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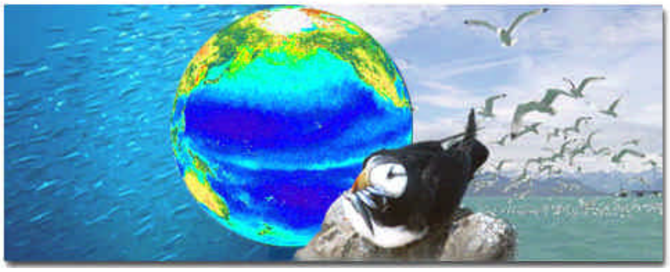
Response of Seabirds to Fluctuations in Forage Fish Density



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Final Report

USGS - Alaska Science Center, Anchorage

Response of Seabirds to Fluctuations in Forage Fish Density

DRAFT
Final Report to:

Exxon Valdez Oil Spill Trustee Council
Restoration Project (APEX) 00163M

&

Minerals Management Service
Alaska OCS Region

Alaska Science Center
U.S. Geological Survey
1011 East Tudor Road
Anchorage, AK 99503

April 2002

Response of Seabirds to Fluctuations in Forage Fish Density

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Response of Seabirds to Fluctuations in Forage Fish Density.

DRAFT Final Report
EVOSTC Restoration Project (APEX) 00163M
Minerals Management Service, OCS Alaska Region

Study History: Since the late 1970s, seabirds in the Gulf of Alaska (GOA) have shown signs of food stress: population declines, decreased productivity, changes in diet, and large-scale die-offs. Small-mesh fishing trawls conducted during the past 45 years reveal that a major shift in fish community composition occurred in the late 1970s: some forage species (e.g., capelin) virtually disappeared, while predatory fish (e.g., pollock) populations increased markedly. These ecosystem changes were part of an overall "regime shift" in the physical and biological environment of the GOA and had profound effects on seabirds. The *Exxon Valdez* Oil Spill (EVOS) occurred more than ten years after the regime shift, and it has been difficult to distinguish EVOS effects from effects of the regime shift on seabird populations. Restoration Project 98163M was initiated as part of the Apex Predator Ecosystem Experiment (APEX) in 1995 to characterize relationships between seabird population dynamics, foraging behavior, and forage fish densities in lower Cook Inlet-- the area in which most seabirds were killed by the EVOS. The ultimate goal was to achieve a better understanding of relationships between seabirds and forage fish in a variable environment, and to assess whether current environmental conditions are favorable to seabirds in the GOA. The Cook Inlet Seabird and Forage Fish Study (CISeaFFS) is a collaborative project of the Alaska Biological Science Center and the Alaska Maritime National Wildlife Refuge, with major funding and logistic support from the EVOS Trustees (APEX), the U.S. Geological Survey, the Minerals Management Service, U.S. Fish and Wildlife Service, Alaska Department of Fish and Game, and the University of Washington.

Abstract: Following the *Exxon Valdez* Oil Spill (EVOS), one concern was that prevailing ecological conditions in the Gulf of Alaska (GOA) would not favor recovery of damaged seabird populations. To address this issue, we examined relationships between oceanography, forage fish and seabirds near three seabird colonies in lower Cook Inlet (LCI) in 1995-1999. Upwelling of cold, nutrient-rich GOA waters at the entrance to the shallow LCI estuary supports a high density of juvenile pollock, sand lance, and capelin; which in turn are exploited by high densities of breeding seabirds (murres, kittiwakes, puffins, etc.) on the east side of LCI. Waters on the west side of LCI are oceanographically distinct (warmer, less saline, outflowing), and much less productive for forage fish and seabirds. Patterns of seabird foraging behavior, productivity and population change reflected patterns of forage fish abundance and distribution, which in turn depended on local oceanography. Most seabird parameters varied with forage fish density in a non-linear (e.g., sigmoidal, exponential) fashion, and in some areas and years, productivity was limited by food availability. Current and projected ecological conditions favor recovery of seabirds from the EVOS at some colonies. In 14 chapters, this report summarizes data and compiles it into 247 tables, figures and appendices. Chapter 14 provides a thorough synthesis of overall project findings. Final analyses and interpretations of data will be published later in peer-reviewed journals (in addition to 51 articles already completed).

Key Words: Cook Inlet, murre, kittiwake, guillemot, forage fish, diet, pollock, capelin, sandlance, reproduction, growth rate, hydroacoustic, trawl, seine, *Exxon Valdez*, Kachemak Bay.

Project Data: *Description and format of data* - Data vary in type and format. Oceanographic data (thermographs, CTD) in .hex and .csv files, hydroacoustic data in raw .dt4 files and .csv integration summary files, fish and bird data archived in Excel and Access databases. Satellite imagery and maps archived in .wmf format or ArcView shape files. *Custodian* - Contact John Piatt, USGS, 1011 E. Tudor Rd., Anchorage, AK 99503; ph: 907 786-3549. For Barren Islands colony data contact Vernon Byrd, USFWS, 2355 Kachemak Bay Dr., Homer, AK 99603; ph: 907 235-6546.

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John Piatt

Summary

The Cook Inlet Seabird and Forage Fish Study (CISeaFFS, or 'Sisyphus') was established in 1995 with EVOSTC (APEX), USGS, MMS and FWS support to measure the foraging (functional) and population (numerical) responses of seabirds to fluctuating forage fish densities around three seabird colonies in lower Cook Inlet. This involved at-sea surveys for forage fish (hydro-acoustics, trawling, seining) and seabirds (line transects), and some characterization of oceanography (AVHRR satellite imagery, CTD profiles, moored thermographs), while simultaneously measuring aspects of seabird breeding biology (egg and chick production, chick growth, population trends) and foraging behavior (diets, feeding rates, foraging time) at adjacent colonies. Seabird data from colonies at Chisik and Gull islands were collected by USGS, data from the Barren Islands were collected by FWS. Field work was conducted during 1995 - 1999. Findings are presented here in 247 tables, figures and appendices. A synthesis of results for murres and kittiwakes is provided in Chapter 14. This report is not a final synthesis of *all* results, rather, it is a milestone on the way to publication of results in peer-reviewed scientific publications (see progress below). This report provides a compilation and summary of major data sets from Cook Inlet research and it accompanies a digital archive of all raw and summary data collected on this project. Detailed analysis and synthesis of fish and seabird data in the archive will follow in peer-reviewed journal articles.

CISeaFFS Publications to Date: The following 51 peer-reviewed articles have been submitted or published at the time of writing this final report, and stand as part of this report. PDF versions are at: www.absc.usgs.gov/research/seabird&foragefish/index.html or can be obtained from the Principal Investigator. Most of these papers arise directly from work conducted in Cook Inlet or Prince William Sound with funding from the EVOSTC and USGS, or they are related publications (indicated with *) that were written by investigators supported wholly or in large part with EVOSTC funds in 1995-2001. Authors supported under EVOSTC funded projects include: Abookire, Drew, Figurski, Harding, Henkel, Kettle, Kitaysky, Litzow, Neuman, Nielsen, Piatt, Robards, Romano, Shultz, Van Pelt, and Zador.

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Introduction

Some seabird populations in the Gulf of Alaska declined markedly during the past few decades (Hatch and Piatt 1995; Piatt and Anderson 1996). Whereas human impacts such as those from the *Exxon Valdez* oil spill can account for some proportion of these declines (Piatt et al. 1990c; Piatt and Naslund 1995), natural changes in the abundance and species composition of forage fish stocks have also affected seabird populations (Decker et al. 1994; Piatt and Anderson 1996). Marine fish communities in the Gulf of Alaska changed dramatically during the past 20 years (Anderson et al. 1994). Coincident with cyclical fluctuations in sea-water temperatures, the abundance of small forage fish species such as capelin (*Mallotus villosus*) declined precipitously in the late 1970's while populations of large predatory fish such as walleye pollock (*Theragra chalcogramma*) and cod (*Gadus macrocephalus*) increased dramatically. Correspondingly, capelin virtually disappeared from seabird diets in the late 1970's, and were replaced by juvenile pollock and other species in the 1980's (Piatt and Anderson 1996). Seabirds and marine mammals exhibited several signs of food stress (population declines, reduced productivity, die-offs) throughout the 1980's and early 1990's (Merrick et al. 1987; Piatt and Anderson 1996). Similar trends in oceanography, seabird population biology and prey availability have been noted in the Bering Sea, although the cycle there appears to be offset by 4-5 years from events in the Gulf of Alaska (Decker et al. 1994, Springer 1992).

Factors that regulate seabird populations are poorly understood, but food supply is clearly important (Cairns 1992b). In many cases, anthropogenic impacts on seabird populations cannot be distinguished from the consequences of natural variability in food supplies

(Piatt and Anderson 1996). Thus, 'management' of seabird populations remains an uncertain exercise. For example, how can we enhance recovery of seabird populations lost to the *Exxon Valdez* oil spill if food supplies in the Gulf of Alaska limit reproduction? Would commercial fishery closures reduce or increase food availability to seabirds? What are the minimum forage fish densities required to sustain seabirds, and how do we maintain those critical densities?

We attempted to answer some of these questions in our study of seabird and forage fish interactions in lower Cook Inlet. Upwelling of oceanic water at the entrance to Cook Inlet creates a productive marine ecosystem that currently supports about 2-3 million seabirds during summer. More seabirds breed here than in the entire northeast Gulf of Alaska (including Prince William Sound) and concentrations at sea (up to 90 kg/km^2) are among the highest in Alaska (Piatt 1994). For these reasons, the greatest damage to seabirds from the *Exxon Valdez* oil spill occurred in lower Cook Inlet (Piatt et al. 1990).

Functional relationships between seabird predators and their prey are poorly known because the vast majority of seabird research has been conducted on colonies without benefit of concurrent studies at sea on prey availability and seabird foraging behavior (Hunt et al. 1991). The response of seabirds to environmental change can vary widely among species, and is influenced by a host of physical and biological factors. Differential adaptations of seabirds for exploiting plankton and fish, widely-varying foraging abilities and breeding strategies, and complex relationships between oceanography and prey dispersion, abundance, and behavior all serve to complicate our interpretation of changes in seabird population biology. Therefore, in order to assess the potential for recovery of seabirds affected by the *Exxon Valdez* oil spill, a concurrent, multi-disciplinary study of oceanography, forage fish, and seabirds was required.

Coordinated studies of seabird breeding biology and feeding ecology in relation to local prey abundance are remarkably few (for examples, see Safina and Burger 1985, 1988; Monaghan et al. 1989, 1994; Hamer et al. 1991, 1994; Uttley et al. 1994). Following a collapse of capelin stocks and concern about the possible consequences for Atlantic Puffins (*Fratercula arctica*) (Brown and Nettleship 1984), detailed studies of the relationships between oceanography, capelin (*Mallotus villosus*), cod (*Gadus morhua*), common murres (*Uria aalge*), Atlantic puffins and baleen whales were conducted in eastern Newfoundland in 1981-1985 (Montevecchi and Piatt 1984, 1987; Piatt and Nettleship 1985; Burger and Simpson 1986; Schneider and Piatt 1986; Cairns et al. 1987, 1990; Piatt 1987, 1990; Schneider and Methven 1988; Methven and Piatt 1989, 1991; Piatt et al. 1989; Schneider 1989; Burger and Piatt 1990; Schneider et al. 1990; Nettleship 1991; Piatt and Methven 1992).

Results of these studies provide an empirical basis for hypotheses about relationships between seabirds and their prey in a variable marine environment (Table 1.1). Relationships between population biology and feeding ecology can be quantified within an established framework of predation theory (Holling 1959; Murdoch and Oaten 1975; Piatt 1987). Adult survival, reproductive success and population growth (the "numerical response") of higher vertebrates depends largely on the rate at which food (energy) can be extracted from the environment (the "functional response").

For individual seabirds, the functional response incorporates all parameters relating to the capture of prey (Table 1.1). Studies have demonstrated or hypothesized that these parameters are non-linear functions of prey density that operate over time-scales of hours to days, and spatial scales of meters to kilometers. For example, foraging time declines with increasing prey density (Cairns et al. 1987; Monaghan et al. 1989, 1994) allowing more free time for other activities (Burger and Piatt 1990). Similarly, as prey densities increase, foraging ranges may contract by 10's of km (Cairns et al. 1990; Monaghan et al. 1994) resulting in a considerable reduction in foraging energy expenditure (Cairns et al. 1987) and greater prey harvests in the vicinity of colonies (Cairns et al. 1990).

Numerical response parameters for seabirds (Table 1.1) are, in the absence of stochastic mortality events (e.g., oil mortality), a direct function of food availability over longer time scales (months and years) and larger spatial scales (100's to 1000's of kilometers). Thus, population change in seabirds reflects day-to-day foraging success integrated over reproductive time-periods and the area over which populations are distributed (Cairns 1987, 1992a,b; Piatt 1987).

The numerical and functional responses of individual species to changes in prey density are almost always non-linear, frequently sigmoidal, and species-specific with regard to absolute density thresholds (Holling 1959; Murdoch and Oaten 1972; Piatt 1990; Piatt and Methven 1991). In other words, some seabird species may prosper at low levels of prey density while others require much higher densities (Piatt 1987, 1990). Cairns (1987) further hypothesized that components of the numerical and functional response in individual species of seabirds are sensitive to different levels (thresholds) of prey density. For example, adult survivorship is probably quite high over a wide range of medium to high prey densities, but at some low, critical level, adult survival diminishes rapidly. In contrast, when seabirds are constrained to forage locally during the breeding season and food demands are high (for both adults and chicks), then moderate to high prey densities are required to maintain high breeding success.

Some species may be able to buffer against variation in their numerical and functional response by adjusting their foraging effort as prey densities fluctuate (Piatt 1987, 1990; Burger and Piatt 1990; Uttley et al. 1994; Monaghan et al. 1994). Other species may have little buffering capacity because they are pushed to their limits even under normal circumstances (Goudie and Piatt 1991; Hamer et al. 1994). Thus, in some species (e.g., murres), chick feeding rates or breeding success may not be affected over a wide range of prey densities because adults simply spend more time foraging to compensate for the change in prey density. Components of numerical and functional responses that may be buffered (Table 1.1) are therefore less sensitive indicators of prey fluctuations (Burger and Piatt 1990).

Numerical and functional responses are scale-dependent, and may be evident only when examined over appropriate temporal or spatial scales (Schneider and Piatt 1986; Piatt 1987, 1990). Weather, wind, and oceanographic processes profoundly influence the biology and distribution of prey species (Schneider and Methven 1988; Methven and Piatt 1991), and may largely determine the temporal and spatial scales at which seabird foraging occurs (Schneider 1989). Although physical processes can influence the density and availability of prey to seabirds, they should not change the basic direction and form of numerical and functional responses (Table 1.1), and probably have minimal effects on thresholds-- which are largely a species-specific function of seabird body size and behavior (Piatt 1987, 1990; Goudie and Piatt 1991).

The challenge in this project was to measure the form and scale of seabird responses to prey fluctuations in light of variability in the marine environment. Quantifying responses of higher vertebrates in the field can be difficult because of logistical difficulties in measuring key parameters (Goss-Custard 1970), and the lack of power to manipulate predator and prey densities over the full range of possibilities (Piatt 1990). For seabirds, it required the coordination of studies on breeding biology and behavior at colonies, and studies of seabird and prey dispersion at sea in relation to local oceanography.

Objectives

1) To describe and quantify the numerical and functional responses of seabirds (Table 1.1) to seasonal and annual fluctuations in local prey density at three colonies in lower Cook Inlet.

2) To describe spatial distributions of seabirds and prey, and measure the absolute densities of some prey schools, around three seabird colonies in lower Cook Inlet.

3) To test a number of hypotheses (Table 1.1) about how responses of different seabird species vary with regard to prey characteristics and oceanographic conditions.

4) To gather baseline data for future reference in lower Cook Inlet on: i) seabird populations, breeding biology, diets, and distribution; ii) prey distribution, relative abundance, and composition; and, iii) basic oceanographic parameters.

Methods

Specific methods employed for each component of the study are described in detail in each of the following chapters. The general strategy employed for the study is described below.

Measuring Responses: A variety of techniques were used to measure the numerical and functional responses of seabirds to prey density (Table 1.1). The basic elements of the study required:

1) The distribution and abundance of prey species was measured hydro-acoustically (using a Biosonics DT4000 digital echosounder) and with trawls (bottom, midwater) over an area extending at least 45 km away from each of the colonies. (e.g., Piatt 1987, 1994; Piatt et al. 1990a; Hunt et al. 1993). Because potential foraging area increases geometrically with distance from the colony, the areal extent of surveys was chosen to balance the need for sampling of important foraging areas within the range of birds against the practical limitations of time and resources. Fish catches were needed to groundtruth the hydroacoustic surveys, and to assess species and age-class composition of remotely-detected prey schools (Piatt 1987; Schneider and Methven 1988). Prey specimens collected from trawls and seabird chicks were examined to assess prey species composition, sex-ratios, body condition, and energetic content. In addition to trawling, we sampled nearshore fish schools using beach seines, cast-nets and SCUBA transects.

2) Concurrent measures of physical parameters such as wind speed, sea state, sea surface temperature and salinity, and salinity-temperature profiles of the water column (e.g., Schneider and Methven 1988; Piatt et al. 1990a; Hunt et al. 1993).

3) Measuring components of the numerical response (Table 1.1). Most of these parameters were easily measured at the colony by direct observation or measurement (e.g., Gaston et al. 1983; Harris and Wanless 1988; Wanless et al. 1982). Estimating survival was a more time-consuming activity and required the banding and re-sighting of adults in subsequent years (Sydeman 1993; Hatch et al. 1994).

4) Measuring components of the functional response (Table 1.1). Diet components required collection of adult and chick prey items, at colonies and at sea (e.g., Piatt 1987; Burger and Piatt 1990). Study of aggregation behavior required simultaneous surveys of seabird and prey dispersion at sea (Piatt 1990, 1994; Piatt et al. 1990a). Aspects of seabird foraging behavior (range, activity budgets, chick feeding rates) were studied by direct observation of birds at nest-sites (e.g., Monaghan et al. 1994; Uttley et al. 1994).

Study Design: The approach used in this study was to quantify the numerical and functional responses of seabirds at spatial scales ranging from fine (m to km, Gull Island in Kachemak Bay) to moderate (10s-100s km, lower Cook Inlet). Similarly, and where possible, variability in response parameters was measured at small (daily, seasonal) and moderate (annual) temporal scales. At fine and moderate spatial scales, two species of seabird (common murre and black-legged kittiwake) were studied in detail at three different colonies in lower Cook Inlet. Ancillary data were collected on 6 other seabird species. In total, the study included two surface-feeding seabirds (kittiwake and glaucous-winged gull), three pelagic-diving seabirds (common murre, horned and tufted puffins), and three benthic-diving seabirds (guillemot, pelagic and double-crested cormorant).

Some of these species forage mostly near shore (<5 km) whereas others feed more offshore (± 60 km; Piatt 1994).

Studies were conducted at and around Gull, Chisik and Barren islands in lower Cook Inlet (see Fig. 8-1). Gull and Chisik islands provided an excellent contrast for studies of numerical and functional responses because they: i) share a similar suite of breeding species; ii) have markedly different population dynamics (Slater et al. 1994); and, iii) differ in their local oceanographic regimes. Whereas Gull Island seabird populations had increased by 40-80% in the 2 decades prior to this study, Chisik Island populations had declined by similar magnitudes over the same time period. The Barren Islands share a similar suite of species and breeding success had varied between poor and excellent in the 2 decades prior to this study (Manuwal 1980; Roseneau et al. 1994).

Hypothesis Testing: The data gathered from this study on numerical and functional responses of seabirds to variations in prey density (Table 1.1) can be used to test a variety of hypotheses about how seabirds respond to changes in their marine environment. Specific hypotheses will be addressed in peer-reviewed publications. For example, at the largest scales of study, we wanted to know whether long-term changes in forage fish abundance were due to changes in marine climate (Anderson et al. 1994), and whether these changes were responsible for seabird population declines (Piatt and Anderson 1996). Analysis of a 45-year data set on forage fish supports at least the first of these hypotheses (Anderson and Piatt 1999). We have already examined hypotheses about how oceanographic conditions influence prey density and distribution in the water column (e.g., Robards et al. 1999, 2002, Abookire et al. 2000), seabird foraging success (e.g., Litzow et al.. 2000, Harding et al. 2002), and, in turn, the reproductive biology and physiology of seabirds (e.g., Kitaysky et al. 1998, Piatt et al. 1999). Hypotheses about the exact form of numerical and functional responses (Cairns 1987), and differences between species in their responses (Piatt 1990, Goudie and Piatt 1991) will be examined in the preliminary synthesis of chapter 14, and in subsequent publications.

Summary of Results

Populations, productivity, diets and foraging behavior of Common Murres and Black-legged Kittiwakes were studied at three seabird colonies in lower Cook Inlet (Chisik, Gull and Barren islands). Ancillary data were also collected on Tufted and Horned Puffins, Cormorants (spp.) and Glaucous-winged Gulls. Pigeon Guillemots were studied in Kachemak Bay only. Oceanographic measurements, seabird and hydroacoustic surveys, trawls, and beach seines were conducted in waters around (<45 km) each colony. In all years, offshore and southern waters of Cook Inlet were dominated by juvenile walleye pollock, important prey for murres and puffins. Nearshore waters of Cook Inlet were dominated by sandlance, which were consumed by adult kittiwakes and murres in proportion to their local abundance. Both species fed chicks more prey that were rich in fat (e.g., capelin, herring). The CPUE of forage fish in either mid-water trawls or beach seines around Chisik Island was typically 1-2 orders of magnitude less than around the

Barren Islands, with Kachemak Bay yielding intermediate CPUE's. Acoustically-measured forage fish biomass was also lowest around Chisik Island, highest in Kachemak Bay and along the Kenai Peninsula, and moderate around the Barren Islands. Water temperatures throughout the summers of 1995-1999 were similar and near the long-term average, but temperatures in winter of 1997/98 were about 1-2 C higher than in previous years owing to warming from El Niño.

The breeding biology of seabirds differed markedly among colonies owing to persistent geographic differences in forage fish abundance described above. Birds at Chisik Island struggled to reproduce, while those at Gull and Barren islands usually had few problems rearing young. Within each colony, breeding and behavioral parameters were similar among years (1995-1999) with the exception of 1998 when breeding success in all species was lower than in other years; presumably a lingering effect of the previous winters' El Niño event. Murres on Chisik Island nearly failed-- the first time we observed a murre failure at any colony since studies began in 1995. Measures of corticosteroid hormones in 1998 suggested that murres on Chisik were highly stressed even before they attempted to lay eggs in July. A large die-off of murres was observed in Cook Inlet in April and May of 1998, and although most birds affected were subadults, this die-off foreshadowed a poor breeding season. Breeding success of kittiwakes at Gull, Barren and Chisik islands was also lower in 1998 than in any other years, and kittiwakes failed at both Chisik and the Barrens. Population censuses revealed that seabirds at Chisik Island continued in a long-term decline, whereas populations at Gull and Barren islands were stable or increasing. Behavioral studies revealed that seabirds worked harder (longer foraging trips, less discretionary time) at colonies where nearby fish densities were lower (Chisik). Preliminary results of survival studies suggest that the survival rate of adult kittiwakes on Chisik Island was substantially higher on Chisik than Gull Island, while survival of murres appeared to be similar between the islands.

Results showed that seabird parameters (breeding success, foraging effort, population trend, etc.) varied most between islands and relatively little between years. We attribute this regional variability and temporal stability in seabird biology to distinct, persistent oceanographic regimes around each colony that determined the availability of fish to birds within those areas. While each colony responded differently to the ENSO perturbation of 1997/98, responses were commensurate with the underlying physical and biological regime observed in each area. As predicted, the numerical and functional responses of seabirds to food density were non-linear in most cases. For example, kittiwake hatching, fledging and breeding success were all sigmoidal functions of prey density. Breeding success was not correlated with prey density in murres because when food got scarce, murres reallocated discretionary "loafing" time to foraging, thereby buffering the ability to rear chicks under poor feeding conditions. For murres, "loafing" time was a sigmoidal function of prey density. Examination of the response curves for each parameter of breeding in murres and kittiwakes suggests that food supplies at Gull and Barren islands— but not at Chisik— are above threshold limits and are presently adequate to support recovery of losses from the Exxon Valdez oil spill.

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Chapter 2. Oceanography of lower Cook Inlet

Gary Drew and John Piatt

Introduction

Cook Inlet is a broad (ca. 50-100 km) and shallow (mostly <50m) tidal estuary that extends 350 km northeastward from the Gulf of Alaska (GOA) continental shelf (Fig. 2.1). Primary and secondary production in lower Cook Inlet is extraordinarily high (Larrance et al. 1977) and, in turn, this productivity supports large commercial and sport fisheries, thriving marine mammal populations, and some of the largest seabird colonies in the northern GOA. Indeed, more seabirds breed and forage in lower Cook Inlet than may be found along the entire northeast gulf coast, including Prince William Sound (Piatt 1994). This high productivity is in large part a function of the local oceanography and a consequence of persistent upwelling of cold, nutrient-rich gulf waters into the lower estuary (Muench et al. 1978).

Because of this link between oceanography, forage fish and seabirds, we collected some basic oceanographic data on an opportunistic basis as well as on some transects designed specifically for the purpose of examining water mass characteristics in lower Cook Inlet. In this chapter, we present a summary of our findings and a selection of data to illustrate main points. We plan to publish these main findings on oceanography in peer-reviewed journals. In the meantime, oceanographic data collected during this project are being used primarily to characterize habitats used by fish and seabirds, and to help explain temporal and spatial variability in abundance of fish and seabirds in lower Cook Inlet (for example, see Robards et al. 1999, 2002; Piatt et al. 1999; Abookire et al. 2000, 2001, 2002). All oceanographic data collected on the project have been archived and are available for analysis by other investigators.

Background

There have been few dedicated studies of oceanography in lower Cook Inlet, and most work was conducted during the 1970s (Burbank 1977, Larrance et al. 1977, Muench et al. 1978, Schumacher and Reed 1980). Additional information may be found in works on the northern GOA that included some research in lower Cook Inlet (e.g., Royer 1981, 1982, Xiong and Royer 1985, Reed and Schumacher 1986). These few resources are adequate to draw a picture of the important oceanographic processes affecting lower Cook Inlet.

At a coarse scale, Cook Inlet can be viewed as a large inland extension of the continental shelf in the northern Gulf of Alaska (Fig. 2.2). The ocean floor rises from about 5000m to 200m at the shelf break. At this spatial scale, there is little variation in bathymetry on the relatively wide (up to 200 km) continental shelf. The shelf break defines the northerly extent of a counterclockwise rotating subarctic gyre that is responsible for westerly offshore currents (Reed and Schumacher 1986). Offshore water circulation is dominated by the Alaska Current (Alaska Stream) which generally flows parallel to the continental slope. Although the Stream may affect inshore circulation, coastal features seem to be separate, or at least different, than those offshore (Reed and Schumacher 1986).

Closer to the mainland, the Alaska Coastal Current (ACC) drives inshore currents on the continental shelf (Royer 1981). The ACC is primarily a density driven current that reaches peak velocity in the fall coinciding with maximum freshwater runoff from rivers along the gulf coast (Royer 1981, Royer 1982). Winds are also thought to be important in constraining the flow of the ACC in a narrow stream and in producing coastal convergence (Reed and Schumacher 1986).

The persistent, westward-flowing ACC is thought to be the primary factor responsible for summer-long upwelling in lower Cook Inlet (Muench et al. 1978). As the ACC enters lower Cook Inlet, it first must squeeze through Kennedy and Stevenson entrances, and then is pushed up onto the relatively shallow estuary shelf at the mouth of the inlet, and onto shallow shelves around the Barren islands and along the Kenai Penisinsula (Fig. 2.3). Within Cook Inlet itself there is a complex circulatory pattern (Fig. 2.3). In general, there is an inflow of mixed ACC water on the east side, and an outflow of less saline, warm and turbid water along the west side of the inlet. These water masses are separated by a distinct “mid-channel rip” (Burbank 1977). The extent of the northern intrusion of seawater on the east side appears to be a function of tidal mixing (Burbank 1977). Most of the water entering Cook Inlet on the east side traverses the inlet and is carried back out on the west side.

In this chapter, we will present some results of oceanographic investigations in lower Cook Inlet from 1995 to 1999, and compare our findings with those of previous studies. More extensive datasets are summarized in Appendices 2.1-2.21.

Methods

Sea Surface Temperature

Images of sea-surface-temperature (SST) were developed using data from advanced very high-resolution radiometer (AVHRR) sensors aboard NOAA Polar Orbiting Satellites. We have archived hundreds of “good” (relatively cloud-free) images from all years of our study. For this report, we selected the best single images available in the month of July during the years 1995-1999. This period coincided with our annual seabird and forage-fish sampling cruise. Raw AVHRR data was calibrated and georeferenced at the Alaska Science Center and then added to a geographic information system (GIS) for Cook Inlet. We originally used the multichannel sea surface temperature (MCSST) algorithm on the data, but results suggested some electronic contamination in channel 5. Consequently, we used surface temperatures derived solely from channel 4.

Water Profiles

We collected temperature and salinity data during the summers of 1995-1999 using a Seabird Electronics SBE 19 SEACAT Conductivity, Temperature and Depth (CTD) recorder. Density was calculated from temperature and salinity. Prior to data collection in 1998, we modified our CTD by adding a fluorometer (to measure phytoplankton standing crop; Wet Labs Inc., Wetstar) and a turbidity sensor (to measure sediments in the water; D&A Instrument Co., OBS-3). Therefore, all CTD casts conducted in 1998 and 1999 included data from the additional sensors (see Chapter 3). Several hundred CTD profiles were collected in conjunction with mid water trawls (Chapter 4) and on several cross-inlet transects (Fig 2.4). These transects were located near seabird colonies to characterize local marine habitats and they were sampled once annually (1995-1999). In addition, repeated samples were taken at three stations (Fig 2.4), Station Z (1995-1996), Eldred Passage (1997-1999), and Inner Bay (1998-1999) in order to investigate within-year variability in water characteristics and primary production.

Temperature Loggers

One or two temperature data loggers (Onset Electronics StowAway and TidbiT) were placed 3-10m below the low tide line near each of the 3 colonies, Chisik Island (Snug Harbor), Gull Island (Kachemak Bay) and East Amatuli Island (Barren Islands). The loggers were programmed to collect data at regular time intervals (varying from 1 to 15 minutes), and data were averaged by day for analyses presented here. These loggers were placed at each of the study sites in order to provide general information on the timing and magnitude of annual temperature cycles. Additionally, several loggers were placed near spawning sites to provide temperature data during spawning of sandlance, and a pair of loggers was placed at 10m and 100m near Hesketh Island to describe the annual cycle of stratification and mixing in Kachemak Bay.

Other Data

We compiled data on water temperatures from two other sources. Continuously-recorded sea surface temperature data were obtained from a monitoring station situated in Seldovia Harbor, situated a few km from our sampling station at Eldred Passage on the south side of Kachemak Bay (Fig. 2.4). Temperatures have been recorded year-round at this site since 1964, and since 1994, temperature data were collected every hour, 365 days a year. For more information on this data, go to the NOAA web site: http://co-ops.nos.noaa.gov and find ancillary observations for station 9455500. We also compiled data from the GAK1 station off the south Kenai Peninsula (near Seward) in the Gulf of Alaska, where vertical profiles of sea temperature and salinity from the surface to 250 m have been taken regularly since 1971. Both temperature and salinity data can be downloaded from the University of Alaska web site: http://www.ims.uaf.edu:8000/gak1.

Results and Discussion

Geographic Variability in Sea Surface Temperature

Sea surface temperature imagery (Figs. 2.5-2.9) confirms the important elements of oceanography that have been described from *in situ* measurements. On their westward approach to the entrance of Cook Inlet, waters south of the Kenai Peninsula tend to be stratified with relatively warm water at the surface. These warm surface waters— evident in most AVHRR images taken during summer— along with our water profiles in Kennedy Entrance (see following section) and historical data from the existing Gulf of Alaska CTD line (GAK 1; Xiong and Royer 1984) suggest that an extensive low-salinity lens may overlay more oceanic waters over the northern GOA shelf during summer months. As these waters approach the relatively shallow underwater land bridge connecting the Kenai Peninsula with the Barren Islands and the Kodiak Archipelago (Fig. 2.3), cooler waters are upwelled and mixed (Reed and Schumacher 1986). More extensive mixing and cooling of surface layers occurs as the current enters lower Cook Inlet and pushes water up onto the shallow estuary shelf (Figs. 2.5-2.9).

Transport of this cold, upwelled water into lower Cook Inlet— described in some detail by all previous investigators (Burbank 1977, Muench et al. 1978, Reed and Schumacher 1986)— can be clearly seen in all years moving up the east side of the inlet from Kennedy entrance to as much as 50 km north of Kachemak Bay. We observed this pattern in all AVHRR images taken at all times of year, although the east-west and north-south extent of the cold-water plume varied with tide state and time of year. Coastal divergence or upwelling is also clearly evident along the tip of the Kenai Peninsula and around the Chugach Islands (Burbank 1977). Similar coastal upwelling is usually observed around the Barren Islands, and along the northeast coast of Shuyak Island in the Kodiak Archipelago. As noted by Burbank (1977), upwelled surface waters appear to bypass middle and inner Kachemak Bay, which remains stratified during summer. Satellite images support the drogue studies of Burbank (1997) which suggested that the majority of westward transport of northward flowing waters to the western side of Cook Inlet occurs just north of Kachemak Bay. The limit of seawater intrusion into the inlet appears to be just south of Kalgin Island.

AVHRR images also confirm Burbank's (19977) conclusions about oceanography on the west side of the inlet. Water in the upper inlet is warm and stratified during summer owing to the large volume of freshwater entering the upper reaches of Cook Inlet (e.g., from the Matanuska, Susitina, and Kenai rivers). This warm, low-salinity water flows southward (Fig. 2.3) until it meets the northward-moving cold plume, where all waters are pushed to the western side of the inlet and continue to flow southward into Kamishak Bay and then eventually around Cape Douglas and into Shelikof Strait. The boundary between cool, inflowing water and warm, outflowing waters is best seen in Fig. 2.7, and this boundary is always marked by a "mid-channel rip" where these water masses converge and where seaweed, logs and debris are gathered at the surface in extensive rip lines (Burbank 1977). This convergence is strongest during flood tide as the northward intrusion of clear and partially mixed seawater tends to wedge itself between the less dense water west of the mid-channel, and less-dense coastal water that flows north from Kachemak Bay (e.g., Fig. 2.7).

Surface temperatures were generally warmer in 1997 and 1998 (Figs. 2.5-2.9; note that all AVHRR images were constructed with the same temperature scale). Temperatures in these years were influenced by the 1997-1998 El Nino/Southern Oscillation (ENSO) event, the strongest ENSO event on record. The warm sea surface temperature anomalies (SSTA) in the GOA during the spring and summer of 1997 were partly related to concurrent large-scale atmospheric anomalies (Lau 1997). The principal processes involved in producing the warm SSTA were enhanced warm-air advection and insolation as revealed by the anomalous distributions of low-level temperature, geopotential height, relative humidity, and cloud cover (Overland et al. 1999). Warming in winter 1997-1998 was likely due to heat propagation by Kelvin waves, and anomalously warm temperatures were observed in the GOA not only at the surface, but throughout the water column (Royer and Weingartner 1999). It is not clear whether residual effects of this heating account for the warm surface temperatures observed in Cook Inlet during summer of 1998.

Vertical Temperature and Salinity Profiles

AVHRR imagery provides a useful tool for describing the oceanography of Cook Inlet, but subsurface features can only be inferred from satellite images of surface layers. Vertical CTD profiles of the water column allow us to fully characterize water masses and marine habitats in Cook Inlet. From 1995 through 1999, 856 CTD casts were conducted in Cook Inlet (Fig. 2.10). Here we present only results from 3 cross-inlet transects to examine spatial variation in water characteristics, and from one station in Kachemak Bay to examine seasonal variation. Complete sets of spatial and temporal profiles from all permanent stations and years and can be found in Appendices 2.1-2.21. Our 3 cross-inlet transects (A,B, and C; Fig. 2.4) were similar in location to transects described in Burbank (1977) that crossed the inlet just south of Chisik Island ("line 30", Fig. 98 in Burbank 1977), westward from Kachemak Bay ("line 20"), and a dog-leg transect from the Kenai Peninsula to the Barren Islands and across to Cape Douglas ("line 00"). CTD data collected during fishing trawls is being analyzed separately with respect to fish distributions (e.g., Abookire et al. 2000).

Again, our results corroborate findings of previous studies (Burbank 1977, Muench et al. 1978, Reed and Schumacher 1986) and conclusions made from AVHRR images. Cold, high-salinity water enters lower Cook Inlet around the Barren Islands and is generally mixed or weakly stratified at this point (Transect A, Figs. 2.12 and 2.13). This cold, mixed plume extends northward through (Transect B) and past (Transect C) outer Kachemak Bay, becoming a narrow tongue at its northern extent. Waters on the west side of Cook Inlet are stratified, and surface temperatures are 1-2 C warmer than to the east— as revealed in AVHRR images (above). However, CTD profiles reveal the full extent of differences between east and west, as the entire water column in the west is much warmer and much less saline than waters to the east, especially off Kachemak Bay and further north. Furthermore, the convergent front ("mid-channel rip") separating the east and west water masses is prominently situated— as the name suggests— in the middle of Cook Inlet. As noted by Burbank (1977), the higher density GOA water can be seen (particularly in Fig. 2.12) to slide beneath the lower density west-inlet water at the convergent front.

