adult kittiwakes as well as large nestlings. Even though eagles and ravens rarely target adult kittiwakes, kittiwakes react to their presence and ravens can be extremely effective egg predators. Predation can affect reproductive performance directly but may also act in concert with food supply – when food abundance is limited, predation may be facilitated by inconsistent nest attendance and reduced nest defense by breeding kittiwakes (Hamer et al. 1993; Gill et al. 2002). Predator activity is inherently patchy and it may have been mere chance that particular colonies in 2002 and 2003 were spared from predators at a time when predation severely reduced reproductive performance in other colonies.

Timing of Breeding – The timing of kittiwake egg lying is in part dependant on the availability of food (Gill et al. 2002). Our results indicated delayed egg laying in 2003 that was correlated with colder ocean temperature, delayed spring bloom (R. Foy, unpublished data) which likely delayed the development of the marine food web and the availability of forage fishes in 2003.

Egg Volume - Egg volume is affected at least in part by food availability during egg development (Gill et al. 2002). Larger eggs in 2002 suggest that early season foraging conditions in this year were better than the other two years of the study.

Chick Growth Rate and Regurgitation Propensity – Food limitation is known to affect chick growth rates by reducing the ability of adult kittiwakes to provision their chicks (Suryan et al. 2002). Our results suggest that kittiwakes were better able for provision young in 2003 vs. 2001 or 2002, either by increasing the frequency of meal delivery or by providing larger meals to nestlings.

Plasma Corticosterone – Baseline levels of corticosterone in blood plasma are thought to reflect an individual's level of energetic stress and physiological condition. Kitaysky et al. (1999) demonstrated that levels of plasma corticosterone of adult black-legged kittiwakes during the breeding season are correlated with body condition, food abundance, and reproductive performance and can serve as a measure of regional productivity of the marine ecosystem. Increased baseline corticosterone in breeding kittiwakes across years during the nestling period but not the incubation period suggests that foraging conditions declined as the breeding season progressed in 2003 and, to a lesser degree, in 2002.

Patterns of Nest Attendance-- The duration of foraging trips and the proportion of time that adult seabirds spend away from the colony foraging are both negatively correlated with food availability in the marine environment (Hamer et al. 1993) and are positively associated with distance traveled away from the colony (Suryan et al. 2000). Shorter foraging trips displayed by breeding kittiwakes during the incubation period in 2002 indicate better foraging conditions relative to 2001. In contrast, in 2002, increased foraging time during the early chick period and increases in both foraging time and trip during in the late chick period all suggest that foraging conditions progressively deteriorated over the 2002 season relative to 2001.

At-Sea Distribution—We observed that kittiwakes foraged at a greater distance from the colony during the nestling period in 2002 vs. 2001.These results suggest that foraging conditions within the bay were poor and that individuals needed to travel further to obtain food in 2002.

Kittiwakes as Bio Indicators: an integrated view of the big picture

While all monitored parameters reflect food availability and are potential indicators of marine conditions and forage fish abundance, they differ with regards to their capacity to be influenced by predation. Basic reproductive parameters (i.e., productivity and all of its component measures of breeding performance; clutch size, laying success, hatching success, and fledging success) are sensitive to the level of predation, while all other parameters are not.

The predator-*in*sensitive parameters that we monitored all share striking similarities in trend across years. Delayed timing of egg laying in 2003 was associated with cool marine conditions and delayed arrival of the spring phytoplankton bloom (R. Foy, unpublished data), the annual phenomenon that jump starts the marine production cycle in temperate latitudes. An increased abundance of capelin in the diet of nestling kittiwakes between 2001 and 2003 was matched by a corresponding decline the prevalence, size and energy content (Van Pelt et al. 1997) of sandlance. The growth rate of nestling kittiwakes was greatest in 2003 but exhibited a downward trend between 2001 and 2002 that was consistent with trends toward longer, more distant foraging trips, increased time spent foraging, and increased corticosterone during the nestling period. These trends suggest that forage fishes were less abundant during the nestling period in 2002 and that kittiwakes had to work harder to provision their chicks. In contrast to these late-season indicators, larger egg size and shorter foraging trips during the incubation period in 2002 suggest that early-season foraging conditions were better in 2002 than in either 2001 or 2003.

The only incongruence within the entire suite of predation-insensitive monitoring parameters was that elevated nestling growth rates indicated better foraging conditions in 2003 whereas elevated levels of corticosterone during the brood rearing period suggests the opposite trend. Possibly, adult kittiwakes suffered elevated levels of corticosterone in 2003 because they foraged at greater distances from their colonies while nestlings exhibited rapid growth because they were provisioned with energy rich capelin. Future analysis of nest attendance data for the nestling period in 2003 will help address this unresolved issue.

In contrast to the great consistency observed among predation-insensitive monitoring parameters, predator-sensitive reproductive parameters exhibited two distinct patterns among years: reproductive performance of some colonies declined across years while that of others exhibited no significant trend. We argue that differing levels of predation are responsible for divergent productivity trends of these colonies because the period of greatest discrepancy in productivity among colonies (egg laying and incubation) is the stage of breeding for which kittiwakes are susceptible to the most abundant predators within Chiniak Bay (ravens, crows, and magpies). In addition, while the few colonies that appeared to escape egg predation displayed no trend across years for clutch size, or for laying, hatching, or fledging success, they did exhibit a borderline significant pattern of productivity that precisely mirrors that observed for nestling growth rate and other predation-insensitive parameters during the nestling period: productivity was greatest in 2003 and displayed a modest decline from 2001 to 2002.

We have argued that foraging conditions cannot be directly responsible for declining reproductive performance observed in many kittiwake colonies across years because colonies have overlapping foraging ranges and share common food resources. Instead, we suspect that declining reproductive performance was due to elevated levels of egg predation in 2002 and 2003 but cannot exclude the possibility that food limitation may have facilitated egg predation by diminishing the breeding tenacity of adult kittiwakes. While larger eggs and shorter foraging trips suggest better early season foraging conditions for kittiwakes in 2002 and argue against the "predator facilitation" hypothesis, foraging conditions for kittiwakes fluctuate on a short time scale (Suryan et al. 2002), and neither egg volume data from the pre-laying period nor nest attendance or corticosterone data from late incubation period are truly contemporaneous with the period of peak egg predation during the first two weeks of incubation (D. Kildaw unpublished data). We require corticosterone and colony attendance data from the early incubation period to better address the predator facilitation hypothesis.

To summarize, kittiwake monitoring parameters suggest the follow trends in marine conditions and forage fish abundance within Chiniak Bay:

2001 - Foraging conditions were consistently good across the entire breeding season for most colonies and parents provisioned nestlings primarily with energy rich age 1+ sandlance that they captured within the confines of the bay.

2002 - Although foraging conditions appeared to be excellent early in the season, egg predators severely impacted the reproductive output of approximately 50% of kittiwake breeding colonies within the bay. Impaired nestling growth rates indicated that foraging conditions had declined markedly by the nestling period and were the poorest of any year of the study. Adult kittiwakes responded by devoting more time to foraging and by undertaking longer foraging trips that extended beyond the periphery of Chiniak Bay.

2003 - Egg laying was delayed by cool marine conditions in the spring and egg predation severely impacted most kittiwake colonies within the bay. Rapid nestling growth suggested excellent foraging conditions in 2003 while kittiwake parents provisioned nestlings on a diet of energy-rich capelin and, to a lesser degree, on lipid-poor YOY sandlance.

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Table 1. Summary of laying success, fledging success, hatching success, and productivity data for all colonies in all years of the study.

Year	Colony	Laying Success proportion of nests ± SD (n)[1]	Hatching Success proportion of eggs ± SD (n)[1]	Fledging Success proportion of chicks ± SD (n)[1]	Productivity chicks fledged/ nest ± SD (n)[1]
1978[2]	all	na	0.60 ± na (1)[3]	0.65 ± na (1)[3]	0.70 ± na (1)[3]
2001	all	0.89 ± 0.02 (9)[3]	0.60 ± 0.12 (9)[3]	0.71 ± 0.11 (9)[3]	0.78 ± 0.23 (9)[3]
2002	all	0.83 ± 0.10 (10)[3]	0.44 ± 0.18 (9)[3]	0.55 ± 0.20 (9)[3]	0.44 ± 0.31 (10)[3]
2003	all	0.75 ± 0.27 (10)[3]	0.44 ± 0.31 (7)[3]	0.61 ± 0.28 (7)[3]	0.44 ± 0.47 (10)[3]
1978[2]	KU	na	0.60 ± na (1)	0.65 ± na (1)	0.7 ± na (1)
2001	GC	0.90 ± 0.06 (5)	0.33 ± 0.18 (5)	0.48 ± 0.27 (5)	0.29 ± 0.32 (5)
2001	GU	0.86 ± 0.05 (5)	0.70 ± 0.12 (5)	0.85 ± 0.06 (5)	0.96 ± 0.17 (5)
2001	KA	0.86 ± 0.17 (5)	0.58 ± 0.27 (5)	0.64 ± 0.37 (5)	0.88 ± 0.51 (5)
2001	KU	0.90 ± 0.04 (10)	0.55 ± 0.18 (10)	0.68 ± 0.26 (10)	0.68 ± 0.30 (10)
2001	MA	0.87 ± 0.06 (11)	0.72 ± 0.08 (11)	0.79 ± 0.07 (11)	0.99 ± 0.14 (11)
2001	PU	0.89 ± 0.10 (4)	0.73 ± 0.09 (4)	0.85 ± 0.01 (4)	1.04 ± 0.14 (4)
2001	BL	0.91 ± 0.04 (4)	0.67 ± 0.11 (4)	0.71 ± 0.11 (4)	0.86 ± 0.24 (4)
2001	SE	0.94 ± na (1)	0.58 ± na (1)	0.72 ± na (1)	0.74 ± na (1)
2001	SV	0.86 ± 0.11 (4)	0.51 ± 0.15 (4)	0.65 ± 0.10 (4)	0.56 ± 0.16 (4)
2002	GC	0.87 ± 0.05 (5)	0.39 ± 0.20 (5)	0.46 ± 0.21 (5)	0.29 ± 0.20 (5)
2002	GU	0.90 ± 0.07 (5)	0.72 ± 0.06 (5)	0.88 ± 0.05 (5)	1.07 ± 0.13 (5)
2002	KA	0.84 ± 0.08 (4)	0.65 ± 0.09 (4)	0.71 ± 0.19 (4)	0.76 ± 0.28 (4)
2002	KU	0.62 ± 0.27 (9)	0.21 ± 0.24 (9)	0.34 ± 0.36 (9)	0.26 ± 0.34 (9)
2002	MA	0.86 ± 0.09 (11)	0.36 ± 0.20 (11)	0.66 ± 0.25 (11)	0.42 ± 0.27 (11)
2002	PU	0.85 ± 0.11 (4)	0.50 ± 0.17 (4)	0.71 ± 0.16 (4)	0.62 ± 0.30 (4)
2002	BL	0.93 ± 0.04 (4)	0.38 ± 0.35 (4)	0.43 ± 0.50 (4)	0.48 ± 0.55 (4)
2002	SE	0.90 ± na (1)	0.22 ± na (1)	0.52 ± na (1)	0.19 ± na (1)
2002	SV	0.85 ± 0.10 (4)	0.58 ± 0.17 (4)	0.26 ± 0.24 (4)	0.31 ± 0.39 (4)
2002	UT	0.68 ± na (1)	na	na	0.00 ± na (1)
2003	GC	0.79 ± 0.06 (3)	0.16 ± 0.10 (3)	0.64 ± 0.39 (3)	0.11 ± 0.10 (3)
2003	GU	0.89 ± 0.01 (3)	0.78 ± 0.04 (3)	0.82 ± 0.04 (3)	1.09 ± 0.06 (3)
2003	KA	0.92 ± 0.01 (2)	0.80 ± 0.12 (2)	0.91 ± 0.05 (2)	1.32 ± 0.26 (2)
2003	KU	0.72 ± 0.12 (6)	0.05 ± 0.08 (6)	0.04 ± 0.08 (6)	0.00 ± 0.00 (6)
2003	MA	0.72 ± 0.14 (4)	0.39 ± 0.07 (4)	0.78 ± 0.01 (4)	0.46 ± 0.25 (4)
2003	PU	0.82 ± 0.04 (2)	0.21 ± 0.14 (2)	0.49 ± 0.17 (2)	0.18 ± 0.17 (2)
2003	SV	0.94 ± 0.03 (4)	0.69 ± 0.06 (4)	0.59 ± 0.22 (4)	0.70 ± 0.28 (4)
2003	UT	0.00 ± na (1)	na	na	0.00 ± na (1)
2003	VE	0.73 ± 0.18 (4)	na	na	0.00 ± 0.00 (4)
2003	MR	0.94 ± na (1)	na	na	0.54 ± na (1)

[1] = number of reproductive plots, [2] = unpub. data from D. Nysewander, [3] = number of colonies

Table 2. Summary of data for hatch date, egg volume, clutch size, brood size at hatch and brood size at fledge for all colonies in all years of the study.

Year	Colony	Hatch Date date in July ± SD (n)[1]	Egg Volume cm^3 ± SD (n)[2]	Clutch Size eggs/nest ± SD (n)[1]	Brood Size @ Hatch chicks/nest ± SD (n)[1]	Brood Size @ Fledge chicks/nest ± SD (n)[1]
1978[3]	all	43.4 ± na (1)[4]	na	1.65 ± na (1)[4]	1.44 ± na (1)[4]	1.48 ± na (1)[4]
2001	all	40.0 ± 1.6 (9)[4]	45.9 ± 0.53 (6)[4]	1.80 ± 0.1 (9)[4]	1.47 ± 0.1 (9)[4]	1.56 ± 0.1 (9)[4]
2002	all	41.9 ± 6.8 (10)[4]	46.3 ± 0.25 (6)[4]	1.67 ± 0.2 (10)[4]	1.39 ± 0.1 (9)[4]	1.49 ± 0.1 (9)[4]
2003	all	44.7 ± 3.2 (9)[4]	45.6 ± 0.58 (5)[4]	1.57 ± 0.2 (9)[4]	1.36 ± 0.2 (8)[4]	1.52 ± 0.1 (8)[4]
1978[3]	KU	43.4 ± na (1)	na	1.65 ± na (1)	1.48 ± na (1)	1.44 ± na (1)
2001	GC	42.6 ± 0.9 (5)	46.2 ± 3.69 (157)	1.69 ± 0.06 (5)	1.28 ± 0.14 (5)	1.29 ± 0.17 (5)
2001	GU	39.9 ± 1.4 (5)	45.5 ± 2.91 (73)	1.80 ± 0.14 (5)	1.66 ± 0.07 (5)	1.59 ± 0.06 (5)
2001	KA	36.3 ± 2.2 (5)	45.8 ± 3.47 (126)	1.99 ± 0.04 (5)	1.59 ± 0.33 (5)	1.59 ± 0.18 (4)
2001	KU	40.8 ± 2.5 (10)	46.5 ± 3.54 (126)	1.76 ± 0.13 (10)	1.47 ± 0.16 (10)	1.36 ± 0.12 (9)
2001	MA	39.7 ± 0.9 (11)	45.2 ± 3.45 (176)	1.92 ± 0.06 (11)	1.65 ± 0.14 (11)	1.50 ± 0.15 (11)
2001	PU	41.1 ± 0.6 (4)	46.4 ± 2.85 (56)	1.75 ± 0.06 (4)	1.60 ± 0.06 (4)	1.53 ± 0.04 (4)
2001	BL	39.2 ± 1.7 (4)	na	1.80 ± 0.12 (4)	1.64 ± 0.16 (4)	1.48 ± 0.14 (4)
2001	SE	39.8 ± (1)	na	1.81 ± na (1)	1.71 ± na (1)	1.52 ± na (1)
2001	SV	40.2 ± 2.2 (4)	na	1.68 ± 0.23 (4)	1.45 ± 0.07 (4)	1.35 ± 0.03 (4)
2002	GC	40.5 ± 2.2 (5)	46.7 ± 3.75 (154)	1.69 ± 0.13 (5)	1.42 ± 0.14 (5)	1.30 ± 0.22 (5)
2002	GU	38.4 ± 1.5 (5)	46.2 ± 3.45 (70)	1.82 ± 0.13 (5)	1.60 ± 0.08 (5)	1.50 ± 0.03 (5)
2002	KA	38.6 ± 7.3 (4)	46.5 ± 3.22 (70)	1.84 ± 0.06 (4)	1.56 ± 0.09 (4)	1.44 ± 0.13 (4)
2002	KU	45.1 ± 5.2 (9)	45.9 ± 3.09 (102)	1.57 ± 0.17 (9)	1.50 ± 0.11 (5)	1.49 ± 0.29 (5)
2002	MA	40.4 ± 5.7 (11)	46.2 ± 3.46 (92)	1.72 ± 0.18 (11)	1.33 ± 0.20 (11)	1.32 ± 0.28 (10)
2002	PU	40.1 ± 2.8 (4)	46.4 ± 3.32 (67)	1.71 ± 0.18 (4)	1.58 ± 0.12 (4)	1.40 ± 0.10 (4)
2002	BL	37.8 ± 1.4 (4)	na	1.82 ± 0.14 (4)	1.40 ± 0.20 (4)	1.58 ± 0.00 (2)
2002	SE	41.0 ± na (1)	na	1.70 ± na (1)	1.46 ± na (1)	1.25 ± na (1)
2002	SV	36.8 ± 1.0 (4)	na	1.86 ± 0.14 (4)	1.61 ± 0.07 (4)	1.27 ± 0.33 (4)
2002	UT	na	na	na	na	na
2003	GC	44.1 ± 1.8 (3)	46.0 ± 3.93 (128)	1.54 ± 0.10 (3)	1.55 ± 0.39 (3)	1.45 ± 0.50 (3)
2003	GU	41.5 ± 1.1 (3)	46.1 ± 2.91 (108)	1.86 ± 0.04 (3)	1.65 ± 0.00 (3)	1.49 ± 0.01 (3)
2003	KA	41.6 ± 0.1 (2)	45.7 ± 5.35 (74)	1.89 ± 0.06 (2)	1.74 ± 0.14 (2)	1.68 ± 0.08 (2)
2003	KU	42.8 ± 1.0 (6)	45.7 ± 3.53 (102)	1.48 ± 0.21 (6)	1.63 ± 0.37 (3)	1.00 ± 0.00 (2)
2003	MA	50.6 ± 2.2 (4)	44.5 ± 3.06 (62)	1.42 ± 0.17 (4)	1.27 ± 0.16 (4)	1.15 ± 0.07 (4)
2003	PU	46.0 ± 1.4 (2)	na	1.61 ± 0.03 (2)	1.27 ± 0.18 (2)	1.09 ± 0.12 (2)
2003	SV	41.8 ± 1.2 (4)	na	1.77 ± 0.15 (4)	1.67 ± 0.07 (4)	1.56 ± 0.13 (4)
2003	UT	na	na	na	na	na
2003	VE	na	45.8 ± 3.72 (25)	na	na	na
2003	MR	na	na	na	1.37 ± na (1)	1.46 ± na (1)

[1] = number of reproductive plots, [2] = number of eggs, [3] = unpub. data from D. Nysewander, [4] = number of colonies

Table 3. Summary of data for chick growth regurgitation propensity and diet composition for all colonies in all years of the study.

Year	Colony	Chick Growth (singleton and A chicks only) g/day ± SD (n)[1]	Regurgitation Propensity proportion of nests ± SD (n)[2]	Diet Composition (proportion by mass) ± SD (n)[3]		
				Capelin	Sandlance	Other
1978[4]	all	16.3 ± na (1)[5]	na	na	na	na
2001	all	16.3 ± 0.5 (6)[5]	0.22 ± 0.06 (6)[5]	0.32 ± 0.15 (6)[5]	0.60 ± 0.19 (6)[5]	0.07 ± 0.04 (6)[5]
2002	all	16.0 ± 0.8 (6)[5]	0.18 ± 0.03 (4)[5]	0.32 ± 0.05 (5)[5]	0.58 ± 0.07 (5)[5]	0.08 ± 0.03 (5)[5]
2003	all	16.9 ± 0.6 (4)[5]	0.19 ± 0.04 (4)[5]	0.47 ± 0.12 (5)[5]	0.42 ± 0.13 (5)[5]	0.09 ± 0.07 (5)[5]
1978[4]	KU	16.3 ± 2.1 (34)	na	na	na	na
2001	GC	16.1 ± 2.0 (39)	0.31 ± 0.07 (221)	0.29 ± 0.21 (35)	0.63 ± 0.17 (35)	0.06 ± 0.06 (35)
2001	GU	16.4 ± 1.4 (29)	0.23 ± 0.08 (172)	0.43 ± 0.25 (30)	0.44 ± 0.18 (30)	0.12 ± 0.11 (30)
2001	KA	16.1 ± 1.3 (26)	0.13 ± 0.02 (158)	0.06 ± 0.12 (24)	0.93 ± 0.12 (24)	0.00 ± 0.01 (24)
2001	KU	16.2 ± 1.9 (35)	0.18 ± 0.11 (220)	0.37 ± 0.37 (31)	0.47 ± 0.34 (31)	0.15 ± 0.18 (31)
2001	MA	15.8 ± 1.8 (74)	0.20 ± 0.09 (418)	0.22 ± 0.20 (49)	0.74 ± 0.16 (49)	0.03 ± 0.07 (49)
2001	PU	17.3 ± 1.3 (26)	0.27 ± 0.18 (144)	0.40 ± 0.41 (24)	0.43 ± 0.26 (24)	0.15 ± 0.20 (24)
2002	GC	15.8 ± 1.7 (30)	0.15 ± 0.06 (200)	0.31 ± 0.33 (28)	0.57 ± 0.31 (28)	0.10 ± 0.09 (28)
2002	GU	16.5 ± 2.3 (27)	0.23 ± 0.06 (169)	0.39 ± 0.11 (40)	0.49 ± 0.12 (40)	0.10 ± 0.08 (40)
2002	KA	14.8 ± 2.1 (14)	0.16 ± 0.12 (146)	0.21 ± 0.23 (21)	0.75 ± 0.24 (21)	0.03 ± 0.06 (21)
2002	KU	17.2 ± 2.0 (3)	na	na	na	na
2002	MA	16.0 ± 2.1 (30)	0.17 ± 0.09 (196)	0.38 ± 0.16 (35)	0.56 ± 0.11 (35)	0.04 ± 0.06 (35)
2002	PU	15.6 ± 2.5 (9)	na	0.52 ± 0.43 (14)	0.41 ± 0.36 (14)	0.05 ± 0.09 (14)
2003	GC	17.4 ± 2.6 (22)	0.21 ± 0.07 (116)	0.59 ± 0.22 (28)	0.34 ± 0.26 (28)	0.06 ± 0.07 (28)
2003	GU	17.3 ± 2.1 (44)	0.22 ± 0.06 (290)	0.57 ± 0.07 (47)	0.22 ± 0.12 (47)	0.20 ± 0.11 (47)
2003	KA	16.8 ± 2.7 (22)	0.12 ± 0.05 (151)	0.25 ± 0.09 (28)	0.58 ± 0.11 (28)	0.10 ± 0.18 (28)
2003	KU	na	na	0.69 ± 0.42 (6)	0.30 ± 0.42 (6)	0.00 ± 0.00 (6)
2003	MA	15.9 ± 2.0 (22)	0.20 ± 0.12 (167)	0.46 ± 0.04 (36)	0.43 ± 0.03 (36)	0.09 ± 0.01 (36)

[1] = number of chicks.

[2] = number of nests, colony means (±SD) computed from means for three time periods that are each based on regurgitation proportions from a minimum of two plot-visit per time period.