We examined inter-annual variability in temperatures at depth from profiles (Fig. 2.13) across Kennedy Entrance (Transect C)(Inter-annual variability on other transects can be seen in Appendices 2.1 - 2.9). As discussed above, water temperatures were anomalously high in 1997 and 1998. Warm water was mostly near the surface in 1997, and profiles from 1998 indicated that water below 50m was approximately 1-2 degrees C warmer in 1998 than in any other year. These results are consistent with observations elsewhere that surface layers in the North Pacific were affected by ENSO in 1997 through atmospheric coupling ("tele-connection effect"), whereas the entire water column was affected by ENSO through transport effects in winter of 1997-1998 (Overland et al. 1999, Royer and Weingartner 1999). In some years, a surface lens of relatively warm, fresh water was seen to overlay colder, more saline GOA water. We believe that this occurred sporadically as remnants of stratified GOA water entered Kennedy Entrance (e.g., see Fig. 2.7) and before it was thoroughly mixed by turbulent upwelling. Except for very nearshore, we never observed stratification in mixed GOA waters north of the Barren Islands on transects A or B, (Appendices 2.1 to 2.9).

Temporal Variability in Temperature and Stratification

Sites in Kachemak Bay that were sampled with a CTD repeatedly during summer, Station Z (1995-1996), Eldred Passage (1997-1999) and Inner Bay (1998-1999), exhibited similar seasonal patterns in warming and stratification (Appendices 2.15-2.21). We conducted more CTD casts at Eldred Passage than anywhere else, and we use these results to illustrate that Kachemak Bay usually remained well mixed until mid- to late May (Julian date 151 = May 31) when waters became thermally stratified (Fig. 2.15). Waters remained stratified until mid- to late September (Julian date 258 = September 15), which was usually beyond the time we conducted CTD casts in Kachemak Bay. However, continuously recording temperature loggers placed near the surface and bottom at Hesketh Island (near Eldred Passage) clearly indicated when thermal stratification began and ended in Kachemak Bay (Fig. 2.16). When near-surface (10 m) and bottom (>80m) temperatures were the same, then the water column must have been completely mixed and uniform from top to bottom. When stratification developed, then surface and bottom temperatures diverged, usually by about 2-4 degrees C (Fig. 2.16). It is evident, therefore, that mixing events (presumably storms) in late August and September, 1997, nearly eliminated stratification several times until about October 15 (Julian date 288), after which waters remained mixed for the duration of fall, winter and spring. Unfortunately, the surface temperature logger failed in summer 1998 so we cannot assess when stratification developed again in the bay. However, we can see (Fig. 2.16) that mixing and permanent loss of stratification occurred earlier in 1998 than in 1997, i.e., around the first week of September. Waters remained well-mixed throughout fall, winter and spring, and thermal stratification developed rapidly again around June 20 (Julian date 171); evident also from the vertical CTD profiles (Fig. 2.15).

Continuously recording temperature loggers that were placed at our 3 main study sites (Gull, Chisik and Barren islands) corroborated our findings from AVHRR imagery and CTD profiles. Surface temperatures near Chisik Island (Snug Harbor) were about 1-2 degrees C higher than temperatures at Gull Island throughout summer (Fig. 2.17). In turn, temperatures at Gull Island were often more than 1-2 degrees higher than temperature at the Barren islands. Surface temperatures were least variable on a day-to-day basis at Chisik, presumably because waters there are well-stratified and vertical mixing is less vigorous owing to relatively mild winds in this area during summer. At Gull Island, surface temperatures were more variable throughout summer (Julian date 160 – 250 corresponds to June 9 – September 6) than those at Chisik, presumably because of weaker stratification, complex circulation in the bay and variable amounts of freshwater outflow that would all tend to modify the composition and mixing of surface layers in the bay (Burbank 1977). At the Barren Islands, surface temperatures were very consistent on a day-to-day basis until about mid-July, when they became highly variable. Erratic temperature fluctuations after that time may have been related to the appearance and break-up of warm stratified surface layers around the Barrens (e.g., contrast the location of warm surface layer near Barrens in Fig. 2.7 with more distant warm layer in Fig. 2.9).

Data collected at the NOAA tide monitoring station in Seldovia (Fig. 2.18) corroborate our data from temperature loggers in Kachemak Bay, and allow us to examine annual temperature cycles throughout the duration of our study. The seasonal pattern of warming and cooling was remarkably similar among years and— as indicated in logger data as well (Fig. 2.17)— mean summer (Jun-Aug) temperatures at Seldovia varied little (Fig. 2.18A). However, the unusually warm winter (Feb-Apr) of 1998 and cool winter (Feb-Mar) of 1999 are evident in the Seldovia time series (Fig. 2.18B).

Over a larger time scale (1971-1999) it appears that our study was conducted during a warm phase in the Gulf of Alaska (Fig. 2.19). Water temperatures in the Gulf of Alaska have been anomalously warm since the late 1970s, following a marked climatic and biological regime shift that occurred in association with changes in location and strength of the Aleutian low pressure system (Anderson and Piatt 1999). Temperatures in surface layers of the Gulf (GAK1) do not reveal the shift as well as deeper waters (Fig. 2.19). This is because surface layers in the GOA south of the Kenai peninsula are often strongly stratified with a warm, low-salinity surface layer (e.g., Figs. 2.7-2.9) and temperatures may be influenced as much by freshwater runoff, winds and insolation (Royer 1981, 1982) as they are by long-term changes in temperature of the Alaska Coastal Current (ACC). In contrast, bottom temperatures at GAK1 clearly indicate long-term temperature trends in the ACC (Royer and Weingartner 1999). Because stratification of GOA water is broken down by turbulent mixing at the entrance to Cook Inlet, surface water temperatures in Kachemak Bay in general, and Seldovia in particular, seem to reflect temperatures in deep GOA waters during both summer and winter (Fig. 2.19). Conditions during our study (1995-1999) were closer to average than those observed for much of the 1980s, with exception of the 1997-1998 ENOS event, which elevated both surface and bottom water temperatures in the Gulf and in Seldovia (Fig. 2.19).

Conclusions

The physical oceanography of lower Cook Inlet is largely defined by five features: 1) bathymetry of the shallow estuary basin, 2) extreme semi-diurnal tidal oscillations, 3) a persistent current (ACC) that enters Cook Inlet on the east side and pushes cold, saline GOA waters up onto the shallow estuary shelf, 3) a persistent outflow of relatively warm, low salinity water along the west side, and, 4) a persistent convergent front between these water masses in mid-channel. Cook Inlet has the second highest tidal fluctuations in North America, and strong tides can affect rates of current flow, the degree of penetration of upwelled water, and the location and strength of the convergent front (Burbank 1977). Currents in the lower inlet are strongly influenced by constraints of bathymetry and the persistent coastal current. These factors result in upwelling of nutrient-rich GOA waters that is highly predictable in time and space. In turn, this supports high levels of primary productivity and standing stocks of fish, seabirds and marine mammals (as documented in the following Chapters).

In general, our 3 main study areas could be clearly distinguished from each other because of the persistent oceanographic features that defined them. Annual variability within each area was relatively small compared to the oceanographic differences between them. We observed an extreme annual perturbation in the form of the 1997-1998 ENSO, which was the strongest on record (Overland et al. 1999). Although effects of ENSO are greatly attenuated by the time they reach high latitudes of Alaska, we documented some clear changes in oceanography and biology (Piatt et al. 1999, and following chapters in this report). The warm surface waters that we observed in Cook Inlet during 1997 appeared to be the result of an atmospheric tele-connection with the tropics, rather than a direct effect of the ENSO— which was just developing in the central Pacific at that time (Lau 1997, Overland et al. 1999). Effects included a decrease in wind stress and surface mixing, reduced cloud cover and increased insolation; all of which served to increase temperatures at the surface by several degrees (Overland 1999). Although the highest sea-surface temperatures anomalies were observed in 1997, the greatest impact of the 1997-1998 ENSO was felt in Alaska during the winter of 1997-1998 and spring of 1998 when water temperatures were anomalously high— not just at the surface, but throughout the entire water column. Changes to ACC water in the GOA were some of the most extreme on record (Royer and Weingartner 1999). The impact of this ENSO on forage fish and marine birds in Cook Inlet will be documented more fully in future peer-reviewed publications. In this report, our main focus is on the regional differences in biology among study sites that resulted from differences in underlying oceanography.

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Chapter 3. Primary and Secondary Production in lower Cook Inlet

Gary Drew

Introduction

Cook Inlet is one of the most productive marine areas in Alaska (Sambrotto and Lorenzen 1986). Little is known about factors influencing primary and secondary production there— or of linkages with higher trophic-level forage fish and seabirds. Whereas the main objective of our research in Cook Inlet was to study functional relationships between seabirds and forage fish, we managed to collect ancillary (not directly funded) data on primary and secondary production in later years of the project. Sufficient data were collected to describe some spatial and temporal patterns of primary and secondary production— neither of which has been well-documented in lower Cook Inlet. Here we present some preliminary findings of this research with minimal discussion. Results will be written up later for publication in peer-reviewed journals (lower priority than bird and fish papers).

Most of the information on primary and secondary productivity in Cook Inlet comes from research conducted during the 1970s as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP). From these studies, we know that primary productivity in lower Cook Inlet peaks in spring (April-May) but remains high in outer Kachemak Bay throughout summer (Larrance and Chester 1979) owing to a continuous re-supply of nutrients by persistent upwelling in Lower Cook Inlet (Winant and Olson 1976, Larrance et al. 1977). Indeed, production in lower Cook Inlet is often > 1g $C/m^2/d$ throughout summer, yielding annual production levels in excess of 300 g $C/m^2/y$ (Sambrotto and Lorensen 1986). These are high levels of production for an inner shelf, and match or exceed values associated with upwelling regions of the Bering Sea and California Current (Springer and McRoy 1992). Spring and summer populations are dominated by diatoms and microflagellates, with chrysophytes, dinoflagellates and green algae appearing less frequently and in much lower abundance (Larrance et al. 1977). There is a transition in phytoplankton species from west to east across the inlet and a seasonal succession of species as well (Larrance et al. 1977). Phytoplankton standing stocks are probably grazed heavily by zooplankton carried in to lower Cook Inlet by the Alaska Coastal Current (ACC) (Sambrotto and Lorensen 1986).

There is a diverse zooplankton community in lower Cook Inlet. Cross-shelf Ekman flow of oceanic Alaska Stream water and meander of the Alaska Stream/ACC results in zooplankton communities with both coastal and oceanic origins (Damkaer 1977, Cooney 1986). Cooney (1984) calculated that zooplankton of oceanic origin may account for as much as 83% of all zooplankton in shelf and coastal regions of the GOA. The persistent counterclockwise motion of both the ACC and the Alaska Stream assures that species composition is similar in most coastal areas of the northern Gulf of Alaska (GOA) (Cooney 1986). Some of the highest standing stocks of zooplankton in the GOA are found in Cook Inlet during spring and summer, following the spring phytoplankton bloom. Peak densities in excess of 1000 mg/m^3 are not unusual. The high biomass of zooplankton in the northern GOA is important directly as a food source for higher trophic level animals, and indirectly as a food source for larval fishes that, in turn, become prey (Vogel and McMurray 1986).

In this study, we did not have the funding or resources to mount a full-scale study of primary and secondary production in Cook Inlet. However, with minimal additional effort, we were able to sample widely distributed stations for phytoplankton and zooplankton during the course of trawl surveys for forage fish. We also sampled some fixed stations. Our main objective was to assess spatial variation in phytoplankton and zooplankton standing stocks in lower Cook Inlet; ultimately to better understand factors influencing the distribution of seabirds and forage fish. A secondary objective was to assess seasonal variability in phytoplankton and zooplankton standing stocks, and relate this to environmental features (winds, stratification, upwelling, nutrients).

Methods

Phytoplankton

Phytoplankton concentrations were measured two ways: by measuring chlorophyll pigment in samples collected directly from filtered water and by using a chlorophyll pigment sensor attached to a conductivity-temperature-depth (CTD) recorder. Direct collections were made in 1997 at the Eldred Passage station and on the Cook Inlet Transect (Fig 3.1). Eldred Passage and Inner Bay stations were sampled using a CTD-mounted sensor throughout the summers of 1998 and 1999 at approximately one-week intervals. The Cross Inlet transect was sampled once each summer, in July of 1997, 1998 and 1999, using a CTD-mounted sensor.

For collections, we used a Niskin bottle to obtain water samples at the surface, 5 m, 10 m, 25 m, and 50 m. Water samples were filtered for coarse debris and a one-liter sample was stored in blacked-out nalgene bottles for later filtration. Within a few hours, samples were subjected to vacuum filtration in a darkened room to isolate phytoplankton from the sample. Filter disks were frozen and sent to the University of Alaska-Fairbanks for analysis. Samples from the Cook Inlet Transect were treated similarly, except that we collected only from 10 m depths at each station, and samples were cooled in ice until they could be filtered. Samples from 1998 were analyzed for phytoplankton chlorophyll concentrations by Peter McRoy at the University of Alaska-Fairbanks (UAF). A lack of dedicated funds precluded analysis of samples from subsequent years.

We validated results obtained using the fluorometer with results obtained from sample collections (above) at Eldred Passage during 1998. As the fluorometer proved an accurate and convenient tool for measuring phytoplankton abundance, we used it exclusively for that purpose in 1999. We used a WETStar fluorometer (WET Labs Inc.) attached to our SBE 19 CTD Profiler (Seabird Electronics Inc.). Flurometry data was downloaded from the CTD with other data from the profiler.

Nutrients

Water samples for nutrient analyses were collected throughout the summer of 1997 at the Eldred Passage station and along the Cross Inlet Transect in June (Fig. 3.1). Nutrient samples were also collected from the Eldred Passage and Inner Bay stations in 1998 and 1999. After filtering out phytoplankton from water samples (above), a 50 ml subsample was extracted from the water sample, labeled and frozen for future analysis. Samples from 1997 were analyzed for total nitrates, ammonia, silicates and phosphates by Peter McRoy at the University of Alaska-Fairbanks (UAF). A lack of dedicated funds precluded analysis of samples from subsequent years.

Zooplankton

We began collecting zooplankton in 1997. Samples were collected opportunistically at most mid-water trawl stations (see Chapter 4), seasonally at Eldred Passage and Inner Bay stations, and at all stations occupied during CTD transects across portions of Cook Inlet (Fig 3.1). Eldred Passage was sampled throughout the summers of 1997-1999. The Inner Bay station was sampled throughout the summers of 1998-1999. The Cross Inlet transect was sampled once each summer, in July of 1997, 1998 and 1999. The transect was lengthened slightly in 1998. This is the only transect that provides us with simultaneously-collected data on spatial variation in oceanography, nutrients, phytoplankton and zooplankton.

Zooplankton were collected using a plankton ring net with a 60 cm diameter mouth opening. The net was 3 m long and had a mesh size of 333 µm. Tows were all conducted vertically, from a depth of 50 m in most instances, or from 5 m off the bottom where the bottom was <50m deep. Samples were rinsed out of collection buckets with a minimum of seawater and then fixed with a 1 to 1 mix of 10% formalin, yielding a final formalin concentration of 5%. Settled volumes were measured on all samples at the Alaska Science Center. More recently, zooplankton samples have been analyzed for species composition and abundance. However, results of this work are not yet completed.

Results and Discussion

Phytoplankton biomass varied among years and areas, but with such a short time series, we can draw few conclusions from these data. One consistent feature, however, was the lack of phytoplankton biomass in the western half of lower Cook Inlet (Figs. 3.2). Standing stocks of phytoplankton were highest in stratified waters (Chap. 2 and Appendices) of outer Kachemak Bay in most years, although high production was observed in mixed waters off Kachemak Bay in 1998 (Fig. 3.3). These results are consistent with previous observations of Larrance and Chester (1979). The west side of the inlet is relatively depauperate in phytoplankton owing to high sediment loads in the water (see also Appendices 2.7-2.9) that prevent light from penetrating surface layers, thereby severely limiting phytoplankton productivity (Larrance et al. 1977). Analyses of water samples collected on our cross-inlet transect of 27 June, 1997, confirmed the cross-inlet pattern of phytoplankton distribution observed with the fluorometer and demonstrated that low concentrations of phytoplankton on the west side were not due to nutrient depletion (Fig. 3.4).

As demonstrated in time-series data from two stations in Kachemak Bay, phytoplankton production began in late April to early May (Fig. 3.4). Peak blooms were generally early in the season, though substantial levels of phytoplankton biomass were present until the end of August in 1998. Following stratification in early June (see Chapter 2 and Appendices 2.17-2.21), most production occurred in the upper 30m of the water column (Fig. 3.4). There were multiple peaks in phytoplankton biomass over the summer, presumably after nutrient supplies were replenished following storm-induced mixing of the water column. We collected data on nutrient concentrations in 1997 at Eldred Passage (Fig. 3.6), but unfortunately the corresponding phytoplankton samples were lost. Nonetheless, these data indicate that significant depletion of nutrients occurs in surface layers at Eldred Passage during summer, particularly nitrates and silicate. Alternatively, differences in the timing of various phytoplankton species blooms may also have been a factor.

More than 200 zooplankton samples were collected throughout lower Cook Inlet at each fish trawl station (Chapter 4), on CTD transects and at fixed stations in Kachemak Bay (Fig. 3.5). Zooplankton standing stocks were generally highest in stratified waters of outer Kachemak Bay (Fig. 3.5) in all years. In 1998, however, zooplankton biomass was exceptionally high in the area of cold-water upwelling outside Kachemak Bay; coinciding with the high measurements of chlorophyll-a made on the same transect (Fig. 3.8). Zooplankton biomass was similarly correlated spatially with phytoplankton biomass on the cross-inlet transect in 1997 and 1999 (compare Fig. 3.8 with Fig. 3.3).

Zooplankton standing stocks varied seasonally also, exhibiting peaks in biomass from mid-May to mid-June (Fig. 3.9). Zooplankton biomass grew quickly and peaked at about the same time that phytoplankton biomass was peaking in stratified waters of Kachemak Bay (Fig. 3.5). Zooplankton biomass at Eldred Passage and Inner Bay stations exhibited similar patterns in abundance within each season (Fig. 3.5).

In summary, our findings corroborate those of Larrance et al. (1977) from 20 years earlier. The key to initiation of a phytoplankton bloom in lower Cook Inlet is stratification of the water column. In addition, water transparency must be adequate to permit 1% of the light incident to the surface to penetrate deeper than about 10m (Larrance et al. 1977)— a constraint that severely limits phytoplankton production on the west side of Cook Inlet. As summer progresses and stratification further develops in Kachemak Bay, nutrient depletion begins to limit phytoplankton production. Phytoplankton blooms may occur repeatedly during summer following storms or advection of nutrient-rich surface waters into Kachemak Bay (Larrance et al. 1977). Outside of Kachemak, but still east of the mid-channel rip (Chapter 2), mixing and water exchange are more frequent. This results in high nutrient loads all summer and allows for potential blooms to occur at any time in mixed waters, such as we observed in July of 1998. In turn, persistently high levels of phytoplankton production support a large standing stock of zooplankton in lower Cook Inlet during spring and summer (Cooney 1986). The areal distribution of zooplankton also reflected that of phytoplankton with high standing stocks in mixed waters on the east side, and a generally low biomass in waters west of the mid-channel rip. We have not completed our analysis of zooplankton species composition and biomass. Final results will be available by April of 2002, and we expect to compile and publish our findings within a year or two after that time.

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Chapter 4. Abundance and Distribution of Pelagic Forage Fish in Cook Inlet

Alisa Abookire and John Piatt

Introduction

We undertook a study of forage fish primarily because of their ecological role in supporting populations of marine birds at our three study colonies in lower Cook Inlet. We wanted to know where fish were concentrated in lower Cook Inlet and which species were most common. The term "forage fish" is generally applied to abundant, schooling fishes that serve as prey for a variety of marine mammals, seabirds and larger fishes. The most abundant forage fishes in the Gulf of Alaska are Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), Pacific herring (*Clupea pallasi*), juvenile walleye pollock (*Theragra chalcogramma*) and lanternfishes (Myctophidae)(Springer and Speckman 1997). Most of these fishes occupy pelagic habitats and are best sampled with mid-water trawl nets. We therefore used a modified herring trawl to collect forage fish around our three study colonies. These samples provided us with information on the distribution, relative abundance and species composition of fish schools in the study area, and served to corroborate hydro-acoustic data on fish abundance (Chapter 7). In addition, trawl collections were subsampled to assess the size-class of fishes available to predators.

Forage fish populations undergo fluctuations in abundance at a variety of temporal and spatial scales (Bechtol 1997, Anderson and Piatt 1999). Most pelagic forage fish have relatively short life spans. Populations are prone to fluctuate rapidly owing to early maturation, high fecundity, high rates of predation and sensitivity to habitat degradation (Anderson and Piatt 1999). Irrespective of changes in abundance, populations may also shift their distributions with short- and long-term changes in the marine environment (Cushing 1995). While we know how some species are distributed with respect to environmental gradients (e.g., Swartzman et al. 1992, 1994), little is known about habitat preferences of forage fish in Alaska. Species that are sensitive to environmental perturbation include Pacific herring and capelin because both have relatively specialized intertidal or shallow subtidal spawning sites (Meyer 1997). Whether due to direct effects of oil, or other environmental factors that predate the *Exxon Valdez* oil spill in 1989, a reduction in abundance of fatty forage fishes is believed to be limiting the recovery of seabirds in the Gulf of Alaska (Piatt and Anderson 1996). When we initiated our study, however, it was not clear which forage fish species were commonly available to seabirds in the Gulf of Alaska.

Therefore, some primary objectives of this study were to: 1) measure the relative abundance of forage fishes within foraging range of seabirds at three colonies in lower Cook Inlet, 2) assess the species composition of forage fish schools in each of the three study areas, and, 3) assess the spatial distribution (both vertical and horizontal) of the common forage fish species in each area, and relate distribution to environmental characteristics. This report provides preliminary results that address each of these objectives. We will continue to analyze trawl data in the future, including statistical evaluation of temporal and spatial patterns of abundance, and of relationships between forage fish and their habitats. We plan to publish several peer-reviewed papers on the ecology of forage fish in lower Cook Inlet in addition to papers already completed that have used these trawl data (Robards et al. 1999b, Abookire et al. 2002).

Methods

Fish collections

We conducted 241 mid-water trawls in lower Cook Inlet during the summers of 1996-1999. Trawling was concentrated within a 45 km foraging range of three seabird colonies in lower Cook Inlet: the Barren Islands, Gull Island in Kachemak Bay, and Chisik Island (Fig. 4.1). Trawls (n=213) were done in conjunction with systematic hydro-acoustic surveys of forage fish around each seabird colony (see Chapter 7, and Fig. 7.5 for details on survey tracks) and were conducted during July 16-25, 1996; July 19 - August 2, 1997; July 21 -August 9, 1998; and July 25 - August 11, 1999. On these surveys, we trawled only where significant sign of fish biomass was noted with the hydro-acoustic echosounder. Fish abundance was recorded with a Biosonics DT4000 echosounder using a 120 kHz transducer. Acquisition threshold was set at –70 dB. When a significant fish sign was detected on the echosounder we drove over the entire signal and then returned to the location where the signal began and towed a mid-water trawl through the hydroacoustic signal. We fished some or all of the acoustic signal, depending on strength of targets while fishing. Of the 213 trawls on acoustic sign, only 159 were considered “good” trawls, suitable for interspecies and interannual comparisons of catch-per-unit-effort and percent composition. In addition, we conducted 23 trawls in Kachemak Bay and near Chisik Island on 20-25 June, 1997. These extra trawl data, and “poor” trawls from above, are used here only for the purpose of examining species distributions, and not for interannual comparisons.

We fished from the R/V *Pandalus*, a 22 meter stern trawler. The mid-water trawl was a modified herring trawl with a 30 foot-wide mouth and a 1/8” cod-end liner with a plastic 1000 µm mesh collecting bucket. Tow duration varied among years. In 1996, the average tow duration was 25 minutes. In order to catch more single-species schools and to better coordinate hydroacoustic signal with catch, we decreased the tow duration to 15 minutes in 1997 and 10 minutes in 1998 and 1999. A transducer was mounted on the headrope and used at all times to determine the depth of the net. A Temperature Depth Recorder (TDR, Wildlife computers model # MK7) was mounted on the headrope and used during every tow to determine the exact depth of the net while fishing (Appendix 4.1). Tow start and end time and location were recorded with a Global Positioning System unit when trawl doors were at the water surface. Each tow was flagged as good (G), questionable (Q), or bad (B) based on efficiency of gear and presumed success in catching the acoustic target. In some cases— such as around Chisik Island— we trawled areas with little or no acoustic sign. Catch-per-unit-effort (CPUE) was calculated as the number of fish captured per 1000 m trawled (for CPUE of all species, see Appendices 4.2-4.4). Distance of trawl was determined from GPS readings of position taken at the start and end of the trawl.

Fish measurements

All fishes were identified, counted, and fork length was measured (to the nearest 1 mm) with an electronic Limnoterra Fish Measuring Board (FMB). If >100 individuals of the same species were captured in a single tow, a random subsample of 50 to 100 was measured. After each tow, the total weight of all fish comprising each species was measured with a Pesola scale aboard ship. Individual fish weights were taken in a variety of ways. In 1996 no fish were weighed. In 1997 individual fish weights were taken aboard the ship with Pesola scales. In 1998 and 1999, at least 30 individual fish per size-class of each species were frozen and weighed on land (after thawing) with an Ohaus electronic scale.

For each study area, 50 fish specimens of each species and size-class were archived (frozen individually in whirl-pak bags) for later use in seabird feeding studies or analysis of fish energetics, stable isotopes, or genetics. Larval fishes were preserved in 5% formalin for possible further identification. Beginning in 1997, jellyfish, euphausids, and shrimps were weighed and squids were counted (Appendix 4.5). Euphausids and squid were also frozen for energetics and fixed in 5% formalin for identification.

Statistical analyses of fish data

Shannon-Wiener Index of Diversity (Krebs 1989) and species richness (the total number of species) were calculated for mid-water trawl data by year and area. Length-frequency histograms and length-weight regressions were calculated for the following common species: Pacific sand lance, Pacific herring, walleye pollock, capelin, Pacific cod (*Gadus macrocephalus*), longfin smelt (*Spirinchus thaleichthys*), pink salmon (*Oncorhynchus gorbuscha*), and Pacific sandfish (*Trichodon trichodon*). These species were chosen because each one comprised at least 5% of the species composition in one area-year (see Table 4.2). Length-frequency histograms were binned into 5 mm fork-length intervals, using data combined from all areas and years. Log(length) versus log(weight) linear regressions were calculated for the common species above (Appendix 4.6).

Results

Relative abundance

A total of 266,446 fish were captured in 159 “good” tows. There was an order of magnitude difference in relative catch rates of forage fishes among the three areas. Overall CPUE was highest at the Barren Islands (3264 ± 1018 fish/km), moderate in Kachemak Bay (1180 ± 373 fish/km) and lowest near Chisik Island (238 ± 78 fish/km). In general, this pattern of relative catches among areas was consistent among years (Fig. 4.2), except in 1999 when CPUE was similar at the Barrens and Kachemak Bay. The high CPUE observed at the Barrens was due mostly to high catches of sand lance recorded near the Kenai Peninsula (inside of the Chugach Islands) rather than to catches in open waters around the Barrens. Indeed, variability in catch of sand lance among years accounted for most (r^2=0.94) of the variation in total CPUE among years (Table 4.1).

Catch composition

Sand lance were the most common (71%) forage fish caught in mid-water trawls in lower Cook Inlet. While they were occasionally superceded in importance by other species in some years, they comprised the highest proportion of catches over all years combined, and in all three study areas (Figure 4.3). Other abundant fishes in the Cook Inlet study area were Pacific herring (18%), walleye pollock (8%) and capelin (2%). In general, differences in catches among the three colony areas persisted among years. Fish schools in the Barrens sampling area often consisted of single-species aggregations; for example pollock or capelin offshore and sand lance or herring nearshore. Similarly, catches in Kachemak Bay were often dominated by one or two species (especially sand lance). In contrast, we rarely recorded single-species fish catches near Chisik Island. Mid-water catches near Chisik were usually small, and, while they were often dominated by one species (e.g., sand lance, pollock), they usually also included many other species such as capelin, longfin smelt, salmonids, pricklebacks (*Lumpenus* spp.), larval flatfishes (Pleuronectidae), and pacific lamprey (*Lampetra tridentatus*). Chisik exhibited the highest species richness, with more than twice as many species caught there than at the Barrens. Species diversity was also highest at Chisik (Table 4.2).

Fish size

Most species captured in the mid-water trawl were “forage size” (i.e., defined by us as fish smaller than 200 mm in length because they are suitable for eating by seabirds). The majority of walleye pollock, Pacific cod, and other gadoids captured in lower Cook Inlet had fork lengths <100 mm, with uni-modal size distributions representing only young-of-the-year (YOY) age-classes (Figure 4.4). Similarly, we caught only YOY salmon. Walleye pollock with lengths >200 mm (n=313, up to 616 mm in length) were captured almost exclusively in Kachemak Bay. Three size classes of herring were captured (Figure 4.4) that corresponded to different age-classes (Stokesbury et al. 1999): young-of-the-year (size < 80 mm), one-year olds (ca. 80-150 mm) and older adults (150-200+ mm). The largest herring captured were 255 mm in length. Most adult herring were captured in Kachemak Bay; only one was captured near Chisik and none at the Barrens. Sand lance captured in trawls included mostly y-o-y (<90 mm), but also some one-year-old (1+, ca. 90-130 mm), 2+ (ca. 125-145 mm) and older age-classes (Robards et al. 1999a,c). Capelin and longfin smelt size-frequencies were bimodal, suggesting mostly YOY and 1+ age-classes, as well as a few older fish. Pacific sandfish are relatively slow-growing, and catches included a few aged 1-2 (<100 mm), but mostly fish aged 3-6 years (Paul et al. 1997). The largest sand fish caught was 232 mm in length. Length-weight regressions for all common species (areas and years combined) are provided in Appendix 4.6.

Distribution

In order to assess patterns of vertical distribution we examined depths at which fish were caught, using data combined over all years and areas. Highest catches of sand lance, juvenile herring, eulachon and longfin smelt were recorded in surface waters less than 40 m in depth (Fig. 4.5). There were occasional catches at 40-80 meters involving 1000s of sand lance. Non-juvenile forage-size herring (80-200 mm, see Fig. 4.4) were most abundant at depths of 40 to 50 m. Walleye pollock and capelin were distributed throughout the water-column, but largest catches were concentrated at depths greater than 40 m. Similarly, juvenile Pacific cod were caught at all depths, but were most abundant at depths less than 40 m.

To assess the geographic distribution of species, we plotted CPUE of all common fishes at each station we trawled in lower Cook Inlet. The highest CPUEs for all species combined were associated with the cold core upwelling area (see Chapter 2) between the Barrens and outer Kachemak Bay and with coastal areas of the Kenai Peninsula, including the shores of Kachemak Bay (Fig. 4.6). Species were segregated into different geographic areas. Sand lance and herring tended to concentrate in coastal areas and in the northern part of the study area (Fig. 4.6). Pollock and capelin were more abundant offshore and in the southern part of the study area (Fig. 4.6). Other common taxa showed a distinct preference for either Kachemak Bay or Chisik Island waters (Fig. 4.7-4.9). Jellyfish were widely abundant in the cold core area (Fig. 4.9).

Conclusions

Abundance and species composition of forage fish schools differed among the three study areas of lower Cook Inlet. Fish were an order of magnitude more abundant around the Barren Islands and in Kachemak Bay than they were around Chisik Island. However, CPUE data must be interpreted cautiously because trawl locations were not random; they were selected on the basis of having exceptionally strong acoustic targets. While we believe that the inter-area comparisons of relative abundance are probably of correct magnitude and direction, we have less confidence that inter-annual variability within each study area reflected real temporal trends. Temporal fluctuations were best measured on hydro-acoustic surveys (Chapter 7).

Catches at the Barrens were typically dominated by one species of forage fish; usually sand lance or juvenile herring near the coast, and juvenile pollock offshore. Species richness was lowest at the Barrens. In contrast, waters around Chisik typically contained small, mixed-species schools of fish and this was reflected in high species richness and diversity of catches. Kachemak Bay was more moderate in its abundance and diversity of species. Spatial patterns in the mid-water forage fish community of Cook Inlet mirror those found in the near-shore fish community (Robards *et al.* 1999b), presumably for the same reason. Productivity of phytoplankton, zooplankton— and apparently fish— is enhanced in eastern lower Cook Inlet by upwelling of nutrient-rich Alaska Coastal Current waters into the lower inlet and outer Kachemak Bay (Chapters 2, 3).

Sand lance abundance in lower Cook Inlet increased dramatically in 1998 and high catches were sustained in 1999. We speculate that this have been related to the El Niño-Southern Oscillation (ENSO) event of 1997-1998. Effects of the ENSO were felt most strongly in Cook Inlet during the winter (late January through April) of 1998, when SSTs were as much as 1-2 º C warmer than normal (see Chapter 2). Sand lance spawn in October and larvae hatch by late December (Robards *et al*., 1999c). Therefore, the warmer ENSO waters in winter 1998 may have enhanced sand lance growth and survival during winter, and subsequent abundance during the following summer. We have begun to consider the biological impacts of the 1997-1998 ENSO in lower Cook Inlet (Piatt et al. 1999) and plan to explore the data further to assess impacts of the ENSO event on fish growth, recruitment and community composition.

Differences among forage fish species in their vertical distribution in the water column and proximity to different seabird colonies should have important consequences for seabirds. In particular, sand lance is most abundant near the surface and occurs in close proximity to Gull Island in Kachemak Bay, and to a lesser extent in proximity to seabirds from the Barrens (if they fly to the Kenai Peninsula). In contrast, pollock and capelin are found most often at depths greater than 30 m, and in abundance just north of the Barrens. We examine how adult seabird diets and meals delivered to chicks reflect this regional pattern of forage fish availability in Chapters 9, 10, and 14. Presumably, inter-species differences in vertical and inlet-wide distribution of forage fishes reflect differences in habitat choice among species. In future publications, we will be looking at how different species are distributed with respect to environmental variables such as temperature, salinity, bottom depth, distance to shore, zooplankton biomass, etc. (e.g., Swartzman et al. 1992, 1994; Abookire et al. 2000, 2002).

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Chapter 5. Abundance and Distribution of Nearshore Fish in lower Cook Inlet

Martin Robards and John Piatt

Introduction

Inshore habitats are routinely used by a variety of small forage fish (e.g., capelin *Mallotus villosus* and sand lance *Ammodytes hexapterus*) both for spawning and feeding during summer. The near shore zone also serves as an important nursery area for juveniles of many large marine fish species (Poxton *et al.* 1983, Orsi and Landingham 1985, Bennett 1989, Blaber *et al.* 1995, Dalley and Anderson 1997). Aside from the commercial importance of these large species (e.g., Pacific salmon [*Oncorhynchus spp.*], walleye pollock (*Theragra chalcogramma*), and herring [*Clupea pallasi*]), their juvenile age-classes can also serve as important forage for marine predators in Alaska. Declines in a variety of predator populations in the Gulf of Alaska have been linked to shifts in abundance and composition of forage fish stocks over the past 45 years (Francis *et al.* 1998, Anderson and Piatt 1999). In order to examine the relationship between seabirds and forage fish more closely, we studied variability in abundance and composition of nearshore fish communities in areas used by breeding seabirds in lower Cook Inlet.

Studies conducted elsewhere have shown that nearshore fish assemblages can change markedly over time (e.g., Horn 1980, Allen 1982, Nash and Gibson 1982, Nash 1988, Bennett 1989), but little was known about temporal or spatial variation of nearshore fishes in Alaska prior to our study. Therefore, one of our primary objectives was to assess variability in abundance, distribution and diversity of nearshore fish communities in three oceanographically distinct areas of lower Cook Inlet. Ultimately, we will use these data to assess prey availability to marine birds and to better understand factors influencing seabird population biology (e.g., Litzow et al. 2000, 2002). Data collection in the first few years of study was also focused on the biology of sand lance (Robards *et al.* 1999b,c, 2002), one of the single most important forage fish in northern oceans (Robards et al. 1999d). We have published some important results of our nearshore fish research, showing variability in nearshore fish communities over time-scales of decades, years, months and days (Robards et al. 1999a). Species composition and CPUE of seine catches also differed significantly with tides and time of day. Geographic differences in oceanography also influences the distribution and abundance of forage fish schools within lower Cook Inlet (Robards et al. 1999a), and at smaller spatial scales within Kachemak Bay (Abookire et al. 2000).