[3] = number of diet samples, colony means (±SD) computed from means of samples within 4 time periods.

[4] = D. Nysewander unpub. data.

[5] = number of colonies contribution to annual mean.

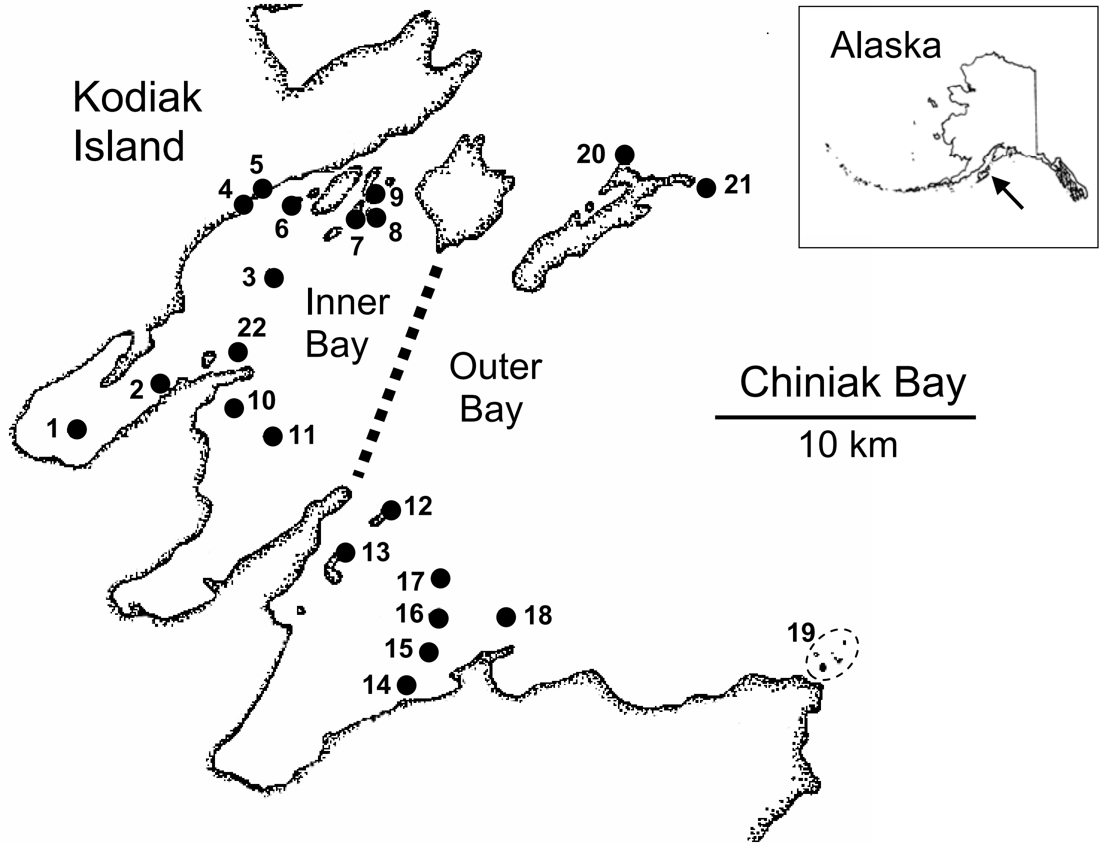

Figure 1. Locations of 22 black-legged kittiwake breeding colonies (see key below) within the Chiniak Bay study area on Kodiak Island, in the western Gulf of Alaska. The dashed line demarcates inner bay and outer bay regions. Colonies are identified by their two-letter abbreviation throughout this report. 1=Mary I. (MA), 2=Blodgett I. (BL), 3=Puffin I. (PU), 4=Gibson Cove (GC), 5=Sealand (SE), 6=Gull I. (GU), 7=Crooked I. (CR), 8=Kulichkof I. (KU), 9=Holiday I. (HO), 10=Marathon Rock (MR), 11=Veisoki I. (VE), 12=Queer I. (QU), 13=Kalsin I. (KA), 14=Utesistoi I. (UT), 15=Svitlak I. (SV), 16=Middle I., 17=Pinnacle Rock (PR), 18=Kekur I. (KE), 19= Cape Chiniak Is. (CH), 20=Long I. Inner (LI), 21=Long I. Outer (LO), 22=Cliff I. (CI)

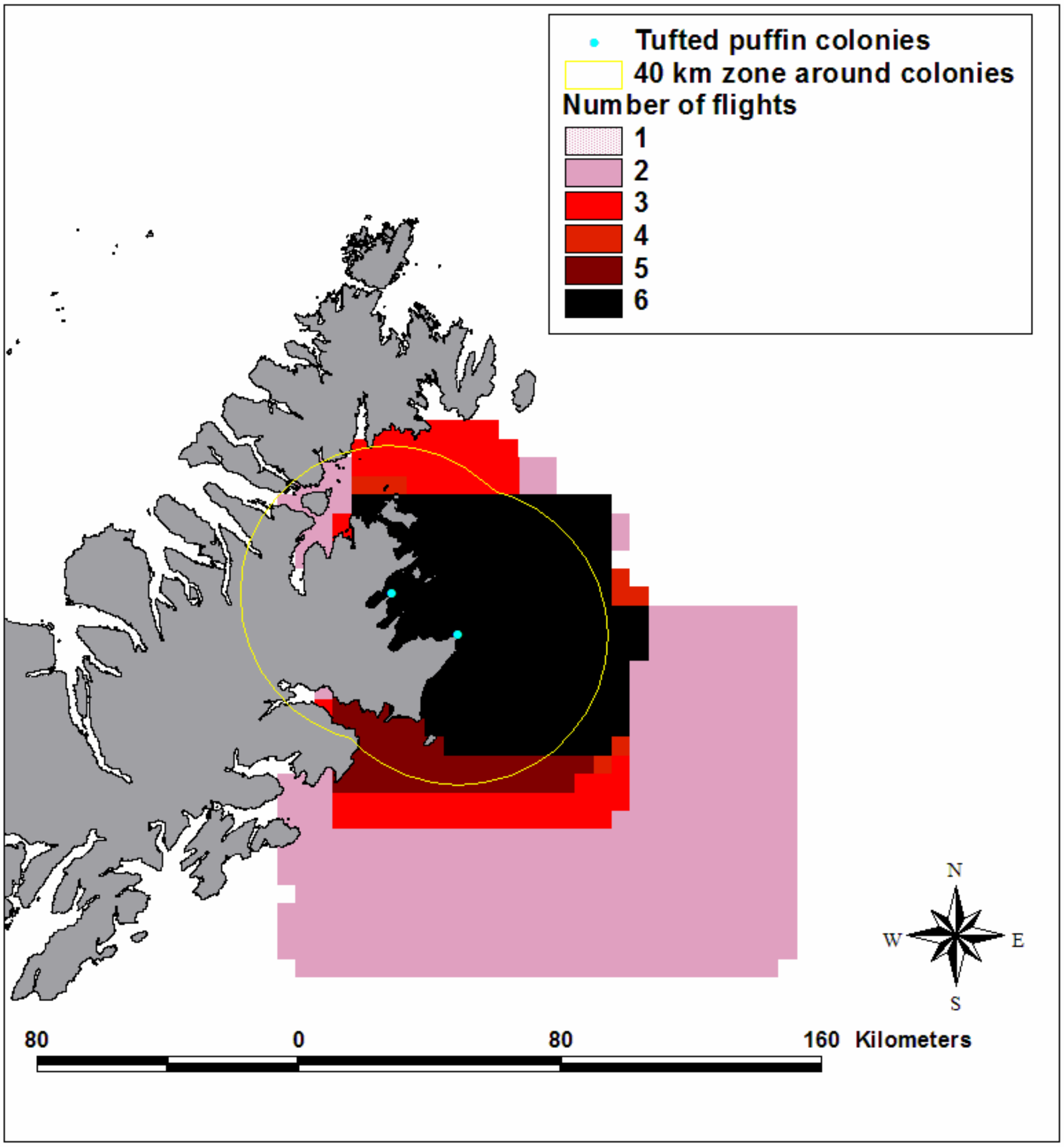

Figure 2. Coverage area of aerial transects flown in 2003 to determine the at-sea distribution of kitiwakes.

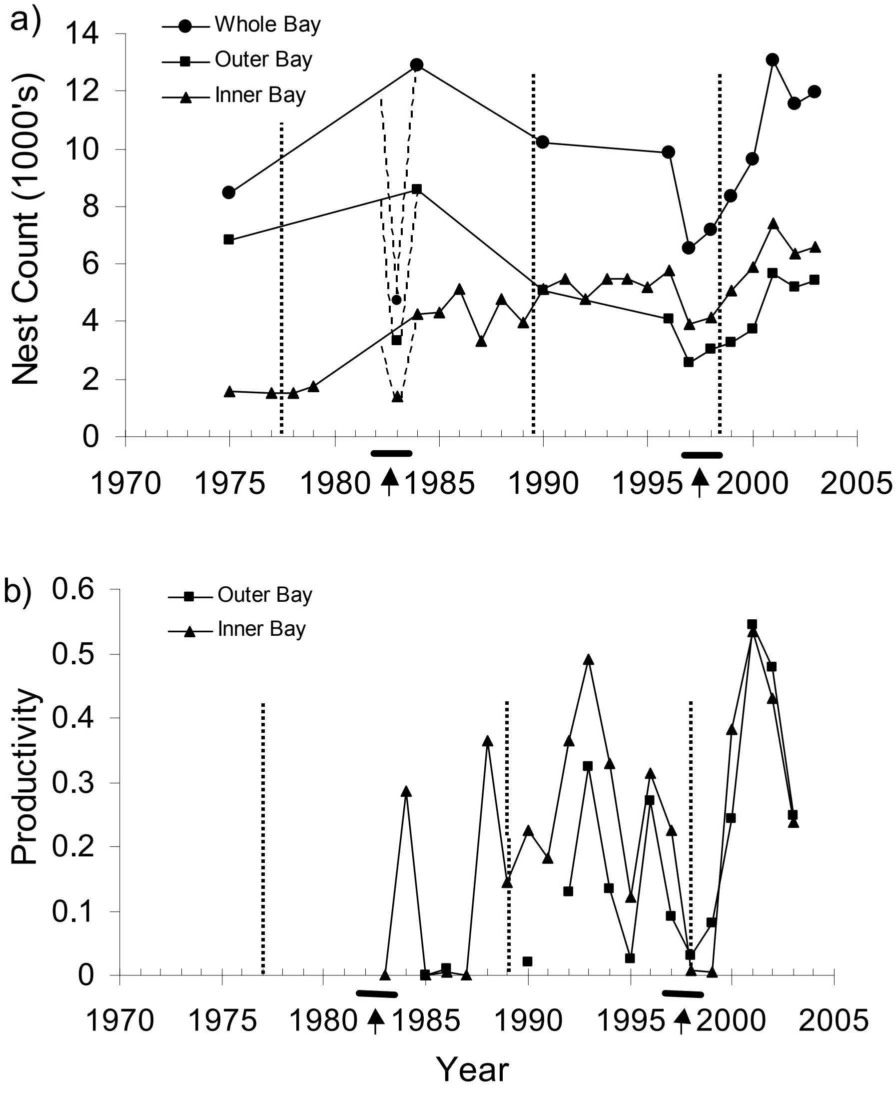

Figure 3. a) Trends in count of kittiwake nests within inner and outer regions of Chiniak Bay between 1975 and 2003. Dashed lines indicate "regime shift" events that occurred in 1977, 1989, and 1998. Bars beneath the x-axis indicate extreme El Nino events. b) Trends in productivity (chicks fledged/nest) of kittiwakes within inner and outer sections of Chiniak Bay. Dashed lines indicate regime shift events that occurred in 1977, 1989, and 1998. Bars beneath the x-axis indicate extreme El Nino events.

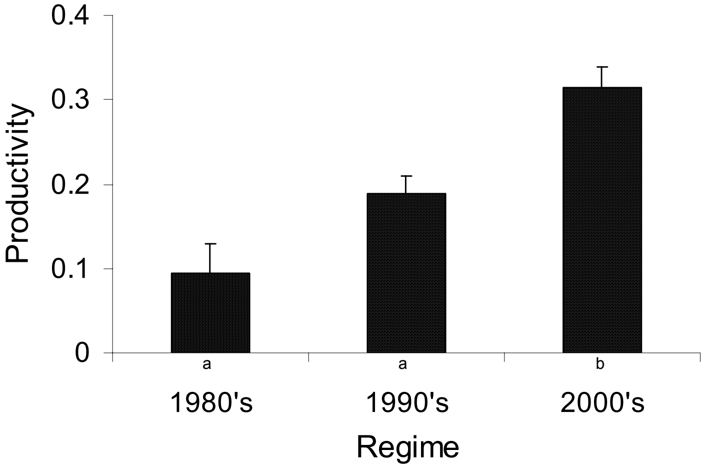

Figure 4. Kittiwake productivity differed among climatic "regimes" in the Gulf of Alaska. Letters at the base of each bar indicate results of Tukey's post-hoc comparisons: bars sharing a letter do not differ significantly.

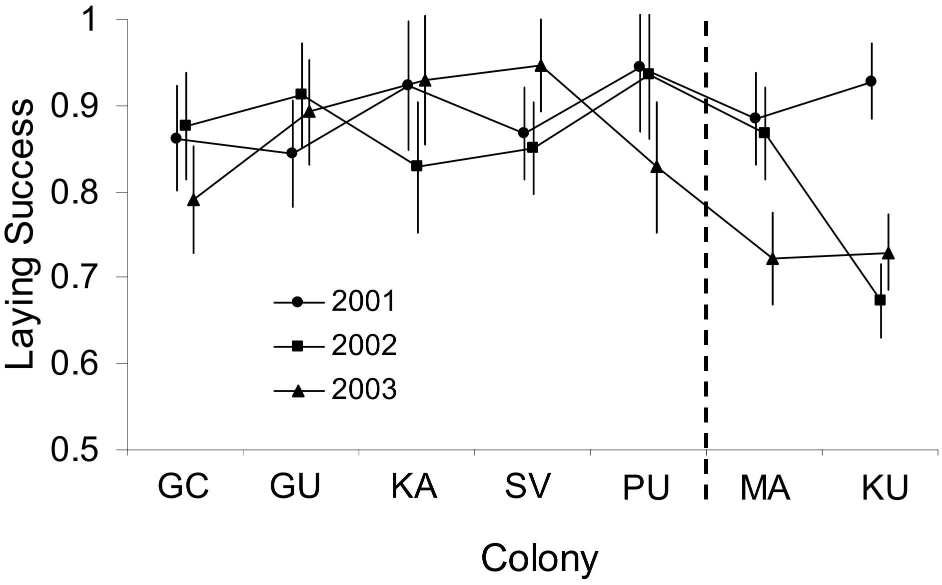

Figure 5. Interaction plot of mean (±SE) laying success (nests with eggs/total nests) of black-legged kittiwakes in 7 colonies within Chiniak Bay, Alaska for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and colony. Colonies were separated into two groups indicated by the vertical hatched line to neutralize the interaction.

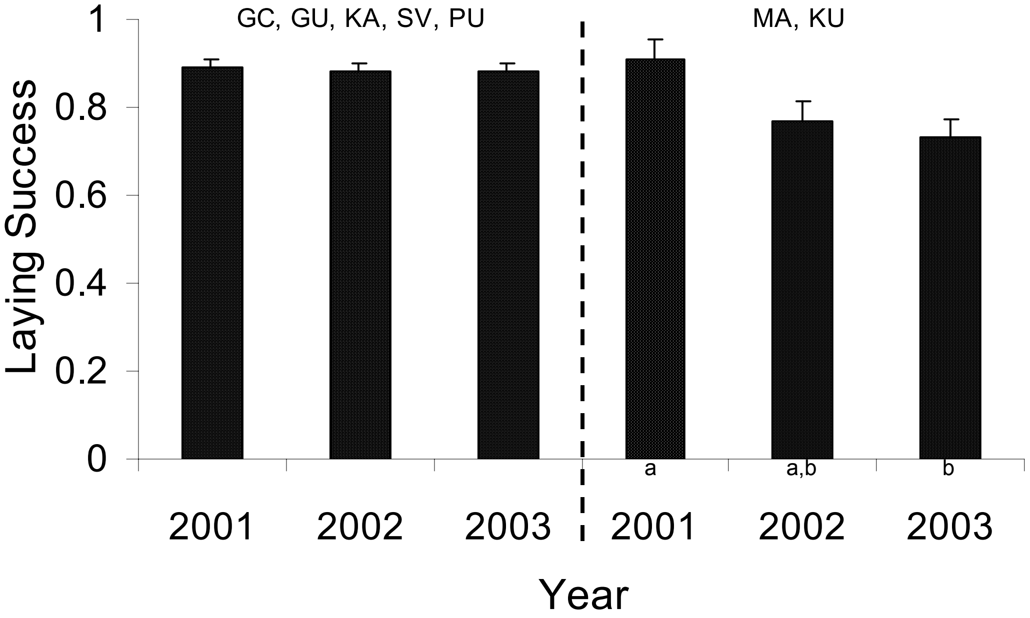

Figure 6. Mean (±SE) laying success (nests with eggs/total nests) for 7 colonies that were divided into two groups to neutralize an interaction between year and colony. Letters at the base of each bar present results of Tukey's post-hoc comparisons within each group: bars that share a letter are not significantly different.

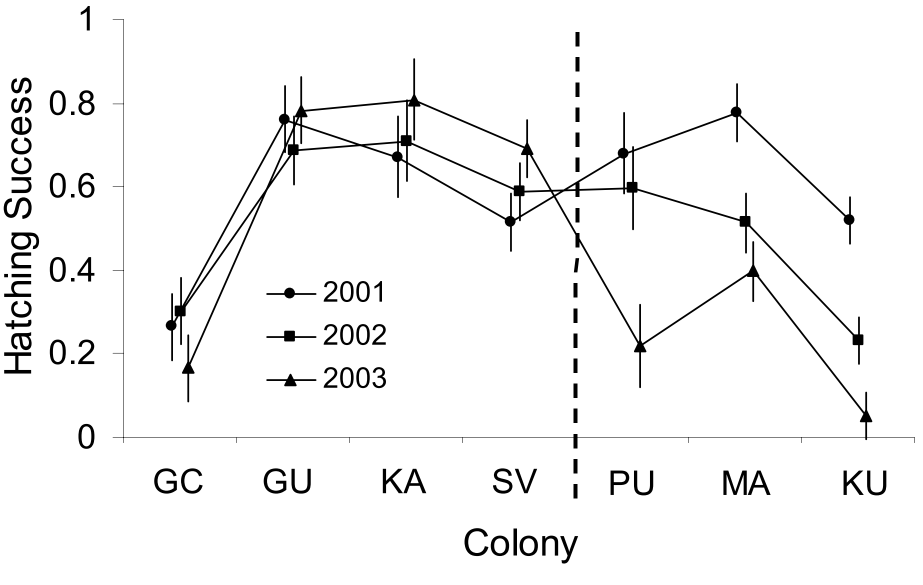

Figure 7. Interaction plot of mean (±SE) hatching success (chicks hatched/total eggs) of black-legged kittiwakes in 7 colonies within Chiniak Bay, Alaska for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and colony. Colonies were separated into two groups indicated by the vertical hatched line to neutralize the interaction.

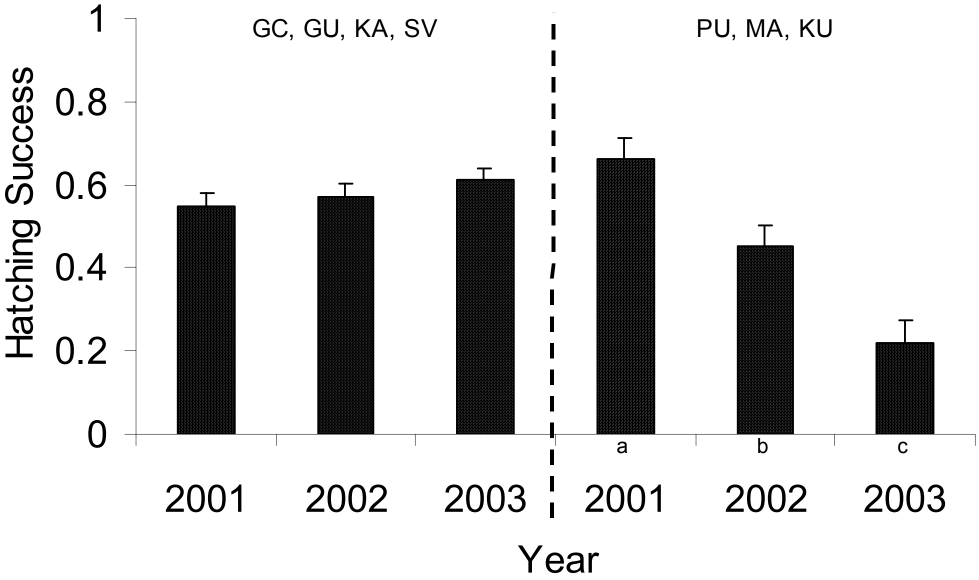

Figure 8. Mean (±SE) hatching success (chicks hatched/total eggs) for 7 colonies that were divided into two groups to neutralize an interaction between year and colony. Letters at the base of each bar present results of Tukey's post-hoc comparisons within each group: bars that share a letter are not significantly different.

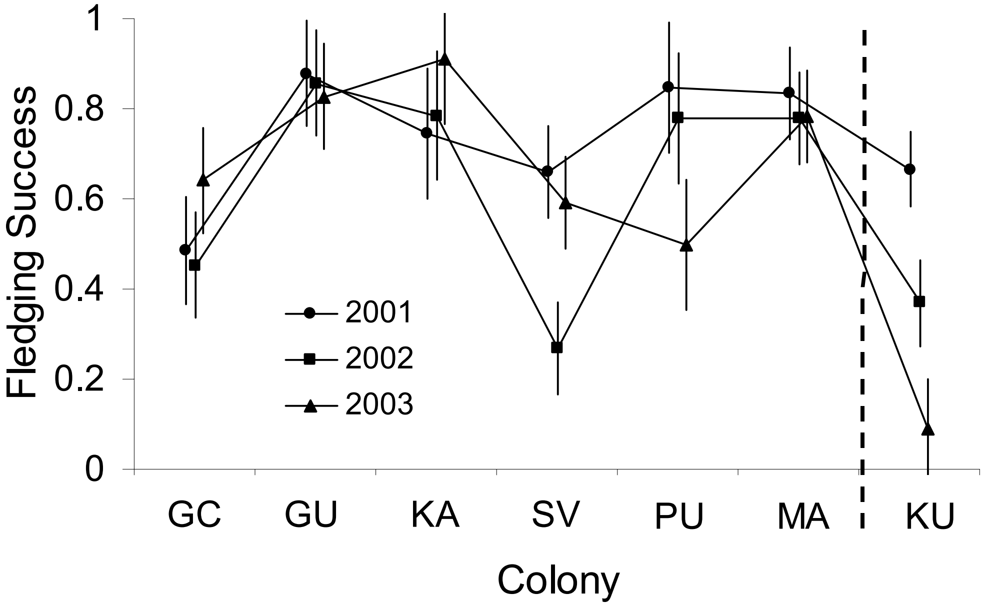

Figure 9. Interaction plot of mean (±SE) Fledging success (chicks fledged/chicks hatched) of black-legged kittiwakes in 7 colonies within Chiniak Bay, Alaska for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and colony. Colonies were separated into two groups indicated by the vertical hatched line to neutralize the interaction.

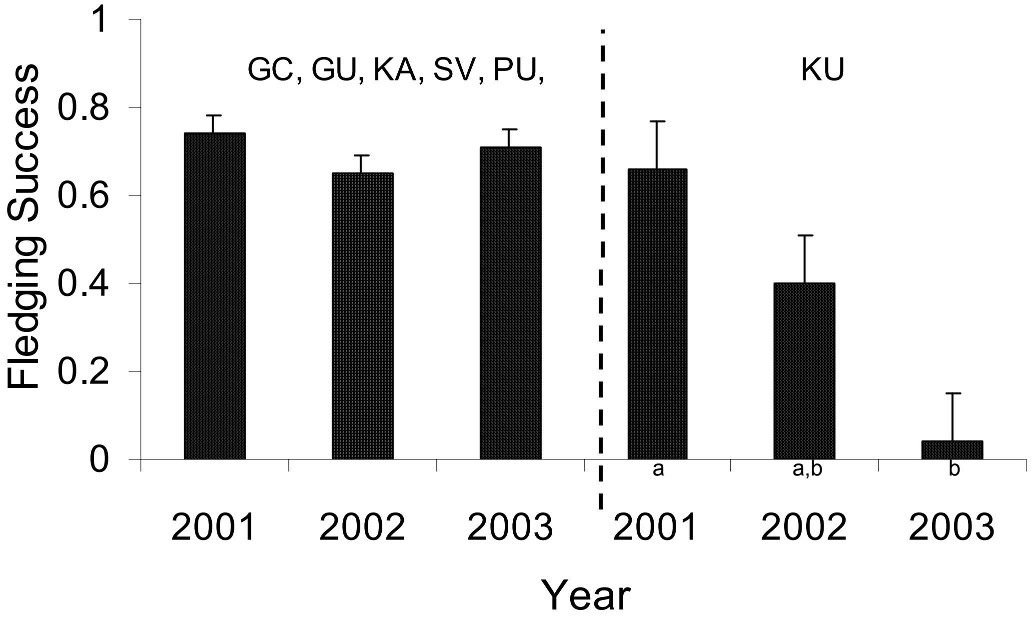

Figure 10. Mean (±SE) Fledging success (chicks fledged/chicks hatched) for 7 colonies that were divided into two groups to neutralize an interaction between year and colony. Letters at the base of each bar present results of Tukey's post-hoc comparisons within each group: bars that share a letter are not significantly different.

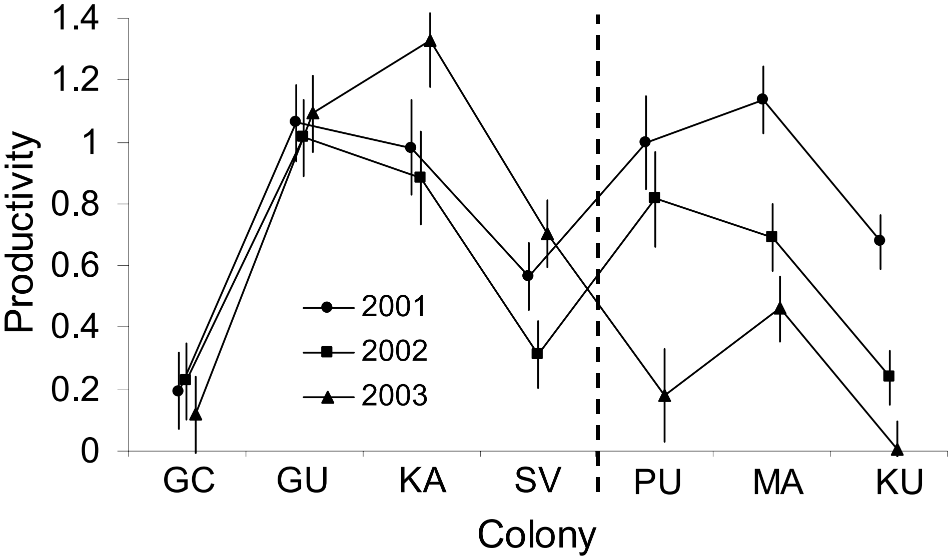

Figure 11. Interaction plot of mean (±SE) overall productivity (chicks fledged/total nests) of black-legged kittiwakes in 7 colonies within Chiniak Bay, Alaska for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and colony. Colonies were separated into two groups indicated by the vertical hatched line to neutralize the interaction.

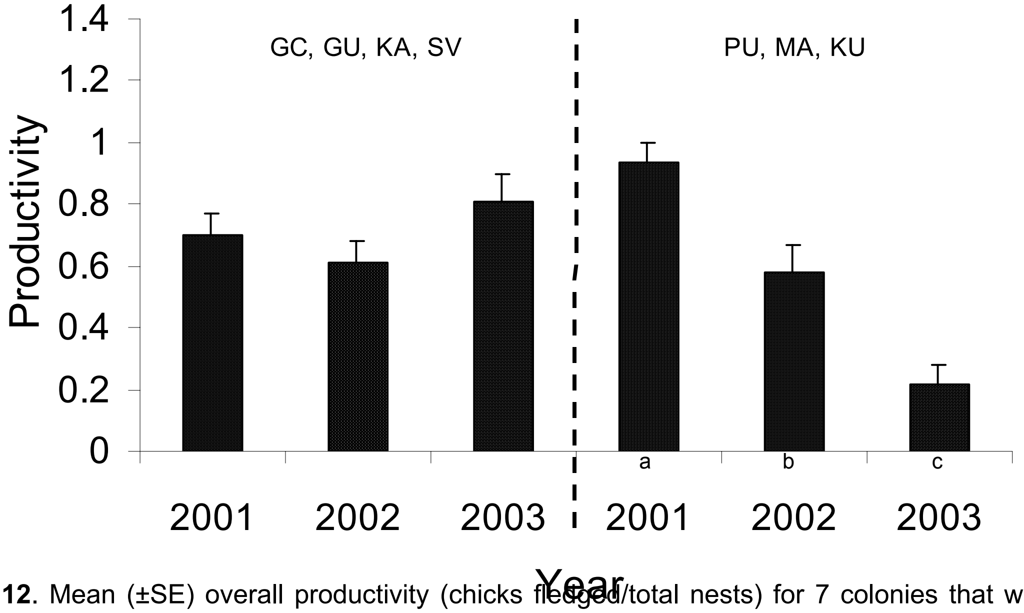

Figure 12. Mean (±SE) overall productivity (chicks fledged/total nests) for 7 colonies that were divided into two groups to neutralize an interaction between year and colony. Letters at the base of each bar present results of Tukey's post-hoc comparisons within each group: bars that share a letter are not significantly different.

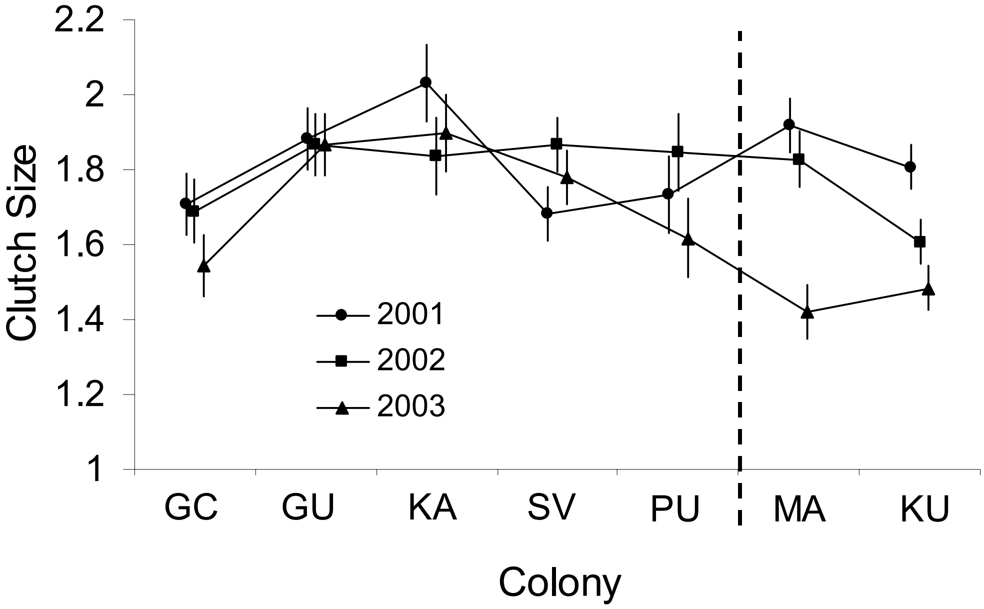

Figure 13. Interaction plot of mean (±SE) clutch size of black-legged kittiwakes in 7 colonies within Chiniak Bay, Alaska for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and colony. Colonies were separated into two groups indicated by the vertical hatched line to neutralize the interaction.

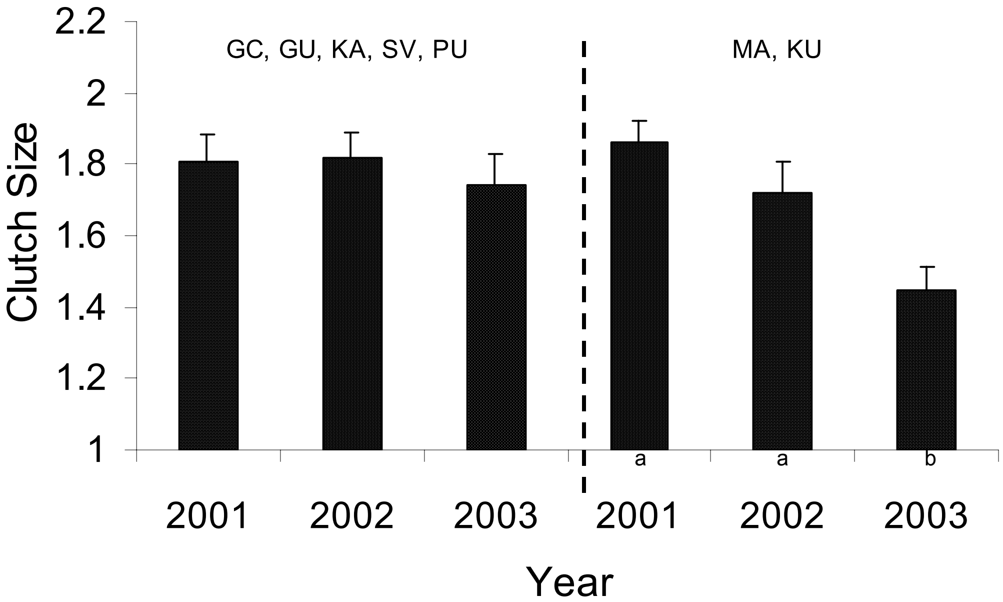

Figure 14. Mean (±SE) clutch size for 7 colonies that were divided into two groups to neutralize an interaction between year and colony. Letters at the base of each bar present results of Tukey's post-hoc comparisons within each group: bars that share a letter are not significantly different.

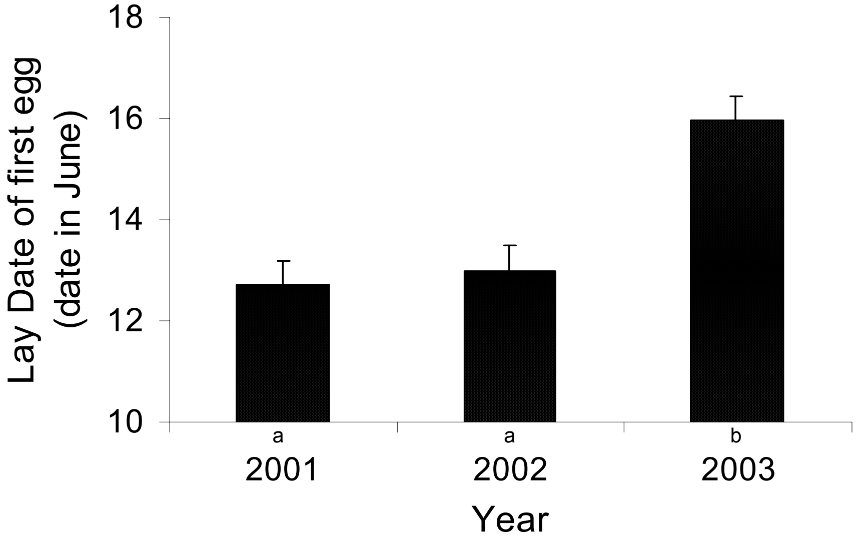

Figure 15. Mean lay date (± SE) of the first egg of black-legged kittiwake clutches for 7 colonies within Chiniak Bay, AK from 2001-2003. Letters at the base of each bar indicate results of Tukey's post-hoc comparisons: bars sharing a letter do not differ significantly.

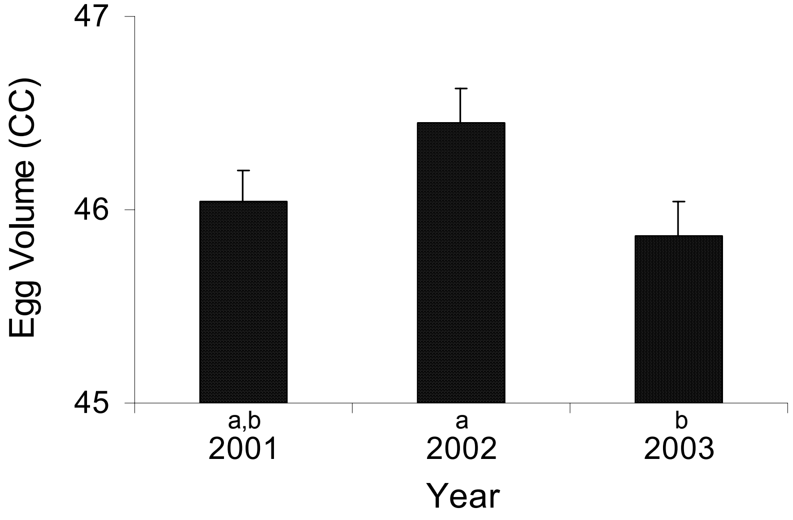

Figure 16. Mean egg volume (±SE) of black-legged kittiwakes for 5 colonies in Chiniak Bay, Alaska 2001-2003. Letters at the base of each bar indicate results of Tukey's post-hoc comparisons: bars sharing a letter do not differ significantly.

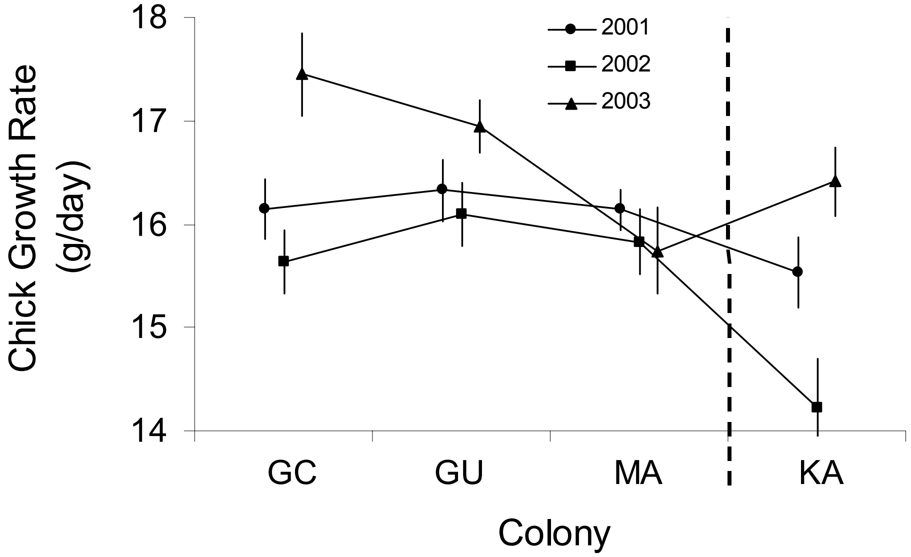

Figure 17. Interaction plot of mean linear growth rate (±SE) of body mass of black-legged kittiwake chicks for 4 colonies within Chiniak Bay, Alaska for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and colony. Colonies were separated into two groups indicated by the vertical hatched line to neutralize the interaction. Growth rate is defined as slope of a linear regression model fitted to mass-at-age data from individual chicks for which a minimum of 3 mass measurements were collected between 3 and 22 days of age, a period within which growth is approximately linear.

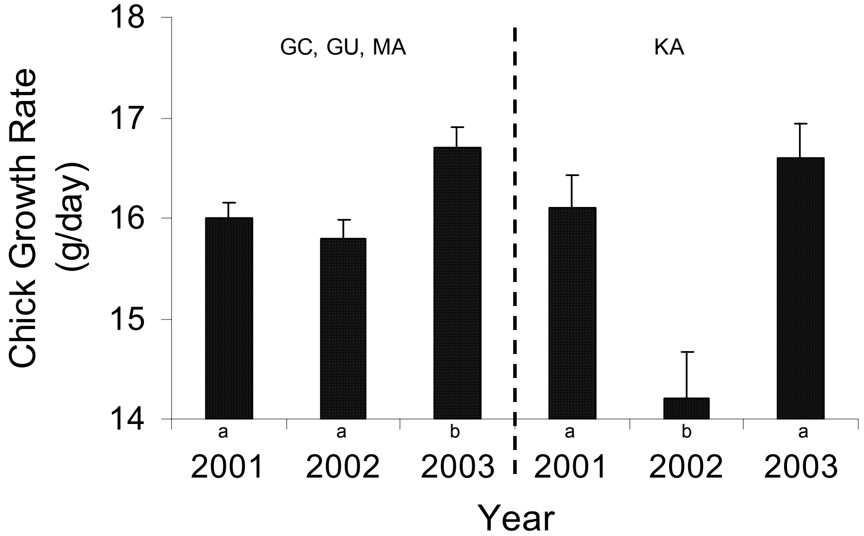

Figure 18. Mean linear growth rate (±SE) of body mass of black-legged kittiwake chicks for 4 colonies that were divided into two groups to neutralize an interaction between year and colony. Letters at the base of each bar present results of Tukey's post-hoc comparisons within each group: bars that share a letter are not significantly different. Growth rate is defined as slope of a linear regression model fitted to mass-at-age data from individual chicks for which a minimum of 3 mass measurements were collected between 3 and 22 days of age, a period within which growth is approximately linear.

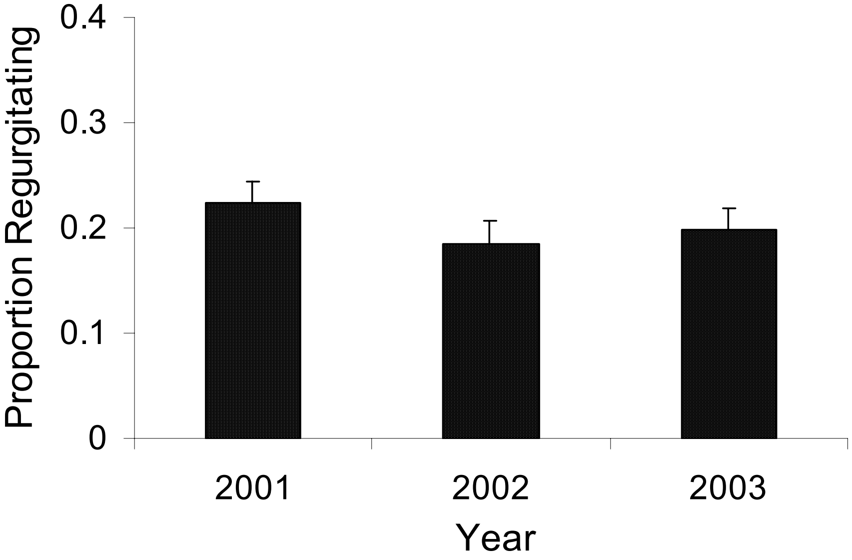

Figure 19. The mean proportion of nestling kittiwakes that regurgitated in response to researcher disturbance did not differ among years ($F_{2,71}$=0.86, *P*=0.43) in Chiniak Bay, AK 2001-2003. Bars represent means (±*SE*) of proportions computed for each plot visit by dividing the number of nests with chicks that provided regurgitations by the total number of nests with chicks. If fewer than 10 nests were sampled on a given plot visit, data were pooled with those of the next nearest visit.

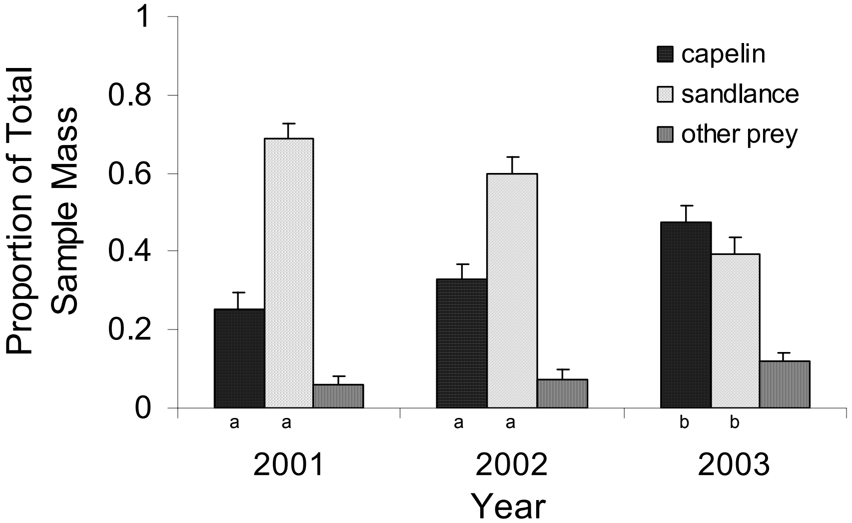

Figure 20. Diets of black-legged kittiwakes in Chiniak Bay, AK 2001-2003. Proportion of capelin in the diet of black-legged kittiwakes increased across years (p=0.004) at the expense of sandlance (p=0.001). Mean proportions (±SE) are indicated and were computed from mean values for diet samples pooled for each colony within 4 seasonal time periods.

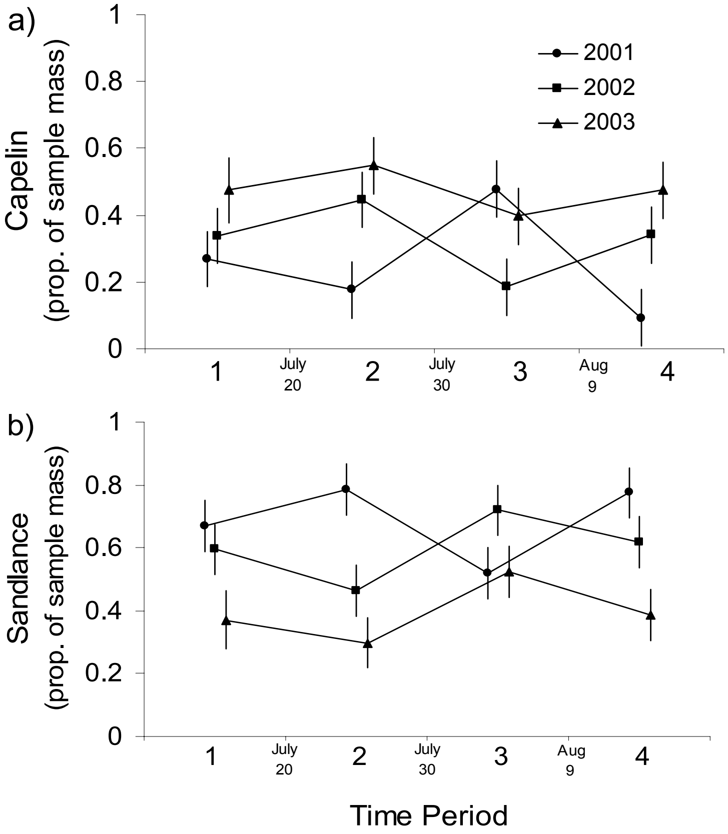

Figure 21. Interaction plots of diet composition (mean ± SE) of black-legged kittiwakes in 4 time periods for 2001-2003. An extreme lack of parallelism between lines illustrates the interaction between year and time period that was driven by increased capelin, and reduced sandlance, during the 3rd time period in 2001.