In this report, we summarize some of the important results of our nearshore forage fish study; documenting the abundance, diversity and distribution of forage fish near shore in lower Cook Inlet. We will continue to analyze and publish results of our nearshore fish research, both for its importance in understanding nearshore fish ecology, and as vital background information to our studies of seabird foraging ecology in lower Cook Inlet.

Methods

Study Sites and Habitats

Kachemak Bay lies along the southeastern shore of Cook Inlet. The bay is 38 km wide at its entrance and 62 km long. The upper 6 km consists of mud flats that are exposed during low tide. Depths are relatively shallow, ranging from about 35 to 90 m, with some deeper areas (100 to 165 m) present off Gull Island along the south-central side of the bay. Water entering the bay originates from the Gulf of Alaska and is largely oceanic (Burbank 1977). Chisik Island, on the western side of Cook Inlet, is situated at the mouth of Tuxedni Bay and receives freshwater from local glacier-fed rivers. Water passing outside the island is also relatively fresh because it receives significant glacier-fed input from large rivers at the head of Cook Inlet (Burbank 1977, Feely and Massoth 1982). Nearshore habitats around Chisik Island contain few sandy substrates and consist primarily of glacial silt and mud flats interspersed with rocky substrates that are exposed at low tides. Near the entrance to Cook Inlet, the Barren Islands are in a transition zone between deep Gulf of Alaska waters and the shallow Cook Inlet estuary. The Alaska Coastal Current enters Cook Inlet north of the Barren Islands, leading to intense upwelling of cold, nutrient-rich waters onto the shallow southeastern Cook Inlet shelf (Burbank 1977). Because of the upwelling and strong tidal action, waters in this area are turbulent and well mixed.

Field Collections

We used beach seines to sample nearshore fish communities. These nets effectively and non-selectively sample shallow, inshore waters with sandy or smooth bottoms (Cailliet *et al.* 1986). Thirty meters of rope were attached to the ends of each net for deployment and retrieval. Nets were deployed from a small boat and set parallel to shore, about 25 m from the beach as described by Cailliet *et al.* (1986). The net was then retrieved by hauling on both end ropes until the net was pulled ashore. Samples were collected about every two weeks in Kachemak Bay during May - September, and once per month throughout the winter of 1996 and 1997 (Table. 5.1). Samples from Chisik Island and the Barren Islands were collected every two weeks for the duration of their respective field seasons. To standardize comparisons among sites and years, we used data collected only between 1 June and 31August in each year for analyses presented in this report. An archived beach seine database contains results of all other sets made in these three areas.

We used slightly different beach seine nets among different locations and years due to ongoing design modifications and/or logistic constraints. While these differences undoubtedly introduced some variability in CPUE into our catch results, we believe that among-net differences in catch efficiency were small relative to among-site differences (but see below). All nets were basically the same, having: 1) a symmetric design with deepest vertical netting at the center and shallowest netting at the two ends, 2) a deeper, center panel of net with 3-6 mm stretched mesh, 3) two tapering wing panels with 6-13 mm stretched mesh on each side of the center panel. We used four different nets, and they differed mostly in their dimensions rather than design. In the following, we present in order for each net: Depth at center, depth where wings meet center panel, depth at end of wings, length of total net, length of wing panels, length of center panel, stretched mesh size of wing panels, stretched mesh size of center panel. Measurements of net dimensions varied slightly with when they were measured (at purchase, after use in field, among years) and by whom they were measured. The “Kachemak” (K) net (3.9m, 3.3m, 2.2m, 44m, 14.7m, 14.7m, 6-13mm, 3mm) was longer and shallower than other nets, and had a small mesh (3mm) strip running along the entire bottom of the net. The “Puget Sound” (P) net was the most shallow (2.4m, 2m, 1m, 37m, 18m, 1m, 6mm, 3mm). The “Apex” (A) net was deeper in the middle and wings (5.4m, 4.4m, 1.5m, 35m, 13m, 9m, 6mm, 3mm). The “Chisik” net (C) was of similar depth to A, but half the length of nets A or P (5.5m, 4.5m, 1.4m, 18m, 6.7m, 4.5m, 6mm, 3mm).

Net “K” was used in Kachemak Bay in 1995-1999, and at Chisik in 1995. Net “P” was used at the Barrens in 1996 only, and net “A” was used there in 1997-1999. Net “A” was used at Chisik in 1996-1997, and net “C” was used there in 1998-1999. In 1998, net “A” was used briefly in Kachemak Bay during late May through mid-June, allowing for comparison of catch efficiency with net “K”, which was used on the same beaches within a few weeks. Excluding two sets with extreme high catches of herring or sand lance, we compared total catch and species richness of 26 sets using net “A” to 28 sets on the same beaches using net “K”. Sets with “A” nets were conducted on 30 May and 11 June; sets with “K” nets were conducted on 13 and 26 June. Sets were usually repeated at high and low tide on the same day, and consecutive sets were often conducted at the same tide state to reduce site variance. A comparison of the average catch at 10 sites using the “A” net versus the “K” net showed that both nets caught similar quantities of fish (“K” catch = 0.72 [“A” catch]; $r^2 = 0.74$; $p<0.01$). We can control for variable effects of tide state and use of single sets (see Robards et al. 1999a), and use only data from sites where duplicate data are available from a site at only one tide stage (low). This use of selected data (comparing 10 sets using net “K” to 10 sets using net “A” at 5 sites) made little difference in the result (“K” catch = 0.67 [“A” catch]; $r^2 = 0.92$; $p<0.01$). Since the “A” and “K” nets were most divergent in dimension and design, we conclude that use of different seine nets contributed little to the observed variability in CPUE between sites or years (see below).

However, this may not be true of catch composition and diversity. Using the data from 54 sets at 10 sites, there was a weak relationship ($r^2=0.26$) between nets “A” and “K” in the average number of species caught per site (No. species in “K” = 0.91[no. species in “A”] + 3.5). In other words, net “K” generally caught 3-4 species more than net “A” at any given site. This difference likely increased later in summer as more species were encountered. Examination of the species lists revealed that catches of pelagic schooling fish (such as herring, salmonids, smelts, juvenile gadids, sand lance, etc.) were similar in both nets, whereas benthic fishes (such as flatfish, sculpins, etc.) were much more frequently caught in the “K” net. Thus, some caution is needed for comparisons of species diversity among sites.

Two sites were sampled at the Barren Islands. Most sets were made at East Amatuli Cove, but 6 sets were made at West Amatuli beach. Eight sites were sampled on Chisik Island, and 38 in Kachemak Bay during 1995-1996. After analyses of these data for temporal and spatial variability in catch per unit effort and species composition (Robards et al. 1999a), we reduced our sampling effort to cover only 12 of the original sites in Kachemak Bay during 1997-1999. Beach seining was generally conducted within a window spanning 1.5 h on either side of high and low tides. A single set was carried out on each site visit as this usually provided good representation of species richness and dominant species rank (Allen *et al.* 1992, Robards *et al.* 1999a).

Fish Measurements

All fishes were identified and counted. Fork length was measured to the nearest 1 mm. If >100 individuals of the same species were captured in a single tow, a sub-sample of 50-100 fish was measured (occasionally more fish were measured if needed for other project objectives). Weights were taken on a sub-sample of forage species (e.g., herring, sand lance, pollock). Weights were occasionally measured on other species. Due to the key trophic role of sand lance in the Gulf of Alaska (Blackburn and Anderson 1997), a much greater emphasis was put on assessing variability in this species, and we measured large samples of adult (age groups >1) and juvenile (age group 0) age classes (as later confirmed from otolith interpretations). Morphometric data are not presented in this report.

Statistical Analyses of Fish Data

The relative importance of fish species in seine catches was examined two ways: By calculating catch-per-unit-effort (CPUE, total number of fish per seine set) and frequency of occurrence (percentage of total sets in which a species was caught). Shannon-Wiener index of diversity (Krebs 1989) and species richness (the total number of species) were calculated for beach seine data by year and area.

Results

Relative Abundance

A total of 847,452 fish, including at least 75 species, were captured in 871 hauls (Tables 5.3 and 5.4). Pacific sand lance dominated the nearshore community in Kachemak Bay and at the Barren Islands and comprised more than 75 % of all fish caught. There were two orders of magnitude difference in catch-per-unit-effort (CPUE) between Chisik Island and the Barren Islands. CPUE in Kachemak Bay was intermediate to Chisik and the Barrens in 1995 and 1996, and similar to the Barrens in 1998-1999 (Table 5.5, Fig.5.1).

CPUE differed markedly among years at the Barren Islands and Kachemak Bay. Mean CPUE at the Barren Islands declined steadily since sampling commenced in 1996. Median catch data suggest a more abrupt decline between 1997 and 1998. In contrast, mean catches in Kachemak Bay increased markedly between 1997 and 1998, although median catches actually show only a slight increase at that time. Chisik Island catches were the lowest amongst our study areas. Mean and median catches were much less variable than those recorded at the other two sites, and patterns of annual variation were similar.

Community Composition

Overall, diversity was highest at Chisik Island (Fig. 5.2). Catches at Kachemak Bay and the Barren Islands (except 1999) were dominated by sand lance. Of the three study sites, community composition was most consistent among years in Kachemak Bay: Sand lance comprised more than 75 percent of the total catch in all years. Herring were the second most important taxa in all years except 1999. The dominance of sand lance within this community increased over the study period and this was reflected in a steady decline of the Shannon-Wiener index (Fig. 5.2) and an increase in the proportion of sand lance in catches (Fig. 5.3). Frequency of occurrence, however, changed little among years (Table 5.6). More than twice as many species were recorded in Kachemak than either Chisik or Barren islands (Fig. 5.2). By frequency of occurrence (Table 5.6), consistently common taxa in Kachemak Bay included also dolly varden, juvenile gadids, greenlings, sculpins, and sole.

Nearshore fish communities at Chisik Island were, on average, more diverse than those at other study sites (Fig. 5.2) and composition of catches was also the most variable among years (Fig. 5.3). Only a single set was conducted in 1995, and so we will not discuss this further. Diversity was particularly high in 1996 and 1998, but different taxa were prominently represented within the community in each year. Data for 1997 suggested lower diversity (Fig. 5.3), but this was largely the result of two large catches of unidentified larval fish (Fig. 5.3). In general, the community at Chisik was not dominated by any one species. Important taxa in some years included herring, sand lance, and salmonids; and to a lesser extent osmerids, pricklebacks, sculpins and flatfish.

Barren Island catches were dominated by fewer species, and catch composition differed markedly among years (Fig. 5.3). Catches in 1996 were very large and comprised almost entirely of sand lance, although gadids, osmerids, lingcod, and sculpins were taken frequently (Table 5.6). Sand lance abundance and frequency of occurrence diminished considerably in 1997 and 1998, while gadids, osmerids, lingcod and sculpins continued to contribute to overall diversity. Finally, in 1999, catches of sand lance plummeted to almost nothing while the frequency or abundance of other taxa (e.g., salmon, gadids, lingcod, sculpins) remained similar to that found in other years One large catch of unidentified larval fish dominated the picture for CPUE (Fig. 5.3). In summary, inter-annual changes in catch composition and specie diversity at the Barren Islands were driven mostly by dramatic changes in abundance of sand lance among years of study.

Discussion and Conclusions

The relative abundance and distribution of fish species in lower Cook Inlet appears to be largely determined by oceanography and sediment influx (Robards et al. 1999). Upwelling of nutrient-rich waters around the Barren Islands leads to high local productivity (Chapters 2 and 3), which in turn results in high abundance of forage fish species. Mixed water entering Kachemak Bay is also nutrient rich and becomes locally stratified, resulting in the highest standing stocks of phytoplankton to be found in lower Cook Inlet (Larrance et al. 1977). As at the Barrens, this apparently translates into high forage fish abundance. In addition, Kachemak Bay harbors a variety of nearshore habitats and oceanographic conditions that help support a high diversity of fish species (Robards et al. 1999, Abookire et al. 2000). In contrast to the Barrens and Kachemak Bay, water flowing past Chisik Island comes from northern Cook Inlet, and it carries high sediment loads from the glacial rivers that feed into it (Feely and Massoth 1982). The silt-load and resulting low light-penetration limit phytoplanktion production in this area to about one-tenth the levels observed in Kachemak Bay (Larrance et al. 1977). Furthermore, the combination of low productivity and abundance of glacial silt and mud that blanket most of the local substrates are probably unfavorable for many fish species. In particular, sand lance prefer clean, sandy substrates near shore (Pinto et al. 1984).

Herring, gadids (walleye pollock and Pacific cod), osmerids (capelin), and sand lance are important forage fish for seabirds in Cook Inlet (Chapters 9-12). Based on beach seine data, it is clear that Kachemak Bay supports the most robust community of forage fish in lower Cook Inlet. Although sand lance dominated the community, other forage fish populations were also abundant and reasonably stable among years; in particular herring and capelin. This offers some buffer to potential predators as individual species fluctuate in abundance among years. For example, while herring virtually disappeared in 1999, there were still large numbers of sand lance for predators to feed upon. In contrast, Chisik Island waters support low numbers of fish and the community changed markedly among years. There would appear to be few choices of prey that offer predators either plentiful food supplies or temporal stability in population size. Finally, nearshore areas around the Barren Islands generally supported large numbers of sand lance and gadids; although 1999 was an exception. Like Kachemak, the Barrens offer high abundance of a few key prey species. One major difference, however, is that while numerous adult sand lance reside year-round in Kachemak Bay— and spawn on local beaches during autumn— only juvenile sand lance are found at the Barrens (Robards et al. 1999a). Sand lance populations at the Barrens may be more dependent on currents to bring YOY sand lance near shore during summer, and hence populations there may be more variable.

In this report we have provided a basic summary of findings on the abundance and distribution of forage fish near shore in Cook Inlet. We will continue to analyze beach seine data and publish our findings in peer-reviewed journals. In particular, we will continue to examine the distribution of individual fish species and communities with respect to environmental features (substrate, temperature, salinity, currents, etc., as in Robards et al. 1999a, 2002, Abookire et al. 2000, 2002), and we will continue to analyze the diets and biology of birds with respect to forage fish availability information gleaned from beach seine surveys (e.g., Litzow et al. 2000, 2002).

Although we measured fish at each site and among years (Table 5.2), morphometric data have not been summarized in this report. Data for sand lance have been analyzed with regard to size, weight and growth rates for different areas in 1995-1997 (Robards et al. 1999b, 1999c, 2000). This work revealed that there was rapid growth of young-of-year (YOY) fish during the summer months, and markedly different growth patterns among areas. For example, sand lance from the Chisik area exhibited slower growth during summer, and fish were much smaller at a given age than fish in Kachemak Bay (Robards et al. 2002). These findings complicate any interpretation of morphometrics data for other species, and we have not completed our analyses of these data. When completed, results for other species will be published in peer-reviewed journals.

Limitations of Study

We note some limitations of using beach seine data to make inferences about near shore fish "communities". Sampling of nearshore habitats with beach seines was limited to sandy and cobble substrates. Strong currents or inshore swells over 0.5 m also prevented effective retrieval of nets. Therefore, fish inhabiting muddy or rocky substrates, mussel (*Mytilus edulis*) and kelp beds, or the surf zone were under-represented in our study. The surf zone is preferentially used by some species because of low numbers of predators and food-rich waters (Bennett 1989).

Also, we used four different nets during the course of our studies in three different areas of Cook Inlet. Comparison of catch efficiency (see Methods) suggested that use of different nets could account for some of the variability that we observed in CPUE and catch composition. However, CPUE appeared to differ much less than 2-fold among nets whereas CPUE differed 10- or 100-fold among areas. Nonetheless, annual variability in CPUE within sites sometimes varied less than 2-fold, and we would tend to discount the importance of such minor fluctuations when different nets were involved. Similarly, it appeared that the "K" net, used in Kachemak Bay every year, tended to catch more species than other nets— perhaps owing to the small-mesh liner running along the net bottom. We would expect to have caught more species at the Barrens and Chisik if we had used a similar net-design at those locations. On the other hand, one reason we caught more than twice as many species in Kachemak Bay than at either Chisik or the Barrens is because we fished far more sets (671, 94, 106, respectively) at far more sites (38, 6, 2, respectively).

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Chapter 6. Benthic and Intertidal Fishes in Kachemak Bay

Alisa Abookire

Introduction

Most of the seabirds that we studied in Cook Inlet eat pelagic schooling fishes that can be sampled with a beach seine or mid-water trawl. The diet of the Pigeon Guillemot (*Cepphus columba*), however, consists of both demersal and pelagic forage fishes, as well as invertebrates (Litzow *et al*. 1998). Demersal and pelagic forage fish differ in their distribution and energy density (Van Pelt *et al*. 1997), and it is believed that Guillemots selectively forage upon the lower quality demersal fish because they are a more localized, reliable prey (Golet *et al*. 2000, Litzow 2000).

Specifically because of our interest in assessing the entire prey base of Pigeon Guillemots, we sampled demersal fish in Kachemak Bay with bottom trawls from 1996 to 1999 and SCUBA transects from 1997 to 1999. Our primary objectives were to: 1) measure the relative abundance of forage-sized demersal fish available to Pigeon Guillemots breeding at several different colonies, 2) measure seasonal and annual variability in abundance of demersal fish, and, 3) relate temporal and spatial patterns in demersal fish abundance to environmental parameters.

Habitat selection by demersal fish and the effect of local oceanography on temporal and spatial patterns of abundance in Kachemak Bay have been explored in a numbers of publications (Abookire 1997, Abookire and Norcross 1998, Abookire et al. 2000, 2001). The influence of demersal forage fish abundance and distribution on the diet and reproductive success of Pigeon Guillemots has also been thoroughly documented (Litzow 2000 , Litzow *et al*. 1998, 2000, 2002a, 2002b). Thus, we have fulfilled our primary research objectives and documented our findings in peer-reviewed publications.

In this report, we provide simple summary documentation and results of trawl surveys (to accompany the database archive), and document results of SCUBA surveys for demersal fish that were originally intended to complement bottom trawl surveys, but in the end, were insufficient for use in assessing prey availability to Pigeon Guillemots. Nonetheless, they may prove useful for documenting nearshore fish communities in Kachemak Bay. It is unlikely that we will pursue further analysis or publication of these data in the foreseeable future.

Methods

Bottom trawls

Bottom trawls were conducted in late summer of 1996-1999. From August 7 to 9, 1996, 10 stations were sampled in Kachemak Bay at Halibut Cove, Peterson Bay, China Poot Bay, Neptune Bay, and Eldred Passage (Fig. 6.1). On June 30-July 2, July 17-18 and August 13-17 of 1997 those 10 stations were repeated, and on August 17, 1997, three new stations were established and sampled near the Seldovia Bay Pigeon Guillemot colony. Details on all trawling stations are provided in Appendix 6.1. In 1998 we changed vessels and captains, and we towed a video camera at each site prior to trawling in order to assess the bottom for rocks or boulders (which could tear the trawl net). The camera was integral to selecting trawl stations. If the site had a smooth bottom and less than 50 % kelp cover, then we trawled it. These videos may be used to help characterize demersal habitat and view sediment types in Pigeon Guillemot foraging areas.

On July 1-2, July 18, and August 14, 1998, we trawled all 13 stations from 1997 except for stations H1 (inner Halibut Cove) and Y2 (by Elephant Rock), which were omitted due to rocks. Stations M1 and S1 were replaced with M4 and S4 due to rocks and obstructions (reefs) seen with the camera. Additionally, four deep (25 m) stations were added; one in Halibut Cove (H3), Neptune Bay (N3), and two outside Seldovia Bay (S5a and S5b). Stations were chosen such that depth ranges 8-10 m, 10-15 m, 15-20, and 20-25 m were represented proportionately between the colony sites, for a total of 15 sites. These depths were chosen because although Pigeon Guillemots forage in water depths from 6 to 45 m, they most frequently forage at depths of 15-20 m (Clowater and Burger 1994).

In 1999, we trawled on 17 and 20 August at the same sites that were sampled in 1998. The only exception is that Y3 (near little Tutka Bay in Eldred Passage) was omitted after two attempts which each resulted in gear damage. The deep site in Seldovia Bay was S5b, as field notes from August 1998 indicate that S5a had an excess of shell debris and kelp which clogged the net. Sampling in June and July was not continued in 1999 due to low CPUE in trawls, which limited statistical analyses of catches among years.

Standard tow duration in 1996 was 10 minutes. Tow duration was reduced to 5 minutes in 1997-1999. Station depth did not exceed 25 m. We towed a 3.05 m plumb staff beam trawl equipped with a double tickler chain (Gunderson and Ellis 1986). Net body was 7 mm square mesh with a 4 mm mesh cod end liner. Tows were flagged as good or bad based on the efficiency of the trawl. If the trawl was twisted, broke a weak-link, torn, or if the net was full beyond the cod-end, then the tow was flagged as a bad tow (Appendix 6.1).

All fishes were identified to species, counted and measured to the nearest mm fork length. Length data are not reported here, but are available in the database archive. All species of fish that were recorded from bottom trawls in 1996-1999, and were measured, are listed in Appendix 6.2.

We analyzed data only for fish with fork length less than 15 cm, mostly because the beam trawl we used tended to capture small fish. Fish were classified as either less than forage-size (< 8 cm) or forage-size (8 – 15 cm). Fish data were standardized to CPUE for an area of 1000 m^2. The area towed was calculated as the effective width of net (0.74; Gunderson and Ellis 1986), multiplied by the width of our trawl (3.05 m), multiplied by tow length as determined by Global Positioning System data. Spatial comparisons were made between Outer and Inner Kachemak Bay, as Homer Spit (Figure 6.1) divides the Bay into two oceanographically distinct areas (Abookire *et al*. 2000).

SCUBA transects

SCUBA dive transects were surveyed at 10 stations around Seldovia and 10 stations around Moosehead Point (Figure 6.1) to assess forage fish relative abundance and species composition near two Guillemot colonies. Although the objectives were the same in 1997 and 1998, dive sites differed among years. Some of the site names may be similar between 1997 (e.g., Moose 5) and 1998 (e.g., MH 5), but the sites in 1997 were not repeated in 1998 for logistic and sampling reasons. In 1997, SCUBA dives occurred on August 18, 25, and 26, and stations were all < 10 m deep. In 1998, SCUBA dives occurred on June 27-29, July 14-15, and August 17-19, and stations were chosen so that 5 stations in each area were < 10 m and 5 were < 20 m. Each diving team took 5 sites in an area (Appendix 6.3).

In 1999, SCUBA data were used to determine the predictability of demersal prey at two stations that were not sampled in previous years, but were known foraging sites for Pigeon Guillemots (M. Litzow, unpub. data). The first SCUBA site was in Seldovia Bay and was sampled on July 18, 19, 20, and 22, for a transect length of 100 m (Appendix 6.3). In 1999, the first two Seldovia dives are "bad" because they did not follow the exact compass bearing as dives 3 and 4. Dives and 3 and 4 (July 20 and 22) were exact replicates. The second site was South of Cohen Island in Eldred Passage, and it was sampled on July 18 and 22, 1999, for a transect length of 60 m. Heavy kelp forest prevented us from swimming the desired 100 m transect length. Sampling was done around low tide. Sediment type (Cobble, gravel, sand, fine sand, silt) was recorded at start, middle, and end of each transect. Percent kelp cover of the entire transect was also recorded (Appendix 6.3).

All fishes on SCUBA transects were visually categorized as less than forage-size (< 8 cm), forage-size (8 – 15 cm), and greater than forage-size (> 15 cm). All species of fish recorded on SCUBA dives in 1997-1998 are listed in Appendix 6.4. Hermit crabs were recorded and categorized with the same three size classes as fish.

No fish larger than forage-size (> 15 cm) are analyzed in this report, as larger fish are more likely to detect and avoid a diver. Sand lance and schooling fish were recorded, but removed from analysis of SCUBA data because zeros of these species are not reliable data. The fish data for 1997 and 1998 are standardized to transect length of 30 m, so that fish counts from 60 m transects were divided in half. Spatial comparisons were made between Outer and Inner Kachemak Bay, as Homer Spit (Figure 6.1) divides the Bay into two oceanographically distinct areas (Abookire *et al*. 2000).

Results

Bottom trawls

We caught 5,901 demersal fish (size < 15 cm) in 95 trawls from 1996 to 1999. More small fishes were captured than forage-size; 2.0 times more in the Outer Bay and 2.8 times more in the Inner Bay. Although the Inner Bay appeared to consistently catch more small fish, relative abundance (CPUE) of forage-size and small demersal fishes was not different between Outer and Inner Kachemak Bay (Table 6.1). Seasonally, relative abundance did increase from early July to August (Table 6.2).

Beam trawl catches were composed of 41 % flatfishes (Pleuronectidae), 21 % cod (Gadidae), 15 % sculpins (Cottidae), 7 % pricklebacks (Stichaeidae), and 5 % ronquils (Bathymasteridae) (Table 6.3). Most of the remaining species were greenlings (Hexagrammidae) and rockfish (*Sebastes* spp.) (see Appendix 6.2 for a complete list). Demersal fish communities in the Outer and Inner Bay had different percentages of the same main fish groups. Demersal fish composition in the Outer Bay had more sculpins and rockfish, while a higher percentage of cod and pricklebacks occurred in the Inner Bay (Table 6.3).

SCUBA transects

We counted 331 forage-size and 350 smaller fish in 72 SCUBA dives from 1997 to 1998. High variability in fish counts on SCUBA transects (Table 6.4) made spatial comparisons of relative abundance inconclusive.

Species observed on SCUBA transects comprised 39 % sculpins (Cottidae), 23 % pricklebacks (Stichaeidae), 10 % cod (Gadidae), 9 % flatfishes (Pleuronectidae), 9 % gunnels (Pholidae), and 6 % greenlings (Hexagrammidae) (see Appendix 6.4 for a complete list). Demersal fish communities in the Outer and Inner Bay had different percentages of the same main fish groups. Demersal fish composition in the Outer Bay had more sculpins and pricklebacks, while a higher percentage of gunnels, flatfish, cod and greenlings occurred in the Inner Bay (Table 6.3).

In 1999, a total of 16 fish were counted on the “good” SCUBA transects near Cohen Island and 371 fish in Seldovia Bay (Table 6.5). Numbers were very low at the Cohen site, such that temporal comparisons of relative abundance cannot be made. Preliminary assessment of the Seldovia dives suggests that demersal fish have high site fidelity and low variability in distribution.

Discussion and Conclusions

Spatial differences in demersal fish abundance were not detected at the scale of Kachemak Bay (see Abookire *et al*. 2000), presumably because bottom waters in Outer and Inner Kachemak Bay had similar substrates, temperatures and salinities. Observed seasonal differences in fish abundance were likely related to the life-history of each species rather than any one physical parameter. On a scale of days, demersal fish displayed low spatial variability in abundance. Such observations were not unexpected, as the arctic shanny (*Stichaeus punctatus*, Keats *et al*. 1993), some greenlings (Hexagrammidae, Hart 1973), and sculpins (Cottidae: DeMartini 1978 , Vdovin *et al*. 1994) display territorial behavior (e.g., males often guard the eggs) and thus tend to have dispersed and stable spatial distributions.

In all years, we observed more small fish than forage-size fish in all of Kachemak Bay, and in both the Outer and Inner bays. Kachemak Bay is a year-round nursery area for flatfishes (Abookire and Norcross 1998), and it appears to be a nursery for other groundfish as well (Robards et al. 1999). Many species of demersal fishes were captured in this study, and different demersal fish communities were detected between Outer and Inner Kachemak Bay. Trawls and SCUBA data concur that a higher percentage of sculpins are found in the Outer Bay whereas gadids are more common in the Inner Bay. While SCUBA transects recorded a higher percentage of pricklebacks in the Outer Bay, bottom trawl catches and beach seines (see Abookire *et al.* 2000 , Litzow *et al.* 2000) showed a higher percentage in the Inner Bay.

Demersal fishes can be challenging to sample, and there are pros and cons to both of the methods we used. The bottom trawl we used was a beam trawl, which is effective, consistent and yields good quantitative results. However, in near-shore environments with many habitats (especially rocks and reefs), gear damage is a common problem. Heavy kelp cover in areas such as Seldovia Bay prevented us from trawling because the kelp clogged the cod-end and fish were not captured effectively. Additionally, strong tidal currents, such as those in Kachemak Bay, can flip the cod-end into the mouth of the net or twist the net so that it does not fish properly. To counter this, we simply trawled during neap tides, but this constrained our time-window for sampling.

SCUBA diving is a good compliment to trawls, because it permits one to sample reefs, kelp beds and other habitats otherwise impossible to sample with nets. However, strong tiderips in Kachemak Bay restricted diving to periods of slack water (one hour centered around high or low tide). This time-constraint, coupled with cold water temperatures, made it a challenge to sample more than 3-5 sites in one day. SCUBA is also limited by the depth which can be safely sampled, and repetitive dives compound the depth constraint. SCUBA is a partially subjective method of surveying fish that relies on a knowledgeable diver who can accurately identify fish and estimate fish sizes visually. Finally, SCUBA is quite costly and labor intensive, and yields a dataset with many zeros and high variability around values of relative abundance. Although we found SCUBA to be of limited value for comparing relative abundance among areas, it was useful in assessment of fish behavior, habitat characteristics, and species composition.

One of the benefits of a multi-year study is that auxiliary species are recognized and range extensions can be recorded. The presence of several unusual fishes was noted in the summer of 1998, coinciding with the arrival of the warm ENSO water in Kachemak Bay. Pacific sanddab (*Citharichthys sordidus*) were captured at three bottom trawl stations in 1998, when only one individual had previously been recorded in Kachemak Bay from September 1994 (Abookire 1997). In 1998, Wendell's warbonnet (*Chirolophis snyderi*) was observed in both a bottom trawl and SCUBA dives, and one yellowmouth rockfish (*Sebastes reedi*) was captured in a bottom trawl. Kelp clingfish (*Remicola muscarum*) extended their northern range and were observed on 1998 SCUBA dives and then in five beach seine sets in 1999 (see Chapter 4). Another northern range extension was noted for the painted greenling (*Oxylebius pictus*), which was captured on August 20, 1999 in a bottom trawl and on May 15, 1999 in a beach seine.

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Chapter 7. Hydroacoustic Forage Fish Biomass and Distribution in Cook Inlet

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Introduction

Most fisheries work in the Gulf of Alaska has focused on adults of species that are commercially marketable (e.g., Megrey *et al*. 1990). Less attention has been given to species that are not commercially harvested— such as sand lance (*Ammodytes hexapterus*) or capelin (*Mallotus villosus*)— even though many of these species are important prey items of commercially valuable fishes and critical in the diets of many seabirds and marine mammals. In addition, studies of larval fish are common (e.g., Stabeno *et al.* 1995) but studies of juveniles (generally, age-0 to age-1 or 2) are more uncommon. These are the age-classes of commercial ground fish such as cod and pollock that are commonly consumed by adult fish, seabirds and many marine mammals (Pitcher 1980, Yang 1995, Brodeur and Bailey 1996, Merrick *et al*. 1997). All these "forage fishes" play a valuable role in food-web dynamics by conveying energy from lower to higher trophic levels (Springer and Speckman 1997).

For this study of the biological response of seabirds to fluctuations in prey density, we needed to develop a robust index of forage fish abundance around three seabird colonies in Cook Inlet. Whereas indices based on fishery catches have been used in some cases to assess prey availability to seabirds (e.g., Monaghan et al. 1989, Hamer et al. 1994, Anker-Nilssen et al. 1997), acoustic surveys have been less commonly employed (e.g., Safina and Burger 1985, Piatt 1987, 1990). This is partially due to difficulties (and costs) in gathering and interpreting acoustic data, and a lack of baseline acoustic data on most forage species. Trawl surveys are relatively straightforward to conduct but they can be strongly biased if trawl stations are selected on the basis of acoustic signal strength (see Chapter 4). Acoustic echo-integration surveys can be used to systematically sample the entire water column of relatively large marine areas, and they can be particularly effective at showing changes in distribution of forage species over time (e.g, Johannesson and Mitson1983, Carscadden and Nakashima 1997). Thus, we used acoustic surveys to measure forage fish abundance in lower Cook Inlet during each summer of 1995-1999.

This portion of the Cook Inlet Seabird and Forage Fish study was designed to assess geographic and annual variability in forage fish abundance in lower Cook Inlet. We conducted hydroacoustic surveys for forage fish within a 45 km radius of three seabird colonies at the Barren, Gull and Chisik islands. Overall objectives of this our study were to: 1) quantify forage fish abundance on transects in lower Cook Inlet and estimate overall forage fish biomass in each seabird study area; 2) relate the distribution of acoustic biomass in Lower Cook Inlet to oceanographic features and other aspects of the physical environment, including primary and secondary production, temperature and salinity, bottom depth and distance from shore, etc.; and, 3) quantify the characteristics of forage fish schools that are of importance to marine predators.

We have begun to relate the distribution and abundance of forage fishes to environmental features of Cook Inlet (Robards *et al.* 1999, Abookire et al. 2000) and similar studies for some important forage species in Cook Inlet have been conducted elsewhere; for example, pollock (*Theragra chalcogramma*) and Pacific sand lance (*Ammodytes hexapterus*) in the Bering Sea (Swartzman *et al.* 1994, 1995, McGurk and Warburton 1992), and capelin (*Mallotus villosus*) in the Labrador Current (Schneider and Methven 1988, Carscadden and Nakashima 1997). The physical environment influences both primary and secondary productivity (Parsons et al. 1984) and helps to structure fish habitats. In turn, dispersion of forage fish strongly influences the spatial aggregation of seabird predators and determines the rate at which prey can be extracted from the environement (Schneider and Piatt 1986, Piatt 1990). Fish school characteristics such as density, degree of aggregation, distance from the water surface and distance from colonies all have important consequences for predators such as seabirds.

Here we present summary data on the abundance and distribution of forage fish in lower Cook Inlet. Summary acoustic biomass estimates are also used in Chapter 14, where aspects of seabird biology and behavior are related to prey abundance. Study of the relationships between acoustic fish biomass and environmental characteristics, between seabirds at sea and fish schools, and of the characteristics of fish aggregations, are all underway as part of a Ph.D. dissertation (S. Speckman, Univ. of Washington, School of Aquatic and Fishery Sciences). Findings will be published in peer-reviewed journals.

Methods

We conducted hydroacoustic surveys for forage fishes in Lower Cook Inlet, defined as the area south of Kalgin Island, in late July and August from 1995-1999 (Table 7.1). Effort was focused around 3 seabird colony sites: the Barren Islands, Gull Island, and Chisik Island. These 3 core study areas support large seabird populations with similar suites of species. Local oceanographic regimes, however, differ greatly among the 3 sites (Chapter 2) and population dynamics of the seabird communities are notably different (Chapter 14).

In 1995, surveys were concentrated within a 45 km radius around each of the 3 seabird colonies (Fig. 7.1). In 1996, coverage was more extensive (Fig. 7.2) and included areas in western Cook Inlet and south of the Barren Islands that were not surveyed in subsequent years. Furthermore, a series of nearshore coastal transects were added in 1996 (Table 7.1, Fig. 7.2) and conducted every year thereafter. In 1997-1999, surveys were similar to and slightly more extensive than those in 1995, concentrating within a 45 km radius of each of the 3 seabird colonies (Fig 7.3). Transects surveyed from 1997-1999 were identical in each of those 3 years, except that the most northerly nearshore transect was not surveyed in 1997. In 1996-1999, transects were established in both "nearshore" and "offshore" habitats. Nearshore transects followed the contours of mainland or island shorelines in zig-zags of 1.8 km length, where waters were generally deeper than 10 m. Offshore transects cut across open water from one shore to another, over depths ranging from 10 m to >200 m.

In 1995 and 1997-1999, surveys were conducted primarily from the *R/V Pandalus*, a 22 m stern trawler operated by the Alaska Department of Fish and Game. Surveys in 1996 were conducted from the *R/V Tiglax*, a 36 m vessel operated by the Alaska Maritime National Wildlife Refuge, U.S. Fish and Wildlife Service. In all years, surveys in some shallow, nearshore areas were conducted from the *R/V David Grey*, an 11 m Uniflite cabin cruiser operated by the Biological Resources Division of the U.S. Geological Survey. Ground speed for all vessels was approximately 11-15 km/hr (6-8 knots).

Hydroacoustic data were collected with a single beam 120 kHz BioSonics DT4000 system with a 6^o beam angle. The transducer was attached to a hydrodynamic sled and deployed off the side of the survey vessel 1-2 m below the water surface. All data were logged directly to a computer in real time. GPS locations were obtained from a Rockwell Precision Lightweight Global-positioning Receiver (PLGR), which have a worst-case horizontal position accuracy of ±10 m at speeds <36 kph (Anonymous 1995). At the beginning of the cruise in each year, the hydroacoustic system (transducer, cable and sounder) was calibrated in the field using a tungsten steel sphere of known target strength.