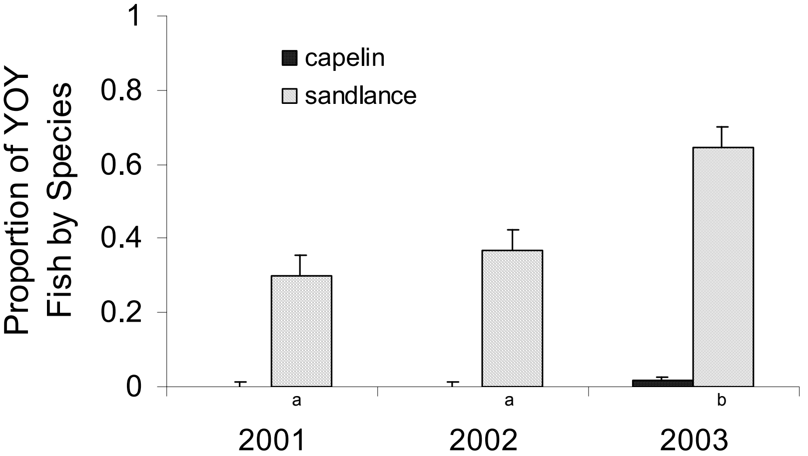

Figure 22. The proportion of YOY individuals in the diets of black-legged kittiwakes by year in Chiniak Bay, AK 2001-2003. Proportion of YOY individuals in the diet increased across years for sandlance but, for capelin, was negligible in all years.

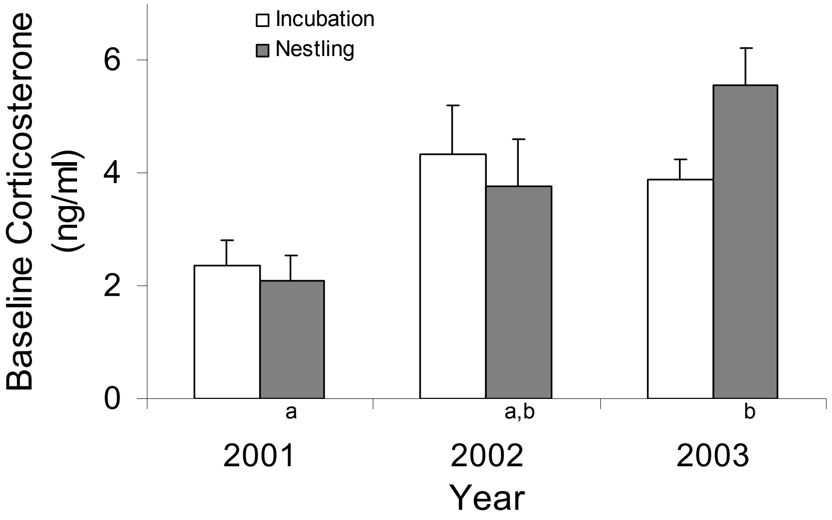

Figure 23. Baseline levels (mean ±SE) of plasma corticosterone for free-living adult black-legged kittiwakes during incubation and nestling periods in Chiniak Bay, AK 2001-2003. Results of pair wise comparisons within each period are denoted with letters: bars that share a letters do not differ.

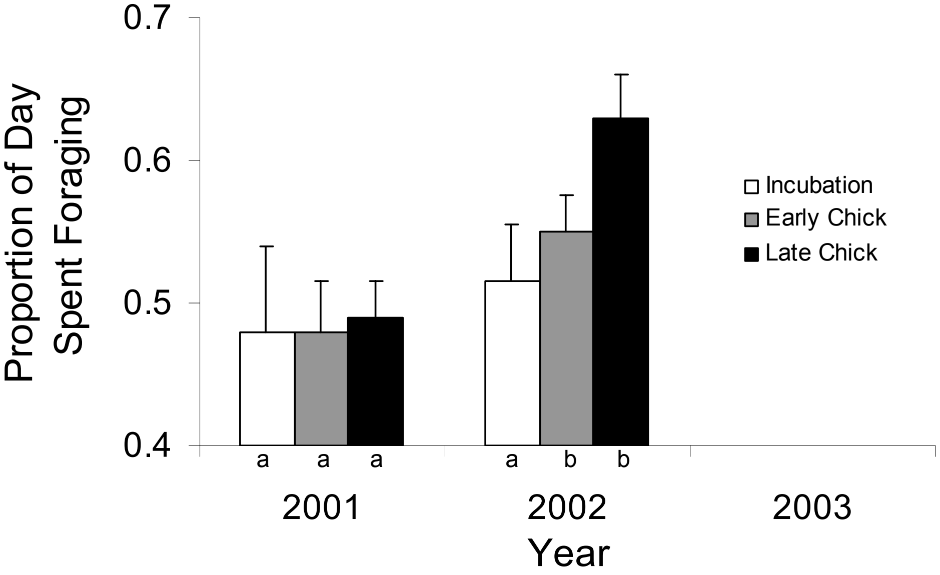

Figure 24. Mean proportion (±SE) of daylight period devoted to foraging by kittiwakes for three periods of the breeding season (Incubation, Early Chick, Late Chick) in 2001 and 2002. Letters denote significant differences between years within each period: bars that share a letter do not differ.

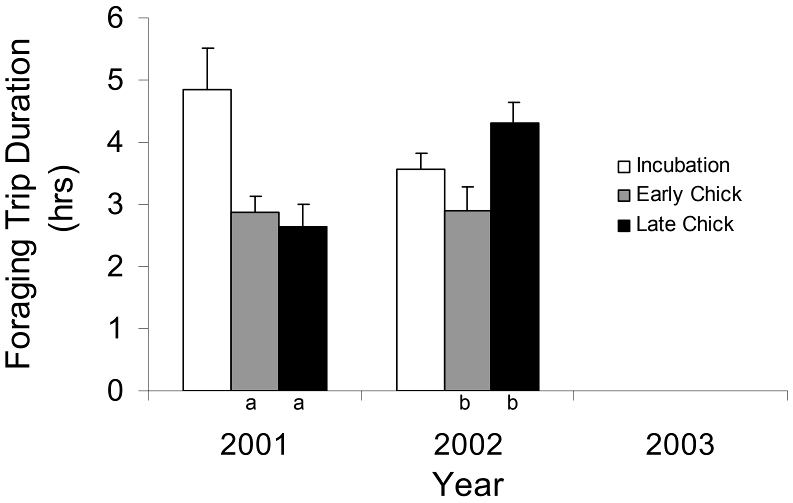

Figure 25. Mean duration (hrs ±SE) of foraging bouts of breeding kittiwakes during three periods of the breeding season (Incubation, Early Chick, Late Chick) in 2001 and 2002. Letters denote significant differences between years within each period letter do not differ.

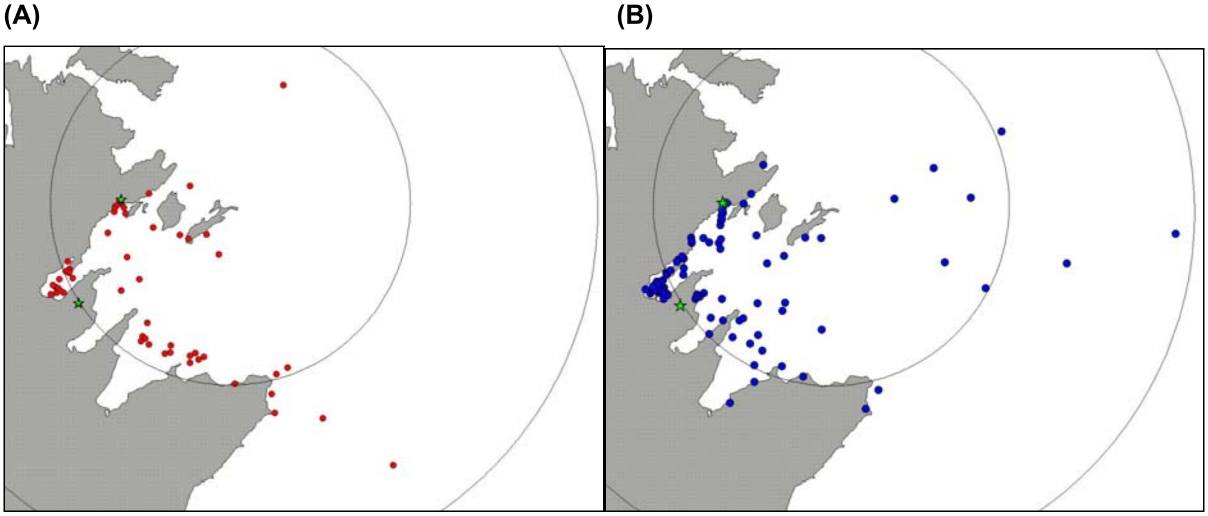

Figure 26. Triangulated locations of kittiwakes equipped with radio-transmitters in Chiniak Bay, Alaska. (A) locations (n = 70) for 27 black-legged kittiwakes in 2001. (B) locations (n = 137) for 36 black-legged kittiwakes in 2002. Concentric rings located at 10- and 20-nautical mile from the north eastern tip of Long Island. Green stars show the location of two triangulation stations.

Reproductive performance of glacous-winged gulls In Chiniak Bay, Kodiak Island, Alaska

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Introduction

Availability of food resources has a significant impact on the reproductive performance of seabirds, both directly due to the amount of energy allocated to offspring and indirectly through parental body condition (Anderson *et al.* 1982; Chastel *et al.* 1995; Monaghan *et al.* 1989; Risch and Rohwer 2000). Fluctuations in the marine environment that affect prey availability translate to extreme fluctuations in productivity of seabirds.

The glaucous-winged gull (*Larus glaucescens*) is an abundant, colony-nesting seabird whose breeding range spans from northern California to central Alaska. Glaucous-winged gulls form monogamous pairs and exhibit bi-parental care for up to three chicks per reproductive season (Verbeek 1993). Glaucous-winged gulls nest locally on the north east side of Kodiak Island, on the offshore islands in Chiniak Bay. The reproductive period begins with nest initiation in late May or early June and ends with chick rearing which continues into late August (Gamble & Buck, unpublished data). Like other seabirds, the reproductive success of glaucous-winged gulls varies significantly among years and throughout breeding colonies in Alaska (Dragoo *et al.* 2003; Krasnow *et al.* 1985; Nysewander *et al.* 1978; USFWS; Verbeek 1993).

While they are pisciverous during times of abundant food resources, glaucous-winged gulls are dietary generalists and can modify their diet to maximize net rates of energy gain (Irons *et al.* 1986). In south central Alaska, a change in diet of glaucous-winged gulls during the reproductive period from predominantly fish to blue mussels correlated with reduced breeding performance (Murphy, 1994).

Because reproductive success of glaucous-winged gulls is both easily monitored and reproductive success of seabirds in general has been shown to be positively correlated with available food resources (Anderson et al 1982; Cairns 1987; Hunt et al. 1996), glaucous-winged gulls may be useful indicators of foraging conditions prior to and during their reproductive period. Reproductive variables of seabirds that are sensitive to the influence of food supply include, but are not limited to hatching success, egg volume, and clutch size. In 2001, we implemented a multi-year study of the reproductive performance of the glaucous-winged gull in Chiniak Bay, Kodiak Island, Alaska.

Methods

Study Area

This study was conducted on the offshore islands of Chiniak Bay, Alaska. Chiniak Bay is located on the north east side of Kodiak Island and hosts seven large and numerous smaller glaucous-winged gull breeding colonies (Fig. 1).

Monitoring

We monitored the reproductive performance of seven colonies from 2001-2003. The sub-set of colonies that we monitored varied by year (see Table 1), but included colonies located on Chiniak, Blodgette, Gull, Kalsin, Mary, Puffin, and Svitlak Islands. Reproductive success of glaucous-winged gulls was assessed by monitoring reproductive parameters of designated plots within known breeding colonies.

We chose plots based on historical monitoring efforts, access, density, and proximity to other breeding seabird colonies.

We followed the fate of every glaucous-winged gull nest on pre-determined plots by visiting each plot every five days, weather permitting, from nest initiation to the date of failure or hatch. We marked each nest with a survey flag and flagged and determined each nest's location within the plot by measuring along an X, Y coordinate grid. Using calipers, we measured greatest length and width (±1mm) of each egg of the clutch and calculated egg volume of the first egg of each clutch using the following equation:

$$\text{Egg Volume (cm}^3\text{)} = 0.000476 \times \text{length (mm)} \times \text{width}^2 \text{ (mm)}$$

Clutch size is the maximum number of eggs observed in any nest. Nests that were depredated or disappeared during mid-lay cycle are included in this calculation. We calculated reproductive success as the proportion of nesting attempts in which at least one egg of the clutch hatched. Therefore,

$$P = N_S / (N_S + N_U),$$

where N_S = number of clutches with at least one hatchling and N_U = number of clutches with no hatchlings.

Finally, we obtained additional data on growth rates of chicks, diets collected from regurgitations of adults and chicks, and measured nest site characteristics. These data will be used in conjunction with the aforementioned reproductive parameters to create a generalized linear model to estimate daily survival rates and characterize the relationship between daily nest survival rates and the appropriate covariates (Rotella *et al*. 2003).

Statistical Analysis

We compared hatching success between years and among colonies by using a Chi-squared Likelihood Ratio. We compared mean egg volume and mean clutch size between years and among colonies with two-factor ANOVAs, and Tukey's multiple comparison tests. We assessed normality of samples within each colony-year class and performed analysis on ranks when appropriate. We obtained a Pearson's Correlation Coefficient to determine the strength of the relationship between hatching success and mean egg volume and mean clutch size and mean egg volume. All data are presented as mean ± *SE.* We considered differences significant at $P<0.05$.

Results

Glaucous-winged gulls of all colonies monitored fledged chicks in 2001, 2002, and 2003 (0.60, 0.64, and 0.53 and n= 303, 330,175 respectively). Reproductive success differed by colony ($P<0.001$, n= 808, df= 6), however it did not differ by year ($P=0.15$, n= 808, df=2 Table 1, Fig. 2). Kalsin and Puffin Island colonies experienced the highest reproductive success in 2001 (0.80), while Chiniak Island (0.93) and Svitlak Island (0.72) had the highest reproductive success in 2002 and 2003, respectively. Mean egg volume differed by colony ($P=0.007$, n=726, df= 6), but did not differ by year ($P=0.28$, n= 726 df=2; see Table 1, Figure 3). In 2001, the Kalsin Island colony had the highest mean egg volume (91.98±0.63 cm^3), while Chiniak Island (92.22±1.02 cm^3) and Svitlak (90.31±1.19 cm^3) had the highest mean egg volume in 2002 and 2003, respectively. Mean clutch size differed by colony ($P<0.0001$, n=726, df= 6), but not by year ($P=0.27$) and there was a significant colony-year interaction ($P=0.02$, n= 726, df= 8, Table 1, Fig. 4). In 2001 and 2002, the Kalsin Island colony had the largest clutch size (2.85±0.06 and 2.89±0.06 eggs, respectively), while in 2003, Kalsin and Svitlak Island colonies had the same largest mean clutch size (2.81 ±0.09 and 2.81±0.08, eggs, respectively). Reproductive success and egg volume were not significantly correlated (P=0.25, r^2=0.07, n=20). Mean egg volume and mean clutch size were significantly correlated (P= 0.02, r^2= 0.26, n= 20, Fig. 6).

Discussion

Reproductive success of glaucous-winged gulls ranged from 53- 64% in 2001-2003. Relative to the range and variability in reproductive success they experience historically statewide, these values are considered fair. Chiniak colonies had reproductive success of 86.2- 92.2% in 1978 (Nysewander and Hoberg 1978), and 1-42% in 1983 (Krasnow *et al.* 1983). In 1991, colonies in the Aleutian chain experienced reproductive success of 14-85% (Dragoo et al. 2003). Interestingly, glaucous-winged gull reproductive success in 2004 was less than 1% in many of the same Chiniak Bay colonies in 2004 (Buck, unpublished data)

Likely, the moderate to high productivity of glaucous-winged gulls in 2001-2003 was due to moderate to high forage availability in those years. This theory is supported by high productivity in tufted puffins (*Fratercula cirrhata*) and black-legged kittiwakes (*Rissa tridactyla*) in those years. Additionally, the break down of oceanographic frontal structure during the breeding season allowed for an influx of forage species into the nearshore habitat where seabirds may forage in close proximity to their colonies (RJ Foy, personal communication). This oceanographic phenomenon was especially pronounced in 2001 and was progressively weakened in 2002-2003. The apparent responsiveness of glaucous-winged gulls to this observed oceanographic change lends further evidence to the postulation that the glaucous-winged gull may be a decent indicator of forage availability.

Acknowledgements

Additional funding was provided to the Alaska Cooperative Fish and Wildlife Research Unit from the US Geological Survey (Award # 1434-HQ-97-RU-01582). We are grateful to Dwain MacIntosh, Katie Murra, Rachael Orben, and Cory Williams for field assistance.

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Table 1. Reproductive success (n), egg volume, and clutch size (mean ± *SE*) of glaucous-winged gulls from 2001-2003 on seven colonies in Chiniak Bay, Kodiak Island, Alaska.

Colony	**Year**	**Reproductive Success (n)**	**Egg Volume (+/- SE)**	**Clutch Size (+/- SE)**
Chiniak	2002	0.93 (29)	92.22 (1.02)	2.69 (0.11)
	2003	0.48 (33)	86.60 (2.59)	2.52 (0.13)
Blodgett	2001	0.20 (25)	88.07 (1.38)	2.41 (0.18)
	2002	0.64 (25)	86.02 (1.43	2.16 (0.17)
Gull	2001	0.30 (43)	n/a	2.43 (0.14)
	2002	0.55 (56)	89.93 (0.84)	2.67 (0.09)
Kalsin	2001	0.80 (50)	91.98 (0.63)	2.85 (0.06)
	2002	0.74 (46)	91.53 (0.84)	2.89 (0.06)
	2003	0.42 (36)	90.58 (1.04)	2.81 (0.09)
Mary	2001	0.77 (64)	89.94 (1.21)	2.55 (0.08)
	2002	0.44 (62)	89.77 (0.97)	2.26 (0.11)
	2003	0.52 (33)	89.98 (0.80)	2.30 (0.14)
Puffin	2001	0.80 (34)	90.15 (1.63)	2.71 (0.08)
	2002	0.83 (41)	89.13 (0.95)	2.63 (0.10)
	2003	0.53 (30)	87.69 (1.27)	2.47 (0.14)
Svitlak	2001	0.72 (87)	88.13 (1.31)	2.74 (0.06)
	2002	0.32 (71)	92.04 (1.05)	2.43 (0.10)
	2003	0.72 (43)	90.31 (1.19)	2.81 (0.08)
All Colonies	2001	0.60 (303)	89.65 (1.23)	2.62 (0.10)
	2002	0.64 (330)	90.09 (1.01)	2.53 (0.11)
	2003	0.53 (175)	89.16 (0.68)	2.60 (0.05)

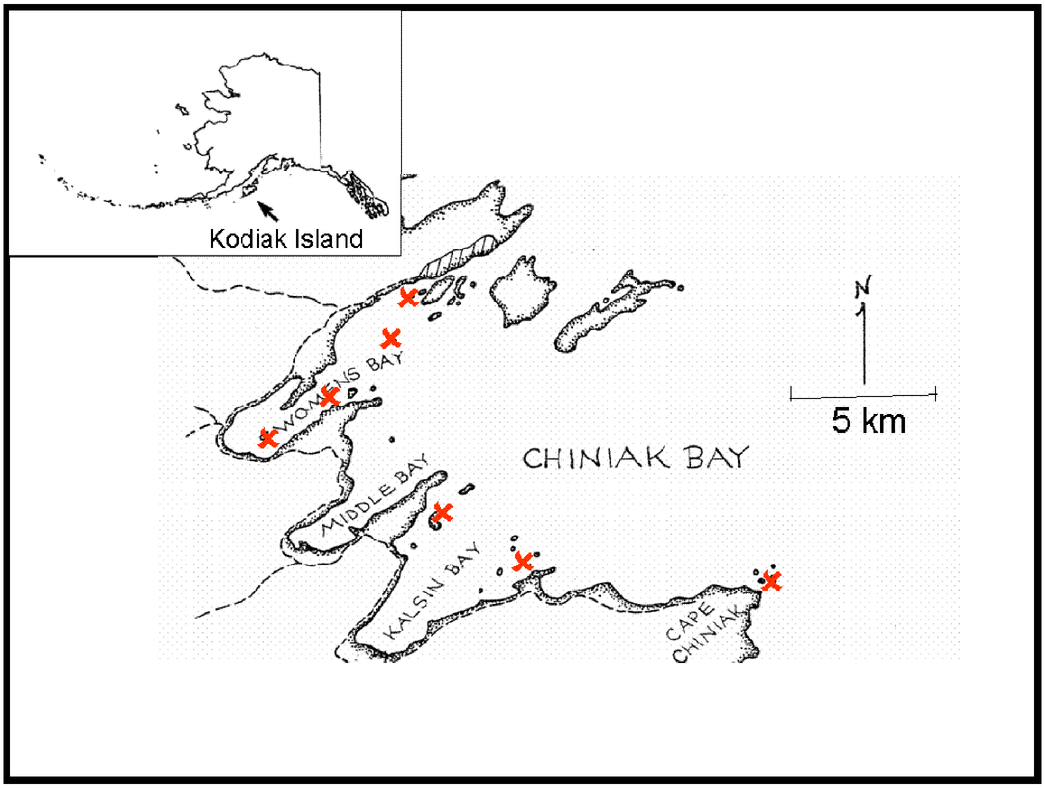

Figure 1. Glaucous winged gulls were monitored at 7 colonies in Chiniak Bay, Alaska on the NE side of Kodiak Island from 2001-2003. Colony locations are designated with X.

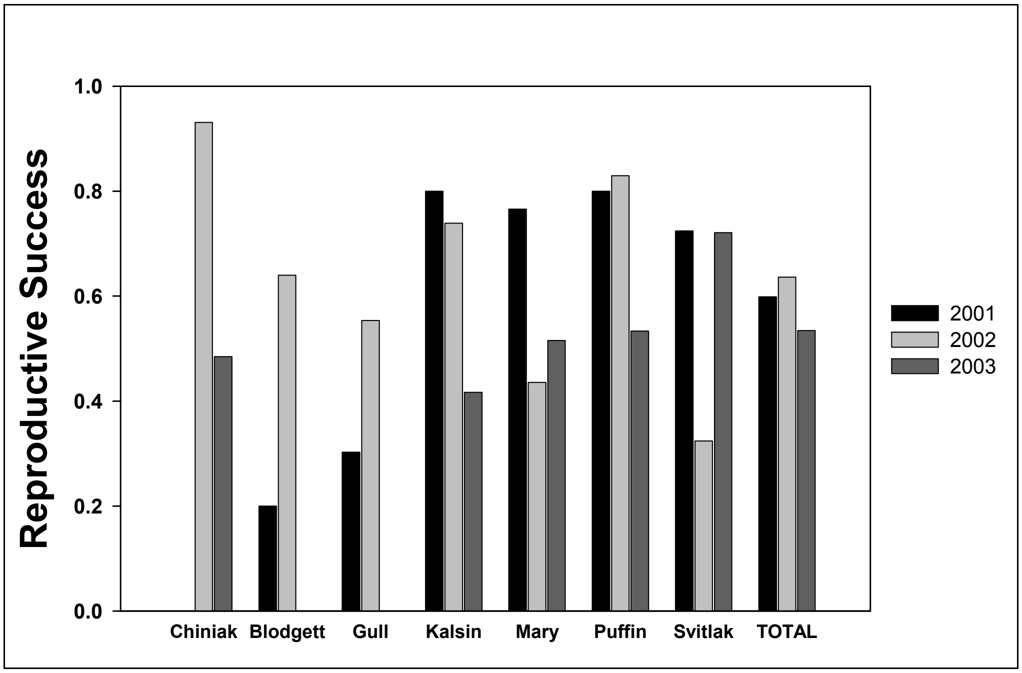

Figure 2. Hatching success of glaucous-winged gulls from 2001-2003 at seven colonies in Chiniak Bay, Kodiak Island, Alaska.