In order to quantify forage fish biomass in each area and year, hydroacoustic transect data were first binned into 10-min (horizontal) by 5 m (depth) blocks and integrated using EchoView© (Sonar Data Pty. Ltd., Hobart, Tasmania) to determine S_A (mean backscattering per m^2) of each block. The integration threshold was set at –60 dB in 1995 and –80 dB in 1996-1999. The use of 10-min (ca. 2-3 km of survey) distance bins was arbitrary. Until a complete spatial analysis of the data have been completed, we have no *a priori* reason for selecting any particular bin size (Schneider 1989, Rose and Leggett 1990). For these initial analyses, we chose a 10-min bin size because it may be an appropriate scale for some of the species we are examining (e.g., capelin, cod; Rose and Leggett 1988, Piatt 1990), and because it is a widely-used transect scale for seabird surveys (Gould et al. 1982). In general, distances surveyed among areas and years were similar, except for 1997 when data from some transects north of the Barrens were lost. Otherwise, variability in the numbers of transects used for analyses (Table 7.2) can be accounted for by differences in vessel speed or currents which altered the time required to complete transects (e.g., particularly in 1999 when ship speed was faster).

Relative measures of acoustic biomass (S_A) were converted to absolute estimates of fish density (fish/m^2) by dividing S_A by σ (backscattering cross-sectional area of single prey) for species with the following known target strengths:

Pollock:	$TS=20Log(L)-66$	(Foote and Traynor 1988)
Cod:	$TS=20Log(L)-65$	(Rose and Leggett 1988)
Capelin:	$TS=20Log(L)-65$	(Rose and Leggett 1988)
Herring:	$TS=26Log(L)-76$	(Thomas and Kirsch 1999a)
Sand Lance:	$TS=24.5Log(L)-84$	(Thomas and Kirsch 1999b)
Physoclists:	$TS=20Log(L)-65.5$	(Foote 1987)

Over all years of the study, the most abundant taxa caught in mid-water trawls (Chapter 4) were sand lance (60%), gadoids (pollock and cod, 23%), herring (12%), osmerids (capelin and smelts, 3%) and "other" (2%). Conversion of relative to absolute biomass is problematical in study areas such as ours, where species overlap in geographic distribution (as revealed by mid-water trawls, see Chapter 4). However, species groups were markedly segregated by depth (Chapter 4). For example, 90% of fish caught in the upper 20 m were sand lance, whereas gadoids dominated (90%) at depths of 60-100m. Herring and capelin were found at intermediate depths.

In order to generate estimates of absolute biomass, therefore, we simply divided S_A in each depth stratum by a composite σ value weighted by the proportion (as determined by trawl data combined over four years) and TS of each group in each stratum. For this purpose, pollock, cod, capelin, smelts and "other" fish were all assumed to have TS values equivalent to a general physoclist (above)-- a simplifying assumption likely to cause little bias considering the similarity in TS among these taxa, and compared to the rather large difference in sand lance and herring target strengths. Estimates of areal fish densities (fish/m^2) were further converted to volume biomass density estimates (g/m^3) by dividing by bin depth (5 m) and multiplying by average weights for fish of mean size used in calculating fish density (year, mean length, range, mean weight of all fishes combined: 1996, 73.4 mm, 19-721 mm, 2.19 g; 1997, 75.5 mm, 15-807 mm, 2.41 g; 1998, 79.7 mm, 20-760 mm, 2.37 g; 1999, 84.5 mm, 23-897 mm, 3.05 g).

Mean and 90th percentile biomass densities were calculated for each area (around Chisik, Gull, and Barren islands) and year (1996-1999). The sample unit was a single 10-min by 5 m block, and sample sizes therefore reflect not only the number of transects (no. of 10-min bins) but also the depth of the water column (to a maximum of 100 m). Mean and 90th percentile biomass densities were calculated from the entire survey area and water column, from the entire survey area but only 30 m surface layer, from offshore transects only, and from inshore transects only. To account for the skewed distribution of acoustic biomass estimates, means were calculated from transformed data as mean (log x+1) values, and then transformed back to original density units (Johannesson and Mitson 1983). In addition to calculating mean densities, sampled blocks were analyzed for the frequency of occurrence of fish biomass densities ranging from 10^{-7} to 10^{0} g/m^3.

Results and Discussion

Overall fish density was higher near Gull Island (in Kachemak Bay) than near the Barrens or Chisik in all years of study except 1999 (Figure 7.4). Mean acoustic biomass densities near Gull were generally 2-3 times greater than near the Barrens, which were generally 2-6 times greater than densities near Chisik (Table 7.3). Thus, acoustic surveys corroborated both trawl and seine results, and suggested an order-of-magnitude difference in forage fish biomass among the waters surrounding each of the three seabird colonies under study.

Acoustic biomass in waters surrounding each colony were roughly similar between 1995 and 1997, but started to decline in 1998, and declined markedly in all areas in 1999 (Fig.

7.4). Declines in abundance were most striking in shallow (Fig. 7.4) and inshore waters (Fig. 7.5). Annual changes in abundance were concordant among areas (Chisik vs. Kachemak r^2=0.78; Chisik vs. Barrens r^2=0.98; Kachemak vs. Barrens r^2=0.87)— suggesting that factors influencing fish abundance were operating at the spatial scale of Cook Inlet. In all areas, fish biomass was concentrated in the upper water column (<30 m depth; Fig. 7.4, Table 7.4) and in inshore areas (Fig. 7.5, Table 7.5). Offshore densities were generally much lower than inshore densities (Fig. 7.5, Table 7.6). Except in 1996, there was little difference among inshore and offshore densities near Chisik, whereas densities were 2-6 times higher inshore in Kachemak Bay (near Gull) and along the Kenai Peninsula (near Barrens) than offshore in all years of study. There is no indication that the 1997-1998 ENSO event had a significant influence on forage fish abundance in the summers of either year— even though a widespread murre die-off in April of 1998 suggested that fish abundance had been reduced during late winter in Cook Inlet (Piatt et al. 1999).

The average distribution of acoustic biomass at depth is more clearly illustrated by grouping data from all years and apportioning it among 20 m depth strata (Fig. 7.6). Biomass in all areas was concentrated in the upper 40 m, owing in part to the fact that sand lance and herring are most abundant at these depths— whether they are found nearshore or in deeper offshore waters (Chapter 4). Juvenile pollock are most abundant at depths of 60-100 m, accounting for the peaks of biomass found at these depths near the Barren and Chisik islands. Stokebury et al. (2000) found almost identical results for herring and juvenile pollock during July in Prince William Sound. If this degree of segregation between gadid and herring/sand lance is typical— and it was in all years that we surveyed fish in lower Cook Inlet— it has important implications for predators that must dive to capture prey underwater.

Another useful way to view the differences in biomass among areas and years is to consider the frequency distribution of integration blocks containing differing densities of fish (Fig. 7.7). In particular, the frequencies of blocks containing 10^{-2}, 10^{-1}, and 10^{0} g/m^3 of biomass are of interest because these include the high-end densities needed to support foraging marine birds and mammals (Safina and Burger 1985, Piatt 1990). The frequency of high-density blocks differed markedly among areas. Kachemak Bay contained far more high-density blocks than either the Barrens or Chisik areas, and in the Chisik area blocks with densities greater than 0.01 g/m^3 were rare. The change in frequency of high-density blocks between years was similar among areas, and the shift in overall frequency distributions was well-correlated among areas (Chisik vs. Kachemak r^2=0.57, Chisik vs. Barrens r^2=0.67, Kachemak vs. Barrens r^2=0.79). This suggests that regional (Cook Inlet wide) effects on fish abundance were more important than effects operating at local scales.

The geographic distribution of acoustic biomass within different depth strata is illustrated in Figs. 7.8-7.11. Shown are the raw backscattering values per unit area (S_A), without any conversion for target strength of fishes caught on transect. Acoustic backscatter was highest in coastal areas and in relatively shallow water (<30m). High biomass densities were also observed in deep waters (>60m) surrounding the Barren Islands (Fig. 7.10).

Integrated over all depths (Fig. 7.11), acoustic biomass was concentrated: 1) around the coast of the Kenai Peninsula, 2) along the south and north shores of Kachemak Bay, 3) in cold, mixed waters (Chapter 2) north of the Barren Islands and to a lesser degree in the cold-water plume that extends north past outer Kachemak Bay. In marked contrast to waters near the Barrens and in Kachemak Bay, waters adjacent to Chisik Island were almost devoid of acoustic signal. In some years (e.g., 1997, 1998), weak targets were recorded in the southeast section of the study area, corresponding to the northern extension of the cold-water plume at those times.

In summary, differences in fish biomass among the three study areas reflected differences in oceanography (see Chapter 2). The Chisik area, with its relatively warm, turbid waters consistently contained the lowest fish biomass. Furthermore, fish aggregations found in the Chisik area had consistently lower average school densities and a much lower frequency of high-density patches (Fig. 7.7). This seems to reflect overall lower levels of primary and secondary production in the Chisik area (Chapter 3), resulting in an area that is unable to support a high biomass of forage fish. The high dispersion of forage fish around Chisik probably increases their likelihood of finding adequate zooplankton food supplies. Kachemak Bay is a stratified and highly productive system (Chapters 2 and 3) that consistently supported the highest forage fish biomass and schools with the highest fish densities. The Barren Islands, also nutrient-rich and productive, supported intermediate levels of fish biomass and school densities. These regional patterns of offshore fish abundance are also reflected in nearshore fish communities, with Chisik supporting 1-2 orders of magnitude lower fish biomass than Kachemak Bay or the Barrens (Chapter 5; Robards et al. 1999).

The main reason we conducted acoustic surveys was to obtain a single index of prey abundance around each seabird colony that we could use to relate with seabird biology and behavior in each year of study. This index is provided in Table 7.3, and used in Chapter 14 as we examine the response of seabirds to fluctuations in prey density. Variability in the distribution of forage fish— both vertical and horizontal— and its implication to foraging seabirds (Chapter 8) will be explored more in future analyses and publications. We are currently using multivariate statistics to evaluate the influence of temperature, salinity, phytoplankton biomass, zooplankton biomass, water depth, and thermocline depth on the composition and distribution of forage fish schools in lower Cook Inlet (S. Speckman, Ph.D. thesis, in prep.). In addition, we will be characterizing fish schools for attributes of importance to predators, such as school density, mean school dimensions, school depth, degree of aggregation, etc., and comparing the attributes among study areas and over time. These analyses will appear in a Ph.D. dissertation for the College of Fisheries Sciences, University of Washington, and we will publish the results in peer-reviewed journals.

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Chapter 8. Pelagic Seabird Abundance and Distribution in lower Cook Inlet

Suzann Speckman

Introduction

Seabird distribution patterns often reflect prey availability. Numbers of birds at sea are generally low in areas with poor food supplies, and higher in areas where forage fish schools form extended aggregations (Schneider and Piatt 1986). Seabirds may switch foraging areas to follow prey movements or to forage in areas of higher prey abundance (Piatt 1990, Schneider 1990, Logerwell and Hargreaves 1996). Oceanographic features such as frontal systems, water temperature and salinity, vertical stratification, and bathymetry can also influence seabird distribution (Decker and Hunt 1996, Piatt 1994) usually by their action in concentrating or dispersing seabird prey species or the zooplanton prey those forage fish consume (Swartzman et al. 1994, 1995, Castillo et al. 1996, Decker and Hunt 1996, Mehlum et al. 1996).

In this study, we set out to contrast the biology of seabirds at three colonies in lower Cook Inlet that have markedly different population dynamics. We measured food supplies around each colony (Chapters 4-7) and while we conducted hydroacoustic surveys for fish, we also censused all seabirds and marine mammals observed on those transects. From these data, we propose to: 1) measure the aggregative response of seabirds to prey density at sea, 2) relate the distribution and abundance of marine birds in lower Cook Inlet to forage fish distribution and oceanographic features, and, 3) estimate the overall population abundance of seabirds and marine mammals in lower Cook Inlet. Analyses are still in progress, and here we present summary information on the abundance and distribution of important marine taxa in lower Cook Inlet during our years of study. The aggregative response is discussed in Chapter 14. The relationship between seabirds and their physical and biological environment will be the subject of a Ph.D. dissertation at the College of Fisheries, University of Washington (S. Speckman, in prep.).

Methods

We conducted surveys for marine birds and mammals in Lower Cook Inlet during late July and August of 1995-1999 (Table 8.1). In 1995, surveys were concentrated within a 45 km radius around each of the three major seabird colonies found in Lower Cook Inlet: Chisik Island on the western side of the Inlet, Gull Island in Kachemak Bay, and the Barren Islands, at the mouth of the Inlet between the Kodiak Archipelago and the Kenai Peninsula (Fig. 7.1). Owing to logistic constraints, we only surveyed waters in the NE quadrant around the Barren Islands. Previous studies had shown that this was the area in which fish-feeding seabirds were concentrated (Piatt 1994). In 1996, coverage was more extensive, and in addition to the core study areas surveyed in 1995, included areas in western Lower Cook Inlet and south and east of the Barren Islands that were not surveyed in subsequent years (Fig. 7.2). In 1997-1999, surveys were similar to and slightly more extensive than those in 1995, concentrating within a 45 km radius of each of the three seabird colonies (Fig. 7.3) but providing a series of transects that were continuous from south to north. The most northerly transect was not surveyed in 1997. In 1996-1999, surveys followed transects established in both "nearshore" and "offshore" habitats. Nearshore transects followed the contours of mainland or island shorelines, where waters were generally deeper than 10 m. Offshore transects cut across open water from one shore to another, over depths ranging from 10 m to >200 m.

In 1995 and 1997-1999, surveys were conducted primarily from the *R/V Pandalus*, a 22 m stern trawler operated by the Alaska Department of Fish and Game. Surveys in 1996 were conducted from the *M/V Tiglax*, a 36 m vessel operated by the Alaska Maritime National Wildlife Refuge, U.S. Fish and Wildlife Service. In all years, surveys in some shallow, nearshore areas were conducted from the *R/V David Grey*, an 11 m Uniflite cabin cruiser operated by the Biological Resources Division of the U.S. Geological Survey. Ground speed for all vessels was approximately 11-15 km/hr (6-8 knots).

Seabird surveys were conducted according to protocols established by the U.S. Fish and Wildlife Service for marine birds (Gould et al. 1982, Gould and Forsell 1989). From 1995-1999 and for offshore surveys in 1996, all swimming birds and mammals within 150 m on either side or 300 m forward of the boat were counted and identified to species and considered "on transect." For nearshore surveys in 1996, transect width was 200m. Instantaneous counts of birds flying within the transect boundaries were made 3 times during each 10-minute time interval (Gould and Forsell 1989). The sum of flying birds and birds on the water for a given time period yields a density estimate (birds/km^2). When possible, birds were recorded in discrete flocks and the following behaviors were recorded: flying, swimming on the waters' surface, actively feeding, standing on flotsam or jetsam, or holding a fish in the bill. Unusual bird sightings outside the transect boundaries or census times for flying birds were recorded as "off transect." Mammals were recorded as "off transect" when identified beyond the transect boundary.

Bird and mammal sightings were recorded by entering them directly into a real-time computer data-entry system (DLOG; Glenn Ford, Portland OR) that plots sighting positions continuously using GPS coordinates. GPS locations were obtained from a Rockwell Precision Lightweight Global-positioning Receiver (PLGR). PLGR units have a worst-case horizontal position accuracy of ±10 m at speeds <36 kph (Anonymous 1995). DLOG also provides the bottom depth and the distance to the nearest shore for all sightings. At all times, 1 person entered data into a laptop computer, located in the wheelhouse, while observers surveyed from the best vantage points of each vessel. On the *Pandalus*, 1-2 observers surveyed from the bow, located 3.4 m above the water's surface. On the *Tiglax*, 2 observers surveyed from the flying bridge, located 8.5 m above the water's surface. Observers on the *David Grey* surveyed from inside the wheelhouse (1 m) in 1995-1996, and surveyed from the top of the wheelhouse (2.4 m) in 1997-1999. The number of observers ranged from 1-3, and the low height of the observation platform in 1995 and 1996 was countered by reducing the transect width. Observers actively scanned with their eyes ahead of and alongside the survey vessel, and species identifications were confirmed using 7- or 10-power binoculars. Sightings were immediately called to the data entry person over hand-held VHF radios. All surveys took place during weather conditions suitable for sighting small seabirds at 150 m. Ancillary data on weather, sea conditions, observation conditions, bird behavior or plumages, and species of fish held by birds were collected for each transect.

For preliminary analyses, bird abundance and density estimates were based on five study areas. The three core study areas, Chisik, Kachemak, and the Barrens, were used for all years of the study, 1995-1999. Two additional areas were added for 1996: Shuyak, the very southernmost area surveyed, and the Central area, in the central and southwestern portion of the lower Inlet (Fig. 7.2). Data from transects conducted in 1996 were divided into appropriate areas to make them comparable with data from other years. All bird distribution maps were plotted using a log(x + 0.5) scale, and unless noted in the legend, all maps on a page were scaled so that a given symbol size represents the same number of birds in all maps on that page. For the purpose here of describing likely foraging areas, bird distribution maps include observations of only birds that were on the water, and do not include flying birds. All birds, regardless of activity, were used for the species summary table and for calculating densities at sea.

Results and Discussion

We surveyed marine birds and mammals along a total of 6192 km of transects (ranging from 763-2052 km/year) during the summers of 1995-1999 (Table 8.1). Survey area comprised a total of 1816 km^2 over the 5 years of the study. More than 135,000 marine birds were observed, representing 45 marine species (Table 8.2). A total of 831 marine mammals representing 10 species was also observed (Table 8.2).

Sea otters comprised the majority (38%) of marine mammals observed in lower Cook Inlet during 1995-1999 (Table 8.2). Other abundant species included harbor seals (21%), Dall's porpoise (13%), humpback whales (11%), harbor porpoises (4%), and Steller's sea lions (3%). Fin whales, minke whales, killer whales and northern fur seals were also observed in some years. Data on marine mammals have been archived and may be further analysed for peer-reviewed publications— although this is not a priority for this project. Nothing further about marine mammals will be presented or discussed here.

Shearwaters, mostly Short-tailed Shearwaters (*Puffinus tenuirostris*), comprised the majority (48.2%) of birds observed (Table 8.2). Other abundant species included Tufted Puffins (13.6%), Black-legged Kittiwakes (9.3%), Common Murres (8.0%), *Brachyramphus* murrelets (6.2%; 8% of which were Kittlitz's Murrelets, *B. brevirostris*), phalaropes (3.0%; 99% of which were Red-necked Phalaropes, *Phalaropus lobatus*), Fork-tailed Storm-Petrels (2.7%), Northern Fulmars (2.3%), Glaucous-winged Gulls (1.8%), Horned Puffins (1.3%) and Pigeon Guillemots (1.1%). The remaining 2.5% of birds was composed of less common species including loons, grebes, tubenoses, cormorants, sea ducks, jaegers, gulls, terns, and alcids.

Of all the areas we surveyed, Shuyak in 1996 had the highest marine bird densities with 324.77 birds/km^2 (Table 8.3). Kachemak supported moderate densities of birds in all years, and the Central region supported low densities of birds in 1996. Among the three core study areas, the highest densities of marine birds were observed around the Barrens in all years, and the lowest densities were observed near Chisik in all years (Table 8.3, Figs. 8.1-8.11). However, most of the difference in density between the Barrens and Kachemak Bay was due to a difference in abundance of shearwaters and Tufted Puffins, both of which were much more common around the Barrens. There was little difference between the Barrens and Kachemak Bay in their densities of common, fish-eating seabirds such as kittiwakes, murres and murrelets.

Shearwaters had the highest densities of any species group observed, with an average of 274.5 birds/km^2 in the Shuyak area in 1996 (Table 8.3). Of the three core study areas, shearwater densities were highest around the Barrens in 4 out of 5 years, and lowest near Chisik in 4 out of 5 years. Shearwater distribution in 1996, when the entire lower Inlet was surveyed, was well-correlated with the northward-flowing plume of cold, upwelled waters that forms north of the Barren Islands (contrast shearwaters in Fig. 8.11 with AVHRR imagery in Chapter 2). Other oceanic species, such as storm-petrels and fulmars, were also found primarily in the oceanic upwelled waters around and to the north of the Barren Islands (Fig. 8.11). As with shearwaters, their range north of the Barrens appears to be constrained by the extent of the cold-water plume, although the association does not appear to be as strong.

Fish-eating seabirds such as murres, puffins, murrelets, guillemots, gulls, and cormorants were concentrated (Figs. 8.1-8.9) in coastal areas around the Barren Islands, along the Kenai Peninsula and along the North and South shores of Kachemak Bay. These are all areas in which forage fish concentrations were highest (see Chapters 4, 7). Deep-diving species such as murres and Tufted Puffins were also widely distributed in moderate to high densities in offshore waters north of the Barrens, particularly in areas with high concentrations of juvenile pollock and capelin (Chapters 4, 7). Tufted Puffin densities were highest around the Barrens in all years, with up to 40 puffins/km^2. In the other study areas, puffin densities remained at or below 3.4 birds/km^2. Murre densities were also highest around the Barrens, although densities were similar to those observed in Kachemak Bay in most years (Table 8.3).

Horned Puffins were concentrated around Chisik— the only location where appreciable numbers breed— with densities ranging from 0.99-4.98 birds/km^2. Marbled Murrelet densities, although highest in Kachemak in all years, were highly variable, ranging from 3.4-12.6 birds/km^2 in Kachemak and dropping as low as 0.87 birds/km^2 at Chisik. Cormorants were recorded in low densities in all areas and years. With the exception of a large feeding flock observed in the area offshore of Chisik Island in 1995, cormorants were limited to nearshore areas. Marbled Murrelets had a wide distribution, and were found in all portions of the study area. They occurred only rarely, however, where waters were >100 m deep (i.e., within about 25 km to the north and east of the Barren Islands).

Kittlitz's Murrelets were more limited in their distribution, and were concentrated within and outside of Kachemak Bay and along the Kenai Peninsula.

Surface feeders— such as Glaucous-winged Gulls and kittiwakes— and Pigeon Guillemots were found occasionally in offshore areas but all showed a strong tendency to forage within a kilometer of the shore. Kittiwake densities were highest in the Barrens (actually along the Kenai Peninsula) in 4 out of 5 years. Glaucous-winged Gull densities were variable, peaking in each of the three core study areas in different years. Guillemots were largely restricted to the shores of Kachemak Bay and the Kenai Peninsula. In 1997, a few guillemots were found in shallow waters on the eastern edge of the Chisik offshore area, but no guillemots were seen on Chisik shoreline transects in five years of study. Guillemots were dispersed, and densities were always below 2 birds/km^2.

In summary, lower Cook Inlet supports some of the highest at-sea densities of marine birds in Alaska (Piatt 1994), with densities of over 100 birds/km^2 in 3 of 5 years at the Barren Islands and over 300 birds/km^2 in the Shuyak region. These concentrations are supported by high levels of biological productivity, which in turn result largely from persistent upwelling of cold oceanic waters around the Barren Islands and Kenai Peninsula and the advection of these nutrient-rich waters northward into the inlet by prevailing currents (Muench et al. 1978, Chapters 2 and 3). In general, the abundance and distribution of marine birds corresponded to patterns of oceanography and/or fish distribution. Procellarids (shearwaters, fulmars and storm-petrels) were associated with cold, nutrient-enriched upwelled waters. Fish-eating birds— such as murres, kittiwakes and murrelets— aggregated in areas with high forage fish biomass concentrations. Whereas murres are capable of diving to great depths, few were observed foraging in deep waters to the immediate north and east of the Barren Islands. Despite the longer travel times, murres from the Barrens Islands foraged mostly in coastal waters along the Kenai Peninsula— perhaps because prey along the Kenai Peninsula are more predictable and energetically cheaper to exploit than prey in deep waters adjacent to the Barrens. It appears that most murres from Chisik ranged far (>50km) offshore towards Kachemak Bay, presumably because of the scarcity of prey closer to home. Black-legged kittiwakes foraged almost entirely along the coast. As we observed with murres, the richest foraging grounds for kittiwakes in all years were in Kachemak Bay and along the Kenai Peninsula, whereas few kittiwakes were observed foraging near Chisik at any time. These patterns of murre and kittiwake distribution help explain measures of foraging range and trip duration, and ultimately, reproductive success in these species (see Chapter 14).

Analyses are still in progress, and here we have presented summary information on the abundance and distribution of marine birds in lower Cook Inlet. The aggregative response of murres and kittiwakes to prey dispersion is discussed in Chapter 14. The relationship between seabirds and their physical and biological environment will be the subject of a Ph.D. dissertation at the College of Fisheries, University of Washington (S. Speckman, in prep.).

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Chapter 9. Common Murre Biology in lower Cook Inlet

Thomas van Pelt and Michael Shultz

Introduction

Immediate impacts of the 1989 T/V *Exxon Valdez* oil spill (EVOS) on Common Murres (*Uria aalge*) in the Gulf of Alaska were well documented (Piatt et al. 1990). Common Murres comprised most (74%) of the oiled bird carcasses recovered from beaches (>30,000; representing 10-30% of the total mortality) and putative short-term effects included a reduction in populations at affected colonies, delayed breeding phenology and low reproductive success (Piatt et al. 1990, Piatt and Ford 1996). One of the most severely affected areas was Cook Inlet, where large numbers of murres were beginning to gather near breeding colonies such as the Barren Islands when oil swept through the region in April and May of 1989. However, there is also evidence that an oceanographic 'regime shift' occurred in the Gulf of Alaska in the early 1980's, resulting in changes in seabird diets and reduction of reproductive success in some marine bird and mammal populations (Piatt and Anderson 1996, Anderson and Piatt 1999). These changes were similar to some hypothesized effects of the EVOS. This raised two important questions: 1) can effects of the oil spill on murres be separated from natural variability, and, 2) how will the regime shift affect the recovery of murre populations impacted by EVOS?

To address these questions, we conducted detailed studies of murre breeding biology and foraging behavior at the three largest murre colonies in lower Cook Inlet: Chisik Island, Gull Island and the Barren Islands. We simultaneously measured forage fish distribution and abundance in waters around those colonies (Chapters 4-7). The purpose of this chapter is to document the methods we used to gather data on murres and present all the basic results in summaries by colony (3) and year (5) of study. Preliminary results of our studies on murres have appeared in several publications (Piatt and Anderson 1996, Zador and Piatt 1998, Piatt et al. 1999, van Pelt 2000). An analysis of the response of murres to fluctuations in prey density is given in Chapter 14. Major results on breeding biology and behavior presented in this chapter will be further analyzed and submitted for publication in peer-reviewed journals.

The Common Murre is a highly colonial seabird with a circumpolar boreal and low-Arctic distribution. Only one egg is laid (although lost eggs may be replaced) and both sexes share incubation and chick provisioning duties. The chick is fed at the nest for 15-25 days, leaves the colony at < 30% of adult mass, and is subsequently cared for by one parent for up to six weeks. The murre colony at Chisik Island (west side of Cook Inlet; 60° 09' N, 152° 34' W) underwent a steady decline to ca. 10-20% of maximum counts made in the early 1970s and currently supports ca. 2500 murres. The colony at Gull Island (east side of Cook Inlet; 59° 35' N, 151° 19' W) has expanded by about 80% since 1984, and currently supports ca. 8500 individuals. The colony at the Barren Islands (58° 55' N, 152° 10' W) lies at the mouth of Cook Inlet, and supports a relatively stable or slightly increasing murre population that is an order of magnitude larger than the colonies at Chisik and Gull Islands (Piatt and Anderson 1996, Zador et al. 1997). The three colonies are separated from each other by about 100 km (Fig. 7.1) and are in oceanographically distinct habitats (Chapter 2). Chisik Island is surrounded by stratified, relatively-warm estuarine waters whereas Gull Island is surrounded by colder, mixed oceanic waters with significant freshwater runoff (Robards et al. 1999). The Barren Islands are surrounded by cold, Gulf of Alaska waters because the Alaska Coastal Current enters Cook Inlet north of the Barren Islands and cold, nutrient-rich waters are upwelled around the Barrens and onto the shallow Cook Inlet shelf (Robards et al. 1999, and Chapter 2).

Methods

Population monitoring

Some population monitoring plots had already been established by Alaska Maritime National Wildlife Refuge (Homer, Alaska) personnel prior to the beginning of our study. To facilitate long-term comparisons, these historical plots were maintained. However, in some cases additional plots were created at the beginning of our study in 1995, and also in later years. We therefore summarized our data in several different ways: 1) using only historical plots, 2) using historical plots and plots created in 1995, and, 3) using historical plots, 1995 plots, and plots created after 1995.

All plots were photographed, and boundaries were clearly marked on the photographs. Using inflatable boats for access, binoculars for viewing, and tally-clickers for counting, all murres within the plots were counted 5-12 times during the season between early incubation and the onset of chick fledging. Sea, wind, and visibility conditions were recorded for each count. Counts were made between 1000 and 1600 hours (the time during daylight hours when attendance is most stable; see Birkhead and Nettleship 1980, Piatt and McLagan 1987, Boersma *et al*. 1995, Roseneau *et al*. 1995). Two observers counted each plot. If the difference between observers was greater than 10% of the total, the count was repeated and initial results were discarded. The plot total was taken as the mean of the two observer counts. The sample unit is the count-day, with all plot counts for each day merged into a total. Plots in population counts therefore serve as an organizational tool and not as a statistical unit (in contrast to productivity plots; see below). Plots also allow for sampling of the entire colony, and help reduce potential bias from counting only one area of a colony (Birkhead and Nettleship 1980).

Murre attendance on cliffs is most consistent from the end of egg-laying through the start of chick fledging (Birkhead and Nettleship 1980, Piatt and McLagan 1987), but logistic constraints during the field season precluded us from conducting all counts within this period. Therefore, following the field season, count 'windows' for each colony-year were defined (based on the reproductive chronology for that year) as mid-incubation to the beginning of fledging. Estimates for mid-incubation were obtained by adding 15 days to peak laying date; the start of fledging is defined as the date on which the first chick was observed to fledge from a productivity plot. Summaries presented here use only counts made within the appropriate mid-incubation to fledging window (Appendix 9.1)**.**

Productivity and breeding chronology

Measures of Common Murre productivity and breeding chronology were derived from data recorded during regular observations of nest-sites (Birkhead and Nettleship 1980). Nest-sites were grouped into plots, and data were analyzed using plot as the sample unit. A minimum of seven plots were subjectively selected (to include different habitat types) at each study location (Chisik, Gull, and Barren Islands). Each plot comprised clusters of 8-40 nest-sites (sites with eggs) on cliff faces, cliff tops, or sections of flat-topped offshore rock. Observations of each plot were made from a marked point that was used each year. Plot boundaries— defined by recognizable, permanent features of the substrate— were clearly marked on photographs taken from the observation point, and on hand-drawn maps that show recognizable features of the terrain. If possible, the same plots were used each year. When it was possible to identify nest-sites used in previous years, nest-site numbers were retained. New nest-sites received new numbers (or the number of an adjacent site plus a letter).

Breeding chronology and breeding success of Common Murres were monitored following a modified version of the Type I protocols detailed by Birkhead and Nettleship (1980). Using digital color photographs or hand-drawn sketches, each site where a murre was present in the pre-laying period was mapped. Plots were monitored using a regular interval of 3 days typically, but this ranged from 2-4 days depending on the year. In an effort to obtain more precise chick fledging ages in 1997 and 1998, plots were checked more frequently (1-2 d) just prior to fledging. The presence of the nesting adults and nest contents were recorded using the following codes:

<u>Adult codes</u>

S	Standing and not in incubation or brooding posture.
L	Laying down and not in incubation or brooding posture.
IP	Incubation posture. A distinct posture assumed by most murres when incubating eggs. Adult sits forward with back humped, tail held down, and wings slightly dropped with tips uncrossed.
BP	Brooding posture. A distinct posture assumed by most murres when brooding chicks. Characterized by wing-mantling--the wing sheltering the chick is dropped.
P	Adult present. Cannot classify posture as any of the above.
N	No adult present.

<u>Nest content codes</u>

E	An egg is seen
C	A chick is seen
Ø	There is no egg or chick
U	Undetermined nest content

Examples: ‘2S’ means 2 adults were standing; ‘SLØ’ means that one adult stood, another lay, and there was no egg or chick; ‘NC’ is an unattended chick; ‘NØ’ is an empty nest-site.

Laying date was defined as the first day we either recorded an adult in an incubating posture or saw an egg at a site where there had not been one on the previous visit. Because murres incubate their eggs closely, rarely revealing the egg to observers, it was necessary to infer some egg-laying dates based on first recording of incubating posture at sites where an adult was observed in an incubating posture on at least three consecutive visits (Murphy and Schauer 1996). For those sites that already had an adult in incubating posture or an egg present when first visited or mapped, laying date was back-calculated from hatch date, using the normal incubation period of 32-33 d (Gaston and Jones 1998).

The presence of just-hatched chicks can also be difficult to view directly. Hatching date was therefore defined as the first day we either recorded an adult in brooding posture or saw a chick at a site where there had not been one on the previous visit. Fledgling age is defined as the inclusive number of days from the hatching date to the day before the date when the chick was first noted absent. After colony departure, chicks continue to be cared for by the male parent for up to two months (Varoujean et al. 1979), but for convenience here, and following methods used in other studies of this species, chick departure from the nest-site is taken as ‘fledging’, and chicks that have departed the nest-site as ‘fledglings’. Since 15 days is the minimum nest departure age in Common Murres (Gaston & Jones 1998), chicks were considered to have ‘fledged’ successfully if they disappeared from the nest-site >= 15 d after hatching; any chicks that disappeared prior to this were assumed to have died.

Hatching success was calculated as the proportion of active nest-sites (sites where the presence of an egg was either inferred or directly observed) that produced a chick, and breeding success was calculated as the proportion of active nest-sites that fledged a chick (Birkhead and Nettleship 1980). Fledging success was defined as the proportion of hatched chicks that fledged successfully. Reproductive success was taken as the proportion of nest-sites where an egg was laid from which a chick fledged.

Calculation of productivity

Owing to logistic constraints, we observed nests at 1-4 day intervals, rather than at the daily intervals recommended (Type I ‘full scale’ method; Birkhead and Nettleship 1980). Intervals were usually an odd number of days, and this simplified our estimation of laying and hatching dates by minimizing fractional dates. For instance, if a nest-site was observed to contain an egg on day and then contained a chick on day 3 (2 d interval between checks), the hatching date would be estimated as day 1.5. However, if the nest-site was next visited on day 4 (3 d interval between checks), the hatching date would be estimated as day 2.

We developed a set of objective rules for analyzing our productivity data (rules, formulas, and spreadsheets for analysis were initially developed by Arthur Kettle, Alaska Maritime

National Wildlife Refuge, Homer). Details are given in Appendix 9.2, with supplementary information on parameters and codes in Appendix 9.3. An important feature of these rules is the effort to improve the precision of hatch date calculations, by excluding nest-sites with between-check intervals > 7 d for both laying and hatching. Since this rule acts only on nest-sites that produce chicks, it can artificially reduce the ratio of eggs to chicks, thereby artificially reducing hatching success. We corrected for this problem by first determining the proportion of nest-sites that were excluded due to excessive interval between checks, then reducing the number of 'egg-only' nest-sites by the same proportion. This rule also reduces the sample size of nest-sites per plot and any plot whose number of nest-sites fell below eight after application of this rule was excluded from analyses.

As documented in other studies of murre productivity, we observed egg predation on many occasions. Thus, it can be assumed that some murre pairs laid and lost their egg in the 1-4 d interval between any two successive observation days, suggesting a slight overestimate of both hatching and reproductive success (Boekelheide et al. 1990). Because our observation effort was generally constant during the seasons, however, any overestimates should also be constant and should not affect the trends documented here. A further problem arises if the observation intervals span the fledging period unevenly, in which case the chick may be ruled to have died when in fact it may have fledged. For example, if a nest-site with chick was checked on day (hatch date + 12 d), then subsequently checked with no chick on (hatch date + 16 d), the chick would be scored as 'disappeared at age 14 d' and therefore dead. But in this example, there is some chance that the chick was in fact alive on (hatch date +15 d), and therefore successfully fledged. Errors of this kind would tend to artificially reduce measures of fledging success and consequently reduce estimates of reproductive success. However, there is an equal probability of the observation interval to cause a chick to be ruled as 'fledged' when in fact it died (e.g., in a situation similar to above example, if a check on (hatch date +13 d) was followed by a check on (hatch date + 17 d), the chick would be ruled as 'disappeared at age 15 d' and therefore fledged, when in fact it could have died on (hatch date +14 d)). We therefore assume these errors to cancel each other; there is no evidence that the chick survival rate is non-linear between age 10-20 d. However, it is important to acknowledge that productivity measures using variable intervals between checks may not be directly comparable to measures presented in other studies that used either daily checks, or different intervals between checks.

Chick diet

Murres bring single fish to their chicks, held in line with the bill and with the tail outwards, leaving about half of the fish visible (Gaston and Jones 1998). Between arrival at the colony and delivery to the chick, there is often a brief appeasement display, during which the fish is held high in the air and is relatively easily seen, thereby facilitating identification. We used binoculars to identify prey items to the lowest possible taxonomic level, and we estimated the length of prey items relative to the length of an adult murre's bill gape (gape length was then accurately measured from a random sample of captured adults), in one-fifth multiples. Identification was based on the color and shape of the prey, and of the caudal, anal, adipose fins of fish. A field guide to Common Murre bill loads and other fish keys were used to aid identification of prey (for a copy, go to: .www.absc.usgs.gov/research/seabird&foragefish/products/index.html).