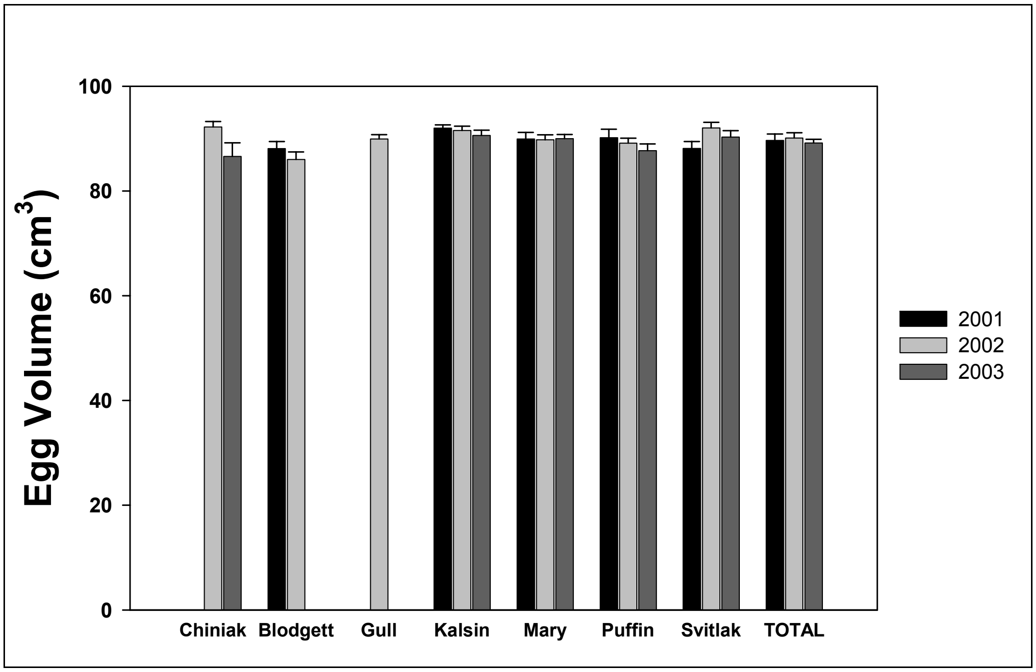

Figure 3. Egg volumes (cm^3± *SE*) of glaucous-winged gulls from 2001-2003 at seven colonies in Chiniak Bay, Kodiak Island, Alaska.

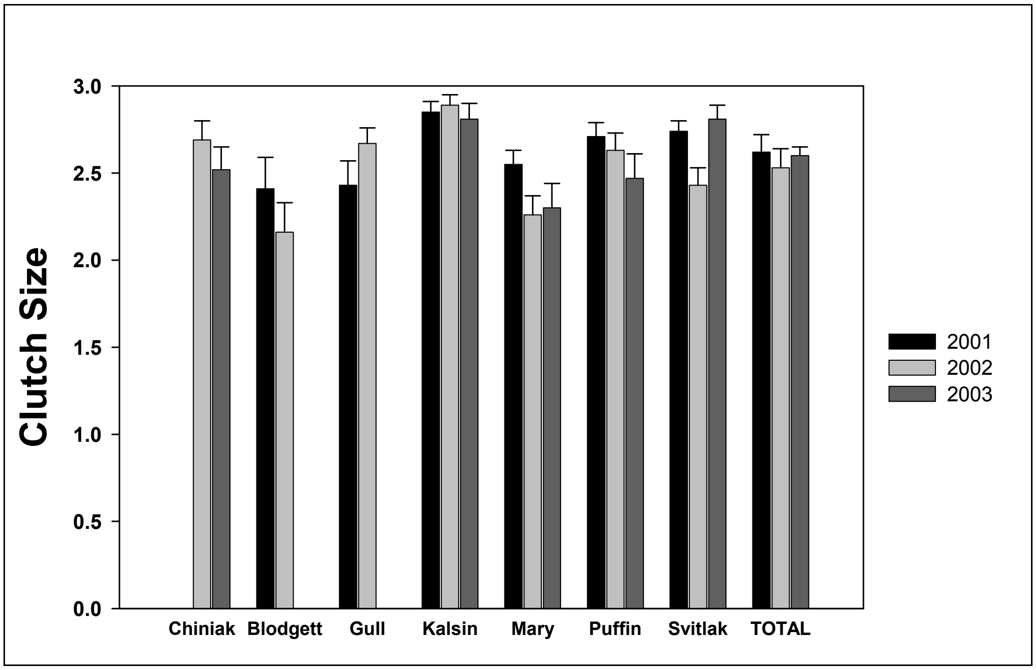

Figure 4. Clutch sizes (mean eggs± *SE*) of glaucous-winged gulls from 2001-2003 at seven colonies in Chiniak Bay, Kodiak Island, Alaska.

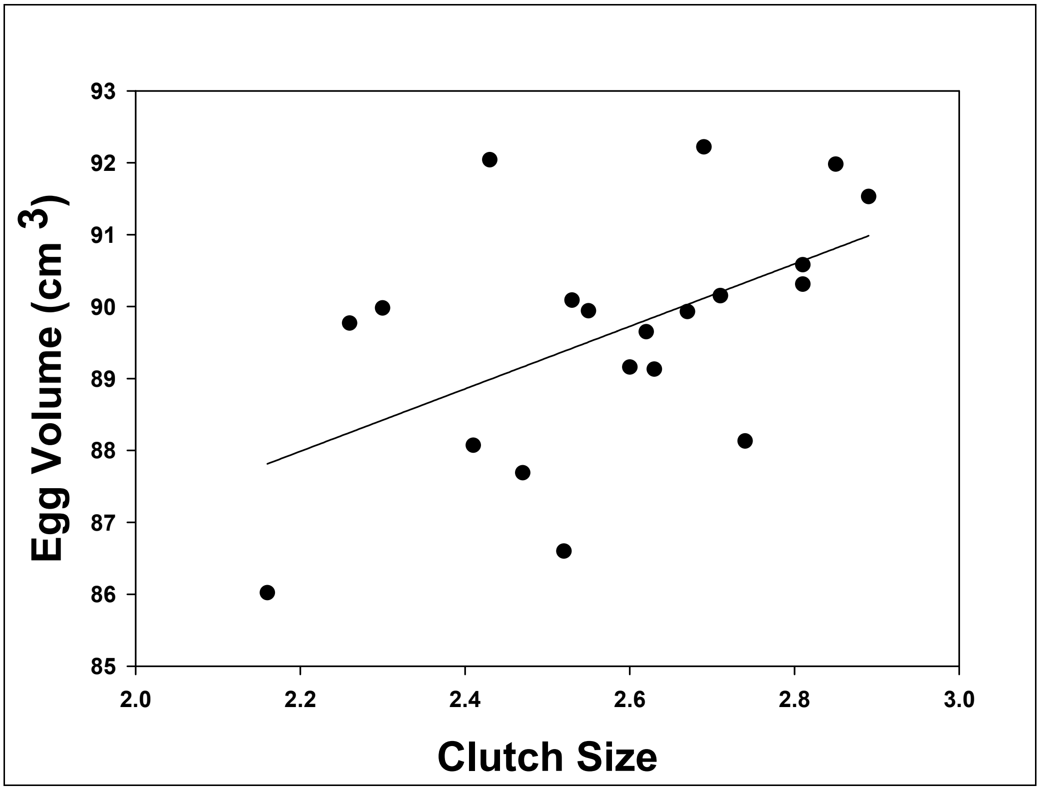

Figure 5. The relationship between mean clutch size and mean egg volume (r^2=0.26) of glaucous-winged gulls from 2001-2003 at seven colonies in Chiniak Bay, Kodiak Island, Alaska.

Body condition of glaucous-winged gulls throughout the reproductive period

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Introduction

Availability of food resources has a significant impact on the reproductive performance of seabirds, both directly due to the amount of energy allocated to offspring and indirectly through parental body condition (Anderson *et al.* 1982; Monaghan *et al.* 1989; Risch and Rohwer 2000). Body condition reflects the physiological state of an animal and influences its present and future fitness. Seabirds live in a dynamic system with wide scale and often extreme fluctuations in marine conditions. Therefore, they need to accumulate sufficient energy reserves during episodes of high food availability to offset the periods of low food availability and costs of energetically expensive events such as reproduction. However, due to their size and corresponding constraints on flight, the extent to which seabirds can accumulate endogenous reserves of energy is limited. Because body condition of adult seabirds is closely coupled to marine conditions, it may be a useful indicator of resource availability (Boersma 1978; Cairns 1987).Thus, a thorough understanding of body condition in long-lived seabirds may prove to be a valuable tool to monitor seabird populations and understand complex marine ecosystems.

Corticosterone is the primary glucocorticoid released by the avian adrenal glands (Holmes and Phillips 1976). While it may be classified as a “stress hormone,” in general, corticosterone functions in the maintenance of homeostasis primarily through mobilization of endogenous energy reserves and by modulating changes in behavior that serves to facilitate individual survival. Corticosterone is thought to be regulated seasonally (Breuner and Orchinik 2002), although the mechanisms are poorly understood in birds across different taxa. In addition to predictable, cyclical natural history events such as migration, overwintering, and breeding, seabirds must contend with unpredictable events like fluctuations in food availability. Food limitation in seabirds elicits elevated levels of corticosterone (Kitaysky *et al*. 2001; Lanctot *et al*. 2003) as well as modulation of normal levels of plasma lipids such as glycerols, free fatty acids, and sterols (Jenni-Eiermann and Jenni 1998). Because rates of secretion and metabolic clearance of corticosterone are the primary pathways for maintenance of homeostasis in response to a stressor, accordingly, high circulating levels of corticosterone may be indicative of real or perceived stressors that a bird encounters. Thus, by monitoring corticosterone levels across the stages of the reproductive period in glaucous-winged gulls, we may have a meaningful measurement of body condition and degree of cumulative stress an individual has encountered.

The products of intermediary metabolism that occur in the bloodstream provide another tool to index body condition. These biomarkers can be effectively used in free-living birds to assess their short-term nutritional and metabolic state (Jenni-Eiermann and Jenni 1998). In short, they work in concert show the nutritional trajectory that an individual bird is on when a blood sample is taken (Williams *et al.* 1999). If one is interested in whether an animal is increasing or decreasing in body condition, information gleaned from hematological assays can be more valuable than non-hematological measures of health that provide only a static estimate of body condition. In a controlled, captive study of plasma biochemistry, Alfonso-Alvarez and Ferrer (2001) found that fasting yellow-legged gulls followed the same classic metabolic model as was shown in captive studies with geese (Le Maho *et al.* 1981). Gulls showed a pattern different from the classic model, however, when they received reduced food as opposed to no food, a likely scenario for a free-living gull.

Although it is recognized that high lipid content is not the only indictor of good body condition and individual health, it is known to correlate with greater reproductive success and survival in several species of birds (Chastel *et al*. 1995). In conjunction with measures of total proximate composition, a body condition index that adjusts for mass-related morphological measurements may provide a useful, relatively non-invasive method of gaining further information about body condition.

The glaucous-winged gull (*Larus glaucescens*) is an abundant, colony-nesting seabird whose breeding range spans from northern California to central Alaska. Glaucous-winged gulls nest locally on the northeast side of Kodiak Island, on the offshore islands in Chiniak Bay. The reproductive period begins with nest initiation in late May or early June and ends with chick rearing which continues into late August (JB Gamble & CL Buck; unpublished data). Reproductive success of glaucous-winged gulls varies significantly among years and throughout breeding colonies in Alaska (Dragoo *et al.* 2003; Krasnow *et al.* 1985; Nysewander *et al.* 1978; USFWS; Verbeek 1993).

Reproductive parameters of seabirds are susceptible to proximate changes in food availability (Anderson *et al.* 1982) and quality (Piatt and Anderson 1996) and are ultimately controlled by body condition (Risch and Rohwer 2000). In 1984, Murphy *et al*. demonstrated that a change in diet of glaucous-winged gulls in south-central Alaska from predominantly fish to blue mussels (*Mytilus edulis*) during the reproductive period correlated with reduced of breeding performance.

Energetic demands of foraging change with stage of the breeding period as reproductive adults switch from a pelagic habit to central place foragers because of ties to breeding sites. This effort is compounded during the nestling period by increased demands of meeting metabolic needs of not only themselves, but also 1-3 growing chicks that approach adult size at fledging. Changes in behavior and metabolic demands associated with reproduction occur within a highly dynamic (day to day, month to month, year to year) foraging environment. If parent birds are in poor body condition, they may abandon reproductive efforts in favor of long-term survival (Chastel *et al*. 1995). Therefore, we investigated how body condition of free-living glaucous-winged gulls changed with stage of reproduction. The results from this research will not only increase our understanding of metabolic tradeoffs associated with reproduction but will also serve as a potentially sensitive instrument by which to indirectly measure fluctuations in food availability in the marine system.

There are a myriad of ways to evaluate body condition of a seabird, however we utilized the methods outlined above to compare less invasive, non-lethal hematological measures in addition to traditional index and total body composition methods. Specifically, we analyzed body condition of glaucous winged gulls throughout their reproductive stages using four different methodologies: circulating corticosterone levels, plasma lipid metabolites, proximate analysis, and body condition index based on morphological characteristics.

Methods

Study Area and Sample Collection

We conducted this study in Chiniak Bay, Kodiak Island, Alaska. Glaucous-winged gulls were captured or collected on or near a total of five colonies within the bay prior to and during the 2002 and 2003 reproductive period (Fig. 1). We captured adult glaucous-winged gulls with either remote controlled bow-net traps or standard humane collection techniques (Ornithological Council 2004). From each captured bird, we recorded morphometric data including body mass (±7g), length of tarsus (±1mm), wing-chord (±1mm), culmen (±1mm) and head-bill (±1mm). We collected either baseline (<3 minutes after capture) or stress series (<3, 10, 30, and 50 minutes following capture) samples of blood from gulls of known reproductive status during pre-breeding, incubation, chick rearing, and post-breeding stages. This capture-stress method standardized the stress load experienced by birds and thus allowed for direct comparisons of adrenal responsiveness among birds and stage of the reproductive period. Additionally, baseline samples were assayed for concentration of various lipid classes rather than samples collected later in the series because measures of metabolites are both time and stress sensitive. Blood was collected from all birds using heparinized microhematocrit or Natelson tubes following puncture of either the alar, jugular, or medial metatarsal vein. Blood samples were kept cool and were transported to the laboratory at the Kodiak Fisheries Research Center where they were immediately centrifuged to separate the plasma and cellular fractions. Plasma was drawn off via long-stemmed Pasteur pipette, transferred to labeled 1.5ml conical snap-cap vials and maintained at -50° until assayed for concentrations of corticosterone and plasma lipids.

We necropsied all birds we collected and obtained morphometric measurements, determined their sex and reproductive status. We removed and froze stomachs for analysis of diets and preserved adipose tissue samples from either the abdomen, furcula, or above the pigeal gland of each bird for later analysis. Each carcass was wrapped in plastic and stored at -50°C until prepared for proximate analysis. Frozen birds were thawed and plucked. Because feathers are not an available endogenous energy source, we collected and weighed feathers. The weight of the feathers was subtracted from the weight of the carcass to provide a feather-free carcass weight. We then ground and homogenized each de-feathered carcass individually for proximate analysis. We pooled sexes for all analyses because glaucous-winged gulls exhibit bi-parental care and do not manifest a high degree of sexual dimorphism.

Corticosterone Assay

Plasma was assayed in duplicate for concentration of corticosterone using radioimmunoassay. Briefly, aliquots of plasma (10 - 25 µl) were measured into centrifuge tubes and allowed to equilibrate overnight with 2000 cpm tritiated corticosterone. Corticosterone was extracted in 4 ml re-distilled dichloromethane added to each sample. Extracts were aspirated with pasteur pipettes and evaporated under nitrogen in a warm water bath. After evaporation of dichloromethane, samples were dissolved in 550 µl phosphate-buffered saline with gelatin and allowed to equilibrate overnight at 4° C. Aliquots of samples were transferred to duplicate test tubes (200 µl each) for radioimmunoassay. In addition, a 100 µl aliquot was placed in a vial for determination of percentage recovery of the initial 2000 cpm. This recovery value was used to adjust final assayed concentrations of corticosterone. Standard curves were set up over the range of 2 - 500 pg. Samples were refrigerated overnight after addition of equal (100 µl) amounts of labeled corticosterone and antiserum. Dextran-coated charcoal (0.5 ml) was added 12 min prior to centrifugation to separate bound and free fractions. Supernatants were decanted into scintillation vials and counted after addition of 4.5 ml Ultima Gold® scintillation fluid. These procedures are described in greater detail elsewhere (Wingfield and Farner 1975).

Plasma Lipid Assay

We used a method of lipid class analysis adapted from Parrish (1987) and Whitsett *et al*. (1986) for small plasma volumes. We extracted plasma lipids with a chloroform-methanol solvent bath (2:1, v/v). The methanol contained 0.01% of the antioxidant butylated hydroxytoluene. We used 0.88% calcium chloride in de-ionized water to wash the chloroform layer, and granular anhydrous sodium sulfate to remove the remaining water from the samples. We reconstituted the resulting lipids with chloroform and stored samples frozen at -70° C until they were analyzed.

We used six standards to identify the lipid classes found in the gull plasma. Free fatty acids, sterols, phospholipids, triacylglycerols, diacylglycerols, and monoacylglycerols were all obtained from Sigma (St. Louis, MO). We used the Iatroscan thin layer chromatography (TLC) method to separate lipids spotted on chromarods with the hydrogen flame ionization detector (FID; Iatron Laboratories, INC. Tokyo, Japan).

Proximate Analysis

We processed homogenized samples individually for composition of protein, moisture, and ash. We calculated percentages of each component for each sample post-assay, based on the original wet mass of the sample. These percentages were added to determine by subtraction the percentage of lipid in each sample. To validate this method, we dried 14 samples and analyzed them for lipid content by Soxhlet extraction using a dichloromethane solvent. The resulting total percentages fell into the 98-102 percentile range. This justifies the aforementioned subtraction method to determine lipids because the subtraction method also falls into this range, indicating low sample variation and high precision.

We calculated the percentage protein in triplicate for each sample from a one gram sub-sample of homogenate that we assayed with a Leco FP-2000 protein/nitrogen determinator (Leco Corporation, St. Joseph, MI). We calculated the percentage moisture in triplicate for each sample by desiccating three four gram sub-samples of homogenate in a 100°C drying oven for 24 hours. We then calculated the total percentage of ash in triplicate for each sample by scorching the desiccated samples on a hotplate and combusting them in an ashing oven at 546°C for 12 hours.

Statistical Analysis

We used ANOVAs or Kruskal-Wallis tests to evaluate whether plasma levels of corticosterone differed by reproductive stage or minute from capture and Dunn's Method to test all pairwise multiple comparisons. We calculated plasma lipid results with Peak Simple version 2.8 software using peak area percentages of lipid classes derived from the resulting chromatographs. We used ANOVAs or Kruskal-Wallis tests on ranks to estimate whether lipid classes varied by stage, and Dunn's Method or a Tukey test for all pairwise multiple comparisons. We used ANOVAs or Kruskal-Wallis tests to estimate whether proximate composition of glaucous-winged gulls varied by reproductive stage, and Dunn's Method or a Tukey test for all pairwise multiple comparisons. We calculated the index of body condition by adjusting for body size and dividing each bird's total mass by its culmen length. We used ANOVAs to estimate whether body condition differed by reproductive stage and Tukey's test for all pairwise multiple comparisons. All data are presented as mean ± *SE.* We considered differences significant at *P*<0.05.

Results

All gulls sampled demonstrated a stress response as indicated by levels of plasma corticosterone during the timed bleed series (Table 1, Fig. 2). Baseline levels of corticosterone tended to increase from the pre-breeding stage to the incubatory and chick rearing stages, and experienced a sharp decline in the post-reproductive stage (*P*=0.064, *n*=49, *df*=3; Fig. 1, Table 1). Levels of corticosterone during a stress series differed significantly between incubation and chick rearing stages (*P*=0.004, *n*=25, *df*= 3; Figure 2, Table 1). Adrenal responsiveness, at 50 minutes post capture, was significantly higher during incubation than the chick rearing stage (*P*=0.01, *n*=25, *df*= 3; Fig. 2, Table 1).

Free fatty acids, sterols, phospholipids, triacylglycerols, diacylglycerols, and monoacylglycerols were all present in glaucous-winged gull plasma (*n*=55, Figs. 3 and 4, Table 2). The primary plasma lipids are triglycerides, free fatty acids, sterols and phospholipids. Monoacylglycerols and diacylglycerols only appeared in trace amounts in the samples and did not significantly contribute to the plasma composition. Free fatty acids and sterols differed with stage of the reproductive period, while phospholipids, monoacylglycerols, diacylglycerols, and triacylglycerols did not. Free fatty acids of glaucous-winged gulls were highest in the post reproductive stage and were significantly different from the pre-reproductive stage (*P*<0.05, *n*=23, *df*=3). Gulls in the pre-reproductive stage also showed significantly lower free fatty acid levels than gulls in the incubatory stage (*P*<0.05, *n*=39 *df*=3), and the chick rearing stage showed intermediate concentrations of free fatty acids.

Plasma levels of sterols in gulls were highest in the chick rearing stage, and were significantly different than levels in the post reproductive stage (*P*< 0.05, *n*=16 *df*=3). Gulls had significantly higher sterol levels in the pre-reproductive stage than in the post-reproductive stage (*P*<0.05, *n*=23, *df*=3), while those in the incubatory stage demonstrated intermediate values.

Proximate composition of lipid, ash, and moisture percentages differed by stage; however, protein did not (*n*=56, Figs. 5 and 6, Table 3). Lipid content declined throughout the reproductive stages, and both pre-breeding and incubatory stage gulls had significantly higher lipid levels than post-breeding gulls (*P*<0.001, *n*=56, *df*=3).

The body condition index of adult glaucous-winged gulls ranged from 16.79 to 30.80 ± 2.89 (*n*=60). Body condition was highest in the pre reproductive stage and declined into the reproductive and post reproductive stages. During the pre-reproductive stage, gulls were at a significantly higher body condition index than in the post-reproductive stage (*P*=0.026, *n*=43, *df*=2; Fig. 7).

Discussion

Lipid reserves of adult glaucous-winged gulls tended to decrease throughout the reproductive period as shown by both their body condition index and total proximate composition. Baseline levels of corticosterone and plasma sterols tended to increase with the demands of the reproductive period, peaking in the chick rearing stage. This supports current theory that as fat reserves of parent birds are depleted, corticosterone is secreted to stimulate the metabolism of alternative energy stores (Kitaysky *et al.* 1999). Our results demonstrate that there is also a rise in levels of free fatty acids with a loss of lipid, which further supports current research that shows free fatty acids should show a decline with mass loss (Jenni-Eiermann and Jenni 1998).