Observation periods were of two types: targeted periods dedicated to observations of chick diet, and ancillary observations made during all-day adult time-budget watches. We did not include fish haphazardly observed during productivity checks, since that could skew observations toward large fish. Each observation was recorded as one of the following three categories: (1) 'Did Not See' (a feeding occurred, but because the delivery was too fast or was obscured, no identification was possible), (2) Unknown (a view sufficient for identification was obtained, but positive identification was not made), or (3) the fish was identified to the lowest practical taxonomic level. 'Did Not See' category fish were not used for diet summaries. We also recorded the fate of each prey item. Only prey that were actually fed to chicks were used for these summaries, since fish used for display may differ from those fed to chicks.

Adult diet

Diets of adult murres were assessed by collection of a sample of ca. 10 individual murres per colony per year. Flying birds were killed by shotgun from an inflatable boat as they were returning to the colony. All collections were carried out under the authority of permits issued by the U.S. Fish and Wildlife Service and the Alaska Department of Fish and Game. Within four hours of death, carcasses were either necropsied in the field, or frozen for later necropsy in the laboratory. Stomachs and proventriculi were dissected out, placed individually in 18 oz plastic bags (Whirl-paks) together with a volume of 50% isopropyl alcohol to equal double the volume of gastric tissue and contents, then frozen. Stomachs were later analyzed under contract by Kathy Turco or Alan Springer (Falco Inc., Fairbanks, Alaska), and biomass of prey were assessed based on otolith numbers and size, using a reference collection maintained at the University of Alaska, Fairbanks.

Adult attendance and provisioning

Adult time budgets were calculated from all-day observations of 8-12 nest-sites at each study location. The same nest-sites were used for all observations within each summer, although failed nests were replaced in later watches. During observations, the time was recorded for each adult arrival, delivery of prey to chicks, exchange of incubation or brooding duty, and adult departure. Each observation-day began when nest-site activities became clearly visible and ended when it was too dark for observations to continue. On Gull Island, some observations were recorded by video and analyzed later; more complete details of the video recording system are given in Zador and Piatt (1999). At Chisik Island in 1998, a few observations were made using video recording. At the Barren Islands, a commute by boat is necessary to access the plot; early-morning and late-night observations were therefore recorded by video and later analyzed at camp. At each study site, we conducted observations on 2-3 observation-days during incubation, and 3 observation-days during the nestling period. The observations were timed to sample the early, middle, and late parts of the incubation and nestling periods. When possible observation days were synchronized among study locations. Where observation nests changed between years, we chose nests near the previous ones, to minimize the possibility of confounding among-plot effects with among-year effects.

Nest attendance was measured in bird-minutes per nest per hour (e.g., a nest with one bird attending for a full hour and its mate attending for half of the hour has 90 bird-minutes that hour). We calculated separately nest attendance during incubation and during the nestling period. Adult provisioning frequency was measured in feedings per nest per hour. Adult duty exchange frequency was calculated in exchanges per nest per hour. A trip from the nest began when an adult left the nest and ended when it returned. Values were calculated separately for trips made during incubation, trips during the nestling period, and trips that ended with chick provisioning. Only complete trips were counted--not trips that were in progress when the observation period started or ended. From preliminary analyses, we concluded that neither nest-site or observation day contributed significantly to variability in behavioral parameters in a given year and we used nest-site as the sample unit.

Chick growth

We were not able to repeatedly capture individual chicks to measure standard variables such as maximum growth rate and midpoint mass. Instead, we captured chicks of unknown age and made single measurements of both mass and wing length (Harris and Wanless 1988, Uttley et al. 1994, Bryant et al. 1999). This was done in at Chisik Island in 1995, 1996, 1997, and 1999, and at Gull Island in 1995 and 1996. In all years, the captures were made in a single bout to ensure that each chick represented a unique and independent measurement, and capture bouts were timed to occur near the midpoint of the chick-rearing period, so that exceptionally early or late chicks were not over-represented. In all years, mass measurements were made using a 300-g spring scale. Wing measurements were made ± 1 millimeter, from the carpal joint to the tip of the longest feather. Over a range of wing-lengths from 25 to 45 mm the relationship between chick weight and wing-length was linear in all years; we therefore sub-sampled data to include only those chicks whose wings were between 25 and 45 mm (inclusive) at time of capture (Harris and Wanless 1988). We used linear regression to measure the relationship between mass and wing length by colony and by year, and we present the regression slope ± standard deviation as the sample unit for comparison between colonies and years.

Fledgling condition

We used captures of fledging chicks to obtain estimates of body condition and age at fledging. These data represent integrated growth over the first 2-3 weeks of development; subtle differences in growth patterns may therefore be missed using this approach, but it should reveal large differences between years or colonies and allows comparisons to other studies that present fledging mass and condition (Harris and Wanless 1988). Fledging chicks were captured either by hand as they made their way across cliff-base rocks toward the ocean, or with dipnets from boats roaming near shore. All captures were carried out under the authority of permits issued by the US Fish and Wildlife Service and the Alaska Department of Fish and Game. Handling times were minimized wherever possible to reduce the stress of capture. Capture dates were timed to overlap with the peak in numbers of fledglings. For the purposes of summarizing the data, we pooled some adjacent days' data into capture 'bouts' in cases where <5 individuals were captured per day. Within each capture day, effort was concentrated during the dusk to early night period, using headlamps to aid captures and data collection. Mass (± 1 g) was measured using a spring scale, and flattened standard wing length ± 1 mm (from the carpus to tip of the longest feather) was measured using a stopped ruler. Some fledglings had wet feathers when captured; mass data from those individuals were not included in summaries presented here. Following capture and measurement, fledglings were released either directly into the sea, or onto the rocks in the area where captured. Processing each fledgling generally took no longer than 1 minute, and fledgling behavior post-handling appeared to be no different from fledglings that were not captured.

Age of fledglings was estimated using a wing length-age regression determined from known-age chicks in a separate study at Duck Island (age [d] = -7.01 + 0.388[wing length in mm]; $n = 13$; $F = 59.97$; $P < 0.001$; Van Pelt 2000). Using body size to estimate offspring age can be imprecise (Cooch et al. 1999); therefore estimated ages were compared with ages determined by chick departure from nest-sites in observed plots. Over three colony-years, the ages estimated by wing length did not differ from ages measured by chick departure (Chisik 1998 $t_{26} = 0.507$, $P > 0.3$; Chisik 1999 $t_{154} = -1.254$, $P > 0.2$; Gull 1999 $t_{68} = -1.107$, $P > 0.2$). Body mass is partly the result of structural body size and may not reflect the quantity of body reserves (Chastel et al. 1996). We therefore scaled mass to body size as an index of body condition, dividing mass by wing length.

Adult body condition

Breeding adults were captured using a telescoping fiberglass pole fitted with a noose. All captures were carried out under the authority of permits issued by the US Fish and Wildlife Service and the Alaska Department of Fish and Game. Handling times were minimized wherever possible to reduce the stress of capture. All birds captured were actively attending a nest-site, egg, or chick. Captured birds were banded with a unique combination of color bands and a metal USFWS band. A small blood sample for sex determination was taken from the wing. Blood was collected and stored in a 1.8 ml vial that had been pre-filled with a buffering solution. The sex of the bird was later identified from red blood cell DNA, using two CHD genes (Griffiths et al. 1996). Body mass (± 5 g) was measured using spring scales; head-plus-bill and tarsus length ± 1 mm using vernier calipers; and flattened standard wing length ± 1 mm (carpus to distal end of longest primary feather) using a stopped ruler. Body mass is partly the result of structural body size and may not reflect the quantity of body reserves (Chastel et al. 1996). We therefore scaled mass to body size as an index of body condition, dividing mass by wing length.

We attempted to capture adults on a regular schedule to represent condition during prelaying, early, middle and late incubation, and early, middle and late chick-rearing. The target sample size per capture session was 10 adults. However, due to logistical considerations not all captures per session could be made on the same day. For the purposes of summarizing the data, we therefore grouped captures into 'bouts' of captures made within a few days of each other.

Adult corticosterone levels

Simultaneous with captures made for measurement of adult body condition, we took blood samples from the alar vein within 3 minutes of capture. Blood was collected in microhematocrit capillary 100 microliter tubes, which were then emptied into 0.5 ml Eppendorf vials. Blood samples were stored on ice, and then centrifuged within 12 hours, after which the plasma was collected and frozen. Plasma samples were later analyzed for corticosterone concentrations by radioimmunoassays in J.C. Wingfield's lab at the University of Washington (for further details on methods used for assays and analyses, see Kitaysky et al. 1999 and references therein).

Results

Population plots

Results for each group of census plots are summarized by colony and shown in Tables 9.1-9.3. There was no consistent trend across the five years of study at either Chisik or Gull Islands, but in 1998 there was a clear drop in numbers at both colonies (Tables 9.1, 9.2). Murres appeared to be increasing slowly at the Barren Islands (Kettle et al. 1999). When results are put in context with historical data, and examined over longer times periods, a downward trend at Chisik Island and an increasing trend at Gull and the Barren islands are apparent (Appendix 9.10). We believe that murre population plots at Gull Island are now saturated with breeding birds, and population increases are better revealed from whole-island counts (Appendix 9.11). Even during the short course of our study, we have noticed an increase in murres on parts of the Gull Island colony that were not used in previous years.

Population estimates

Entire island counts were conducted to estimate the absolute size of populations on each island. Two whole-island counts were conducted on Chisik Island and four counts on Gull Island between 1995-1999. These data corroborate results of population plots censuses and showed that between 1995-1999, the Gull Island population continued to increase (Appendix 11). When the data collected between 1995-1999 are summarized with historical counts, they show a continuing decline in the murre population on Chisik as numbers went from an estimated 20,000-25,000 murres in 1970 to 3,500 in 1997. On Gull Island, the population has fluctuated over the past 23 years but overall the population has persisted to increase from 3,200 birds in 1976 to an estimated 10,725 birds in 1999. Whole island counts of murre populations at the Barren Islands are problematic, and there are no good historic data with which to assess whole-island population trends (Piatt and Anderson 1996, Roseneau et al. 1995).

Productivity

All measures of productivity tended to be broadly consistent within colonies, but there were dramatic departures from this in 1998 and 1999. Across the five years of study, mean hatching success varied among the Chisik, Gull, and Barren Island colonies (Table 9.4), and there was no consistent trend across years. However, hatching success was markedly depressed at Chisik Island in 1995 and1998, at Gull Island in 1999, and was relatively low at the Barren Islands in 1998 (Table 9.4). Fledging success was consistently high at the Barren Islands, and tended to be higher at Chisik Island than at Gull Island across the four years for which concurrent data were available, with the exception of 1998 when fledging success at Chisik Island was sharply reduced in comparison to Gull Island (Table 9.5). Breeding success followed a similar pattern to the other measures of productivity, with the highest average success at the Barren Islands, nearly equal average success at Chisik and Gull Islands, no detectable trend across years, and exceptionally low success at Chisik Island in 1998 and at Gull Island in 1999 (Table 9.6).

Breeding chronology

Mean egg laying dates showed greater variation at Chisik Island (range 6 July to 26 July) than at Gull Island (range 9 July to 13 July); birds at Chisik Island tended to lay later than at Gull Island, but this trend was inconsistent across years (Table 9.7). Murres at the Barren Islands tended to be the first to lay eggs among the three colonies, and their mean laying dates were relatively consistent between years (range 1 July to 7 July). Egg laying was severely delayed at Chisik Island in 1998 (Table 9.8). The pattern in mean hatching dates between colonies and years was similar to the pattern in egg-laying (Table 9.8), as expected given a relatively consistent incubation duration of ca. 33 days in this species.

Chick diet

Summaries of the taxonomic composition of chick diets are presented in Table 9.9 (detailed species composition is provided in Appendices 9.4–9.6). Osmerids and sand lance were the dominant species across the whole study area, together accounting for 50-90% of chick diets. There were some conspicuous differences among the colonies: Chick diet at the Barren Islands was overwhelmingly dominated by Osmerids (capelin), while Gull Island chicks were fed a variety of species across years, but in particular, sand lance. Chick diets at Chisik Island were consistently dominated by Osmerids (smelts), together with a varying mixture of sand lance and gadids. There was a notable trend of increasing osmerids in chick diets at Gull Island, from 6% in 1995 to 56% in 1999 (Table 9.9; Appendix 9.5), and sand lance consumption increased at Chisik Island between 1997-1999, from 12% to 36% (Table 9.9; Appendix 9.4).

Adult diet

Summaries of the taxonomic composition of adult diets are presented in Table 9.10 (detailed species composition is provided in Appendices 9.8–9.10). Pooling data across years, osmerids and sand lance dominated diets at all three colonies, accounting for 55% to 86% of adult diets (Table 9.10). However, there were some notable differences between colonies and years. At Chisik Island, sand lance consistently dominated adult diets across all years, while significant consumption of osmerids occurred only in 1996 and 1999. Gadids were important in 1995, but less so in all other years. At Gull Island, sand lance were overwhelmingly dominant in all years except 1998, when osmerids mostly replaced sand lance. Gadids were important only in 1997. At the Barren Islands, gadids were dominant in 1995-1997, while osmerids increased to dominate in 1998. Sand lance were virtually absent from adult diets at the Barren Islands until 1999, when they represented over 70% of the diet.

Adult attendance and provisioning

Summaries of adult attendance during incubation are given in Table 9.11, using nest-site as the sample unit (see Methods). Attendance was consistently higher at Gull Island than at Chisik Island (Table 9.11). There were no consistent trends across years at either colony, and little inter-year variation in attendance at either Gull or Chisik Islands. Attendance during incubation at the Barren Islands was relatively high (Table 9.11), and was consistent between years with the exception of 1997 when attendance was exceptionally high.

Attendance during the chick-rearing phase is summarized in Table 9.12, using nest-site as the sample unit. Again, attendance was consistently higher at Gull Island than at Chisik Island, although the difference was marginal in 1996 and 1999. Attendance at Chisik Island was consistently low, with little variation between years. There was marked variation between years at Gull Island (Table 9.12). Mean attendance at the Barren Islands was similar to Gull Island, and there was also considerable variation between years (Table 9.12).

Chick-feeding rates are shown in Table 9.13, using nest-sites as the sample unit. Trip durations are shown in Table 9.14, using nest-sites as the sample unit. Chick-feeding rates were consistently higher at Gull Island than at Chisik Island, and trip durations were generally shorter at Gull Island than at Chisik Island. Barren Island feeding rates were similar to Gull Island, while Barren Island trip durations were intermediate between Gull Island and Chisik Island. There was no obvious trend across years in provisioning rates or trip durations at any colony; however, there were some years with extreme parameter values. Chick-feeding rates at Chisik were relatively low in 1996 and 1998 compared to other years, and at Gull Island they were relatively low in 1998 (Tables 9.13). Foraging trip durations at Chisik Island were much longer in 1996 than in other years, and at Gull Island they were relatively shorter in 1997 than in other years.

Chick growth

The ‘growth rate’ (see Methods) of chicks from the Chisik and Gull colonies varied considerably among years, with significant differences between years at both colonies (Table 9.15; ANCOVA; Chisik $F_{3,\,128} = 3.08$, $P = 0.03$; Gull $F_{1,\,37} = 10.02$, $P = 0.03$). To compare between colonies, we pooled data from the two years (1995-1996) where overlapping data was available. Slopes did not differ (ANCOVA $F_{1,\,115} = 1.73$, $P = 0.19$). No growth rate data were obtained from the Barren Islands.

Fledgling condition and age

The size, condition, and estimated age of fledglings captured when departing the colony are given in Tables 9.16-9.18. With data from all three years pooled, it appears that chicks from the Barren and Gull Islands fledge in slightly better condition (index 3.17-3.18) than chicks from Chisik Island (index 3.07). There was no apparent trend in condition among years or within sites. Chicks fledged at an average age of 18-24 days, based on estimates of age derived from observations at productivity plots (Table 9.19) or from the size of fledglings as they departed the colony (Table 9.16-9.18). In general, there was little variation and no apparent trend in chick age among colonies and years. Ages were not estimated from Barrens fledgling data, and productivity data were not collected at fine enough resolution to age chicks (A. Kettle, pers. comm.).

Adult condition

Summaries of the size and condition of adults are given in Tables 9.20-9.21. Adults were not captured at the Barren Islands. Pooling data over all three years, the size and condition of adults at Chisik and Gull Islands were virtually identical. There were no apparent size differences between years at either colony, but birds at Chisik Island were heavier and consequently in better condition in 1997 compared to 1998-1999, while birds at Gull Island were in poorer condition in 1997 compared to other years (Tables 9.20-9.21).

Adult corticosterone levels

The baseline levels of corticosterone hormone concentrations (ng/ml) for adults at Chisik and Gull Islands are summarized in Table 9.22. There was high variation in corticosterone levels across breeding phases and years. Concentrations of corticosterone in adults at Chisik Island in 1998 were relatively high throughout the entire breeding season, in contrast to other colony-years, when concentrations either increased across the season (Chisik and Gull in 1997) or varied across the season (Chisik in 1999, Gull in 1998 and 1999; Table 9.22).

Discussion and conclusions

There were no striking trends in population plot counts during the five years of this study. However, there was considerable among-year variation in counts. For example, there was a drop in numbers at Chisik Island in 1998 that was probably linked to the ENSO event of 1998 (Piatt et al. 1999). This kind of annual variability often precludes analysis of trends over short time periods. Consideration of trends over larger time frames than this study (Appendices 9.10, 9.11, Roseneau et al. 1995, 1998) suggest that murres are increasing at the Barren Islands by 4.4% per annum (1989-1999), increasing at Gull Island by 8.8% per annum (1984-1999, whole island counts), and decreasing by 8.9% per annum at Chisik Island (1971-1999).

With a few exceptions, measures of productivity (hatching, fledging, and breeding success) were broadly consistent within colonies and among years. These results follow the well-established reproductive patterns observed in this species, with stable and high levels of breeding success across a range of moderate to good food availability and ecological conditions, but occasional years of exceptionally low productivity when conditions fall below some threshold (Boekelheide et al. 1990, Burger and Piatt 1990, Piatt and Anderson 1996). Owing to the scarce food supply around Chisik Island (Robards et al. 1999, Chapters 4,5 and 7) we expected murres there to do worse than those at Gull Island— and not better, as observed. The low attendance measured at Chisik Island must reflect increased parental effort in reproduction, and buffering of productivity against low food abundance (Burger and Piatt 1990, Uttley et al. 1994, Monaghan 1996). The fact that fledglings at Chisik Island were in similar condition to those at Gull Island may also be ascribed to buffering efforts. We would expect such increased efforts to come at a cost, most likely a reduction in adult condition and/or survival. There were no large differences in body condition of adults between the colonies, however, and we are still assessing adult survival at both colonies (EVOSTC funded project 01338). Results of that work will likely add to our interpretation of work presented here.

The purpose of this chapter was to document methods used to collect data on Common Murres, and to summarize the main results of our studies on this species. The ultimate objective is to interpret how various parameters of murre biology and behavior vary with food supply. To that end, a preliminary synthesis on the response of murres to fluctuations in food supply is presented in Chapter 14. Results presented in this chapter will be further analyzed and submitted for publication in peer-reviewed journals.

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Chapter 10. Black-legged Kittiwake Biology in lower Cook Inlet

Michael Shultz

Introduction

Black-legged Kittiwakes *(Rissa tridactyla)* are among the most abundant nesting seabirds in the Gulf of Alaska (GOA) and Cook Inlet (Irons 1996, Sowls et al. 1978). Kittiwakes are small, pelagic gulls that breed colonially, build nests on cliffs by the ocean, and feed mostly on small forage fish that they capture at the surface. They typically locate prey while flying and then seize those prey from the surface or after plunging into the upper water layer (Irons 1996). Surface feeding species were impacted less by the *Exxon Valdez* oil spill (EVOS) than diving species. Of the 29,175 oiled birds recovered before 1 August 1989, only 2.4% were surface feeding gulls (*Larus* and *Rissa spp.*) (Piatt et al.1990). There was a large die-off of seabirds in August and September of 1989— apparently due to starvation— in which kittiwakes comprised 14% of carcasses recovered (Piatt et al. 1990).

Some seabird populations declined dramatically in the GOA over the past few decades (Hatch and Piatt 1995, Piatt and Anderson 1996). A proportion of these declines can be attributed to anthropogenic factors such as the EVOS, but natural changes in availability of forage fish that began in the late 1970's also affected seabird populations. This major ecosystem reorganization, or "regime shift", was characterized by a precipitous decline of some forage fish species such as capelin and a marked increase in large, predatory fish such as pollock (Piatt and Anderson 1996). Coincident with this regime shift, Black-legged Kittiwake populations declined at some colonies in the GOA, while other populations increased (Hatch and Piatt 1995; Piatt and Anderson 1996; Zador et al. 1997).

Because of their abundance in the EVOS area and history of study, kittiwakes were chosen for further study to assess the relative importance of natural and EVOS effects on seabird populations in the GOA (Irons 1996). They are densely colonial, highly visible cliff-nesters, and evidence suggests that they respond readily to both long and short-term changes in the environment (Aebischer et al. 1990). The breeding biology of kittiwakes has been well studied in many areas of the world, including Prince William Sound (PWS) (e.g., Irons 1996) and lower Cook Inlet (e.g., Bailey 1975a,b Manuwal and Boersma 1978, Dippel and Nysewander 1992, Slater et al 1984). Despite a wealth of studies at colonies, however, only one previous study has examined relationships between breeding biology and changes in food supply (Hamer et al. 1991).

To improve our understanding of relationships between kittiwake biology and food supply, we conducted detailed studies of kittiwakes at the three largest colonies in lower Cook Inlet: Chisik Island, Gull Island and the Barren Islands. We collected data on kittiwake population trends, breeding chronology, breeding success, chick growth, time-activity budgets, chick diet and energy provisioning rates, adult diet, stress hormone levels, and adult survival, from 1995-1999. We simultaneously measured forage fish distribution and abundance in waters around those colonies (Chapters 4-7). The purpose of this chapter is to document the methods we used to gather data on kittiwakes and present all the results of our research in summaries by colony (3) and year (5) of study. An analysis of the response of kittiwakes to fluctuations in prey density is given in Chapter 14. Major results on breeding biology and behavior presented in this chapter will be further analyzed and submitted for publication in peer-reviewed journals.

Methods

Study Areas

We conducted our study from 1995-1999 at Chisik and Duck Islands (collectively referred to as Chisik), Gull Island (including 60' Rock) and the Barren Islands. The three colonies are separated from each other by about 100 km (Fig. 7.1) and are in oceanographically distinct habitats (Chapter 2). Field crews were present at each colony continuously from late May through August in 1995-1997, and from late May through mid-September in 1998-1999. Personnel (PI, Arthur Kettle) from the Alaska Maritime National Wildlife Refuge (AMNWR) collected data at the Barren Islands.

Chisik and Duck Islands are located on the western side of lower Cook Inlet at about 60° 09' N, 152° 34' W. Both islands are part of the Alaska Maritime National Wildlife Refuge. Chisik Island is 2606 ha in area, has a peak elevation of 815 m, and is located about 0.8 km from the mainland. Duck Island is 0.4 km east of Chisik, covers about 2.4 ha, and reaches a maximum elevation of 49 m. Chisik and Duck Islands support approximately 20,000 Black-legged Kittiwakes (Zador et al. 1997) that nest mostly on the southern portion of Chisik, with smaller numbers nesting in the central portion of Chisik's eastern coast, and along the cliffs of Duck Island. Biologists censused kittiwake populations here in the early 1970s (Snarski 1970, 1971 a-c, 1974) and personnel from AMNWR monitored populations and reproductive success intermittently through the 1980s and 1990's (Jones et al. 1980, Kafka 1984, Muhlberg 1984, Beringer and Nishimoto 1988, Slater et al. 1995). Recent estimates indicate that Black-legged Kittiwake populations have declined by more than 80% at this colony over the last 30 years (Zador et al. 1997).

Gull Island is located in Kachemak Bay on the eastern side of lower Cook Inlet. The island is 5 km southeast of the Homer Spit (59° 35' 10" N, 151° 19' 45" W) and is owned by the Seldovia Native Association. The island consists of four spires of fractured bedrock that erupt sharply from the water and are connected only at extreme low tides. We also conducted a limited amount of monitoring at 60-foot Rock (59° 33'N, 151 ° 28'W), a small rocky island about 6 km south of the Homer Spit, owned by AMNWR. Few birds have nested on 60-Foot Rock in recent years, so we concentrated our efforts on Gull Island. Black-legged Kittiwakes have been monitored at Gull Island and on 60-foot Rock by private consultants and AMNWR biologists periodically since 1976 (Erikson 1976, Nishimoto et al. 1987, Nishimoto and Beringer 1989, 1990). Recent estimates indicate that Gull Island kittiwake populations have increased by at least 60% over the last 25 years (Zador et al. 1997). The Black-legged Kittiwake population at Gull Island is currently around 10,000 birds. Kittiwake populations at 60-Foot Rock have also increased by 20% over the last 15 years, and the current population is around 180 birds.

The Barren Islands (58°55'N, 152°00W) support the largest seabird populations in the northern Gulf of Alaska, including 10's of thousands of Black-legged Kittiwakes (Bailey 1976). Details of seabird populations and the islands can be found in Bailey (1976) and in APEX reports by Kettle et al (2000). There were no systematic plot censuses prior to EVOS funded work.

Populations

We monitored numbers of adult birds in population plots to obtain an index of population change among years and colonies. All 10 population plots used at Gull Island and 8 plots at Chisik Island were historic population plots established and monitored by AMNWR personnel. At Gull Island, we monitored 10 historical plots, while at Chisik, 5 new plots were established and monitored in addition to historical plots. Plots were counted every 3-5 days between 1000h and 1600h, from middle incubation to the start of chick fledging, when colony attendance is least variable (Byrd 1989). All population plots were counted using binoculars from a boat except for new plots on Chisik, which were counted from land (in blinds) using binoculars. Repeated counts of individual plots on a given day were treated as replicates, and their totals summed to obtain a single count for that day. Each of these "count-days" were treated as samples and averaged to obtain a mean population count for the season.

Productivity

We used productivity plots to collect data on reproductive parameters of kittiwakes. Each plot was selected from "viewable" sections of the colony, had clearly defined boundaries, and was used in all years of the study. We tracked individual nest sites within plots by using hand drawn maps or computer printouts of photographs taken with digital cameras. We drew plot boundaries and labeled nest sites with unique numbers on plot maps. Approximately 10 plots containing an average of 30 nest sites were monitored on the same day, every 3 days from the nest building stage through chick fledging. We considered chicks to be fledged at 32 days of age as little mortality is observed at the colony after this time.

We observed the status of nests and nest contents from observation points on the island using binoculars (10x40, 8.5x42). By observing nests and their contents on a fixed schedule we were able to obtain estimates of laying and hatching chronology, laying success, hatching success, fledging success, reproductive success, productivity, and clutch size. On some occasions predation events or siblicides were observed. We used study plot as the sample unit for estimating each parameter. The mean and standard deviation of the plot means were used for annual estimates. Reproductive parameters were defined as follows:

Laying and hatching chronology (median lay and hatch dates)
Laying Success (% of nest structures where $\geq$ 1 egg is laid)

Hatching Success (% of eggs laid that hatch)
Fledging Success (% of chicks hatching that fledged)
Reproductive Success (% eggs laid that fledged chicks)
Productivity (chicks fledged per nest structure)
Mean Clutch Size (eggs per nest with eggs)
Brood Size at Hatch (chicks per nest with chicks at hatch)
Brood Size at Fledge (fledglings per nest with fledglings)

We also obtained a productivity index in all years at Gull Island, and in 1997 and 1999 at Chisik Island. We conducted one colony-wide census of nest structures, during middle incubation, and another colony-wide census of large chicks during late chick rearing. We used the ratio of large chicks to original nest structures to obtain an index of productivity.

Nest Attendance, Meal Delivery Rates, Foraging Trip Duration

We measured kittiwake activity budgets to quantify feeding rates, foraging trip duration, and time spent at the nest. We conducted kittiwake activity watches from 0700-2100 on 3 occasions during the chick-rearing period. For each watch we chose a different group of 8-10 nest sites that were highly visible and were representative of the colony in terms of brood status and chronology. The first watch was conducted when chicks were approximately 10 days of age and each successive watch was performed on chicks 7 to 10 days older than the previous watch. Prior to an activity watch, one adult from each nest was captured and marked, either with dye or unique color bands to distinguish among pair members.

During each watch, observers recorded the time of arrivals and departures of each member of a pair associated with that particular nest site. This allowed us to quantify the total time spent at the nest site for each individual and generate a statistic termed “bird-minutes per hour”, or the combined number of minutes both pair members spent at the nest each hour. For example if one bird only was present at a particular nest site from 0700-0800, then for that hour block and that nest site, total bird-minutes were equal to 60. If both birds of a pair were present for a complete hour block, then bird minutes were 120 for that hour. If total bird-minutes were less than 60, then both adults were absent for some period of time, leaving the chick unattended.

We also collected data on meal delivery rates. When a parent arrived at the nest site and subsequently fed a chick, the time that the bird arrived at the nest site was recorded as the meal delivery time. That meal may have been fed to the chick all at once or in many small boluses, but this was still considered to be one meal. From this data we calculated a meal delivery rate, or the number of meals delivered per nest per hour. From these same observations of meal deliveries we also calculated foraging trip durations. The time that an individual spent away from the nest prior to having returned with a meal was considered to be a foraging trip bout.

From preliminary analyses, we concluded that neither nest-site or observation day contributed significantly to variability in behavioral parameters in a given year and so we used nest-site as the sample unit. We then calculated a mean per nest site per day for each behavioral parameter, and then a grand mean, to generate a parameter value for each colony in each year (colony-year).

Chick Growth Rates

We used designated areas of the colony to measure growth rates in each year of the study. Each area contained 5-10 nest sites with chicks. To minimize disturbance, we did not use these areas for other experimentation. We photographed growth rate areas and assigned individual nest numbers to each nest site. In order to obtain accurate ages of chicks, nests were checked daily just prior to their expected hatch dates. Growth rates on both chicks (if two present) in each nest were taken every 4 days. Just after hatching, chicks in two-chick nests, were marked (using permanent marking pens on their heads and webbing of one foot) to distinguish between alpha and beta chicks. When chicks were large enough, we banded them with USFWS metal bands on the right leg. In 1998, at Gull Island, colony (royal blue) and cohort (yellow) bands were also affixed to the right leg before chicks fledged (colony, over USFWS metal, over cohort). Birds were not banded at the Barren Islands.

The following growth and development measurements were taken for each nestling every four days:

Headbill: The distance from the tip of the mandible in a straight line to the posterior edge of the cranium.

Diagonal Tarsus: (right leg) The distance from the point of the joint between the tibia/fibula (calf) and tarsus (foot) to the point of the joint between the tarsus and the base of the middle phalange (toe) in front (achieved by bending the foot up and the toes down and measuring diagonally from top of toes to the bottom of the heel).

Flat Wing : (right wing) The distance from the bend of the wing (wrist) to the tip of the longest primary (tip of the developing teleoptile). We flattened and straightened the wing for this measurement.

10th Primary: (right wing) The length of the outer (10th) primary (from emergence from skin to tip, down not included).

Mass: Using a Pesola scale we recorded mass to the nearest gram. If the chick regurgitated before it was weighed, we weighed the regurgitation and added its mass to the mass of the chick. Before releasing the chick we refed the regurgitation. In the unusual circumstance that the chick refused to accept the regurgitation, it was collected and used as a chick diet sample. No more than one regurgitation was collected from an individual chick in a season.

Fledging Wt.: We measured "fledglings" (day 30 post-hatch, " 1 day) body weight, wing length, and outer (10th) primary for a minimum sample of 40 broods.

We calculated growth rates as the slope of the linear regressions of mass versus age during the linear phase of growth, defined as age 6-22 days. For calculating mean growth rate in a given year, we treated each chick as an individual sample unit. We also calculated growth rates for alpha and singleton chicks pooled, and beta chicks.

Adult Body Condition

We captured breeding adult kittiwakes to obtain an estimate of their body condition. We captured birds at the nest using a 9 m telescoping noose pole. Birds were sampled at pre-determined intervals from the pre-laying stage through chick fledging. We did not capture birds in 1995 and only a limited number in 1996, however, in 1997-1999 we attempted to capture a minimum of 7 birds during 6 sampling windows throughout breeding: pre-laying, early, middle, and late incubation, and early, middle, and late chick rearing. Few birds were captured during the pre-lay stage, as birds proved difficult to capture when not protecting nest contents. Captured birds were measured as with kittiwake chicks, excluding measurements for 10th primary length (see Chick Growth section). Immediately after capture and prior to measuring, a small blood sample was taken for genetic sexing. (For detailed methods of blood collection techniques, see Kitaysky et al. 1999a). We banded each bird with a colony color band over a metal USFWS band on the right leg and a unique 3-band color combination on the left leg. No birds were banded at the Barren Islands. Banding of birds prevented recaptures, enabled re-sighting of individuals for the study of over-winter survival (results not presented here), and for studies of nest attendance patterns (see below). We used the ratio of wing length to body mass as an index of body condition.

Chick Diet

To assess chick diet composition we collected chick regurgitations every 4 days during the chick-rearing period, when chicks were 10 to 30 days old. Many of these samples were collected from chicks used for chick growth studies, however no more than one sample was collected from any individual chick. Regurgitations were also taken from adults that were bringing back food for their chicks. Other samples were collected as part of a dedicated effort to collect diet samples from non-growth rate chicks. These samples were collected at random from accessible nests. Diet samples were stored in Whirl-Paks® labeled with the date, time, colony, nest identification number, and the fresh weight of the sample and then frozen for later analysis of composition. We weighed samples (nearest 0.01 gram), prior to freezing, on an Ohaus electronic scale. Samples were analyzed for composition and proportional biomass at the University of Alaska Fairbanks by Alan Springer and Kathy Turco.

Energy Provisioning Rates

A sub-sample of complete chick meals were analyzed for composition and energy content (KJ / g) by Patrick Jodice and Daniel Roby of the Cooperative Fish and Wildlife Unit at Oregon State University, Corvalis, Oregon. Used in conjunction with meal delivery rates determined in this study, it was therefore possible to calculate energy provisioning rates (KJ / nest day).

Adult Diet

We obtained adult diet samples by collecting stomachs from adult breeding birds at each colony. We collected 7-10 adult kittiwakes with a shotgun adjacent to the breeding colony during the late chick rearing period. In most cases birds were weighed and measured prior to being frozen, however, in some instances birds were frozen, later thawed, and measurements taken during the necropsy process. During necropsies, birds were weighed and measured, scored for fat, sexed, aged, breeding status determined by brood patch stage, and stomachs were removed. Measurements were taken following methods described in "Adult Body Condition" section. Stomachs were preserved in ethyl alcohol for later analysis of diet composition from fish otoliths. Samples were analyzed for composition and proportional biomass at the University of Alaska Fairbanks, by Alan Springer and Kathy Turco. Tissue samples were also taken from the liver, heart, and breast muscle for stable isotope analysis.

Stress hormone levels

We measured circulating levels of stress hormone (corticosterone) in the blood of adult kittiwakes throughout the breeding season. This study was initiated on a small scale in 1996 and in subsequent years an intensive effort was sustained through the course of the breeding season. From 1997-1999, samples were taken from 6 stages of the breeding cycle as described in the section on "Adult Body Condition". For some sampling periods we measured baseline circulating levels of corticosterone, while for others we conducted a full "stress series" (See Kitaysky et. al. 1999 for detailed methods of blood collection and analysis procedures). We present only data for baseline corticosterone levels in this report

Results and Discussion

Population

We monitored annual variability and trends in population size with counts of birds in designated plots (Table 10.1). Population plot count windows are given in Appendix 10.1. There were no obvious trends during the five years of this study, although kittiwakes declined considerably at Chisik Island. When these data are viewed in context of historical plot and whole-island counts conducted prior to 1995, however, the population at Gull Island appears to have stabilized in recent years, while the population at Chisik Island continues to decline (Appendices 10.2 and 10.3). At Gull Island, populations increased dramatically (+8.8% per annum) from 1976 to 1988, and since then (1989-1999) numbers have been remarkably stable (essentially no change in 10 years). We believe that kittiwake breeding habitat is saturated on Gull Island. It is a small island, and it appears that every cliff ledge, nook and cranny is in use by breeding kittiwakes. In contrast, kittiwakes continue in a long (1971-1999) steady (-4.3% per annum) decline in number at Chisik Island. Cliff habitat once occupied by breeding birds— as evidenced by old nest cups or xanthophyllous lichens— is becoming more abundant on Chisik Island. At the Barrens there are no long-term historical data. However, plot counts conducted since 1993 suggest that populations have increased (+5.2% per annum) at the Barrens (Roseneau et al. 1995, Kettle et al. 2000). A different set of kittiwake plots at the Barrens counted from 1989 to 1992 also suggest an increase (+8.6%) in kittiwakes (Dipple and Nysewander 1992, Nysewander and Byrd, unpubl. data), although counts were highly variable and the trend is not statistically significant.