While proximate compositional analysis may be the ideal and definitive measure of body condition, corticosterone, plasma sterols and free fatty acids, as well as body condition indices appear to predict body condition in the glaucous-winged gull. These methods provide a minimally invasive way to study free-living glaucous-winged gulls, and may assist with future predictions of prey abundance and ecosystem health.

Acknowledgements

Additional funding was provided from the Alaska Cooperative Fish and Wildlife Research Unit through the US Geological Survey (Award # 1434-H.Q-97-RU-01582). We thank Dr. Kathleen O'Reilly (University of Portland) for assaying our blood samples for corticosterone, Dr. Alexandra de Oliveira and Bob Pfutzenreuter (University of Alaska Fairbanks Fisheries Industrial Technology Center) for training, lab access, and AdO's modified lipid protocols, Dr. S. Dean Kildaw, and Dwain MacIntosh, Katie Murra, Rachael Orben, and Cory Williams for field assistance.

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Table 1. Baseline and peak levels of plasma corticosterone (mean ± *SE* (*n*); ng/ml) of glaucous-winged gulls across the reproductive period.

	Pre Reproduction	**Incubation**	**Chick Rearing**	**Post Reproduction**
Baseline	1.758 ± 1.78 (17)	1.822 ± 1.82 (13)	1.663 ± 1.66 (12)	0.577 ± 0.577 (8)
Peak	n/a	32.78 ± 8.39 (14)	26.39 ± 12.96 (11)	n/a

Table 2. Percentages of plasma lipids (mean ± *SE* (*n*)) of glaucous-winged gulls across the reproductive period.

	Pre Reproduction	**Incubation**	**Chick Rearing**	**Post Reproduction**
Phospholipid	53.25 ± 11.77 (17)	47.94 ± 10.41 (22)	49.89 ± 12.11 (10)	48.69 ± 7.38 (6)
Sterol	3.6 ± 0.72 (17)	3.58 ± 0.71 (22)	3.65 ± 0.88 (10)	3.02 ± 0.45 (6)
Free Fatty Acid	4.76 ± 4.50 (17)	9.39 ± 11.33 (22)	5.84 ± 3.86 (10)	5.86 ± 9.58 (6)
Triacylglycerol	38.10 ± 9.80 (17)	39.51 ± 10.88 (22)	40.3 ± 10.01(10)	40.66 ± 5.21 (6)
Diacylglycerol	0.14 ± 0.39 (17)	0.10 ± 0.26 (22)	0.13 ± 0.23 (10)	0 ± 0 (6)
Monoacylglycerol	0.15 ± 0.24 (17)	0.15 ± 0.24 (22)	0.17 ± 0.29 (10)	0.18 ± 0.31 (6)

Table 3. Percentages of lipid, protein, moisture and ash (mean ± *SE* (*n*)) of glaucous-winged gulls across the reproductive period.

	Pre Reproduction	**Incubation**	**Chick Rearing**	**Post Reproduction**
Lipid	10.25 ± 4.20 (28)	9.91 ± 2.57 (13)	10.94 ± 4.73 (4)	6.84 ± 2.17 (11)
Protein	19.64 ± 2.42 (28)	20.55 ± 1.41 (13)	19.25 ± 3.73 (4)	20.57 ± 1.38 (11)
Moisture	65.51 ± 3.96 (28)	65.42 ± 2.20 (13)	66.23 ± 1.49 (4)	67.33 ± 1.36 (11)
Ash	4.49 ± 0.92 (28)	4.12 ± 0.62 (13)	4.10 ± 0.57 (4)	4.84 ± 1.13 (11)

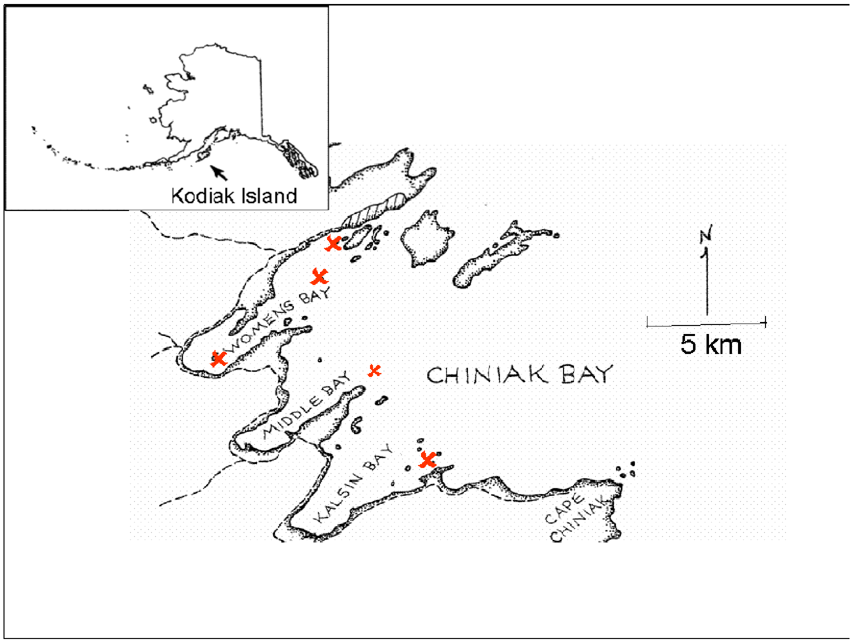

Figure 1: Glaucous-winged gulls were sampled at 5 colonies in Chiniak Bay, Alaska on the northeast side of Kodiak Island in 2002 and 2003. Locations of colonies are designated by an X.

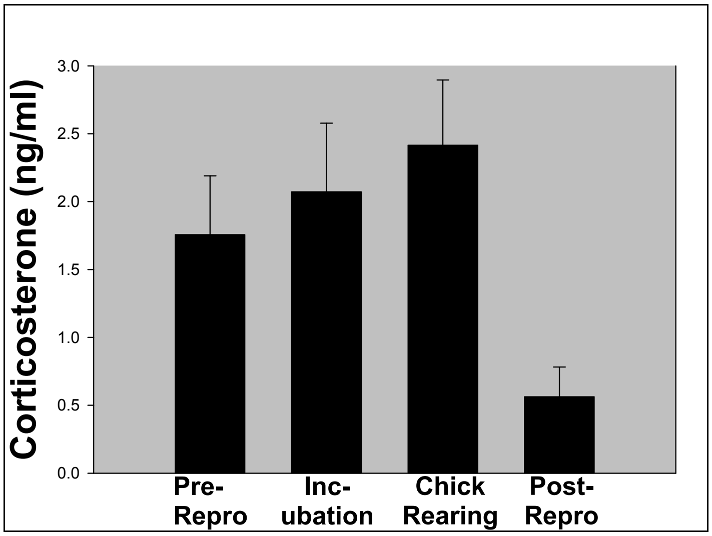

Figure 2: Baseline levels of plasma corticosterone from free-living glaucous-winged gulls throughout the reproductive period (mean ± *SE, n*=50).

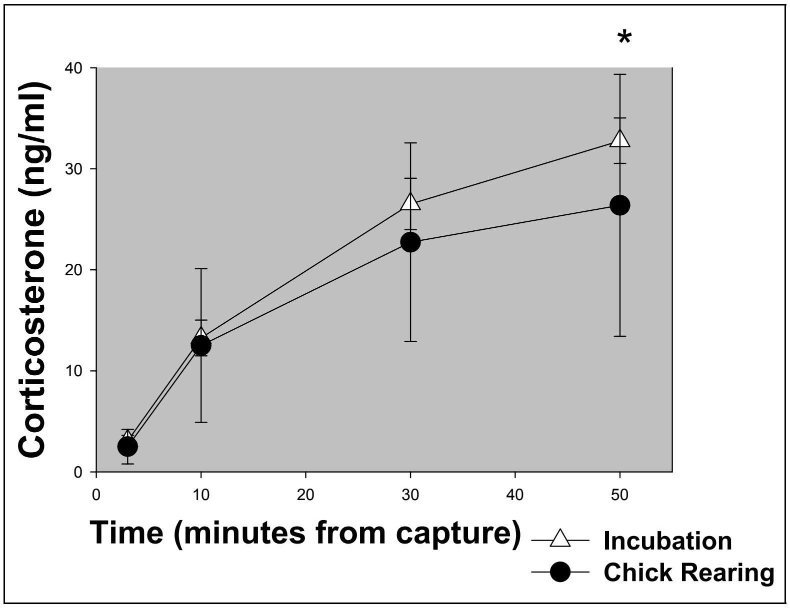

Figure 3. Plasma corticosterone levels of glaucous-winged gulls during stress series in the incubation and chick rearing stages (mean ± *SE, n*=25). * indicates a significant difference at *P*<0.05.

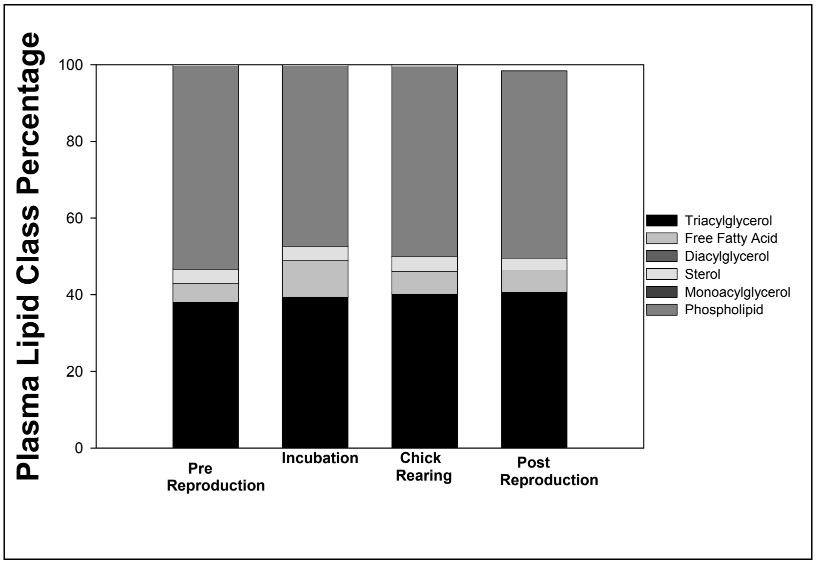

Figure 4. Percentages of plasma lipid classes of glaucous-winged gulls across the reproductive period (*n*=55).

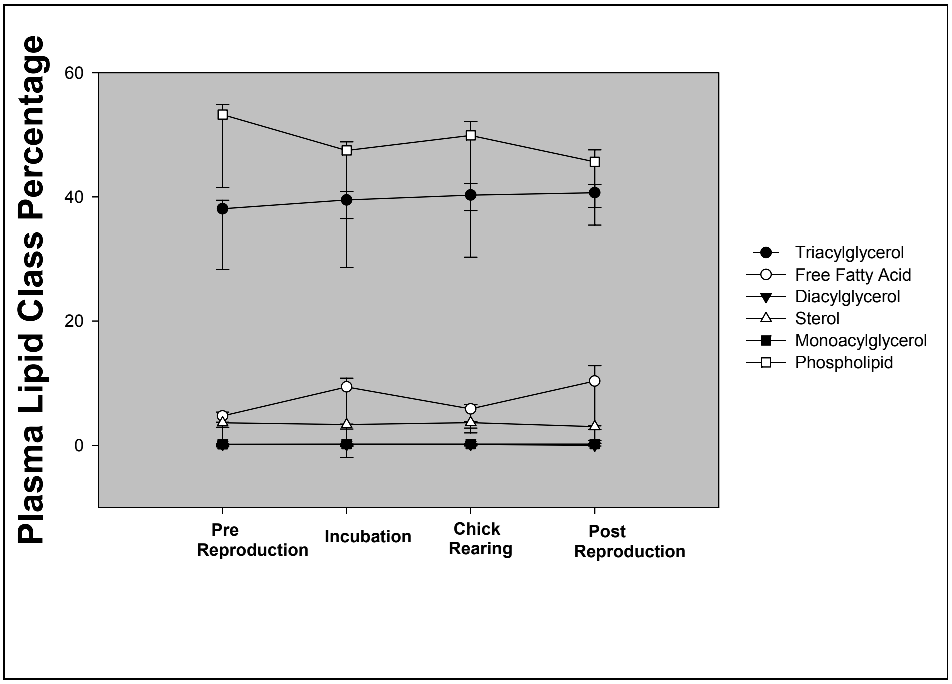

Figure 5. Percentages of plasma lipid classes of glaucous-winged gulls across the reproductive period (mean ± *SE, n*=55).

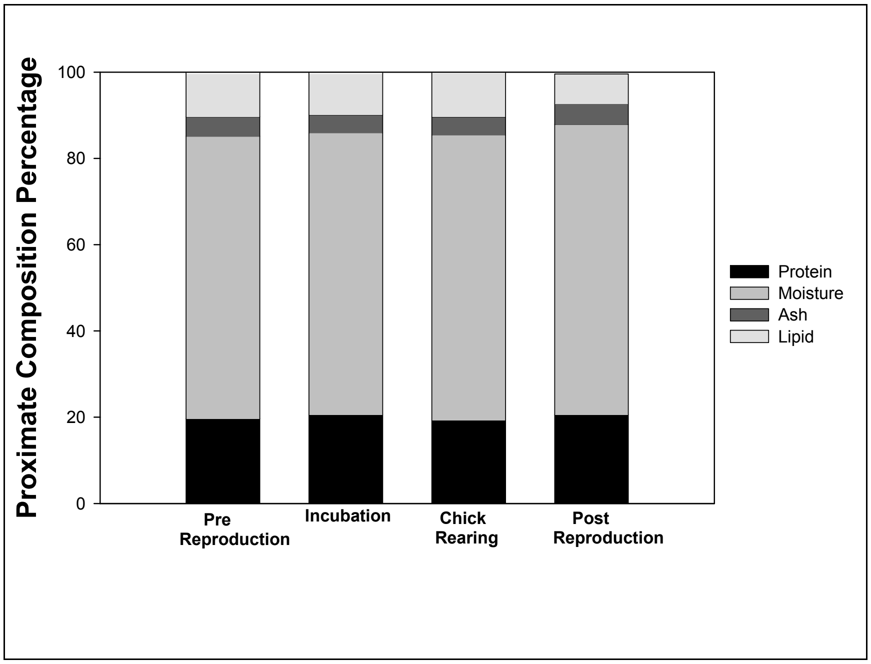

Figure 6. Proximate composition of glaucous-winged gulls across the reproductive period (*n*=56).

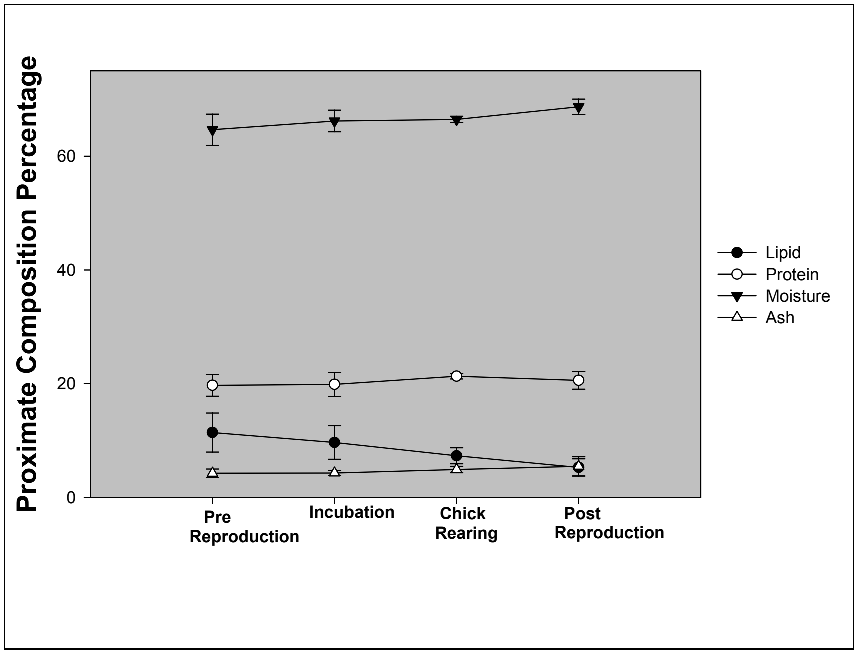

Figure 7. Proximate composition of glaucous-winged gulls across the reproductive period (mean ± *SE*, *n*=56).

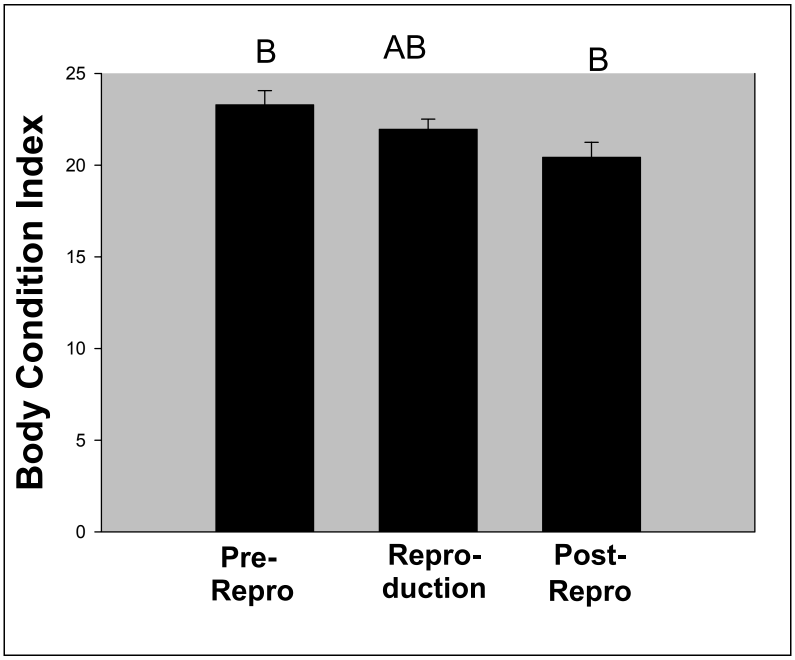

Figure 8. Adult body condition of glaucous-winged gulls throughout the reproductive period (mean ± *SE*, *n*=60). Differing letters above bars indicate significant differences at *P*<0.05.

Foraging distribution, diet, and breeding biology of tufted puffins In Chiniak Bay, Alaska

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Introduction

Since the late 1970's, populations of Steller sea lions (*Eumetopias jubatus*) in the Bering Sea (BS) and Gulf of Alaska (GOA) have declined dramatically (Merrick et al. 1997). Populations of northern fur seals (*Callorhinus ursinus*), harbor seals (*Phoca vitulina*), and several species of piscivorous seabirds have also been declining, leading researchers to speculate that large-scale changes in ecosystem structure may have affected prey resources available to certain apex predators (Castellini 1993; Springer 1993). Recently, attention has focused on the potential effects of climate driven changes in sea temperature and sea-ice conditions on ocean ecosystems and apex predators (Springer 1998). Current research suggests that primary production and ecosystem dynamics in the BS and GOA are affected by fluctuations between warm and cold regimes on a multi-decadal time scale, termed the Pacific Decadal Oscillation (Francis et al. 1998; McGowan et al. 1998). Declines in populations of marine mammals and seabirds coincided with the 1977 shift from a cold to a warm regime which likely affected the abundance and distribution of their prey (Agler et al. 1999; Anderson and Piatt 1999). Declines in populations of seabirds in the GOA were coupled with a shift from diets comprised primarily of lipid-rich capelin (*Mallotus villosus*) to diets dominated by lower-quality Pacific sandlance (*Ammodytes hexapterus*) and walleye pollock (*Theragra chalcogramma*; Piatt and Anderson 1996). In 1998, sea-surface temperatures of the California Current (CC) and GOA cooled by several degrees, while zooplankton biomass in the northern CC increased dramatically, suggesting that another regime shift, in the opposite direction as the 1977 shift, had occurred (Peterson and Schwing 2003). However, it is unclear whether this regime shift was as pervasive as that of 1977 and more research is required to determine if conditions are returning to their pre-1977 state.

Given the dramatic decline of several populations of apex predators and the importance of lipid-rich forage fish in the diets of many apex predators, there is currently a need to better understand the effects of changing oceanographic conditions on the distribution and abundance of forage fish species. Seabirds are useful as biological indicators of prey availability, providing important information on the abundance and spatial, temporal, and age distributions of species that are difficult to assess using conventional techniques (Montevecchi 1993; Hunt et al. 1996; Diamond and Devlin 2003). Recent research has shown that the diets of puffin chicks can be used to assess the availability of important forage fish species, as well as the early life-stages of several species of commercial importance (Baird 1990; Hatch and Sanger 1992; Barrett 2002). It has also been demonstrated that variation in reproductive performance of puffins is related to ocean climate conditions (Durant et al. 2003; Gjerdrum et al. 2003; Harding et al. 2003). In 2001, we began monitoring a suite of reproductive parameters, including egg volume, fledging success and rates of nestling growth at a number of tufted puffin (*Fratercula cirrhata*) colonies located within Chiniak Bay on Kodiak Island, AK. In 2003, we expanded the scope of this study to include a detailed investigation of the diets and foraging distribution of tufted puffins at colonies located in the inner bay and near the outer-edge of the bay. Our primary objectives include investigation of inter-annual changes in reproductive success, determination of effects of changes in diet composition on reproductive parameters, and determining if foraging conditions differed over a relatively small spatial scale (<25km) and what effect, if any, this had on reproductive parameters.

In 2003, we also began collecting blood and adipose tissue samples for Quantitative Fatty Acid Signature Analysis (QFASA) and Stable Isotope Analysis (SIA). QFASA and SIA are non-lethal alternatives to conventional methods of diet determination. Until recently, stomach content analysis of collected birds was the only technique available to assess diet outside of the chick-rearing period. Unfortunately, this technique provides only a snap-shot of what the bird has been eating prior to collection and it is subject to well known biases associated with the under-representation of soft bodied organisms (Bradstreet 1980) and the retention of hard parts (Wilson et al. 1985). Indirect techniques, such as QFASA and SIA, provide an integration of diet over a longer period, avoid the inherent biases associated with stomach content analysis and can be used on birds captured or collected outside of the chick-rearing period, providing data on seasonal changes in prey abundance.

Methods

Study sites

We conducted this study in Chiniak Bay, Alaska (57˚40'N, 152˚20'W) from 2001-2003. Tufted puffins (*Fratercula cirrhata*) are one of the most abundant and widely distributed seabirds breeding in Chiniak Bay. No recent census data for tufted puffins in Chiniak Bay is available; however Dick et al. (1976) recorded over 8300 breeding pairs on 21 island colonies in 1975. We monitored reproductive success, growth rates, and/or nestling diet at five colonies distributed throughout Chiniak Bay (Figure 1). We monitored reproductive parameters at two inner bay colonies (Puffin and Kulichkoff Islands), one colony in Kalsin Bay (Svitlak Island) and one colony at the outer edge of the bay (Chiniak Island) and obtained information on the diet composition of nestlings and the foraging distribution of adults at the two largest colonies in Chiniak Bay; Cliff Island (approx. 500 breeding pairs) in the inner bay and Chiniak Island (>5000 pairs) at the outer edge of the bay. Blood and adipose tissue samples were collected from tufted puffins caught on Chiniak Island.

Reproductive parameters

We began monitoring tufted puffin burrows on 24 June in 2001, 7 June in 2002, and 11 July in 2003. We excavated vertical holes into the nest chamber of burrows with chambers that could not be reached through the entrance and subsequently sealed access holes using square cut plywood or flat rocks that were easily identified and removed for subsequent nest checks. We determined egg size by measuring the length and maximum breadth of all eggs using calipers (±0.1mm) and developed an index of egg volume ($\text{length}*\text{breadth}^2$). This index has a strong linear relationship with fresh egg mass in the Atlantic Puffin (r^2=0.972; Birkhead and Nettleship 1984). We weighed chicks to the nearest gram using Pesola spring scales and measured flattened wingchord from the wrist to the wingtip (± 1mm). We attempted to re-visit all burrows every five days, but inclement weather sometimes prevented access to some colonies, so visits were made every 4-8 days. For cases in which hatch date was unknown, we used a wing length vs. age regression derived from known age nestlings to estimate age (Gjerdrum 2001). We calculated growth rates as the slope of the linear regression equation relating mass and age between ages 10 and 30 days, the near-linear portion of the growth curve. Nestlings with fewer than three measurements of mass between 10 and 30 days of age were excluded from growth rate analyses. We defined fledging success as the number of chicks to reach a minimum wingchord of 130mm per egg hatched. Chick mortality is highest during the first 10 days post-hatch, therefore we excluded burrows that were first checked after July 20, because inclusion of these older nestlings would artificially increase fledging success rates.

Nestling diet

Samples of food items delivered to nestlings were collected on 15/16 August 2002 at Chiniak Island and throughout July and August of 2003 on Cliff and Chiniak Islands. A prey sample is defined as all prey items collected from one burrow on one sampling date, but is not necessarily one bill load (prey samples may be comprised of partial bill loads or multiple bill loads). We collected the majority of samples by screening burrows either individually using small wire screens (15x15 cm) or in mass (20-30 burrows at a time) with a 7x10m seine net. Either method effectively prevents adults from entering with food loads. Often these adults drop their bill loads at burrow entrances. And finally, a minority of samples was collected opportunistically when observers came across fresh prey samples inside the nesting chamber or near burrow entrances where no screens or nets had been placed. Once retrieved, prey samples were kept cool using an ice pack and cooler and transported to the city of Kodiak where they were stored frozen until analyzed. All samples were thawed, weighed to the nearest 0.1g, and separated into individual prey items that were identified to species, weighed to the nearest 0.1g, and measured to the nearest 1mm (snout to fork for fish samples). Pacific sandlance, capelin, and Pacific sandfish accounted for greater than 95% of the prey items fed to nestlings (see results section), thus all other species were pooled into an “other” category for statistical analyses.

QFASA

We biopsied subcutaneous adipose tissue (Iverson and Springer 2002) from adult and nestling tufted puffins for later analysis of fatty acid signatures. Adults were captured using a 7x10m seine net draped over a cluster of 20-30 burrow entrances. As birds tried to exit their burrows they became entangled in the net and were quickly retrieved by nearby observers. We captured nestlings in the nesting chamber by reaching in through burrow entrances. Biopsies involved the extraction of approximately 100-300mg of adipose tissue from a <1cm long incision located at a site just anterior to the uropygial gland and 1cm lateral to the spine. Samples were immediately placed in chloroform containing 0.01% BHT (butylated hydroxytoluene) as an antioxidant and placed on ice until transported (within 12 hours) to the city of Kodiak where samples were then stored frozen (-30ºC) until analysis. Adipose tissue samples were collected from adults during 3 time-periods; pre-incubation (26 May-2 Jun), late-incubation (1 Jul-6 Jul), and late-chick rearing (22 Aug-4 Sep). Adipose tissue collection from nestlings occurred during the late chick rearing period (22 Aug-4 Sep).

Biopsies of adipose tissue are currently being processed. Total lipids are being extracted from adipose tissue samples according to the method of Folch et al. (1957) as modified by Iverson et al. (1997). Fatty acid methyl esters (FAMEs) are being prepared from the lipid extracts using Hilditch Reagent in methylene chloride, capped under nitrogen and heated for one hour. Analysis of FAMEs will be performed in duplicate using a temperature programmed gas-liquid chromatograph according to the methods of Iverson et al. (1997).

Stable isotope analysis

We obtained blood samples from nestlings and adults captured during the late chick-rearing period (22 Aug-4 Sep) by puncture of the superficial brachial wing vein with a 24g needle. Blood was initially collected in heparinized 250µl Natelson blood collecting tubes, then transferred into 1.5 ml microcentrifuge tubes and stored on ice for transport to freezer facilities in Kodiak. Whole blood samples were freeze dried, powdered and analyzed in duplicate using a Europa 20/20 continuous flow mass spectrometer at the UAF stable isotope facility. Accuracy of the Europa was continuously checked using peptone as a known standard. Overall accuracy for the Europa is ±0.2‰ for N and ±0.15‰ for C. Stable isotope concentrations are reported using ‘δ’ notation according to the following:

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ for nitrogen is atmospheric N_2, and the Peedee Belemnite (PDB) from the Peedee Formation of South Carolina is the standard for carbon.

Samples of prey items collected at the colonies are currently being processed for stable isotope analysis. Prey items are being freeze dried, powdered, lipids extracted using a Soxhlet apparatus with chloroform solvent, and dried at 60˚C for 24 h to remove any residual solvent (Hobson et al. 1994). Once processing is complete, samples will be analyzed in duplicate by mass spectroscopy.

Foraging distribution

We set out to determine foraging distribution of tufted puffins from 2 colonies (Cliff Island and Chiniak Island) in 2003 during their reproductive season using radio-telemetry. Adult tufted puffins captured inside their burrows were weighed to the nearest gram with a pesola spring scale, measured for standard morphometrics (tarsus, wingchord, headbill and culmen), and outfitted with a radio transmitter using the subcutaneous anchor method (Newman et al. 1999). Radio transmitters (model A2720, Advanced Telemetry Systems, Isanti, Minnesota) weighed 7.5g or 9g (<1.5% body mass) and were equipped with a 20cm long whip antenna. Transmitters that weighed 7.5g were new and had an antenna mounted at 45° to the horizon, whereas the 9g transmitters had been refurbished and were equipped with a horizontally mounted antenna. We determined the status (egg, chick, or empty) of each burrow at the time of capture and re-visited burrows every 4-9 days to determine chick growth and fledging rates. We monitored the distribution of radio-tagged individuals by flying aerial transects of a fixed grid (10km or 15km) on six occasions between 22 July and 18 August. Aerial transects were flown at 2000-3000 meters using a Cessna 206 equipped with paired four-element Yagi antennas mounted on the wing struts. The initial survey covered an area that extended 40 km in all directions (excluding land) from Chiniak and Cliff Islands. We expanded the area flown on subsequent flights in the direction of signals that were detected outside of the original survey coverage area. Aerial coverage for all flights combined is shown in Figure 2. An observer continually scanned frequencies at a rate of 0.5 frequencies per second using an R-4000 receiver (Advanced Telemetry Systems Inc., Isanti, Minnesota) connected by coaxial cables and a left/right switchbox to the antennae. The observer recorded strength (on a scale of 1-5) and direction (right or left) of any detected signals. The location of tufted puffins was estimated by plotting location of all detected signals using ArcView 3.2 (ESRI Inc.), and calculating a weighted mid-point location of detected signals, or fix. We estimated the precision of fixes attained by aerial telemetry by 'fixing' on reference transmitters placed on anchored buoys at known locations. Land-based telemetry receiving stations with data collection computers (Advanced Telemetry Systems, Isanti, Minnesota) were set up at both colonies to determine if adults continued to attend the colony following attachment of radio-transmitters. Because a large number of birds failed or abandoned their young (see results), we separated birds into two groups; 'attending' adults are birds that still had chicks and continued to attend the colony whereas 'failed' adults no longer had a chick and/or no longer attended the colony. As the season progressed, the status of individual birds changed, such that an adult may be considered 'attending' in one flight and 'failed' in subsequent flights.

Statistical analyses

All statistical analyses were performed using SAS 8.0 (SAS Institute) with the α-level set at 0.05. Data are presented as means ± standard deviation (SD). The effects of year and colony on reproductive parameters (egg volume index and chick growth rates) were analyzed using analysis of variance (ANOVA, Type-III sum of squares). For dietary analyses, mean proportions of each prey type were computed for each bill load and these mean proportions were used in all statistical tests because individual prey items within a bill load are not independent. The effect of colony location (inner vs. outer bay) on diet composition was determined using multivariate analysis of variance (MANOVA). We tested for significant differences in $\delta^{15}N$ and $\delta^{13}C$ values between adults and nestlings using a Student's *t*-test followed by a bonferronni correction for multiple comparisons. A *t* test was used to test for differences in nestling growth rates between radio-marked and control parents. We tested for differences in fledging success between radio-marked and control groups using 2X2 chi-squared contingency tables.

Results

Reproductive parameters

Tufted Puffins successfully reared and fledged nestlings at all colonies in all years with the exception of Kulichkoff Island in 2003. On July 14 of 2003, the first day nests were checked on Kulichkoff Island, only 2 of 25 burrows contained eggs indicating that most birds either failed in the early stages of incubation or did not attempt to breed at all. Both of the active burrows on Kulichkoff subsequently failed; one at the incubation stage and one at the chick-rearing stage. There was no significant difference in egg volume index between colonies ($ANOVA_{colony}$ $F_{4,216}$ = 1.32, p=0.26), nor was there a significant difference between years ($ANOVA_{year}$ $F_{2,216}$ = 0.04, p=0.96). Fledging success varied from a low of 41.2% at Svitlak Island in 2003 to a high of 100% at Puffin Island in 2003 (Table 1). The low rate of reproductive success on Svitlak Island was due to the disappearance of 9 of 10 nestlings between July 21 and July 26. The cause of the disappearance of these chicks is unknown. Fledging success for chicks hatched after July 21 on Svitlak Island was relatively high (80%; n=5). Growth rates of nestlings were highly variable, ranging from a low of 4.6 to a high of 22.96 g/day (Table 1). There was no significant difference in mean growth rates between colonies ($ANOVA_{colony}$ $F_{3,111} = 1.47$, p=0.22), nor was there a significant difference between years ($ANOVA_{year}$ $F_{2,111} = 0.64$, p=0.53).

Nestling diet

Table 2 summarizes the diet composition of tufted puffin nestlings on Chiniak and Cliff Islands. In 2002, 34 prey samples were collected on Chiniak Island and consisted of 75 individual prey items comprising four species of fish including 57.2% (by mass) capelin, 24.6% sandlance, 8.4% Pacific sandfish (*Trichodon trichodon*) and 9.8% unidentified salmonid species (salmonidae spp.). In 2003, we obtained a total of 265 samples of prey (190 from Chiniak Island plus 75 from Cliff Island) comprised of 641 individual prey items (weighing 2723g in total) comprising eight species of fish and one species of invertebrate (squid). Three fish species, capelin, sandlance, and sandfish, represented >95% (by mass) of the prey delivered to nestlings at both sites. The bill loads delivered to nestlings on Chiniak Island in 2003 was comparable to 2002 except for the complete absence of salmonids in 2003 (Fig. 3). There was a significant difference (ANOVA $F_{3,261} = 131.86$; p<0.0001) in diet composition of nestlings at the inner bay site compared to the outer bay site in 2003, with chicks at Chiniak Island consuming primarily sandlance (49.4% by mass) and capelin (44.7%), while Cliff Island nestlings were fed mostly sandfish (74.1%) and to a lesser extent, capelin (15.5%; Fig. 4). At Chiniak Island in 2003, a seasonal shift in the composition of nestling diets occurred, with a peak in capelin consumption occurring during the week of July 14-21 (Fig. 5).

QFASA and stable isotope analysis

A summary of all blood and adipose tissue samples collected from Chiniak Island is shown in Table 3. Adipose tissue samples collected from adults and nestlings are currently being processed, thus no results are reported here. The relationship between $\delta^{15}N$ and $\delta^{13}C$ values of whole blood samples taken from adults and nestlings is shown in Figure 6. The mean $\delta^{15}N$ value for adult whole blood samples of 14.46‰ was significantly higher than the mean value for nestlings of 14.27‰ (one outlier removed; t=3.18, p<0.01). Using a trophic level enrichment factor of 3‰ for nitrogen (Hobson et al. 1994), the trophic difference between adults and nestlings is 0.067 trophic shifts. The mean $\delta^{13}C$ value for adults of -17.27‰ was also significantly higher than the mean value for nestlings of -17.47‰ (one outlier removed; t=2.84, p<0.01). Samples of prey items for stable isotope analyses are currently being processed.

Telemetry

Radio-transmitters were attached to 17 birds on Chiniak Island and 15 birds on Cliff Island. Four of the nine adults that were still incubating at the time of capture successfully hatched their young: however, none of these chicks survived to fledge. Fledging success for nestlings with a radio-marked parent was 30% (n=10) for nests that were first checked before July 20 and 38% (n=21) for nests that were first checked before 2 August. Both of these values are significantly (X^2=6.36 or 23.77; p<0.01 or <0.0001) lower than the fledging success of control nests (71%; n=65). Nestlings with a radio-marked parent had a mean growth rate of 6.08 ± 4.39g/day (n=6), which was also significantly (t=5.45; p<0.0001) lower than the growth rate of 14.59 ± 3.54g/day attained by control groups (n=52).

In total, six aerial telemetry surveys with varying coverage areas were conducted between 22 July and 18 August, 2003 (Fig. 2). We located 24 of 32 radio-marked puffins during the six aerial surveys and 15 (47%) of these birds were located more than once. A total of 59 locations were obtained for the 23 birds (mean=2.6 locations/bird) equipped with 7g transmitters with antennas mounted at 45° to the horizon, whereas only 7 locations were obtained for the 9 birds (0.78 locations/bird) equipped with 9g transmitters with horizontally mounted antennas. All estimates of locations (n=9) of reference transmitters from aerial telemetry were within 5km of actual locations with 78% (7 of 9) of estimates within 3km. The locations of 'attending' adult birds and 'failed' adult birds from Chiniak and Cliff Islands are shown in Figures 7 and 8, respectively. Failed breeders from both islands were distributed further from the colonies compared to attending adults. As the season progressed, both the percentage of birds detected per flight and the percentage of birds detected within 40km of the colonies declined despite an increase in survey effort (Fig. 9).

Discussion

Reproductive parameters

In terms of egg volume, nestling growth rates, and rates of fledging success, it appears that tufted puffins breeding in Chiniak Bay between 2001 and 2003 performed comparably to puffins at other major colonies in Alaska during successful years (reviewed in Piatt and Kitaysky 2002). Egg volume index and rates of nestling growth showed no significant inter-colony or inter-annual differences between 2001 and 2003 (Table 1), suggesting that feeding conditions throughout the bay were relatively stable during this time period. However, breeding birds are sometimes able to buffer their offspring from reduced food supply by shifting their time allocation such that more time is available for foraging (Uttley et al. 1994). Across the same time span (2001-2003) some colonies of black-legged kittiwakes (*Rissa tridactyla*) exhibited declining productivity (D. Kildaw unpub. data). Puffins may be less susceptible to changes in the abundance of key prey species such as sandlance and capelin within Chiniak Bay because they can utilize alternative prey species including sandfish and salmonids that are not readily available to surface feeding gulls. Differences in reproductive success between colonies were only readily apparent in 2003 when the majority of puffin chicks on Svitlak Island disappeared and when burrow occupancy at Kulichkoff Island during the latter phases of incubation was exceptionally low. However, the majority of the reproductive failure at Svitlak Island occurred during a single 5-day time period and Kulichkoff Island is located very close (3.5km) to Puffin Island which had high levels of burrow occupancy, normal chick growth rates and 100% fledging success, suggesting that chronic poor feeding conditions were not likely responsible for the observed breeding failure. The causes of the low burrow occupancy rate on Kulichkoff Island and the disappearance of 9 of 10 nestlings during a single 5 day span are unknown but may have resulted from mammalian predators. Short-tailed weasels (*Mustela erminea*) were observed on Kulichkoff island in 2002 (K. Murra pers. comm.), and two puffin chicks were found partially eaten in their burrows in 2004 (Williams unpub. data).

Nestling diet

Although no significant differences were found in egg volume index, rates of nestling growth, or fledging success rates between inner (Puffin Island) and outer bay (Chiniak Island) colonies, there was a significant difference in nestling diet composition between the two sites in 2003. The two colonies are separated by less than 22km, yet nestlings at Chiniak Island were fed primarily capelin and sandlance, while Cliff Island chicks ate mostly sandfish (Fig. 4). This confirms the findings of Hatch and Sanger (1992), which suggested that tufted puffins are generalist predators that will shift their diet in response to what forage types are currently available. However, this is the first study to show such a dramatic difference in diet composition over such a small spatial scale.

Interestingly, in 1986, the only other year nestling diet data is available for Cliff Island, chicks were fed a diet consisting primarily of capelin and sandlance (see Table 2; data from Hatch and Sanger 1992). Diet samples collected from Chiniak Island in 2003 (Fig. 5) demonstrate that diet composition can also fluctuate within a single breeding season. Thus, diet composition of nestling puffins may vary over relatively small spatial and temporal scales. Although preliminary, analysis of the diet data collected from this study suggests that puffin diet may provide insight into seasonal and inter-annual changes in prey abundance and distribution. The ultimate cause of changing diet composition in this study is unknown, but likely reflects changes in oceanographic conditions affecting prey distribution. A long term data set on tufted puffin productivity from Triangle Island in British Columbia demonstrates that puffin diet and reproductive success are affected by changes in sea surface temperatures (Gjerdrum et al. 2003). Collection of a long-term data set on puffin diet and oceanographic conditions in Chiniak Bay will likely provide insight into the effects of changing climatic conditions on the abundance and distribution of forage fish species in this region.

Stable isotope analysis

Previous studies using analysis of stomach contents (Baird 1991) and analysis of stable isotope signatures (Hobson et al. 1994) have suggested that invertebrates play an important role in the diets of adult tufted puffins in the Gulf of Alaska during the chick rearing period. Piatt and Kitaysky (2002) concluded that adult tufted puffins consume mostly invertebrates year-round. Stable isotope analysis in this study suggests that adults were feeding at the same trophic level as nestlings. Since nestlings were fed exclusively fish, this suggests that adults were also consuming primarily fish. However, the isotopic values of adults in this study were very close to what Hobson et al. (1994) obtained for adults at the Shumigan Islands, once these values are corrected for differences in fractionation between blood and muscle tissues (Hobson and Clark 1992). This suggests that there is either a difference in fractionation rates between chicks and adults, or that the estimated diet-muscle tissue fractionation value of +2.5‰ for nitrogen (from Mizutani et al. 1991) used by Hobson et al. (1994) is unrealistic. Alternatively, the model built by Hobson et al. (1994) may have overestimated the contribution of invertebrates to the diet of adults because there was insufficient data on the isotopic composition of smaller size classes of planktivorous fish consumed by tufted puffins. Analysis of stable isotopes in prey samples and experimental manipulations to accurately determine rates of diet-tissue fractionation are needed to improve the accuracy of estimates of trophic-level feeding based on stable isotopes.

Radio telemetry and foraging distribution

Radio telemetry is a useful technique to determine at-sea distribution (Whitworth et al. 2000) and time-budgets (Litzow and Piatt 2003) of breeding seabirds. However, our results suggested that parental effort of adult tufted puffins was significantly altered by the attachment of transmitters. Although some adults abandoned in response to the initial capture and radio attachment procedure, most adults continued to visit the colony and presumably feed their young for some time (days to weeks) after being radio-tagged. The disappearance of most adults from the study area in later flights (Fig. 9) and the decrease in the number of adults visiting the colony (Williams, unpub. data), suggests that most adults prematurely abandoned their young.

Because attachment of radio-transmitters affected the reproductive effort of breeding puffins, information on at-sea distribution presented in this study should be interpreted cautiously. Figures 7 and 8 clearly demonstrate that the at-sea distribution of tufted puffins was non-random. Previous studies using at-sea surveys have shown a spatial association between puffins and their prey (Swartzman and Hunt 2000). Data on nestling diets and information obtained from aerial telemetry surveys of radio-marked adults suggests that capelin and sandlance was readily available to puffins foraging outside (south-east) of Chiniak Bay, whereas birds foraging within the bay primarily fed sandfish to their young.

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Table 1. Percentage mass of forage species collected from bill loads of tufted puffins at Cliff and Chiniak Islands, Alaska in 1986, 2002, & 2003.

	% Mass			
Prey Species	*Cliff Island*		*Chiniak Island*	
	1986*	2003	2002	2003
Capelin	57.7	14.8	57.2	44.8
Sandlance	40.1	5.4	24.6	49.4
Pacific Sandfish	-	75.2	8.4	5.8
Salmonid	-	1.8	9.8	0
Other fish	2.3	2.8	0	<0.1
Invertebrates	0	<0.1	0	<0.1
Sampling dates	4/5 Aug; 5/6 Sep	15-29 Aug	15/16 Aug	4 Aug - 5 Sep
No. Samples	34	75	34	190
Total # Prey Items	N/A	175	75	566
Total weight (g)	529	928	441	1795

*According to Hatch and Sanger (1992)

Table 2. Summary of reproductive parameters for tufted puffins at study colonies in Chiniak Bay, Alaska in 2001-2003.

Colony	*Year*	*Mean Egg Volume Index cm^3± SD. (n)*	*% Fledging Success (n)*	*Mean Growth Rate g/day ± SD (n)*
Puffin	2001	170.09 ± 12.36 (25)	95.2 (21)	14.03 ± 5.09 (20)
	2002	168.37 ± 10.58 (31)	66.7 (15)	13.53 ± 4.32 (12)
	2003	166.07 ± 17.79 (3)	100.0 (13)	13.38 ± 4.02 (17)
Svitlak	2001	173.19 ± 11.72 (18)	92.9 (14)	13.65 ± 2.11 (8)
	2002	169.23 ± 13.21 (27)	85.7 (7)	13.91 ± 3.74 (7)
	2003	165.97 ± 13.60 (11)	41.2 (17)	13.88 ± 2.63 (7)
Kulichkoff	2001	170.88 ± 13.56 (21)	100.0 (14)	14.49 ± 2.32 (11)
	2002	171.51 ± 10.41 (24)	72.7 (11)	16.42 ± 2.06 (8)
	2003	178.48 ± 16.22 (2)	0.0 (1)	N/A
Chiniak	2002	175.42 ± 11.81 (22)	100.0 (2)	11.18 ± 4.61 (3)
	2003	171.58 ± 13.03 (39)	76.5 (34)	15.50 ± 3.26 (28)
All Colonies	2001	171.22 ± 12.46 (64)	95.9 (49)	14.08 ± 3.90 (39)
	2002	170.81 ± 11.68 (59)	72.7 (33)	14.15 ± 3.87 (30)
	2003	170.22 ± 13.02 (55)	70.8 (65)	14.59 ± 3.54 (52)

Table 3. Summary of tissues collected from tufted puffins at Chiniak Island, Alaska in 2003.