Productivity

Black-legged Kittiwake productivity (chicks fledged per nest structure) averaged for all colony years, was highest at Gull Island (mean=0.48) and lowest at Chisik (mean=0.02). Productivity at the Barrens was similar to that at Gull Island (mean=0.43) (Table 10.2). Productivity was lowest in all years at Chisik. Variation in productivity among years was greater at the Barrens (0.04-0.72) than at Gull (Gull 0.34-0.65) or Chisik (0.00-0.04). Productivity varied inconsistently among colonies in a given year, except for 1998 when productivity was the lowest of any year at all three colonies. This was likely due to anomalous water conditions associated with an El Nino Southern Oscillation (ENSO) event of 1997-1998 (Piatt et al. 1999). Warm sea-surface temperatures developed rapidly during June in the GOA and persisted until May/June of 1998. Despite the ENSO event and resulting reduction in food supply throughout the GOA, kittiwakes at Gull Island still produced 0.32 chicks/pair, while they failed reproductively at Chisik and the Barrens. This is indicative of the stability of the oceanographic conditions and food supply in Kachemak Bay relative to other areas of Cook Inlet (Chapter 2,3).

As an adjunct to measures of productivity gathered from intensive study plots, we also obtained an "index of productivity" at Gull Island in each year, and in two years at Chisik Island (1997 and 1999) (Table 10.11). This was based on an all-island nest census conducted in mid-incubation and another census of chicks during late chick-rearing. The index of productivity was similar to productivity estimates derived from intensive plot monitoring ($r^2 = 0.91$; plot estimate = 1.04[index estimate]).

Mean laying success (Table 10.3) and clutch size (Table 10.4) were similar among colonies, with Gull slightly higher than the Barrens, which was in turn higher than Chisik. In some years, however, laying success and clutch size were higher at Chisik than at the other colonies. Hatching success was similar between Gull and the Barrens, and both were much higher than at Chisik (Table 10.5). In contrast, brood size at hatch (number of chicks hatched per nest with chicks) was highest at Chisik Island (Table 10.6). These numbers illustrate that much of the regulation of productivity at Chisik is exerted early in the breeding season, during incubation. Fledging success was highest at Gull island and very low at Chisik, where almost no chicks have fledged successfully in the last five years (Table 10.7). Brood size at fledge (chicks fledged per nest with fledged chicks) followed the same pattern (Table 10.8).

The median date of egg-laying varied over 11-19 days in June depending on the colony (Table 10.9). For all three colonies, median egg-laying occurred between 5 June and 29 June. Median lay was earliest on average at Chisik (mean = 12 June), two days later at Gull, and two days later again at the Barrens. Median hatching tended to be more synchronous than median lay (Table 10.10), ranging from 2 July – 28 July among colonies. Median hatch was also earliest at Chisik and latest at the Barrens, but hatching phenology differed by 4-5 days among colonies. Thus, on average, Black-legged Kittiwakes initiated nesting earliest at Chisik Island and latest at the Barrens Islands. This consistent pattern may be related to environmental regimes: At any given time, water temperatures are warmest at Chisik Island and coldest at the Barrens (See Chapter 2).

These differences in temperature may influence the timing of peaks in plankton and forage fish production, which in turn, may influence timing of breeding in kittiwakes.

In summary, productivity parameters were generally highest for Gull Island, and lowest for Chisik Island. Productivity parameters measured early in the season (laying success and clutch size) were similar among colonies, but as the season progressed, disparities in breeding success among colonies became more pronounced. Productivity varied inconsistently among colonies in any given year. Although Gull Island had the highest average productivity for all years, kittiwakes at the Barrens were considerably more productive in 1995 and 1996. In 1998, productivity parameters were depressed at all three colonies, presumably in response to the 1997-1998 ENSO event. By any standard, kittiwakes at Chisik island failed in all years of study (Irons 1996), presumably owing to a lack of food (Robards et al. 1999, Kitaysky et al. 1999b). Relationships between reproductive parameters and food supply are examined in Chapter 14.

Colony Attendance, Feeding Rates, and Foraging Trip Durations

We collected data on colony attendance, feeding rates, and foraging trip durations in all years when a sufficient sample size of nests with chicks were available for behavioral watches. Attendance (mean bird-minutes per hour) was lowest at the Barren Islands and highest at Gull Island (Gull mean=59.8; Chisik mean=57.7; Barrens mean=54.3) (Table 10.12). Chick feeding rates were highest at Gull Island and lowest at Chisik (Gull mean=0.22; Barrens mean=0.18; Chisik mean=0.13)(Table 10.13). Chick feeding rates were more variable among years at the Barren Islands than at Gull or Chisik. Foraging trip durations were similar at Chisik and the Barren islands, but much shorter at Gull Island (Gull mean=196.4; Chisik mean=308.3; Barrens mean=314.8) (Table 10.14). Differences among colonies were consistent among years and appear to reflect differences in foraging effort and range (Chapter 8). Attendance and feeding rates were always highest, and foraging trip durations were always shortest at Gull Island— where foraging occurred with a few km of the colony (Chapter 8). Foraging trips were long at the Barren islands, because birds had to travel to distant foraging grounds along the Kenai Peninsula (Chapter 8). Despite this, Barrens birds managed to maintain adequate food deliveries to chicks because food supplies were plentiful along the Kenai Peninsula (Chapters 4 and 7). Birds from Chisik traveled longer and further than those from Gull or the Barrens (Chapter 8), but were incapable of locating adequate food supplies.

Chick Growth

We were not able to obtain growth rate measurements at Chisik Island in 1995, 1998, and 1999 because of reproductive failure. Chick growth rates were highest at the Barrens and lowest at Chisik Island (Table 10.15). Chick growth rates did not reflect differences in feeding rates and foraging trip durations. Growth rates at Chisik and Gull Island were similar in 1997, despite a large difference in productivity (Gull 0.60, Chisik 0.02 chicks/nest). One explanation is that the only chicks to fledge successfully at Chisik in 1997 were from the best quality parents and so they had relatively high growth rates. For related reasons, adults that cannot adequately feed young probably also leave them unattended and vulnerable to predation. So basically, if a chick survives to be measured by us, it is likely to be a well-fed chick. These results suggest that chick growth rates are poor indicators of food supply— not because starving birds are unusual, but rather because they tend to get eaten by predators, leaving a biased sample of well-fed birds to measure.

Adult Stress Hormone Levels

We measured circulating levels of corticosterone (stress hormone) in the blood of adult kittiwakes throughout the breeding season, from 1997-1999. Baseline levels of corticosterone (ng/ml) were slightly higher on average at Chisik Island, than at Gull Island (Table 10.16). If we compare stress hormone levels just during chick rearing at both colonies, the differences are greater (Gull mean=8.4, Chisik mean=12.2). In general, baseline stress levels increased during the season and particularly during late chick-rearing in most years it was measured. Because kittiwakes at Chisik often failed during the chick-rearing period, we were not always able to collect samples. Gull Island birds had higher baseline levels of corticosterone in 1998, when productivity was very low, than in either 1997 or 1999, when productivity was very high. Overall, baseline stress levels were not as high as we had predicted at Chisik, the food deprived colony, probably because birds there suppress their baseline stress response (Kitaysky et al. 1999a). A full analysis of stress in breeding kittiwakes during 1997-2001 at Gull and Chisik islands is currently under way (Kitaysky et al., in prep.).

Chick Diets

Chick meals consisted largely of sand lance *(Ammodytes hexapterus)* at Gull, Chisik and Barren islands (Table 10.17). Pacific herring *(Clupea harengus pallasi)* was the next most important prey at Gull and Barren islands, while smelts made up the second largest proportion of diet biomass at Chisik. Chick diet composition is shown in detail in Appendices 10.1-10.2. Chick meal size was highest at the Barren Islands, slightly lower at Gull Island, and the lowest at Chisik Island (Table 10.18). Taking into consideration meal size and composition, overall energy provisioning rates (KJ / nest day), were highest at Gull Island and below the minimum required for growth at Chisik (Romano 2000). Kittiwake chicks fed on lower quality diet— or in amounts that impair physiological development— have reduced growth and fitness (Kitaysky et al. 1999, Romano 2000).

Adult Diet

Adult kittiwake diet varied much more so than chick diets among colonies (Table 10.19), and better reflected the local composition of prey stocks (Chapters 4, 5). Gull and Chisik Island birds fed primarily on sand lance (greater than 50% composition), but consumed significant proportions of osmerids (smelt at Chisik, capelin *(Mallotus villosus)* at Gull), invertebrates (mostly euphausiids), gadids (cod), and a wide variety of other fish. At the Barren Islands, adult kittiwakes fed primarily on walleye pollock *(Theragra chalcogramma)* (greater than 35% composition), capelin, sand lance and a significant fraction of other prey (see also Appendices 10.8-10.10). There were few apparent trends. Capelin increased in the diet of kittiwakes at Gull and Chisik Islands from 1995 to 1999, but were absent from the diet of Barren Island birds in 1999. In general, adult diets were more diverse than chick diets, and contained a much higher proportion of low quality prey such as cod and pollock (van Pelt et al. 1997).

Adult Body Condition

Adult body condition was measured at all three colonies from 1997-1999 (Tables 10.20 - 10.22). The index of adult body condition (mass / wing) ranged from 1.11 to 1.38 among capture bouts, and from 1.24 to 1.30 among colony years. Mean body condition for all years was similar among colonies. Body condition did vary slightly within a colony and among years, but it is not clear how this relates to other breeding parameters. It is likely that body condition is influenced by many different factors and requires careful interpretation. When foraging conditions are poor, birds may acquire a large fat reserve as a buffer. However, in some instances a large fat reserve may reflect an abundance of food. These are two obviously very different scenarios that could both yield high body condition indices. One clear result is that body condition declined seasonally in all years at Chisik, while at Gull and the Barren islands, it tended to fluctuate through the season. This seasonal decline in body condition at Chisik parallels the observed seasonal declines in reproductive performance.

Conclusion

The main purpose of this chapter was to document methods used to collect data on Black-legged Kittiwakes and to summarize the main results of our studies on this species. The ultimate objective is to interpret how various parameters of kittiwake biology and behavior vary with food supply. To that end, a preliminary synthesis on the response of kittiwakes to fluctuations in food supply is presented in Chapter 14. Results presented in this chapter will be further analyzed and submitted for publication in peer-reviewed journals.

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Chapter 11. Pigeon Guillemot Biology in Kachemak Bay

Michael Litzow

Introduction

Pigeon Guillemots (*Cepphus columba*) are loosely colonial breeders, able to raise two chicks to adult weight in the nest, and forage near shore on a diverse diet that includes invertebrates, demersal fish and pelagic fish (Ewins 1993). Approximately 680 oiled Pigeon Guillemot carcasses were recovered following the *Exxon Valdez* oil spill (Piatt *et al.* 1990) and this number probably represents 10 – 30% of total Pigeon Guillemot mortality from the spill (Piatt *et al.* 1990, Piatt and Ford 1996). A variety of studies have shown that Pigeon Guillemot have experienced more persistent oil spill effects than other bird species in Prince William Sound (Osenberg *et al.* 1994, Wiens and Parker 1995, Murphy *et al.* 1997). As of 1998 guillemot populations in oiled areas of Prince William Sound were roughly one third of pre-spill levels, while populations in unoiled areas were similar to pre-spill levels (Irons *et al.* 2000). Further, guillemot populations at six oiled islands in Prince William Sound have declined from 1990 to 1998, while the population at an unoiled site in the Sound has increased over the same time period (Golet *et al.* in press). Adult Pigeon Guillemots in oiled areas of the Sound were still apparently being exposed to residual oil in 1999, as indicated by elevated levels of the enzyme CYP1A in livers of birds from oiled areas (Golet *et al.* in press). However, these authors concluded that the toxic effects of residual oil alone were probably not sufficient to explain population-level oil spill effects that have persisted for a decade.

Another hypothesis to explain persistent oil-spill effects centers on the role that food availability may play in recovery. Populations of lipid-rich forage fish in the Gulf of Alaska declined rapidly during the late 1970s and 1980s due to changes in oceanographic conditions (Anderson and Piatt 1999). These changes in food availability may have resulted in population declines for high trophic level predators (Piatt and Anderson 1996, Merrick *et al.* 1997), and Pigeon Guillemots may have been among the species affected (Hayes and Kuletz 1997). Further, populations of Pacific sand lance (*Ammodytes hexapterus*), a high-lipid fish that is a favored prey of guillemots, may have been reduced by the oil spill (Golet *et al.* in press and references therein). These changes in food availability might have slowed recovery of guillemots from population-level oil spill effects by reducing the ability of the population to replace oil-killed breeders with new recruits (Piatt and Anderson 1996, Golet *et al.* in press).

As part of apex predator studies funded by the *Exxon Valdez* Oil Spill Trustee Council, we studied Pigeon Guillemot foraging ecology and reproductive biology in Kachemak Bay during 1996-1999. These followed up on previous studies of guillemot biology and diets in Kachemak Bay in 1994-1995 (Prichard 1997). The objective of our study was to assess the role that food availability plays in determining Pigeon Guillemot reproductive success. Specifically, we hypothesized that: (1) Pigeon Guillemot chick diets reflect spatial and temporal patterns of local prey availability, and (2) Pigeon Guillemot reproductive success increases with access to abundant lipid-rich forage fish. Our results in testing these two hypotheses are reported elsewhere (Litzow *et al.* 1998, 2000, 2002, Litzow 2000, Litzow and Piatt 2002).

The purpose of this chapter is to summarize the methods and results of our study in a format useful to other researchers who are interested in the Kachemak Bay population of Pigeon Guillemots. Our findings provide a baseline data set that will allow assessment of the impact of future natural or anthropogenic changes on that population. In addition to our data from 1996-1999 we present data from the same area that were collected by Alex Prichard during 1995 for his Master's thesis at the University of Alaska, Fairbanks (Prichard 1997).

Methods

Study area

We collected data in Kachemak Bay (59° N, 151° W), which is located on the east shore of lower Cook Inlet. Pigeon Guillemots nest in approximately 30 small colonies (*sensu* Ewins 1985) of 2 – 15 nests each and in numerous solitary sites on the south shore of Kachemak Bay. The bay is bisected into oceanographically distinct inner and outer sections by the Homer Spit (Fig. 14.1). The Outer Bay is dominated by input from the Gulf of Alaska and is well mixed and relatively cold and saline, while the Inner Bay is influenced by river runoff and tends to be more stratified, warmer, and less saline (Abookire *et al.* 2000). These oceanographic differences create important differences in foraging ecology for Pigeon Guillemots nesting in the two areas; breeders in the Inner Bay have access to more high-lipid schooling fish than those in the Outer Bay (Abookire *et al.* 2000, Litzow *et al.* 2000). The basis of our study was to compare differences in reproductive biology between the two areas. We studied nests in ten main colonies (Fig. 11.1), as well as many other nests that were solitary or in small groups. We considered pairs nesting at China Poot Bay, Moosehead Pt., Peterson Bay, Halibut Cove and Mallard Bay to be the Inner Bay population, and all others to belong to the Outer Bay population.

Population monitoring

We monitored Pigeon Guillemot populations with two techniques: once-annual surveys of the south shore of Kachemak Bay and replicated censuses at known colonies during incubation and early chick rearing. Annual shoreline surveys followed methods of Sanger and Cody (1994) and were conducted between 25 May and 11 June. In 1995 counts were made within one hour of an afternoon high tide, and during 1996-1999 counts were made within two hours of a morning high tide. We surveyed guillemots from a skiff travelling 4-8 knots approximately 50 m from shore. All Pigeon Guillemots on land and within 100 m of shore were counted. Surveys began at the entrance to Seldovia harbor and ended at the un-named point near Chugachik I. that forms the northernmost point of Bear Cove. The coast of all islands and mainland in this area was surveyed, excluding Tutka Bay and Sadie Cove.

We conducted colony censuses during incubation and early chick rearing (29 May – 9 July) at 26 colony sites (Figure 14.2). The borders of these colony sites are pictured in Appendix 14.1. Counts were made within two hours of a morning high tide, and we counted all guillemots on land and within 100 m of shore. At most sites we counted guillemots for a set time (Table 14.1) and we recorded the highest number of guillemots present in the census site during that time, including birds that flew through the site. At larger sites (Table 14.1) we counted guillemots from a moving skiff, travelling 4-8 knots approximately 50 m from shore. We made two replicate counts at each of these sites, and again retained the highest accurate count. At four of these moving count sites (Guillemot Meadows, Seldovia Bay, Seldovia Pt., and Hesketh I.) one observer counted guillemots on land and inshore of the boat and another observer counted guillemots between the boat and a point 100 m from shore. At the other two sites (the Motherlode and Mallard Bay) we found it easier for the two observers to cooperate in keeping a running tally of all guillemots in the census site as the boat moved through the area. All population counts were made when conditions (i.e. weather, sea state, visibility) were good enough to ensure that we weren't missing any birds.

To compare our census results among years we aggregated eleven individual sites into five larger census areas (Seldovia Bay, Hesketh I., Yukon I., Neptune Bay, Moosehead Pt.; Table 14.1). We pooled counts made at all of the smaller census sites in an area on a given day into a single replicate count for that area. The eleven individual sites were consistently sampled during 1996-1999, and the resulting five areas give good spatial coverage for the guillemot population on the south shore of Kachemak Bay.

Chick diet

Pigeon Guillemots carry single fish in their bills when provisioning chicks, and usually rest on the water in front of the colony before delivering to the nest, making prey identification relatively easy. We collected data for at least one year at each of ten guillemot colonies (Fig. 14.1). We observed chick provisioning at two to five nests during feeding watches. Watches were conducted during 3.5 h shifts distributed evenly across different tide stages and times of day (0600-2000) in 1995 ($n = 30$ nests). From 1996 to 1999 we conducted all-day watches (0600-2200 or 0500-2300; $n = 22$ nests in 1996, 26 in 1997, 24 in 1998, 15 in 1999). Provisioning adults were observed from anchored boats (using binoculars) or from blinds (using telescopes). Study colonies were all in areas of moderate to high boat traffic, and the presence of an anchored boat had no apparent effect on the behavior of observed birds. Each chick meal was identified to the lowest possible taxonomic level, and we estimated the length of chick meals relative to the length of an adult guillemot bill, in multiples of half bill-lengths. Prey categories included Pacific sand lance (*Ammodytes hexapterus*), salmonid (Salmonidae), sculpin (Cottidae), gadid (Gadidae), flatfish (Pleuronectidae), gunnel (Pholidae), *Lumpenus* prickleback (*Lumpenus* spp.), ronquil (*Bathymaster signatus, Ronquilus jordani*), arctic shanny (*Stichaeus punctatus*), unidentified blenny (Blennioidea), and hermit crab (Anomura). Schooling prey species have a distinctive silver color, and we placed prey items that we could not positively identify into "unidentified schooling fish" and "unidentified demersal fish" categories. Other items were simply "unidentified".

We also recorded a variety of ancillary data: the direction that a guillemot arrived from when coming to the colony with a meal, the time of day that the bird landed at the colony, delivered the meal, landed on the water after delivery, and again departed the colony, and the direction that a bird flew away from the colony after delivering. We consistently recorded times of arrival at the colony and delivery, but the other data were more difficult to record.

Nesting biology

We visited nests every five days to determine the fate of eggs and chicks and to weigh and measure chicks. In 1995 we began visiting nests during early incubation (late May – early June) and during 1996-1999 we began visiting nests during late incubation (mid June) in order to minimize disturbance. Most nests were visited by rappelling down to them from cliff-tops above. Chicks were assigned a rank based on their age: alpha (the older of a two-chick brood), beta (the younger in a brood) or singleton (when only one egg in a clutch hatched, or when one chick in a brood died at age ≤ 5 d). Because of the cryptic nature of nests, we often discovered nests only after chicks had hatched. In these situations we assigned alpha status to the larger chick and estimated chick age based on flattened wing length, using measurements from a set of known-age captive-reared chicks at the Seward SeaLife Center for comparison (Table 14.2; G. Divoky, pers. comm.). We only assigned age based on wing length in situations where length was ≤ 40 mm.

We measured nesting phenology in every year of the study. We calculated median hatch date as our measure of nesting chronology, using the hatch date of the first chick in a nest as our metric. We minimized our visits to nests during pre-lay and incubation in order to minimize disturbance-caused nest abandonment, so we did not collect data on lay date.

We measured Inner Bay chick growth rates during 1995-1999, and Outer Bay growth rates from 1995 to 1998. During each visit we weighed chicks with spring-loaded scales and measured flattened wing length and the length of the tenth primary. We used growth rate (slope of linear regression of mass on age) between the ages of 5 and 20 d for comparisons of chick growth (Emms and Verbeek 1991). We also present growth rate for chicks aged 8-18 days to allow comparison with studies that use this metric. Growth rates of alpha and singleton chicks are generally similar, while beta chicks typically grow more slowly (Ainley *et al.* 1990, Shultz and Sydeman 1997). We therefore present growth data for two classes of chicks (alpha / singleton and beta).

Reproductive success was measured in every year of the study. Because we rarely followed nesting attempts from the day of initiation, a simple calculation of reproductive success as the number of chicks fledged per nest would overestimate productivity because we would fail to account for nests that had failed before we had a chance to discover them. We therefore used the Mayfield method to account for nests that failed before discovery (Mayfield 1975, Johnson 1979). This method accounts for eggs and chicks that are lost before discovery by calculating a daily survival rate (*DSR*) for each nesting phase. *DSR* is calculated as:

1 – (number of losses / number of exposure days).

The nest was treated as the sample unit, and losses were assumed to have occurred at the midpoint between the observation when the loss was first noticed and the previous observation. For example, if we observed a nest with two eggs on three consecutive visits at five day intervals, and then found that after another five days one egg was gone and the other was in the process of hatching, then this nest would have one egg loss in 27.5 days of egg exposure.

One of the assumptions of the Mayfield method is constant mortality within a given phase of breeding, and this was clearly not true for chicks during our study (see Results). Since mortality was greater for young chicks than old chicks we calculated separate *DSR* values for chicks age 1-15 d and 16-30 d (Prichard 1997). We recognize that this approach may have shortcomings, since mortality within the two age classes still varies with age. However, these age-dependant changes in mortality within a phase were minimized by breaking chick rearing into two phases, and we believe that the resulting estimates accurately reflect spatial and temporal changes in reproductive success during the study.

The proportion of individuals surviving through incubation and the two phases of chick rearing is then calculated as DSR^{n}, where n = the number of days in incubation or a phase of chick rearing. We used a mean value for incubation length (31 d, Ewins 1993), and $n = 15$ for each of the chick phases. We calculated chick survival only to 30 d because chicks may fledge any time post 30 d (Ewins 1993), and it is difficult to determine whether chicks older than 30 d have fledged or been depredated.

We also calculated the number of eggs layed during a given nesting attempt. Situations where two females layed in a single nest were treated as two separate nesting attempts. We occasionally observed the laying of replacement clutches after original clutches had been lost. In these situations we treated both clutches as a single nesting attempt, so some nesting attempts consisted of more than two eggs, the maximum clutch size for Pigeon Guillemots (Ewins 1993). Nests are often difficult to see into, and contents can occasionally be missed by a biologist dangling from a rappel rope, so we considered a replacement clutch to have been layed only in situations when original clutches were missing on two consecutive visits.

Many eggs in the study that survived incubation without obvious damage failed to hatch, so we calculated the proportion of surviving eggs that actually hatched as:

1 – (number of eggs failing to hatch / number of eggs surviving incubation).

Our estimates of reproductive success (chicks fledged / nesting pair) during 1995-1998 were then calculated as the product of five parameters: the number of eggs layed per nesting attempt, the proportion of eggs that survived incubation, the proportion of surviving eggs that hatched, the proportion of chicks surviving to age 15 d and the proportion of chicks surviving from age 16 d to 30 d.

In 1999 we reduced our nest-observing effort and visited many nests only twice. We first checked nests during 14-15 June to see if they were active (i.e., contained eggs). We then visited active nests during late chick rearing (28 July to 1 August) to see if they contained chicks. We calculated an index of reproductive success as: C / A, where C = the number of chicks found during the second visit, and A = the number of nests active during the first visit. During 1996-1999 we also calculated brood size at fledge, which is the number of chicks fledged from nests where at least one chick fledged.

Adult measurements

We incidentally obtained morphometric measurements of breeding adults during studies of adult foraging behavior. Adults were captured between 8 June and 11 August, and were mostly known or suspected breeders. We measured mass and length of flattened wing, 10th primary, headbill, tarsus and culmen.

Practical considerations

Kachemak Bay is a good site for future Pigeon Guillemot research because of the existence of historical data and because the Inner and Outer Bay provide two very different habitats that can be studied simultaneously. However, there are drawbacks. First, nesting density is lower than in some other areas of Alaska. More importantly, Pigeon Guillemots in Kachemak usually nest on high cliffs and nests can often be accessed only by rappelling 1-50 m down a cliff face. The rock of these cliffs is typically rotten and loose, making rappelling more dangerous. Future study crews should include people who are well experienced with rappelling and jumaring, and should use static rappel line and helmets.

Study colonies varied widely in the effort that was required to access nests. If current patterns of nest dispersion persist, Seldovia Bay, Moosehead Pt. and China Poot Bay should form the foundation of any future studies – these areas provide relatively high nesting densities and nests are among the easiest to access. Neptune Bay also provides a relatively high concentration of nests, but the colony failed repeatedly in the later years of the study. Halibut Cove contains a large nesting population, but nests are dispersed and time consuming to access. The Yukon Island colony contains few nests. These nests are generally easy to reach, but require dangerous scrambles along high, unstable cliff tops – we rigged safety lines between trees, but there were not enough trees to protect the whole approach. Many guillemots nest on Hesketh Island, but accessing these nests is too difficult to make the area useful for research.

Results

Population monitoring

Results for each census site are presented in Table 11.3. We detected no trend in the results from the aggregated census areas until 1999, when populations in every area were down from the previous year (Table 11.4). Total counts for the annual shoreline survey fluctuated between 467 and 634 Pigeon Guillemots, but there was no trend in these results (Table 11.5).

Nesting phenology

Median hatch date varied from 28 June to 4 July in the Inner Bay, and from 29 June to 1 July in the Outer Bay (Table 11.6).

Chick diet

The taxonomic composition of nestling diets is presented in Table 11.7. There was a strong spatial pattern to diets in Kachemak Bay as guillemots in the Inner Bay consistently fed chicks a higher proportion of sand lance than those in the Outer Bay.

Chick growth

Chick growth parameters are presented in Tables 11.8 and 11.9. Growth parameters of alpha and singleton chicks were generally similar between study areas, but beta growth rates were consistently higher in the Inner Bay than the Outer Bay.

Reproductive success

Clutch size was similar between the two study areas, but guillemots were more often able to raise two chicks in the Inner Bay than in the Outer Bay (Table 11.10.). Reproductive success was also consistently higher in the Inner Bay (Table 11.10.), and chicks fledged at a younger age in the Inner Bay (Table 11.11). As noted earlier, chick mortality rates declined with chick age (Table 11.12).

Adult measurements

We did not measure enough adults for powerful comparisons between the two areas (Table 11.13).

Discussion and Conclusions

Population status

Pigeon Guillemot populations in Kachemak Bay were generally stable during the study. The decline in abundance of guillemots at all five census areas in 1999 (Table 11.4) was similar to a decline in the numbers of breeding Common Murres (*Uria aalge*) in the same year in Kachemak Bay (Chapter 9). The decline in Pigeon Guillemot numbers may reflect a decrease in the number of birds attempting to breed in 1999 due to factors such as poor winter foraging conditions rather than an actual decline in population.

Chick growth rates

There was little difference between study areas in alpha / singleton chick growth rates (Table 11.8), but growth rates were consistently lower for beta chicks in the Outer Bay than in the Inner Bay (Table 11.9). Other studies have typically pooled chicks in analyses of growth rate, regardless of brood status, and are therefore difficult to compare with our results. Emms and Verbeek (1991) reported mean growth rates for Pigeon Guillemot chicks age 5-20 d on Mitlenatch I., British Columbia as c. 16 g / d for alpha and singleton chicks and c. 12 g / d for beta chicks, values well below those from either of our study areas.

Reproductive success

Our estimates for reproductive success ranged between 0.10 and 0.71 chicks / breeding pair, and success was always higher in the Inner Bay than in the Outer Bay (Table 11.10). These estimates are lower than those reported for Prince William Sound (0.25 – 1.25 chicks / pair; Oakley and Kuletz 1996) and are also lower than values reported for the

Farallon Islands, California (mean of 0.9 chicks / pair over 13 years; Ainley *et al.* 1990). Methodological differences may account for some of the difference among studies; neither of the other studies used the Mayfield method. This probably did not affect the Farallon estimate, since nest sites at that area are well known and all breeding attempts can be detected. Prince William Sound, however, is more similar to Kachemak Bay in that nest sites are cryptic and often not discovered until some time after nesting has begun, so reported values for that area may be overestimates because of the failure to account for failed nests that were never detected.

Our breeding success estimates are also sensitive to three assumptions we made about parameter values used in the Mayfield method: duration of incubation, duration of chick rearing, and mortality rate within the two phases of chick rearing. Although the duration of incubation may vary (Ainley *et al.* 1990), our value of 31 d is based on averages from a variety of studies (Ewins 1993) and is probably representative. Our assumption that chick rearing lasts 30 d is probably also fairly robust, since chick mortality is low after this age – we only ever found two dead chicks age > 29 d. Issues concerning constant chick mortality are addressed in Methods; we present relevant data in Table 11.12.

Predation of eggs, chicks, and breeding adults was difficult to quantify, but clearly an important factor in determining breeding success. Known or suspected nest predators in the study area include Steller's Jays (*Cyanocitta cristata*), Northwestern Crows (*Corvus caurinus*), Common Ravens (*Corvus corax*), mink (*Mustela vison*) and river otters (*Lutra canadensis*). Vermeer *et al.* (1993) estimated reproductive success as 0.41 chicks / pair at the Queen Charlotte Islands, in an area with high nest predation rates.

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Chapter 12. Horned Puffin Biology on Duck (Chisik) Island

Ann Harding

Introduction

The Horned Puffin is one of three North Pacific puffin species, with a summer breeding distribution that ranges from 50° to 70° North Latitude (Amaral 1977). In contrast to the burrow-nesting habits of the Atlantic Puffin *Fratercula arctica*, Tufted Puffin *Fratercula cirrhata* and the Rhinoceros Auklet *Cerorhinca monocerata*, the Horned Puffin almost always nests among boulders or in rock crevices, making access to chicks difficult and complicating study of their breeding biology. Horned Puffins lay a single-egg clutch. The average incubation period is 41 days, and both parents share incubation duties (Amaral 1977). After hatching, the chick is brooded constantly by a single parent for the first 5-7 days. The chick develops slowly, with a typical nestling period of 38-42 days (Amaral 1977). Both parents feed the chick, making several food deliveries per day. Sandlance (*Ammodytes hexapertus*) is the most important prey component of Horned Puffin chick diet, averaging 65% of the diet throughout the North Pacific (Piatt and Kitaysky 2001). From long-term studies of Atlantic Puffins (e.g., Ashcroft 1979, Harris et al. 1997) we know that puffins can respond to limiting food supplies with reduced growth rates, extended fledging periods, shifts in chick diet, and even complete breeding failure (e.g., Barrett and Rikardsen 1992).

Horned Puffins were not a primary study species for our project in lower Cook Inlet, and bred on only 1of 3 main study colonies. However, Chisik Island contained a relatively large and accessible population, and so we took the opportunity to include Horned Puffins in our larger study of seabird responses to changing food supplies. Thus, we studied the breeding biology, chick growth, chick diet and adult attendance of Horned Puffins on Duck Island from 1995 to 1999. The main objectives of our study were to: 1) Examine inter-year variability in Horned Puffin breeding parameters and measure the response of Horned Puffins to annual fluctuations in prey availability, and, 2) Examine the diurnal and seasonal attendance patterns of adult Horned Puffins in order to develop a standardized population monitoring protocol.

These objectives have been met in an M.Sc. dissertation (Harding 2000) and manuscripts that have submitted for publication (Harding et al. 2002a,b). This chapter summarizes information we gathered on the breeding biology, chick growth, chick diet and adult attendance of the Horned Puffin over five years of study (1995-1999) in lower Cook Inlet, and briefly examines some of the results in the context of other studies. Results presented here also provide an archive of data for future investigations.

Methods

Productivity

Reproductive success was measured during 1995-1999. Horned Puffins are sensitive to disturbance during the incubation phase of their breeding cycle, and may abandon breeding in response to disturbance of their nest sites. Productivity measures therefore have to be based more on observations made by following nest-sites from late incubation to fledging. Laying success cannot be practically assessed, and measures of hatching success and breeding success may be overestimates and biased towards those eggs that have survived until the end of incubation. It is not even practical to measure egg survival rates in order to use the Mayfield methods for adjusting hatching success (as in Pigeon Guillemots, Chapter 11).

Towards the end of incubation in each year, the island was searched for active nest-sites with visible nest-chambers. The timing of this check was based on knowledge of Horned Puffin breeding chronology at Duck Island in previous years. The first check was conducted about one week before the expected first hatch date. Most of the east side of the island was excluded from study due to dangerous rock conditions. Active sites were identified with a painted number on an adjacent rock. Site numbers remained consistent between years. Nest-sites were visited every 3-5 days during the hatching period and every 4-7 days until fledge. During each visit the nest chambers were checked using a headlamp, and the presence of adult, egg or chick was recorded. Visits were brief so as to minimize disturbance. When sight of an egg or chick was blocked by an adult, the adult's brooding posture and the presence of egg shell fragments were used as evidence of hatch. In the few nest-chambers where chicks could move out of sight, chick fate and nest-site chronology were determined using evidence of chick presence; chick vocalization, guano and the presence of dropped fish were recorded.

Hatching, fledging and breeding success were calculated for each year, using nest-site as the sample unit. The timing of the first nest-check during incubation varied between years (23 June to 16 July). To control for a possible inter-year bias in recorded egg-loss and therefore hatching success, we excluded nest-sites where an egg was followed and lost before July 15. It was not possible to follow all chicks to fledging due to the early departure date of field crews at the end of each seasons. To enable calculation of fledging success and control for the different field-crew departure dates between years, it was necessary to have a 'cut-off' age for chicks considered to have survived until fledging. We investigated chick mortality with age. Considering chicks from all 5 years (n=161), twenty chicks died in total; with 80% of deaths occurring at age 10 days or less, and with zero mortality after 20 days old. Once chicks had survived to 20 days, we observed no mortality in the 59 chicks we were able to track to 35+ days old, 30 of whom did not fledge until ≥40 days old. For the purpose of fledging success, we therefore assume that chicks ≥20 days survive until 'fledging'.

Mean fledging age was calculated by including all chicks from productivity data and known-age measured chicks which left their nest-site at ≥20 days old. Fledging age were determined to ± 0-3 days. Due to early departure of field crews, we were only able to calculate fledging age in 1996, 1998 and 1999. No meal collections took place at any productivity site. Median chick hatch date was used as a measure of annual breeding chronology. For the years 1996-1999, median hatch date was calculated by including only chicks with a hatch date range of less than 5 days. In 1995, where most hatch date ranges were approximately 8 days, median hatch date was calculated using all chicks with a hatch date range of less than 9 days.

Chick meal collection

The diet of Horned Puffin chicks on Duck Island was sampled between 1995 and 1999. Five methods for chick meal collection/prey identification were used: "Screening"— Entrances to nest-sites were blocked using re-usable metal grid screens (Hatch and Sanger, 1992). Adults prevented from entering the nest-site may drop the food at the screened entrance. Screens were wedged between the boulders to make a strong barrier and nest-sites flagged to help relocation. After about 2 h, nest-sites were revisited, screens removed and food samples collected. "Gill net"— Gill nets (2-3 cm mesh) or mist nets were draped over boulder piles, blocking the entrances to several puffin nest-sites. Nets were set and observers hid out of sight. Adults delivering meal loads became tangled in the net and dropped their bill loads. The adults were immediately untangled, measured and released, and the dropped bill load collected. "Pick ups"— Chick meals are often dropped by flying or landing adults. Freshly dropped fish were collected throughout each season. Many complete bill loads were collected whilst working in large caves with multiple horned puffin nest-sites. Adults arriving with fish were often startled by a worker's presence and dropped their whole bill-load. "Visual observation"— Bill loads held by adults standing on the boulders and cliffs were recorded. The prey species were identified using 10 x 42 binoculars and the number of fish in the bill load counted. "Experimental halter"— In 1998, a supplemental feeding experiment was conducted to examine the ability of adults to adjust provisioning effort. In order to obtain an accurate measurement of food delivery, a halter made from black pipe-cleaner wire was designed to prevent prey consumption and allow collection of individual prey items. The pipe cleaner was twisted around the base of the bill, to prevent bill opening and fish ingestion, and fitted loosely around the neck and head to anchor the noose in place. Chick movement, breathing and vocalization were not impaired. Halters were fitted at dusk and removed after 48 hours. Sites were visited 4-5 times daily at regular intervals during both days, and all fish were collected from the nest chamber. The nooses were removed once per 24 hours in order to feed chicks with the equivalent amount of food normally provided by their parents.