	Adults		*Nestlings*	
Collection Date	Fat samples	Blood Samples	Fat samples	Blood samples
26 May-2 Jun	16	0	-	-
1-6 July	20	0	-	-
22 Aug-2 Sep	24	23	23	23

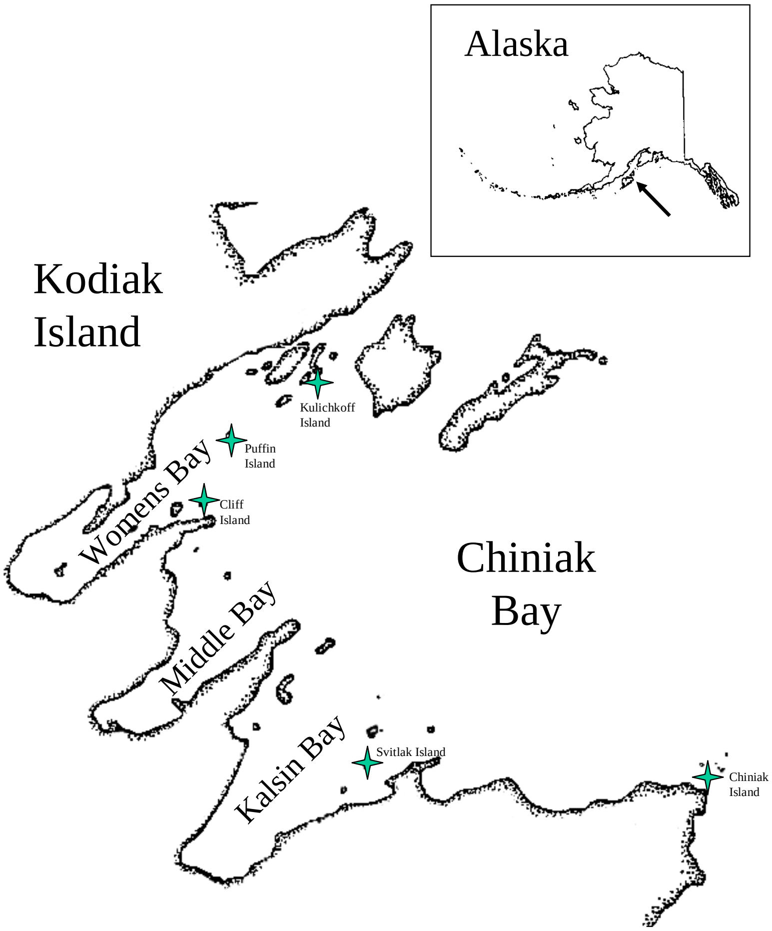

Figure 1. Study area in Chiniak Bay, Kodiak Island. Blue stars represent tufted puffin monitoring sites.

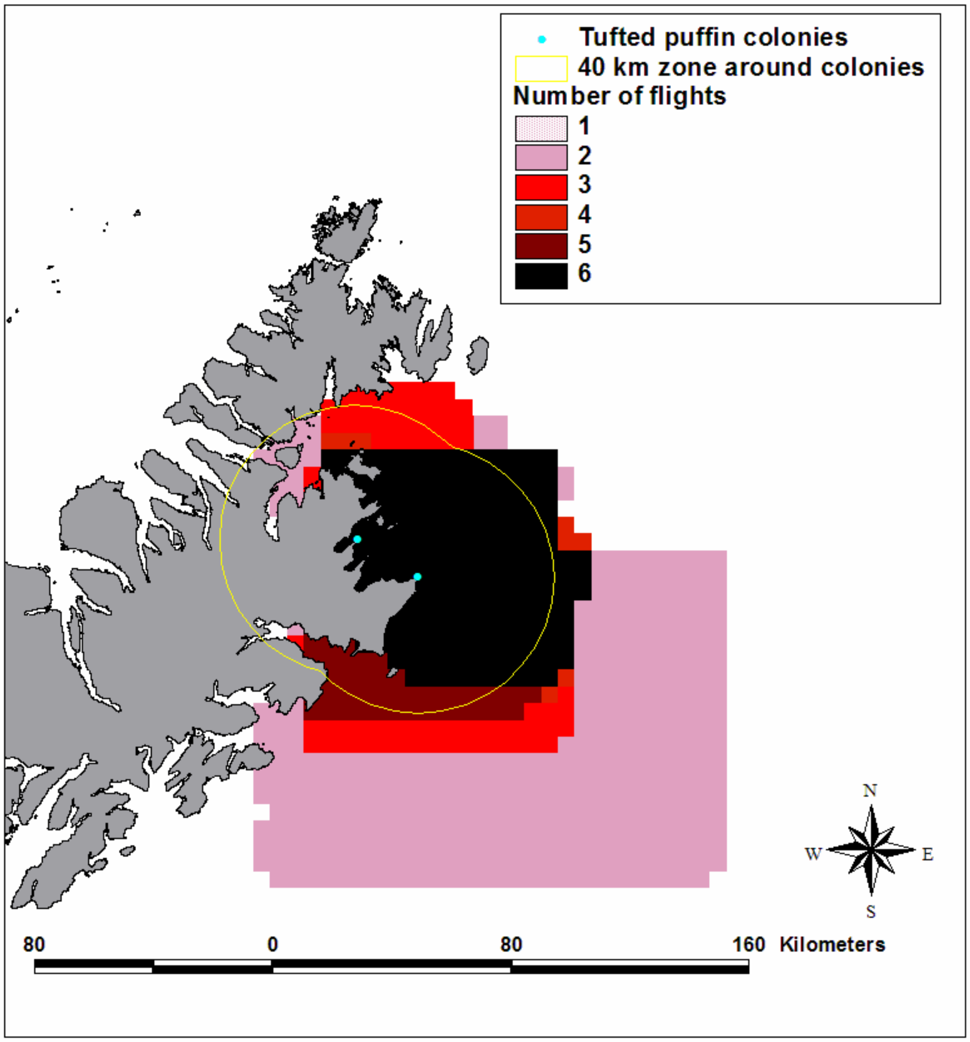

Figure 2. Aerial survey coverage area by 25km^2 grid blocks in Chiniak Bay and surrounding waters, 2003. Blue dots represent colonies with radio-marked tufted puffins and yellow circles represent a 40km buffer around those colonies.

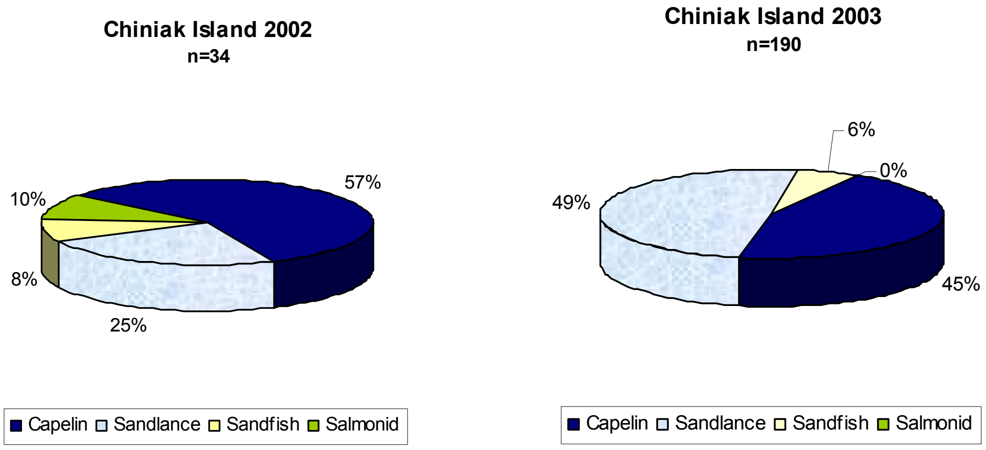

Figure 3. Percent composition by mass of tufted puffin nestling diets during 2 years from Chiniak Island.

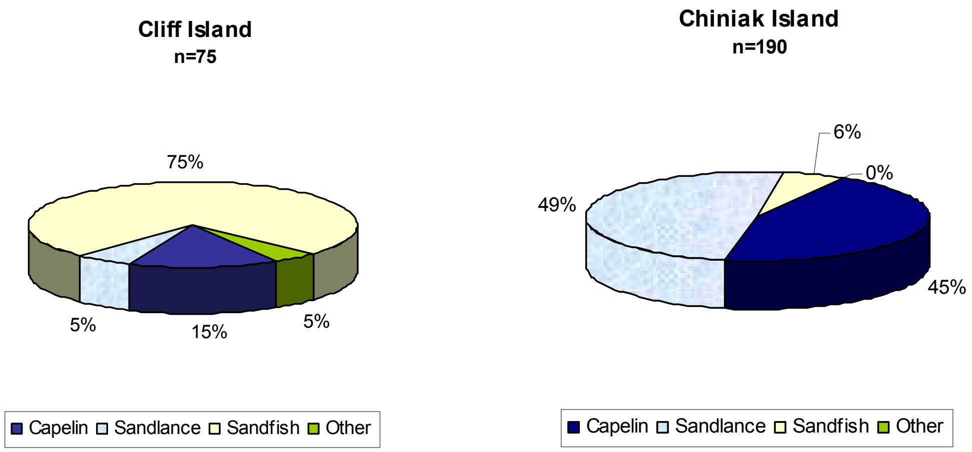

Figure 4. Percent composition by mass of tufted puffin nestling diets at two colonies in Chiniak bay during 2003.

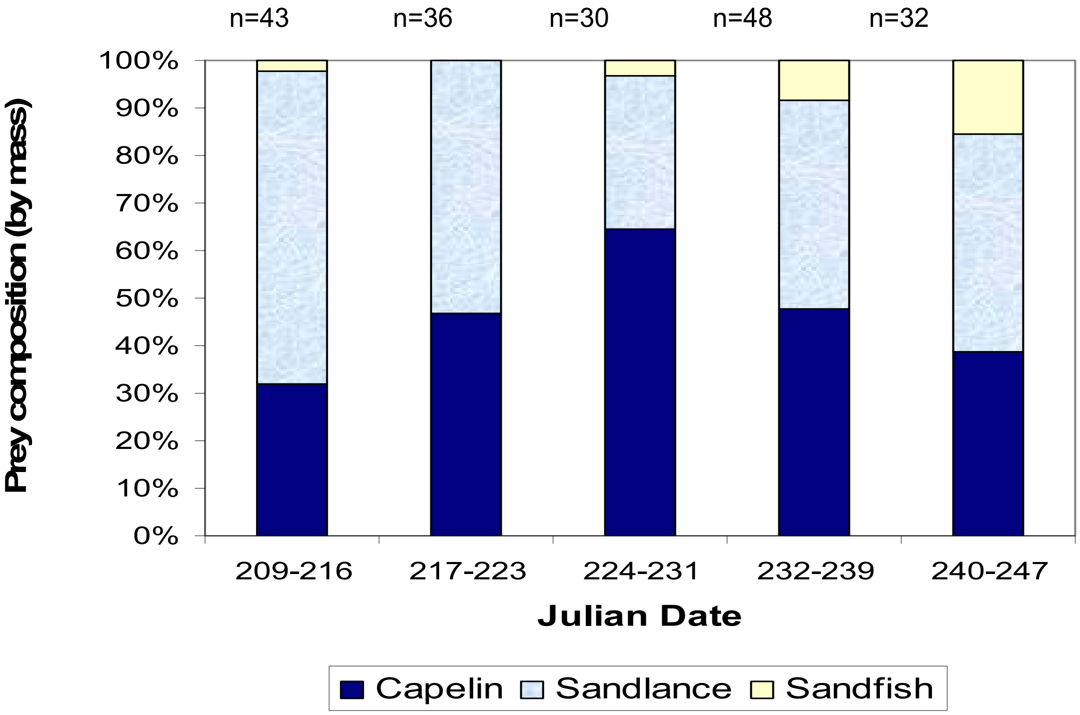

Figure 5. Seasonal diet composition of tufted puffin nestlings by mass at Chiniak Island, Alaska in 2003.

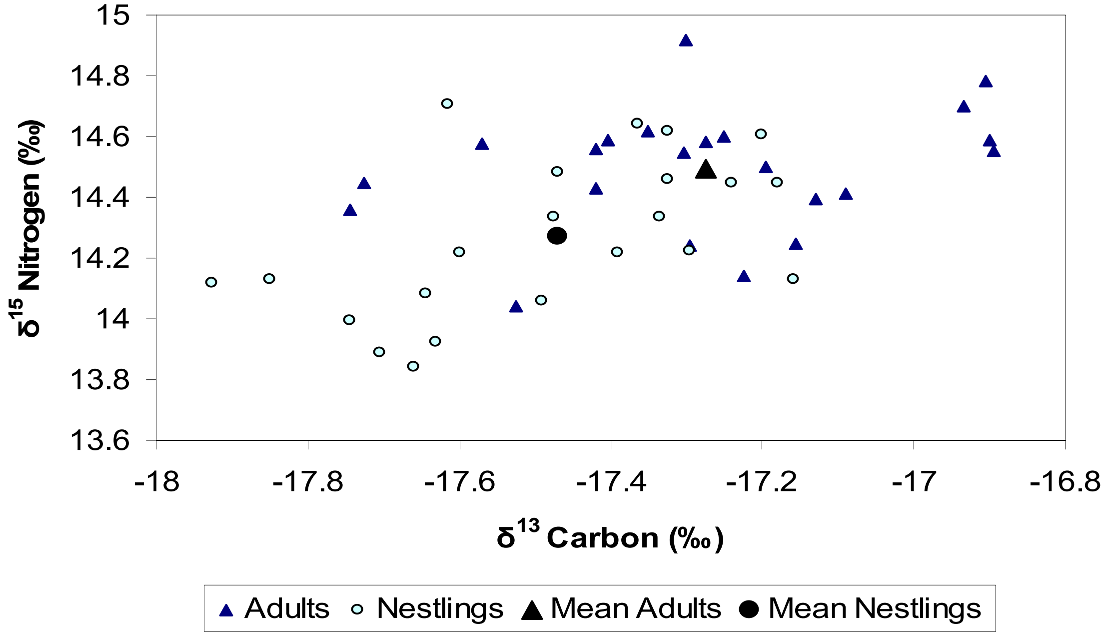

Figure 6. Stable carbon and nitrogen concentrations in whole blood of adult and nestling tufted puffins at Chiniak Island during August of 2003.

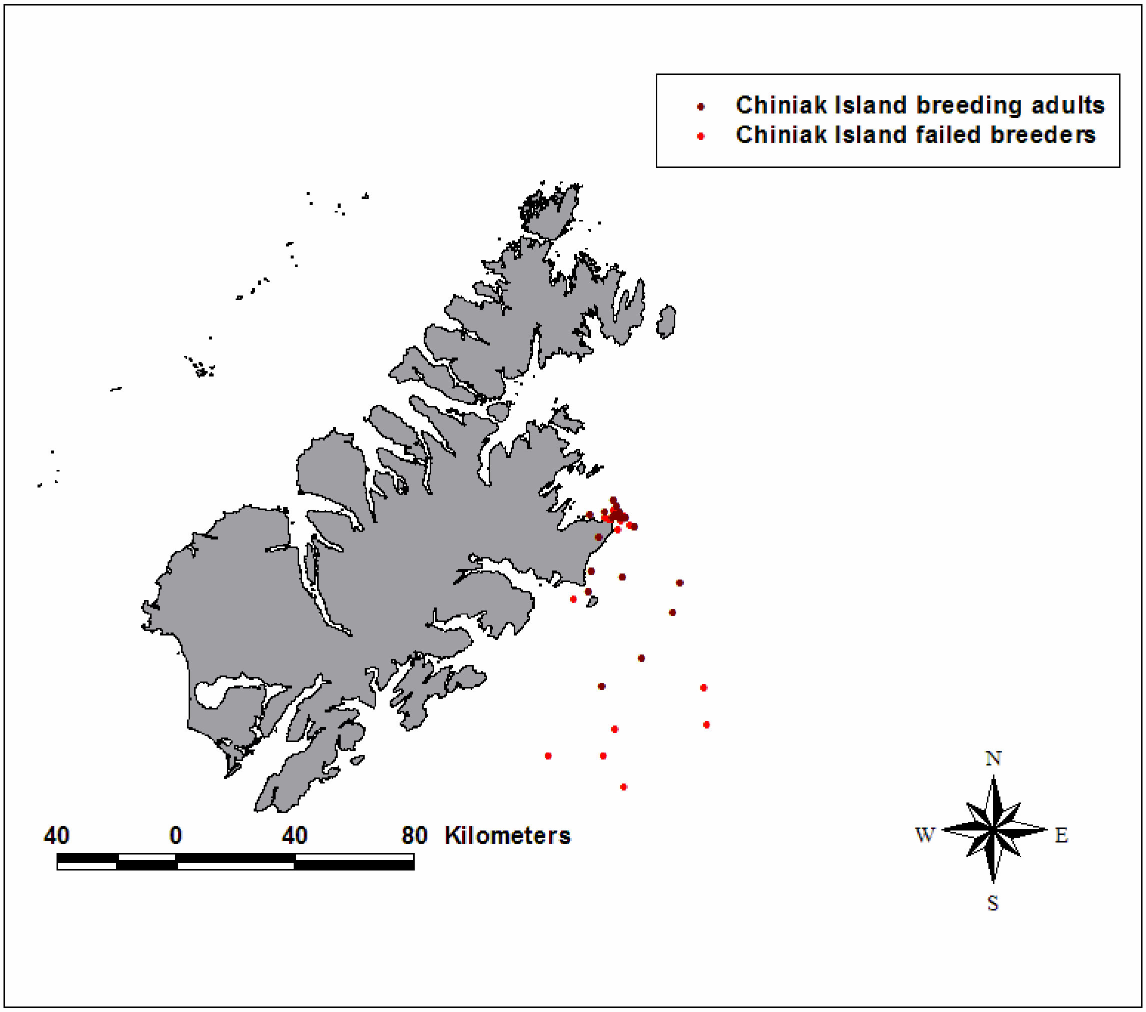

Figure 7. Estimated locations of radio-marked tufted puffins from Chiniak Island in the nearshore waters of south-eastern Kodiak Island, 2003. Locations are grouped by current reproductive status.

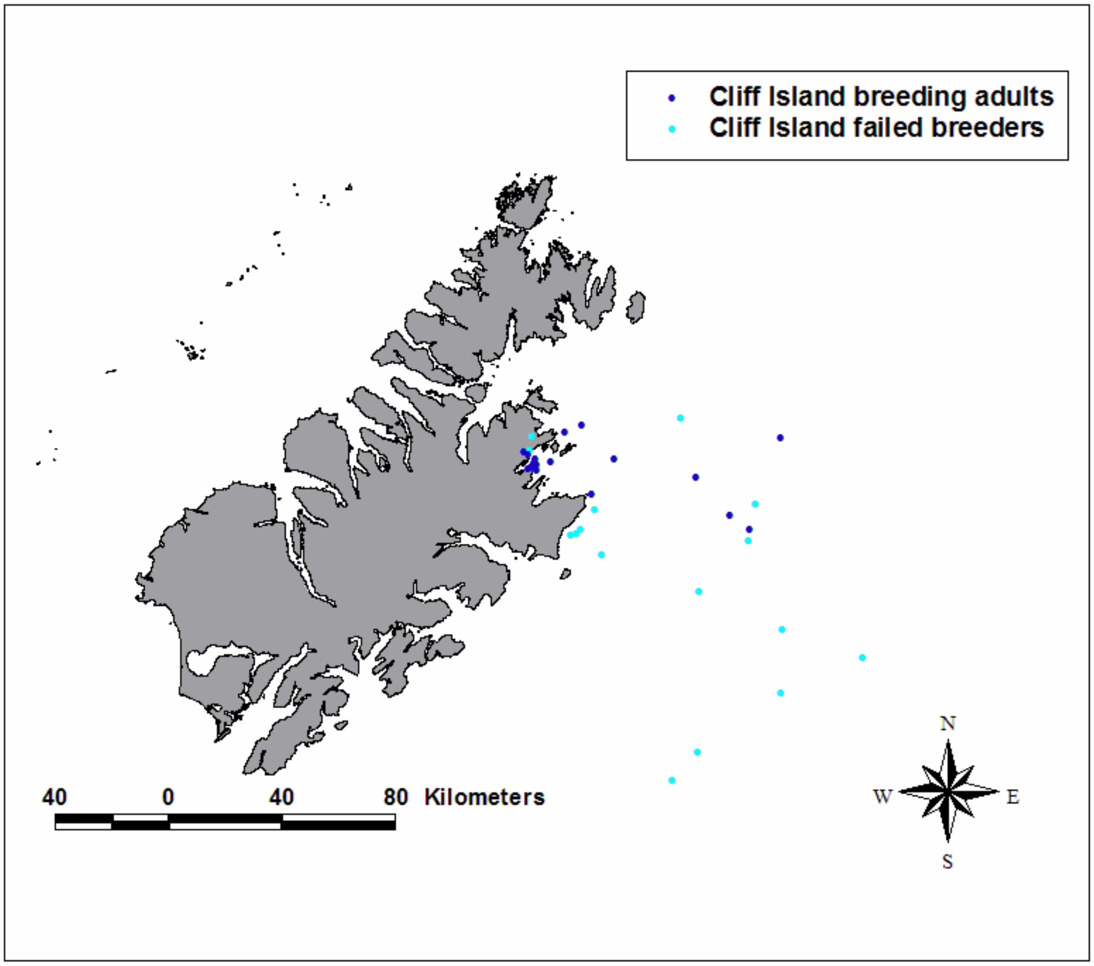

Figure 8. Estimated locations of radio-marked tufted puffins from Cliff Island in the nearshore waters of south-eastern Kodiak Island, 2003. Locations are grouped by current reproductive status.

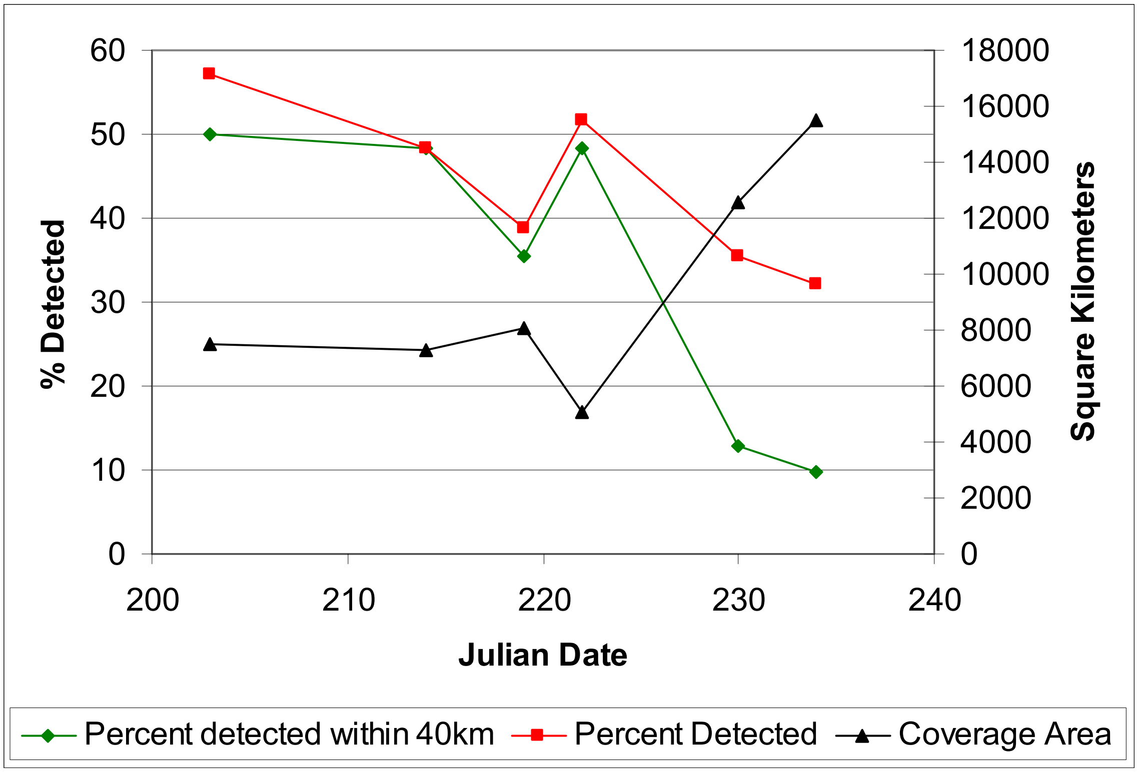

Figure 9. Seasonal changes in survey coverage area and percentage of radio-marked tufted puffins detected during aerial surveys in the south-eastern waters of Kodiak Island, 2003.