All prey collected were identified, weighed (using an electronic balance, ± 0.01g) and measured (fork length in mm). Energy values of prey were calculated using published wet mass energy density conversions (Van Pelt et al. 1997, Paul et al. 1998). All meal collections were identified as either a complete or incomplete bill load. Loads classified as bill-loads were either dropped loads, gill-net loads where no fish were lost, or a visual identification of load contents.

Feeding rates

Daily meal delivery rates to Horned Puffin chicks were recorded for 2-3 days in both 1996 and 1997. It was impossible to simultaneously observe many nest-sites because Duck Island has a low density of nest sites and the majority of crevice or cave nest-sites have multiple or shared entrances. It was possible to observe 4-5 burrow or simple crevice nests in two locations on Duck Island. One area was observed from the Cliff Blind on the West coast of Duck Island and the other area was located on the slope at the West end of North Cove. The North Cove area was observed from the top of the cliff path. In both areas, 4-5 active nest-sites were identified and numbered on a photograph. Sites were observed from 0630-2200 and all adult arrivals, departures and food deliveries were recorded. Owing to the speed of delivery it was impossible to identify bill load size or meal composition. Since adults were not banded or marked, it was not possible to measure individual trip durations or nest-site attendance. The total number of daily meal deliveries were calculated per chick.

Chick Measurements

Chick growth was measured in all years (1995-1999). Nest-sites with accessible chicks were located and numbered with paint. Site numbers remained consistent between years. The young were first handled when they were >5 days of age. For the few nest sites with accessible chicks that were found later in the season, where hatch date was unknown, chicks were aged using the following linear regression ($r^2 = 0.86$) of age on wing-length (Fig. 12.1) for chicks of known age: chick age (days) = 0.26 wing length (mm) - 0.54. Chicks were visited every 4-7 days during the chick-rearing period, and every 3-5 days during the fledging period. During each visit, the following body dimensions were measured with Vernier calipers (following Wernham and Byrant, 1998): tarsal length, total head plus bill length (measured as the greatest distance from the central back of the head to the tip of the upper mandible, with the upper surface of the calipers resting on the top of the head), culmen (from the tip of the upper mandible to the anterior edge of the growing cere), and straightened wing length using a stopped ruler, and body mass using a Pesola balance. Individual chicks were measured by the same person. Repeat measurements were always within 0.5 mm for head-bill, 0.2 mm for culmen and tarsus, 1.0 mm for wing length and 1.0 g for mass. Due to the crevice nesting habits of horned puffins, the number of chicks measured and the number of individual chick visits were limited by the accessibility of their nest chamber. Due to the early field crew departure date in most years, we were unable to collect many data on fledging measurements or peak mass. Blood samples were taken from 14 chicks in 1998 and 21 chicks in 1999.

Adult Measurements

Breeding adult Horned Puffins were measured in 1998 and 1999. Adults were either captured in their nest chamber during the chick-rearing period or trapped using a gillnet placed over the nest entrance during food delivery. Standard body measurements were taken (as for chicks). Three extra bill measurements were also made; bill width, at the proximal base of the nostril, bill depth and cutting edge (Fig. 12.2). To prevent recapture of the supplemental feeding experiment birds during the 1998 breeding season, captured adults were banded with a metal AVISE band on the left leg, and a single, numbered plastic band on the right leg. Genetic blood samples were taken from 11 adults in 1998 and 18 adults in 1999.

Fledgling Measurements

Towards the end of the 1998 and 1999 breeding season, the shoreline was searched at night using headlamps. Fledging chicks were intercepted during their journey to the sea. Standard body measurements were taken (as for chicks) before release. Blood samples were taken from six fledglings in 1998.

Plot census

In 1996, six population plots were established within North Cove and monitored between 1996 and 1999. A description of each plot is below. To maintain consistent plot boundaries, plots were highlighted on photos taken from the observation site. Photos are archived at USGS, Alaska Science Center. The observation site over-looks North Cove and is permanently marked with an orange stake. Plot descriptions are as follows: Plot 1: Boulders on the vegetated slope between the two cottonwood trees. Plot boundary outlined on photos. Estimated area, 11x7m. = 77m²; Plot 2: Area of scree at the base of the cliff. Plot boundary marked with blue paint and outlined on photos. Area, 11x7m. = 77m²; Plot 3: Large boulders on the beach. Plot boundary marked with blue paint and outlined on photos. Area, 12x6.5m. =78m²; Plot 4: Boulders on the cliff. Plot boundary outlined on photos. Estimated area, 25x3m. = 75m²; Plot 5: Area of cliff on the far West side of North cove. Plot boundary outlined on photos. Estimated area, 15x5m. = 75m²; Plot 6: Area of scree at the base of the cliff. Plot boundary marked with blue paint and outlined on photos. Area, 25x13m. = 325m².

The attendance of Horned Puffins at the colony peaked in the evening between 1930 and 2145. Between 2030 and 2145 daily, the number of birds on each plot were recorded at 15 min intervals. Birds were counted using 10x 42 binoculars. Due to shortening daylight hours, counts towards the end of the season were advanced to begin at 2015. Tufted Puffins were counted and recorded separately.

Colony Census

Island counts were conducted in 1995-1999. During an evening peak in colony attendance, the shoreline of Duck Island was circumnavigated on foot, by either one or two observers, and all Horned and Tufted Puffins were counted. Birds counted included all those visible on land and all individuals rafting (within an estimated 200 m from shore). In addition, the number of birds wheeling in flight were estimated. Observer, weather, tide and sea conditions, and the count start and end times were recorded.

Seasonal Colony Attendance

Seasonal colony attendance of Horned Puffins was recorded in 1997, 1998 and 1999. Daily counts were made from 27 June to 31 August in 1997, from 26 May to 4 September in 1998 and between 23 May and 14 September in 1999. Counts were conducted from the marked population plot observation point overlooking North Cove. Birds were counted using 10x 42 binoculars. 'Rafting' and 'loafing' birds were counted separately at 15 minute intervals during the daily evening peak (between 2030 and 2145). Up to 5 counts were made during this period each day, and these were used to calculate mean daily values for the number of birds counted on water, land and total (land and water combined). ‘Rafting birds’ included all birds on the water inside the cove boundaries and within 200 m from shore; a set buoy was used for reference. ‘Loafing birds’ included birds on all north-facing land visible from the population plot observation point (including the 6 population plots). Due to shortening daylight hours, counts towards the end of the season were advanced to begin at 2015.

Diurnal Colony Attendance

Diurnal colony attendance was monitored for 2 days in 1996, 3 days in 1997 and 1 day during the 1998 breeding season. Counts were conducted from the marked population plot observation site overlooking North Cove. Birds were counted using 10x 42 binoculars. Horned Puffins present in North Cove were counted from 0500-2300 at 30 minute intervals. Two separate counts were conducted at each half hour. ‘Rafting birds’ include all birds on the water inside the cove boundaries and within 200 m. from shore, a set buoy was used for reference. ‘Loafing birds’ include all birds on land within the North Cove boundaries (including the 6 population plots).

Results

Productivity

Breeding success was high and similar among years (Table 12.1), and there was no significant difference in hatching success, fledging success or overall breeding success between years. Although no consistent effort was made to resight banded birds, there is evidence of nest-site fidelity, with 5 of the 11 birds banded in 1998 opportunistically resighted in the same burrows in1999. Median chick hatch date ranged from 19 July in 1996, to 29 July in 1998 (Table 12.1).

Chick Diet

A total of 2796 prey items were collected during 1995-1999 (Table 12.2). Sand lance was the dominant prey species (Fig. 12.3), constituting over 94% of the chick’s diet in each year. Most of the other prey consisted of capelin (*Mallotus villosus*) or salmon species (*Onchorhynchus* sp.). Invertebrates comprised an extremely small part of chick diet, with only 2 squid and 8 euphausiid among the total of 2796 prey items collected. There was no significant difference in the proportion of sand lance in the chick’s diet between years ($\chi2$=6.36, df=4, p >0.05). Sandlance differed in size between years, with relatively small individuals delivered to chicks in 1996 and 1997, and larger individuals in 1999 (Table 12.3). Sandlance length ranged from a mean of 85.2 mm in 1996 to 100.2 mm in 1999 (total range = 31-223mm). Mean mass ranged from 2.1g in 1996 to 3.3 g in 1999.

There was no significant difference in mean mass of fish per bill load (ANOVA: F=0.8, df=3,57, p=0.97), or the mean number of prey items per load (ANOVA: F=1.54, df=3,124, p=0.2) between years 1996 to 1999 (Table 12.4). Mean bill load mass over all 5 years was 16.4 ± 0.8 g (n=63), mean number of prey items per load was 6.2 ± 0.3 (n=132). Daily meal delivery rates were recorded for a total of 5 days in 1996 and 1997; means ranging from 2.6 to 6.8 meals per day are presented in Table 12.5.

Chick growth

To compare growth among years, I calculated growth rate (using linear regression) for different body components during the linear phase of growth (10-30 days for body mass and wing length; 0-15 days for culmen and tarsus length). These data were used to calculate a single growth rate, for each body component, for each chick. There was a significant difference among years in mass growth rates of chicks (Table 12.6), with much slower growth in 1998 than in other years.

We were only able to measure puffin chick fledging ages in 1996, 1998 and 1999. There was a significant difference in chick fledging age between the 3 years (ANOVA: F=15.66, df=2,69, p=<0.001). Means are shown in Table 12.7. Although growth rate was lowest in 1998, chicks fledged at the youngest age (34.7 days).

Adults and fledgling measurements

A total of 38 breeding adult puffins were caught in 1998 and 1999. Morphometrics are presented in Appendix 12.1. Mean adult wing length was 198 mm (SD= 7.32, n=38), mean adult body mass was 531g (S.D. = 44.27, n=38). Very few fledglings were caught, and their measurements are provided in Table 12.8.

Seasonal and diurnal attendance

The seasonal colony attendance of Horned Puffins is presented in Fig. 12.4. We are in the process of examining seasonal patterns and the annual and daily variability in attendance (Harding et al. 2002b). However, some general patterns are apparent: 1) there is high variation in daily colony attendance, 2) late incubation is characterized by the highest numbers of puffins, 3) the numbers of attending birds drop during the first two or three weeks of chick-rearing. Diurnal attendance was monitored for 6 days in total during 1996, 1997 and 1998. Diurnal attendance for 1997 is shown in Fig. 12.5. A morning and a larger evening peak were observed. Puffin numbers were low between 1300 and 1500 hours. Attendance is highest during the evening peak, between 1930 and 2130.

Population plots and colony census

We are in the process of examining the population plot data for 1996-1999 (Harding et al. 2002b). Daily variability in counts is reflected in the seasonal attendance data (Fig. 12.4), with the 'land' counts including the 6 population plots. Colony counts of Horned Puffins are presented in Table 12. 9; Tufted Puffin counts in Table 12.10. We are also examining the population counts with respect to phenology and the data from seasonal colony attendance.

Discussion and Conclusions

Since we have no measure of laying success and only followed eggs from late incubation, it is difficult to compare the hatching and breeding success on Duck Island with other studies on Horned Puffins. The mean fledging success for the 5 years (91.4%) is relatively high compared to other studies in which fledging success ranged from 25-100%, with a mean of 75% (n=39) (Piatt and Kitaysky 2001).

Complete breeding failure in the Atlantic Puffin has been frequently reported, and has usually been attributed to extremely poor food availability, and often attributed to overfishing (eg., Anker-Nilssen 1987, Barrett et al 1987, Barrett and Rikardsen 1992, Martin 1989, Lid 1981). Breeding failure has also been recorded in the Tufted Puffin and the Rhinoceros Auklet (*Cerorhinca monocerata*) (Vermeer 1979, 1980), and in the Horned Puffin (Byrd et al. 1993). Although it seems that puffins have some flexibility and can extend their chick feeding period during seasons of short food supply, life history theory predicts that under seasons of extreme short food supply parents will abandon their breeding attempt, reducing the risk of mortality associated with high parental effort.

Although Common Murres experienced an almost complete breeding failure in 1998, suggesting that local feeding conditions were extremely poor, the lack of detectable difference in reproductive success for puffins on Duck Island between years suggests that Horned Puffins can successfully rear a chick to fledging over a wide range of food availabilities. Breeding failure has been rarely recorded in the Horned Puffin, and evidence from other studies suggests that the variability in the reproductive success of Horned Puffins between years and at different colonies is incredibly low. Horned puffin fledging success over 39 colonies years averaged 73% (range = 25-100) (Piatt and Kitaysky 2000). Our data is however limited by lack of knowledge of the proportion of birds that attempt to breed between years, and we were unable to measure incubation success, a suggested key factor for reproductive success in puffins (Hatch and Hatch 1990).

Chick diet over the 5 years of this study was dominated by sand lance, constituting over 94% of the diet in each year. Capelin and juvenile salmonids comprised most of the other prey, each constituting approximately 2% of the chick diet. Pacific lamprey and sandfish are unusual prey species for Horned puffins, but were observed in small numbers in the chick diet on Duck Island. The diet of Horned Puffin chicks on Duck Island is high in sandlance, even for a species known to specialize, with 60% of chick diet throughout the North Pacific range comprised of sandlance (Piatt and Kitaysky 2000). Horned Puffin chicks are fed almost entirely fish, with sandlance, capelin and gadids the most important prey species across their North Pacific range (Piatt and Kitaysky 2001). Horned puffin chicks are fed relatively few other prey species in comparison to the Tufted Puffin (Hatch and Sanger 1992). For example, the chick diet of Tufted Puffins on Suklik in 1985 consisted of 32 fish species and 7 kinds of invertebrate, whereas Horned Puffin chicks were fed only 13 fish species and 2 kinds of invertebrates. Sandlance constituted 83% of the Horned Puffin chick diet, and only 48% of the Tufted Puffin chick diet (Hatch and Sanger 1992).

The size of sandlance delivered to chicks differed between years, from a mean of 85mm in 1996 to 100mm in 1999 (total range=31-223). Other studies have recorded ranges in sandlance size from 56-164mm (Wehle 1983) and 25-164mm, mean=70mm (n=3746) (Hatch and Sanger 1992). Chicks in this study received bill loads weighing on average 16g (range=2.5-35.5g), and comprising an average of 6 prey items (range; 1-22). Other studies have recorded a similar number of prey items per bill load from 1-11 (n=15) (Wehle 1983) and a mean of 7 (n=619) (Hatch and Sanger 1992). Bill load mass in this study is relatively high compared to other studies, which report an average of 9.3 g per load (n=12 colony years) (Piatt and Kitaysky 2001). This difference may be explained by the different methods of meal load collection. Whereas most studies have collected meal loads by blocking nest-sites using re-usable metal grid screens (Hatch and Sanger 1992), this study only classified and weighed bill-loads either where a whole load was observed dropped or when loads were collected using a gill-net and it was known that no fish were lost. The bill load size and mass recorded in this study present a more accurate measure than most other studies. Loads collected using the screening methods are probably underestimated since adults may eat food if prevented from delivering to the chick, and meals may be taken by gulls (pers. obs).

Due to their habit of nesting in crevices, at often scattered locations, little is known about chick feeding frequency in Horned Puffins. Data from this study are limited, ranging from a mean of 2.6-6.8 meals a day over 5 days of observation. These are similar frequencies to those reported on the Barren Islands (2-6 meals/day) (Manuwal and Boersma 1977).

The large range in chick growth rates observed over the 5 years of this study (mean of 3.7-12.8g/day) is similar to the range reported in other studies, from a record low of 3.4g/day in the Semidi Islands to 12.6g/day at the Shamagin Islands (Petersen 1983). In 1979, puffin chicks on Duck Island grew at 10.7 ± 0.7 g/day (n=12) (Jones and Petersen 1979), approximately the same rate as we observed in 1997. Chick growth rate depends on food intake. In an experimental study, Horned puffin chicks fed *ad libitum* (108g/day) grew at 11.2 ± 0.54 SE g/day, whereas chicks fed 53g/day grew at 6.45 ± 0.46 SE g/day (Kitaysky 1999), results suggesting that chicks in 1997 (growth= 10.5g/day) may have been receiving close to *ad libitum* food.

Food limitation is known to reduce the growth rate in puffin chicks (Harris 1984), with well documented evidence from both experimental studies (Harris 1978, Hudsen 1979, Kitaysky 1996, Kitaysky 1999, Øyan and Nilssen 1996) and in the field (eg. Barrett et al 1987, Barrett and Rikardsen 1992, Harris 1985, Tzchanz 1979). We assume that the amount of food received by a chick to be related to the local availability of prey. Growth rates in 1998 were exceptionally low (3.7 g/day), in comparison to chick growth in the other 4 years (9.4-12.8g/day), evidence suggesting that food availability was severely limiting the growth of chicks in 1998.

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Chapter 13. Biology of Other Seabird Species in lower Cook Inlet

Michael Shultz and Thomas Van Pelt

Introduction

Species background and study area

This project was focused on four key seabird species; two that bred on all three colonies within our study area (the pelagic, deep-diving Common Murre [Chapter 9] and the pelagic, surface-feeding Black-legged kittiwake [Chapter 10]), and two found at one or more of our study colonies (the pelagic, diving Horned Puffin [Chapter 12] and the coastal, diving Pigeon Guillemot [Chapter 11]). However, we also collected ancillary data on several other seabird species that comprise part of the seabird community in lower Cook Inlet. These included:

The Glaucous-winged Gull (*Larus glaucescens*) is a common resident along the northwestern coast of North America. These large, omnivorous gulls are generally an inshore species, but they may also forage or scavenge from fishing vessels far out at sea. Glaucous-winged Gulls generally nest at high densities in large or small colonies on off-shore islands, forming apparently monogamous breeding pairs with a clutch size of 1-4 eggs (mean clutch size range 2.1-2.9 eggs; Verbeek 1993).

The Tufted Puffin (*Fratercula cirrhata*) is an abundant seabird in lower Cook Inlet (Piatt 1994, Chapter 8) and breeds in large numbers on the Barren Islands and in smaller numbers at Gull and Chisik islands. Tufted puffins burrow into soil where they raise one young in their nest chambers. They forage widely on a great variety of pelagic prey including sand lance, capelin and juvenile pollock (Piatt et al. 1997). Like its congener, the Horned Puffin, the Tufted Puffin forages offshore and sometimes far from its breeding colonies.

The Pelagic Cormorant (*Phalacrocorax pelagicus*) and the Red-faced Cormorant (*Phalacrocorax urile*) are two of the three species of cormorants that breed in Alaska. They differ from the third cormorant species, the Double-crested Cormorant (*Phalacrocorax auritus*), in that they are strictly marine birds. All the cormorants tend to forage nearshore, and feed heavily on benthic prey. Pelagic Cormorants nest on coastal headlands or islands throughout Alaska and the Asian North Pacific. Red-faced Cormorants nest in a much smaller region of the North Pacific that stretches from northern Japan through the Aleutian Islands. Both species lay clutches of 3-7 eggs, with means from 2.9 to 3.8 eggs per nest (Hobson 1997). The Double-crested Cormorant is widely distributed across North America, and is commonly found along seacoasts and inland waters. Unlike the other cormorant species, these are gregarious birds that can form large colonies in diverse terrain: on the ground, on cliff-faces, and in trees or artificial structures. The modal clutch size for this species is 4 eggs, with a range of 1-7 eggs per nest.

Our work on these species was conducted at two colonies in Cook Inlet, Gulf of Alaska, between May-September in 1995-1999. The colony at Chisik Island (including Duck Island; west side of Cook Inlet; 60° 09' N, 152° 34' W) supports a significant population of Glaucous-winged Gulls and Double-crested Cormorants, with small populations of Pelagic Cormorants and Tufted Puffins. The Gull Island colony (east side of Cook Inlet; 59° 35' N, 151° 19' W) supports significant populations of Glaucous-winged Gulls, Tufted Puffins, and smaller populations of Pelagic and Red-faced Cormorants. The two colonies are separated by ca. 100 km and are in oceanographically distinct habitats, with Chisik Island surrounded by stratified, relatively warm estuarine waters and Gull Island by colder, mixed oceanic waters with significant freshwater runoff (Robards et al. 1999 and references cited therein).

There is increasing evidence that an oceanographic 'regime shift' occurred in the Gulf of Alaska in the early 1980's, resulting in changes in seabird diets and reduction of reproductive success in some marine bird and marine mammal populations (Piatt and Anderson 1996; Anderson and Piatt 1999). These changes were similar to some hypothesized effects of the T/V *Exxon Valdez* oil spill (EVOS) on relatively well-studied seabird species such as murres and kittiwakes (see Chapters 9 and 10). It is also likely that other members of the seabird communities (e.g. cormorants, gulls, and puffins) have also been affected.

To learn more about foraging, breeding, and population changes in colonies of Glaucous-winged gulls, Tufted Puffins, and Double-crested, Pelagic, and Red-faced Cormorants, we gathered data on these species at Chisik and Gull Islands, while we investigated the oceanography and forage fish distribution around those colonies. The purpose of this chapter is to summarize the methods we used and to present the results of our study in a format useful to other researchers. Eventually, these results may be integrated with those of other species to develop a synthesis of how the seabird community responds to changes in food supply.

Methods

Productivity

Glaucous-winged Gull— We monitored Glaucous-winged Gull reproductive parameters from 1995-1999 at Gull and Chisik islands. Since both islands are covered in dense vegetation by late June, we found it nearly impossible to accurately determine individual chick fates and therefore followed nests only through hatching. On Gull Island, hatching success data were collected from 2 plots in 1995 and 5 plots in other years. Plots contained approximately 10 nests in 1997-1999, and 15-20 nests in 1995-1996. Plots were checked every five days during incubation for nest contents and every 2 - 3 days when chicks were expected to hatch. At Chisik Island, 2-3 productivity plots containing approximately 10 nests were monitored from 1997-1999. In 1996, one plot containing 30 nests was followed. Nests in plots were checked every 3-7 days and their contents recorded. In 1995, we estimated hatching success with a two-visit method. During the late incubation/early chick-rearing period, areas on Duck Island known to contain nesting gulls were surveyed. Contents of all nests found 24 June were recorded, and nests containing eggs were revisited 29 June to determine egg fate. An index of hatching success was calculated from the numbers of chicks seen per nest counted.

We used study plot as the sample unit for estimating each parameter, except at Chisik Island in 1996 where nest site was the sample unit. The mean and standard deviation of the plot means were used for annual estimates. Reproductive parameters are defined as follows:

Hatching chronology (median hatch date)
Hatching Success (% of eggs laid that hatch)
Hatching Productivity (chicks hatched per nest with eggs)
Clutch Size (eggs per nest with eggs)
Brood Size at Hatch (chicks per nest with chicks at hatch)

Pelagic Cormorants— We monitored Pelagic Cormorant productivity at Gull Island from 1995-1999. In 1995-1997, all nests visible from on top of the island were followed, whereas from 1998-1999, nests in 11 productivity plots were followed. Nests were checked with 8 X 42 or 10 X 42 binoculars every 4 - 6 days from incubation through fledging. Nest contents (i.e. numbers of eggs and chicks) were recorded during each visit. Pelagic Cormorant fledging age is highly variable, however around 40 days is typical (Hobson et. al. 1997). We assumed chicks to have fledged if they disappeared after 40 days of age. However, since newly hatched chicks are brooded very closely for the first 10 days, it was difficult to obtain an accurate hatch date by direct observation. To account for this we assumed that a chick had "fledged" if it was present 30 days after the first chick observation (typically around 10 days after hatch).

We calculated productivity estimates with nest as the sample unit from 1995-1997 and plots as the sample unit for 1998 and 1999. Reproductive parameters are defined as follows:

Hatching chronology (median hatch dates)
Hatching Success (% of eggs laid that hatch)
Productivity (chicks fledged per nest structure)
Mean Clutch Size (eggs per nest with eggs)
Brood Size at Hatch (chicks per nest with chicks at hatch)
Brood Size at Fledge (fledglings per nest with fledglings)

We obtained an index of productivity for all Pelagic Cormorant nests on Gull Island from 1995-1999 and on cliffs at Moosehead Point (1 km from Gull) in 1995. Adults and nests were counted once during mid-incubation and all visible chicks were counted just prior to the fledging period. Counts were completed using 8 x 40 or 10 x 40 binoculars with two observers in a boat 5 - 30 m off shore. Since nest contents were not visible from the water, nest status was inferred from adult posture. Only active nests (i.e. contained incubating adults) were counted. Counts were averaged between observers. The same nests were surveyed for chicks. All chicks visible from the water were counted, and totals were averaged between observers. Productivity was determined from the ratio of chicks to nests.

Red-faced Cormorants— An index of productivity (chicks per active nest) was calculated for all Red-faced Cormorant nests on Gull Island from 1995-1998 using the same methodology we used for Pelagic Cormorants.

Double-crested Cormorant— Data on this species was collected at Chisik in all years (1995-1999). However, the colony was located on cliff faces approximately 1250 – 1750 m away from the observation site, at an elevation of 300 – 450 m above the observation site, making observations very difficult. We attempted to overcome this by using a high-quality spotting scope with a 20-60x eyepiece, but observers were still unable to confidently identify nest contents. We attempted to delineate plot boundaries to measure changes in population or nesting effort, but observers had little confidence in both the precision of those boundaries and the counting of nests within the boundaries. In 1995, we were able to identify some Fully Feathered Chicks (FFC); giving a minimum productivity of 0.64 fledglings per nest (18 FFC from 28 nests). However, in 1996-1999, observers had little confidence in the identification of FFCs. Despite these limitations, we were able to estimate the population at around 8-45 nests each year on the high cliffs on the North East side of Chisik Island.

Population monitoring

We monitored populations of all species on population plots at Gull and Chisik islands, from 1995-1999. Some population monitoring plots had already been established by USFWS Alaska Maritime National Wildlife Refuge personnel prior to the beginning of our study. To facilitate long-term comparisons, these historical plots were maintained; however, in some cases additional plots were created at the beginning of our study (1995), and also in later years. We therefore summarize our data separately for historic plots and newly created plots.

All plots were photographed, and boundaries were clearly marked on the photographs. Using inflatable boats for access, binoculars for viewing, and tally-clickers to ease counting, all birds within the plots were counted 5-12 times during the season between mid-incubation and the onset of chick fledging. Sea, wind, and visibility conditions were recorded for each count. Counts were made between 1000 and 1600 hours (the time during daylight hours when attendance is most stable; see Birkhead and Nettleship 1980; D.E. Dragoo, unpubl. data; Boersma *et al.* 1995; Roseneau *et al.* 1995). Two observers counted each plot; if the difference between observers was greater than 10% of the total, the count was repeated. The plot total was taken as the mean of the two observer counts. The sample unit is the count-day, with all plot counts for the each day merged into a total. Plots in population counts therefore serve only as an organizational tool and not as a statistical unit (in contrast to productivity plots; see below).

Attendance was most consistent from the mid-incubation through the start of chick fledging, but logistic complications during the field season meant that not all counts fell within this period. Therefore, following the field season, count 'windows' for each species and each colony-year were defined (based on the reproductive chronology for that year) as mid-incubation to the beginning of fledging. Estimates for mid-incubation were obtained by adding half of the incubation period for each species to peak laying date; the start of fledging is defined as the first chick observed to fledge from a productivity plot. Plot counts outside these windows were retained for archival purposes, but the summaries presented here use only counts made within the appropriate mid-incubation to fledging window**.**

Since we did not monitor Tufted Puffin breeding success, we estimated breeding chronology based on chick ages from growth data collected in 1997. We aged chicks by assuming they reached asymptotic weight at around 35 days of age (Gaston et al. 1998). This was sufficiently accurate for our purposes given that nearly all counts fell well within these windows.

We conducted whole island counts of adult Pelagic and Red-faced Cormorants and nests during mid-incubation in most years. Counts were completed using 8 x 40 or 10 x 40 binoculars with two observers in a boat 5 - 30 m off shore. Two observers counted a section of the colony; if the difference between observers was greater than 10% of the total, the count was repeated. The section total was taken as the mean of the two observer counts. This procedure was repeated until the whole island had been censused.

We completed whole island censuses of Glaucous-winged Gulls during incubation in 1995, 1997, and 1998 at Gull and Chisik island. At Gull Island, the counts were completed on the same day between 1000-1400. The same methods were used as for Pelagic and Red-faced Cormorant censuses, except that at Gull Island the counts were conducted from land. At Chisik Island, counts were completed from an inflatable boat; on Duck Island from land.

Tufted Puffin chick growth

The Tufted Puffin population at Gull Island numbers about 100 pairs, and very few of these burrows are accessible without disturbing nesting Common Murres *(Uria aalge)* and Pelagic Cormorants. As a result, we obtained chick growth rates for only 5 individuals in 1997. We checked burrows every 4 days, after chicks were no longer being brooded to measure and weigh chicks. We measured mass with a 500 gram Pesola spring balance to the nearest 5 grams, flattened wing length with a 100 cm wing-ruler, and culmen (from the tip of the upper mandible to the anterior edge of the growing cere and tarso-metatarsus ("tarsus") lengths with Vernier calipers.

Results

Glaucous-winged Gull

Productivity— Glaucous-winged Gull productivity parameters, averaged for all years, were similar between Gull and Chisik Islands (Table 13.1). Clutch size was slightly higher at Chisik, while hatching success was slightly lower than at Gull, resulting in similar overall productivity (chicks hatched per nest with chicks). Gulls initiated nesting at Chisik Island 5 days earlier on average, than at Gull Island (Table 13.1).

Population— Numbers of Glaucous-winged Gulls in population plots were variable among years, but there was no apparent trend in the population at Chisik and Gull Island (Table 13.2). When counts from 1995-1999 are compared to historical counts there again appears to be no trend in the populations at either colony (Appendix 13.1). Gulls nesting on 60 Foot Rock were counted only in 1995, but in light of historical estimates this small population may be increasing. Population plot count windows calculated from yearly nesting chronology are summarized and compared with the actual count windows in Appendix 13.2. In addition to population plot counts, colony censuses were completed in 1995, 1997, and 1998 at Gull and Chisik islands (Table 13.3). When these data are compared to historical counts there is no clear trend in the data from Chisik. At Gull Island, the population seems to have stabilized after a fairly rapid increase during the 1970's and 1980's (Appendix 13.3).

Pelagic Cormorants

Productivity— We estimated Pelagic Cormorant productivity in plots and by index checks, at Gull Island from 1995-1999 (Table 13.4). Productivity of Pelagic Cormorants in plots was relatively consistent among years, except for 1995, when it was well below the average for 1996-1999 (0.29 vs. 0.71 chicks per nest). Much of this low reproductive output in 1995 can be accounted for by a small average clutch size. We also checked the productivity index in all years at Gull Island (Table 13.5). Productivity estimates using index methods were generally much higher than those from plots, except in 1998 when the opposite was true.

Population— There were no Pelagic Cormorants in population plots at Chisik Island from 1995-1999. Numbers of cormorants in population plots at Gull Island declined from 1995-1999 (Table 13.6). Plot counts conducted from 1986-1994 indicate that the population had been stable from 1986-1988, declined noticeably in 1989 and then steadily increased until 1996 (Appendix 13.4). Population plot count windows calculated from yearly nesting chronology are summarized and compared with the actual count windows in Appendix 13.5. Whole island counts of adult birds and nests were conducted from 1995-1998. These results and those from counts completed from 1976-1994 show a similar pattern as the results from population plot count data (Appendix 13.6).

Red-faced Cormorants

Productivity— Estimates of productivity derived from index checks showed a similar pattern among years as those for Pelagic Cormorants (Table 13.5). However, overall productivity averaged among years was slightly higher for Pelagic Cormorants (Pelagic; mean=0.98, sd=0.59, n=4; Red-faced; mean=0.88, sd=0.61, n=4)

Population— Whole island counts of adult birds and nests were conducted from 1995-1998. These results and those from counts completed from 1976-1994 indicate a possible decline in the population from a high of 62 individuals in 1976 to a low of 16 in 1997 (Appendix 13.6)

Tufted Puffins

We counted Tufted Puffins in population plots from 1997-1999 (Table 13.7). Population plot count windows are summarized and compared with the actual time windows when counts were completed, in Appendix 13.7. We measured puffin chick growth in 1997 at Gull Island. The results for individual chicks are summarized in Table 13.8.

Discussion

Glaucous-winged Gull

Gull identification— Williamsen and Petyon (1963) collected a series of gulls from a large breeding colony in the Cook Inlet region, near Anchorage, Alaska, that showed intermediate plumage characteristics between Herring Gulls *(Larus argentatus)* and Glaucous-winged Gulls. This colony was an inland colony and surrounded several large lakes on the Susitna flats. Most of the gulls tended to more closely resemble Herring rather than Glaucous-winged Gulls, based on the extent of dark coloration in the sub-terminal bands of the primaries, iris color, and eye ring color. They later found evidence of interbreeding from other colonies around Cook Inlet and concluded that interbreeding between the two species is "common and widespread" in the Cook Inlet region. They also reported that according to knowledge of breeding distributions at the time, that interbreeding was only to be expected in the Cook Inlet region west to the base of the Alaska Peninsula and on Forrester and Muir Islands in Southeast Alaska. Patten and Weisbrod (1974) later mentioned evidence of inbreeding between these two species, also based on plumage and bare part coloration, from the Glacier Bay region.

Glaucous-winged Gulls nesting on Gull Island also showed characteristics intermediate between these species. Most gulls closely resembled Glaucous-winged Gulls, but a full gradient of characteristics between typical Glaucous-winged and Herring Gull phenotypes nested on the island. The color of the sub-terminal bands of the primaries varied from black to light gray and was not useful for identification. Iris color and orbital ring color were also equally variable. Gull Island is an offshore oceanic island that is more typical of Glaucous-winged Gull habitat than Herring Gull habitat.

Productivity— Hatching success at Gull (59%) and Chisik Island (52%) was comparable to estimates reported for colonies elsewhere in Alaska: 67% (Patten 1974), 46% (Murphy et al. 1974), 62% (Baird 1990), 80% (Hatch and Hatch 1990). Clutch size values (Gull; 2.3, Chisik; 2.4) were slightly lower than some other colonies in Alaska: 2.9 (Patten 1974) 2.1 and 2.6 at Squab Island (Murphy et al. 1984), 2.6 (Hatch and Hatch 1990). Chisik Island birds initiated nesting earlier and laid larger clutches, however they also had lower hatching success than at Gull Island. Although we did not follow gull chicks to fledging, the pattern through hatching is similar to that which is seen for Black-legged Kittiwakes at Chisik Island: they typically lay clutches comparable and sometimes exceeding those at Gull Island, however hatching is noticeably lower at Chisik, and almost none of these chicks survive to fledge. This is probably the result of birds arriving at the start of the season in relatively good condition, however once they have laid eggs and become dependent on local resources, the paucity of food close to Chisik Island results in low net reproductive success.

Pelagic Cormorants

Productivity— Productivity values derived from plots (62%) were noticeably different than those derived from the productivity index counts (98%). Productivity plots contained only a small sample of all nests, while the index included all nests on the island. The productivity index is a less accurate estimate of productivity than the plot data in that the number of "fledglings" is actually the number of large chicks present just prior to fledging. Pelagic Cormorants are relatively asynchronous breeders and as a result some younger chicks are considered "fledged" when certainly some of these would have died before fledging. However, as an index of among year variability and trends in productivity, this method may be more desirable in that it accounts for all areas of the colony.

The range of productivity values at Gull Island (plots, 0.29-0.83) was lower than that reported for Anacapa Island, California (1.69-2.64, Hobson 1997), but was within range for the Farallon Islands (0.0-2.83, Boekelheide et al. 1990). Productivity at the Farallones was more variable among years than at Gull Island. The range of mean annual clutch sizes at Gull Island (2.17-3.83) were similar to those reported from the Farallon Islands, California, indicating that Gull Island cormorants may have lower hatching and/or fledging success. Hobson (1997) reported that Bering Sea colonies have greater hatching success but lower fledging success than British Columbia colonies. This may be due to greater chick predation or the effects of weather and climate or food cycles on chicks.

Population— Historic population plot counts of Pelagic Cormorants at Gull Island dating back to 1986 indicate that their numbers have fluctuated considerably. From 1986-1988, the population was stable, it dropped dramatically in 1989, steadily increased from 1989-1994, and then steadily declined in 1995-1999. The overall trend from 1986-1999 has been a declining one, with a high of 55 birds in plots in 1986 and a low of 18 in 1999. It is possible that the dramatic drop in breeding birds in 1989 was due to EVOS effects, but this does not explain the continuing long-term decline at this colony.

Tufted Puffins

Chick mass growth for Gull Island in 1997 (15.75 g / day), was similar to the range of values reported for this species at the Barren Islands in 1976 (16.5 g/day) and 1977 (16.5 g/day)(Amaral 1977), and to average growth from 11 different studies on the west coast (15.2 g/day, Piatt et al. 1997). At Gull Island in 1997, food abundance was relatively high as evidenced by hydroacoustic surveys (Chapter 7), beach seine catches (Chapter 5) and by Common Murre *(Uria aalge)* and Black-legged Kittiwake *(Rissa tridactyla)* breeding success.

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Chapter 14. Response of Seabirds to Fluctuations in Forage Fish Density: Can Seabirds Recover from Effects of the *Exxon Valdez* oil spill?

John Piatt

Introduction

This chapter contains a synthesis of five years (1995-1999) of study in lower Cook Inlet. Some initial findings have been published (see Chapter 1) and we continued to collect data on some seabird parameters (e.g., foraging behavior, reproductive success, survival, stress, etc.) in summers of 2000 and 2001. For this synthesis, the focus will be on Common Murres and Black-legged Kittiwakes because these were the bird species of primary interest in the study, and the species for which data were collected at all three colony sites in lower Cook Inlet.

First, I will review the background for this study and discuss the theoretical considerations that went into the study design. Second, I will provide a summary of the major findings about the marine ecosystem in lower Cook Inlet (as presented in Chapters 2-7) and discuss the implications for seabirds. Third, I will summarize how seabirds responded to variation in food supply-- the major focus of this study. Finally, I will consider what the data suggest about the status of seabird populations in the Gulf of Alaska, and the likelihood that seabird populations can recover from effects of the *Exxon Valdez* oil spill.

Background

Why the Study was Initiated

Immediate impacts of the Exxon Valdez oil spill (EVOS) on seabirds in 1989 were well-documented. Common Murres comprised most (74%) of oiled bird carcasses recovered from beaches (>30,000) and a variety of direct and indirect evidence suggested that about 250,000 seabirds were killed (Piatt and Ford 1996). Putative short-term effects on murres included a reduction in populations at affected colonies, delayed breeding phenology and low reproductive success (Nysewander et al. 1993). The greatest impact was in the Gulf of Alaska and particularly lower Cook Inlet, where large numbers of murres were beginning to gather near breeding colonies when oil swept through the region in April and May. Models of murre population dynamics (Ford and Wiens et al. 1982) suggested that it could take 20-70 years for murre populations to recover to a stable age distribution *if* environmental conditions were favorable (Piatt et al. 1990).

However, evidence accumulated during the 1990's that environmental conditions were *not* favorable to seabirds in years following the oil spill. A "regime shift" had occurred in the Gulf of Alaska (GOA) during the late 1970's, apparently resulting in marked changes in seabird diets, lowering of reproductive success and population size, and occasional 'wrecks' (large-scale die-offs) in some marine bird and mammal populations (Piatt and Anderson 1996, Francis et al. 1998). Furthermore, this regime shift appeared to affect seabirds in ways similar to hypothesized effects of the spill. This new information raised several questions: To what degree were seabirds affected by natural changes in the GOA environment before the spill? Could effects of the spill be separated from natural variability? In light of the regime shift, what was the current status of seabird populations in the GOA and how long would it take murres and other seabirds to recover from effects of the spill?

To address these questions, the EVOS Trustee Council (EVOSTC) initiated the Apex Predator Ecosystem Experiment (APEX) in 1994 to assess whether current conditions favor a recovery of seabirds from the spill. Initially focussed on Prince William Sound, APEX studies expanded in 1995 to include Cook Inlet, where funding and logistic support from the U.S. Geological Survey, U.S. Fish and Wildlife Service, Minerals Management Service, and the Alaska Department of Fish and Game made it possible to conduct seabird and forage fish studies around three colonies (Chisik, Gull and Barren islands) that had been impacted by the oil spill. In Cook Inlet, investigations included studies on oceanography and forage fish biology, distribution and abundance; and at colonies, studies of seabird foraging behavior, diets, time-budgets, chick growth rates, physiological condition and reproductive success. Most data were collected on Common Murres and Black-legged Kittiwakes, which breed at all colonies studied in lower Cook Inlet. Ancillary data were also collected on other species (Glaucous-winged Gulls, Pelagic Cormorants, Tufted and Horned Puffins, and Pigeon Guillemots); of which only Glaucous-winged Gulls breed at all colony sites. In this preliminary synthesis, we will restrict our analysis and discussion to murres and kittiwakes. Consideration of the entire marine bird community will follow when all data have been compiled and analyzed.

Theoretical Considerations and Study Design

The main question in 1995 was: Is the recovery of seabirds in Cook Inlet currently limited by food supply? The response of seabirds to environmental change can vary widely among species, and is influenced by a host of physical and biological factors. Differential adaptations of seabirds for exploiting plankton and fish, widely-varying foraging abilities and breeding strategies, and complex relationships between oceanography and prey dispersion, abundance, and behavior all serve to complicate our interpretation of changes in seabird population biology. Therefore, in order to assess the potential for recovery of seabirds affected by the *Exxon Valdez* oil spill, a concurrent, multi-disciplinary study of oceanography, forage fish, and seabirds was required.

Coordinated studies of seabird breeding biology and feeding ecology in relation to prey abundance are rare (e.g., Safina and Burger 1985, 1988; Piatt 1987, 1990; Monaghan et al. 1989, 1994; Hamer et al. 1991, 1993; Uttley et al. 1994). Nonetheless, results of these studies provided an empirical basis for hypotheses about relationships between seabirds and their prey in lower Cook Inlet (Chapter 1). Relationships between seabirds and their prey can be quantified within an established framework of predation theory (Holling 1959; Murdoch and Oaten 1975; Piatt 1987). Population change (the "numerical response") in higher vertebrates depends largely on the rate at which food (energy) can be extracted from the environment (the "functional response"). Predator responses to changing prey density are usually non-linear in form and often exhibit threshold dynamics.

The challenge in this study was to measure the form and scale of seabird responses to prey fluctuations in light of variability in the marine environment of lower Cook Inlet and difficulties in measuring food abundance. Quantifying responses of higher vertebrates in the field can be difficult because of logistical difficulties in measuring key parameters (Goss-Custard 1970), and the lack of power to manipulate predator and prey densities over the full range of possible values (Piatt 1990).

In this study, we set out from the beginning to study seabirds and prey resources at colonies known from historical work to be chronically failing (Chisik I.), thriving (Gull I.) and possibly stable or recovering from the oil spill (Barren I.). Our hope was that these historic differences did indeed result from regional differences in food supplies, and that by studying all three colonies for five years we would obtain enough data to construct response curves for important seabird parameters (recognizing that it takes one year to obtain one data point per parameter, e.g., breeding success versus food density). Further, we hoped that this approach would allow us to examine a variety of parameters simultaneously in order to determine which parameters are most strongly influenced by food abundance, and how responses might vary among species in terms of thresholds, sensitivity and variability.

Before we examine relationships between seabirds and food supply, I will review our general findings about the Cook Inlet marine ecosystem and how seabirds exploit food resources in this system.

The Marine Ecosystem in Lower Cook Inlet

Oceanography and Biological Productivity

The engine that drives productivity in lower Cook Inlet is the persistent upwelling of cold, nutrient-rich water at the entrance to Cook Inlet. A plume of cold GOA water that extended from the Barrens to Kachemak Bay was evident in all AVHRR images of sea surface temperature analyzed in 1995-1999, and persisted throughout summer in all years (Chapter 2). High concentrations of nitrates and silicates were associated with this plume, and these nutrients supported high levels of primary productivity in the plume and especially in stratified waters adjacent to the plume in Kachemak Bay (Chapter 3). Phytoplankton production intensified in the upper 30m as stratification developed in May, and continued with varying intensity throughout summer-- suggesting a periodic replenishment of surface nutrient levels following the mixing of surface layers by wind events. Waters on the west side of lower Cook Inlet were oceanographically distinct (warmer, less saline, weakly stratified, turbid, outflowing), and much less productive. A distinct front between western and eastern waters was always observed on cross-inlet transects (Chapter 2), and primary production west of this front never approached levels observed east of the front (Chapter 3).

The east-west difference in oceanography and primary production was reflected at all higher trophic levels. The abundance of zooplankton (Chapter 3), forage fish both offshore (Chapter 4,7) and nearshore (Chapter 5,7), and seabirds (Chapter 8) was in all cases 1-2 orders of magnitude higher on the east side of lower Cook Inlet (Figs. 14.1-14.3). In contrast, species diversity was higher in the west and many fish species (e.g., sandfish, eulachon, smelt) were largely restricted to these waters (Chapter 4). The growth rate of resident forage fish such as sand lance was significantly lower in Chisik waters than in Kachemak Bay. Initially, we thought that sand lance growth was similar among areas, until examination of otoliths and growth rates revealed that fish of the same length were, in fact, one year older at Chisik (Robards 2000). Thus, all evidence suggests that lower Cook Inlet is segregated into two distinct oceanographic domains with striking differences in productivity and biology among them.

Whereas the east-west contrast in oceanography and productivity accounted for most of the spatial variation in biology observed in lower Cook Inlet, other sources of variability were also evident in the eastern domain. The well-mixed, cold waters in the lower inlet-- particularly offshore-- were dominated by juvenile pollock and capelin, whereas sand lance and herring preferred stratified coastal waters of the Kenai Peninsula and Kachemak Bay, and shallow offshore waters north of Kachemak Bay (Chapters 4,5). The overall abundance of zooplankton and fish was much higher in stratified coastal waters of Kachemak Bay and along the Kenai Peninsula than in mixed, cold, offshore waters of the lower inlet (Chapters 3,7). Finally, fish were markedly variable in the vertical dimension as well. Most acoustic biomass was concentrated in the upper 30m in all areas, but in Chisik and Barrens waters, schools were also concentrated at depths of 60-100m. There was also a clear segregation of species by water depth; sand lance and herring dominated above depths of 40m, whereas pollock and capelin dominated below 60m.

In summary, the areal patterns of productivity in lower Cook Inlet are largely a function of the bathymetry and oceanography. The bottom topography of the region steers GOA water into the shallow Cook Inlet estuary and ultimately structures nearshore and offshore habitats in all areas. The inflow of cold, nutrient-rich GOA water in the eastern domain and outflow of warmer, low-salinity water in the western domain creates the basic oceanographic setting for plankton, fish and seabirds. Mid-inlet fronts, eddies, stratification, mixing, river outflow, and winds all have some influence on local patterns of productivity, but the meso-scale (10's to 100's km) pattern is one of stability and persistence. Biological patterns of abundance and distribution persisted among years because the basic underlying oceanography changed little among years. This suggests that food supplies for seabirds are a lot more predictable than one might expect-- at least in terms of the meso-scale distribution of forage fish biomass.

Seabird Foraging Ecology

The distribution of seabirds at colonies and at sea in Cook Inlet reflects regional patterns of productivity and forage fish abundance. More seabirds breed in lower Cook Inlet than throughout the entire NE Gulf of Alaska (GOA), including Prince William Sound (Sowls et al. 1978). Densities of seabirds at sea were generally high in the eastern cold-water domain of lower Cook Inlet, and equaled those observed in extremely productive habitats elsewhere in Alaska such as the Bering Shelf edge and Bering Strait.

Different seabird species foraged in different domains in Cook Inlet, and sometimes in different habitats within those domains (Chapter 8). Oceanic species such as Northern Fulmars, Fork-tailed Storm-petrels, Ancient Murrelets, and phalaropes were found mostly in oceanic waters to the west and south of the Barrens or in frontal waters between the west and east domains in lower Cook Inlet. Shearwaters and Tufted Puffins were extremely abundant around the Barren and Shuyak islands, and were tightly associated with the cold-water plume in the eastern domain. Horned Puffins, which breed in abundance only at Chisik and feed almost entirely on sand lance (Chapter 12), foraged mostly in waters on the north side of Kachemak Bay where sand lance dominated in trawl catches. Pigeon Guillemots, which typically forage close to home and feed largely on benthic fish and sand lance found near shore (Chapter 11) were rarely encountered away from the coast, and populations were concentrated along the south shore of Kachemak Bay and the Kenai Peninsula. Marbled Murrelets, which feed mostly on sand lance, were widely distributed in all areas but were particularly abundant along the shores of Kachemak Bay and the Kenai Peninsula, and offshore on the north side of Kachemak Bay.

Murres and kittiwakes exhibited markedly different foraging distributions. Murres were dispersed throughout the study area, and their distribution was very similar to the overall distribution of acoustic biomass (Chapter 7)-- i.e., concentrated in coastal areas of Kachemak Bay and the Kenai Peninsula, offshore north and east of the Barren islands, and extending north into the Chisik survey area as far as the cold-water plume extended in any given year. Thus, murres appear to routinely travel 20-60 km to forage from the Barren islands, 10-40 km from Gull Island, and at least 30-60 km from Chisik Island.

In contrast, kittiwakes were concentrated near shore in all areas, and only a few scattered flocks were observed offshore (in the central and northern parts of the cold-water plume). Kittiwakes in Kachemak Bay foraged mostly along the south shore, and generally within 5-30 km of the colony at Gull Island. Few kittiwakes were observed on the water between the Barren Islands and the Kenai Peninsula, and we assume that Barrens birds must fly at least 25-40 km before finding prey. Other than a small, coastal shoal south of Chisik, there appeared to be no good coastal foraging areas around Chisik Island, and birds foraged 25-50 km offshore in the direction of Kachemak Bay.

Diets of adult murres and kittiwakes reflected food supplies around each colony. Whereas more than 90 species of fish were caught near shore, and 40 species were caught in offshore trawls, communities were overwhelmingly dominated (>95%) by four species: sand lance, herring, pollock and capelin (Chapters 4-6). Diets of adult murres and kittiwakes were dominated by the same species in similar proportions to local abundance except that herring were generally eaten less and capelin eaten more in proportion to their relative abundances (Chapters 9,10). Sand lance dominated murre and kittiwake diets at both Chisik and Gull, while pollock comprised a much larger proportion in diets of birds from the Barrens. Less common fish species with restricted distributions were observed in diets of local birds (e.g., smelts, eulachon, and sandfish at Chisik, cods in Kachemak). The size classes of prey eaten by adults was similar to the size classes caught in trawls and seines. Taken together, the evidence suggests that adult murres and kittiwakes generally eat what is most available to them within foraging range of their colonies.

In contrast to adult diets, chick diets were poor indicators of relative prey availability. Murres in all areas fed chicks a much higher proportion of osmerids (capelin at Barren and Gull islands, smelts at Chisik) than was available in local waters. Sand lance, herring and juvenile salmon (at Chisik) comprised most of the remaining chick diets. Similarly, kittiwakes chick diets were dominated by sand lance, with herring and osmerids comprising most of the remainder. Clearly, adult murres and kittiwakes choose to feed their chicks prey that are oily and rich in calories, a behavior frequently observed in other seabird species and of obvious adaptive value. In general, and despite colony differences in composition, diets of murre and kittiwake chicks were similar among colonies in terms of energetic value because where one prey was scarce (e.g., capelin) it was replaced in chick diets elsewhere by prey of similar energetic value (e.g., sand lance or smelt). Much greater variability was observed in the rates of food delivery than in the energetic content of meals (Chapters 9,10).

The choice of where to feed, and what to feed upon, has direct consequences for all other aspects of seabird breeding biology. For example, kittiwakes from the Barrens must travel at least 25 km before they even begin their search for suitable patches of food along the Kenai Peninsula whereas kittiwakes at Gull Island can often find prey within 1 km of the colony. The effort expended by Barrens' kittiwakes is rewarded, however, because they generally locate high density patches of prey and deliver large (multiple-fish) meals back to their chicks. Chisik Island kittiwakes spend as much time foraging as Barrens' birds, but have difficulty finding any prey patches. Consequently they deliver smaller meals to chicks less frequently, and usually fail to rear chicks to fledging.

In contrast, murres can deliver only one fish at a time to chicks and foraging range imposes an even greater constraint on chick-rearing murres than it does on kittiwakes. Murres from the Barrens may fly only 10-20 km to locate pollock or capelin schools (although they may have to dive >40 m to obtain food), whereas murres from Chisik must fly 30-60 km to exploit sand lance concentrations in northern Kachemak Bay.

Thus, even before the effects of annual variability in prey abundance are felt (see below), these species- and location-specific foraging constraints must affect parental foraging effort and total parental investment in reproduction differently at each colony. These relationships will be examined in detail in future analyses and publications. Preliminary analyses suggest that variation in food abundance is still the overwhelming factor influencing seabird behavior and biology, and we will now consider some gross patterns-- acknowledging that some of the "noise" in these patterns can, in fact, be explained by local constraints on biology.

Response of Seabirds to Variation in Food Supply

The numerical and functional responses of animals to changes in prey density are almost always non-linear and co-existing species that feed on shared prey resources usually respond differently to fluctuations in prey density (Holling 1959; Murdoch and Oaten 1975; Piatt 1990; Piatt and Methven 1992). In this study, we set out to measure and contrast the form of murre and kittiwake responses to variation in forage fish density in lower Cook Inlet. We measured a variety of functional and numerical response parameters of seabirds at three different colonies, while simultaneously measuring the abundance of prey around those colonies.

For convenience, we can expand on the term "functional response"-- which Holling used specifically to describe the relationship between a predator's rate of prey consumption and prey density-- to include all parameters related to foraging and capture of prey, delivery of prey to offspring, aggregation at sea, foraging time budgets, or even maintenance of body condition. For seabirds, functional response parameters are typically measured over time-scales of minutes to days, and spatial scales of meters to 10's of kilometers. In theory, we could have measured functional response parameters on an hourly or daily basis and constructed response curves with measures of prey density collected over the same time periods. Similarly, predator-prey aggregation response curves can be constructed from line transect data collected over hours (e.g., Piatt 1990), and we are analyzing our own survey data for that purpose (Speckman, *in prep*.). In practice, however, it generally required 3 weeks to measure prey density within seabird foraging range of our three study colonies, and logistic constraints and funding limited this effort to once per breeding season. Therefore, our analyses of functional response parameters use data that were collected periodically during the breeding season and then averaged to obtain one mean value to regress against one mean value of prey abundance obtained in each colony area per year.

Similarly, Holling used the term "numerical response" to specifically describe the relationship between a predator's rate of population change and prey density. Again, we can expand this definition in our study of seabirds to include components of population change such as hatching, fledging or breeding success, recruitment, and survival. These parameters are— in the absence of stochastic mortality events (e.g., from severe weather, oil pollution, etc.)— mostly a function of food availability over longer time scales (months and years) and larger spatial scales (100's to 1000's of kilometers). Thus, population change in seabirds reflects day-to-day foraging success integrated over reproductive time-periods and the area over which populations are distributed (Cairns 1987, 1992a,b; Piatt 1987). In practice, we obtained one measure of each numerical response parameter per colony per year, and regressed that against the mean density of forage fish observed around each colony during the early chick-rearing period in each summer.

The Parameters

We measured forage fish abundance within a 45 km range of each colony by conducting systematic hydroacoustic surveys supplemented with mid-water trawls to classify targets

(Chapter 7). These data were reduced to a single estimate of mean biomass per colony per year (Figure 14.1). Trawl and seine data are not used for examining response curves because they are point measures of abundance, and biased (e.g., trawls were conducted only where significant acoustic sign was observed).

We measured a variety of parameters (Figs. 14.2 and 14.3) at colonies for Common Murres (COMU) and Black-legged Kittiwakes (BLKI). Details of methods for data collection are found in Chapters 9 and 10, although additional details are provided here for some parameters.

Functional response parameters that involved behavior included: aggregation of birds at sea (foraging bird density), attendance of adults at nest-sites, chick-feeding rate, and foraging trip duration. Foraging density at sea was calculated by dividing the total number of birds observed on the water on strip transects in each area by the total number of square kilometers surveyed in that area (i.e., we have not binned the data into smaller transect units and calculated mean ± s.d. densities. The question of appropriate scale for grouping data will be addressed in future analyses, Speckman *in prep*.). There were methodological problems with the bird census data collected in 1995 and these results are not included in the present analysis. Attendance data can be expressed two ways. First, we can express attendance data in mean bird-minutes of attendance per nest per hour. For example, if only one member of a nesting pair attends the nest in every hour of the day, then mean attendance is 60 bird-min/hr. If at least one member is present all day, and both members of a pair are present for 15 minutes of every hour all day, then mean attendance would be 75 bird-min/hr. In the latter case, birds would have an extra 4 hours (16*15/60) of discretionary time in a 16 hour day that could be used for other activities. Discretionary time is calculated as the percentage of each hour that both members of a breeding pair are present. Thus, 75 bird-min/hr of attendance equals 25% of each hour with discretionary time (100*(75-60)/60). Foraging trip durations were determined from observations of birds with known departure times that returned with food for chicks, and therefore represent that amount of time taken by the adult to feed itself and gather food for its young.

Functional response parameters that involved physiology included: chick growth rate (BLKI only), fledgling body condition (COMU), age at fledging (COMU), and adult body mass (COMU) or condition (BLKI). For kittiwakes, we could measure growth rates of alpha and beta chicks by taking repeated measures of mass over time at selected nest-sites. We could not measure fledgling body condition in kittiwakes because large chicks come and go from nests and it was never clear when "fledging" had actually occurred. In any case, growth rates are a good proxy for fledgling body condition. For murres, we could not measure growth rates of chicks because it caused too much disturbance at the colony. However, we could capture fledglings (jumplings) on evenings when they jumped to sea from their nest sites, and therefore could obtain a good measure of fledgling body condition. Age at fledging for murres was calculated from plots where we studied breeding phenology. Two data sources were used to assess body condition of adults: adults captured at colonies for stress studies or birds collected at sea for diet studies. In either case, we used only data collected during late July-early August to compare with fish abundance data collected on cruises at that time. For murres, we examined absolute body mass because birds from all three colonies were identical in size and there is no need to calculate a "condition index" of mass/wing-length which corrects for size differences among colonies. For kittiwakes, size did differ slightly among colonies, probably because of differing ratios in collections of males and females (which are dimorphic). Therefore we examined body condition indices (mass/wing-length) in kittiwakes. Finally, we examined physiological levels of stress by measuring blood plasma concentrations of corticosterone (Kitaysky et al. 1999). These data will be analyzed and interpreted in detail under a different EVOSTC funded project (00479).

Numerical response parameters included clutch size (BLKI), laying success (BLKI), hatching success, brood size at fledging (BLKI), fledging success, and overall breeding success. These parameters have self-explanatory names, and details of how they were measured are given in Chapters 9 and 10. Since murres lay only one egg and they do not build nests, clutch size, brood size and laying success were not measured.

Our original ambition was to obtain data on each parameter from each colony in every year (i.e., 15 colony-years of data per parameter) in order to have a robust data set with which to construct response curves (Chapter 1). We generally succeeded in obtaining 12-15 colony-years of data for most parameters (Figs. 14.2, 14.3) , but in some cases we could not do so well because of logistic constraints (e.g., measuring COMU chick age at fledging not feasible at Barrens), because of biological constraints (e.g., kittiwakes rarely produced enough chicks at Chisik to allow measures of adult attendance, chick-feeding rate, foraging trip duration, or chick growth rates), or because it took years to refine our methods (e.g., capture of COMU jumplings at night).

With only one exception, all data collected on all murre and kittiwake parameters are included in the following analyses of response curves and inter-annual variability. In other words, no data have been culled, and if a particular colony-year of data is missing (Figs. 14.2, 14.3) it is because it was not collected for reasons given above. Out of 266 colony-year-species parameter values considered here, only 3 were excluded from analyses. These were behavior data on kittiwake attendance, chick-feeding rate, and foraging trip duration collected at the Barrens in 1997 (open circles in Fig. 14.5). These data were all calculated from the same observational data set, and for some reason all have improbable values; suggesting some systematic bias. We will re-examine these data at a later time, but for now I have simply excluded them in statistical analyses.

Functional and Numerical Responses to Fluctuations in Prey Density

We predicted (Chapter 1) that both murres and kittiwakes would exhibit non-linear functional responses to prey density. Responses can be positive or negative. We did not measure all the parameters initially proposed for study (Table 1.1), and we added a few along the way. In all cases, we tested the strength of relationships using a variety of linear and non-linear models, and selected models that best fit the data (Table 14.1). More than half of all relationships were, in fact, non-linear and prey density explained a significant amount of variation in parameter values. In the following, we will consider predicted and observed relationships on a case by case basis, and discuss some of the implications of observed relationships (or lack thereof).

We are not just interested in the *form* of relationships between parameters and prey abundance. By contrasting results obtained under a variety of conditions, we also gain insight into the range of parameter values likely to be encountered under 'natural' conditions. This offers insight into the biology of murres and kittiwakes-- especially when we also consider species-specific adaptations and constraints for dealing with changes in food abundance.

Behavioral Parameters

First, we consider parameters that require a behavioral response to changes in prey density. These parameters relate to the *acquisition* of food energy from the local environment, i.e., tracking food at sea (flock dispersion), foraging success away from the colony (as indicated by foraging trip duration), success in feeding chicks (measured as daily rate of meal delivery) and foraging effort (indirectly indicated by the re-allocation of discretionary time to foraging). In general, very little is known about how these parameters vary with food supply for any seabird species, and I will explore our findings for murres and kittiwakes in some detail.

Dispersion at sea

The distribution of murre and kittiwake flocks at sea reflected the distribution of prey: 70-80% of the variance in bird density in the 3 study areas was explained by forage fish density using a sigmoidal (logistic) regression model (Figs. 14.4, 14.5; Table 14.1). This form of aggregative behavior was predictable. Most higher vertebrate predators studied to date exhibit thresholds in their choice of foraging patches (Murdoch and Oaten 1975, Piatt and Methven 1992) and seabirds are no exception (Piatt 1990, Mehlum et al. 1999). The simplest explanation for this behavior is that predators seek to maximize their rate of energy intake, and therefore spend little time in areas where prey densities limit capture rate (Hassell and May 1974). More detailed analyses of aggregation behavior as a function of spatial scale are being conducted (Speckman, *in prep*).

Inflection at the threshold was sharp for murres, resulting in more of a step-function than a sigmoidal curve. The steepness of the response around the threshold explains why we observed a dramatic decline in bird densities in Kachemak Bay when forage fish densities dropped to around threshold values in 1999 (Fig. 14.1). Both murres and kittiwakes were conspicuously scarce in traditional feeding areas in 1999 (Figs. 8.1 and 8 .2).

The sigmoidal nature of the aggregation response reveals that murres and kittiwakes *do* have definable limits in their ability to locate and capture prey in local waters. This foraging constraint has an impact on all other parameters of seabird ecology. If prey densities within the 45 km area we surveyed around each colony fall below threshold levels, then birds must range further from colonies— if possible— to find food. Otherwise, they fail to adequately provision chicks or themselves, with predictable consequences for reproduction.

Foraging trip duration

As predicted, foraging trip duration (FTD) for both murres and kittiwakes was a non-linear, negative function of forage fish density (Fig. 14.4, 14.5). As discussed above (Seabird Foraging Ecology), the functional relationship is confounded by the fact that good foraging grounds are found at different distances away from each colony, and so foraging trip durations (FTD's) are not *just* a function of food abundance-- particularly for kittiwakes. Nonetheless, variation in food density accounted for about 50-60% of variation in FTD's using a negative exponential model (Table 14.1).

Under a range of moderate to high food densities, murres were absent for about 2 hr per foraging trip whereas kittiwakes were absent about 3 - 3.5 hr per trip. As prey density fell, FTD's increased exponentially with murres foraging 3-4 hrs and kittiwakes foraging 5-6 hrs [note these are averages, some individuals foraged much longer]. Regression of data measured at Gull and Chisik, which are less confounded by travel to distant foraging grounds, suggests that-- all else being equal-- kittiwakes spend about 1.4 hr more than murres on foraging trips ($r^2=0.65$, $p=0.05$, $FTD_{BLKI} = 0.97*FTD_{COMU} + 82$). Similar values and inter-specific differences in FTD's were observed during years of 'good' and 'poor' food supply at Sumburgh Head, Shetland, where murre foraging trips averaged 1.3 and 3 hours, respectively (Monaghan et al. 1994), while kittiwake foraging trips averaged 2.3 and 6.2 hr, respectively (Hamer et al. 1993). Average murre (3.6 hr) and kittiwake (5.0 hr) foraging times at Bluff, Alaska, also differed by 1.4 hr (Watanuki et al. 1992). Average Common Murre foraging trips at the Gannet Islands, Labrador were 1.3 and 1.6 hr in 1982 and 1983, respectively (Birkhead and Nettleship 1987).

These results suggest that kittiwakes are less efficient than murres in acquiring food. Murres must acquire more food than kittiwakes to sustain themselves each day because of their differences in body size (average in Cook Inlet ca. 1040 g vs. 405 g, respectively), costs of flight (wing loading: 1.86 g/cm^2 vs. 0.39 g/cm^2; Gabrielsen 1994) and foraging method (diving vs. surface-feeding). From measures of field metabolic rates (FMR) during chick-rearing of Common Murres and Black-legged Kittiwakes (Gabrielsen 1994), and assuming an 87% assimilation efficiency (Romano 2000), we can calculate that murres (2.14 kJ/d/g FMR) and kittwakes (2.03 kJ/d/g FMR) feeding on sand lance (<100 mm, ca. 5.0 kJ/g wet; van Pelt et al. 1997, Anthony et al. 2000) would need to eat 512 g and 189 g, respectively, of fish per day (or 49% and 47% or their body masses, respectively). [Note that respective values for juvenile pollock (3.5 kJ/g, 74% assimilation) would be 859 and 317 g/day, or 83% and 78% of body mass].

In addition to food for self-maintenance, and on average for the chick-rearing period, murres need to acquire about 200 kJ/d of extra food to feed chicks (Gabrielsen 1994) whereas kittiwakes need to collect about 420 kJ/d extra (Gabrielsen 1994). This represents an increase above self-maintenance of 8% and 44%, respectively. Thus, in order to rear one chick to fledging, including self-maintenance costs, murres and kittiwakes would have to gather 552 and 273 g of sand lance daily, or 53% and 67% of adult body mass, respectively. [Respective values for juvenile pollock would be 789 and 390 g/d, or 76% and 96% body mass]. For kittiwakes rearing two chicks, the cost of self maintenance goes up (2.29 kJ/d/g; Gabrielsen 1994) and chick demands double (840 kJ/d) so that adults would need to acquire 381 g of sand lance per day, or 94% of body mass daily. [Respective values for pollock: 544 g/d, 134% body mass].

Thus, parent murres need to acquire about twice as much food each day as parent kittiwakes and they typically acquire what they need in about half the time. This difference in efficiency probably arises mostly from the fact that kittiwakes are restricted to feeding only on schools of fish found within ca. 0.5m of the sea surface (Baird 1994), whereas murres can dive to depths of ca. 200m (Piatt and Nettleship 1985) and can therefore exploit virtually the entire water column of lower Cook Inlet. Even if most of the exploitable fish biomass is above 50 m (Chapters 4,7), murres still have access to 100 times more foraging habitat than kittiwakes at any distance from a colony. Furthermore, we observed that surface-shoaling behavior of fish occurred mostly in coastal waters, and so kittiwake foraging habitat was more restricted than murre habitat in the horizontal dimension as well. Finally, murres (ca. 80 km/hr) can fly faster than kittiwakes (ca. 60 km/hr) and can therefore range further in a given time period. This may be particularly valuable when daylight is limiting (below). Because potential foraging area increases as a function of the distance from colony *squared*, murres can access nearly twice (1.8x) the area kittiwakes can in the same amount of flight time.

Chick-feeding rate

Because FTD's increase exponentially as prey densities fall, the ability of murres and kittiwakes to feed their chicks diminishes rapidly at low prey densities owing to rapidly increasing energy costs and time constraints. As one would expect, the cost of foraging goes up with increased time spent foraging (Gabrielsen 1994). A Common Murre increases food demand about 8.5% more above resting needs for every hour it spends at sea (Gabrielsen 1994). Perhaps more importantly, the amount of *time* available for foraging is limited-- and this appears to be the critical factor limiting chick provisioning at low prey densities. For example, peak food demands for adult kittiwakes in Cook Inlet extend from about 10 July to 15 August (Chapter 10). In mid-July, there are little more than 18 hours of daylight and by mid-August there are less than 16 hours from sunrise to sunset. Since kittiwakes feed diurnally, they are constrained by these time windows in how often they can feed chicks.

While chick feeding rates (CFR's) are ultimately limited by daylight, kittiwakes can adjust the quality and quantity of food delivered in each meal to chicks. In general, the quality (energy density) of meals fed to chicks varied little (mean= 4.7 kJ/g; C.V.=8.5%) because adults apparently went out of their way to feed oily forage fish to chicks at all colonies (Chapter 10; Roby et al., unpubl. data). A more important source of variability was in the mass of meals delivered (C.V. 31.6%). Because they can capture, carry and then regurgitate multiple prey to chicks, kittiwakes can vary the size of meal loads delivered. It is difficult, however, to assess the true mass of chick meals delivered by adults because of uncertainties in the collection of regurgitated samples (e.g., was it full or partial meal because regurgitation was incomplete, or because adult partially fed chick before capture?). These data need further detailed analysis. What we can say for now is that the largest meal delivered by an individual was 62 g, and that average meals in years with good food supplies were about 30 g (Chapter 10), which if comprised all of sand lance (<100 mm), would be about 150 kJ/meal.

As predicted (Chapter 1), kittiwakes exhibited a sigmoidal response in chick feeding rate (CFR) to prey density (Fig. 14.5), and the asymptotic rate of chick meal delivery estimated by logistic regression was 0.21 meals/nest/hr (±0.02, $p<0.001$). This means that over a range of moderate to high prey densities, and with foraging trips of about 3.3 hr (200 min, Fig. 14.5), average adults delivered 3.8 meals per 18-hr day. Baird (1994) reported the same feeding rate for kittiwakes in the Gulf of Alaska (mean 3.8; range 2.4-6.5 meals/d). If 'good' meals containing 150 kJ/meal were delivered, then nests received 570 kJ/d, i.e., enough to sustain growth of about 1.35 chicks (which was, in fact, the asymptotic brood size at fledging, Fig. 14.5).

Below threshold levels of prey abundance (estimated by regression at 0.0135 g/m^3, $p<0.001$), CFR's declined rapidly to as little as 2.0 meals/d (0.11 meals/nest/hr/18h). Note that we have relatively few measures of CFR below threshold prey density because kittiwake chicks failed to survive and we could not measure behavioral parameters in those cases. CFR was correlated ($r^2=0.40$, $p=0.037$) with foraging trip duration and we can calculate from regression ($CFR= -0.0076*FTD + 5.34$) that in order to deliver 3.0 meals/d, FTD's must not exceed 308 min/trip in an 18 hr day; or 257 min/trip during late chick-rearing (16 hr day). Even then, those 3 meals would need to weigh about 30 g (150 kJ) each to achieve maximal growth rates of one chick.

Thus, 5 hr (300 min) is the approximate critical FTD above which kittiwakes begin to have problems maintaining one chick in lower Cook Inlet, and it corresponds to a maximum CFR of about 3 meals/d (0.17 meals/nest/hr/18h, Fig. 14.5). Adults would be hard-pressed to deliver enough food for chicks in 2 meals/d, and so it is not surprising that 3 meals/d is a critical level of effort required. Suryan et al. (2000a) reached the same conclusion for kittiwakes in Prince William Sound: "it appears that an average distance over 45 km and duration > 5 hrs is approaching the limit that adults can maintain while successfully provisioning young". Similarly, Hamer et al. (1993) concluded that foraging trips of 2-3 hrs recorded at various colonies in northeast England and at Sumburgh Head in 1991 represented "the norm for kittiwakes rearing chicks in conditions of good food supply" whereas an FTD of 6.2 h observed at Sumburgh Head (about same latitude as Cook Inlet) in 1990 led to complete breeding failure in kittiwakes. The critical FTD (5 hr) and CFR (3 meals/d) values observed in our study would, of course, be different at higher latitudes where kittiwakes have much longer day-lengths in which to forage (e.g., Svalbard, Gabrielson 1994).

In contrast to kittiwakes and against predictions (Chapter 1), murre CFR's were not a sigmoidal function of prey density— possibly because foraging effort at low prey density was buffered by re-allocation of discretionary time (see below). For murres, CFR declined slightly and linearly with decreasing prey density (Fig. 14.4). Because the peak of murre chick-rearing in Cook Inlet occurs between about 10-30 August, daylight hours available for foraging ranged from 14-16 hr during chick-rearing. Thus, the average CFR of 0.26 meals/nest/hr translates into an average daily delivery rate of about 4.1 meals/d (range 3.0-5.3) in a 16-hr day.

Since murres deliver only one fish at a time to chicks, the issue of meal size is less complicated than for kittiwakes. However, murres did select energy-rich fish (mostly osmerids, sand lance, herring; Chapter 9) and delivered larger fish (often >100 mm) than they ate themselves (generally <100 mm). It was very difficult (and disturbing to birds) to collect fish delivered by adults, so we have very limited data on fish size other than visual estimates of size compared to bill length (e.g., Uttley et al. 1994). For now, we estimate that the mean size of fish delivered was about 6.4 g, and therefore murres were fed an average of about 26 g/d (range 19-34). Even if we assume that chicks were fed fish with higher energy content (e.g., 5.7 kJ/g for sand lance >100 mm; Anthony et al. 2000), we can calculate that chicks received only 148 kJ/d, which is less than the average required intake estimated from metabolic study (200 kJ/d, Gabrielsen 1994) and much less than estimated from other field studies (Barrett et al. 1997). However, higher estimates of energy delivery rates are often the result of higher-- and perhaps faulty (van Pelt et al. 1997)-- estimates of fish energy density rather than higher rates of meal delivery. In any case, our data and these issues need further consideration before reaching any final conclusions.

One certainty, however, is that our observed rates of meal delivery and resulting mass of fledgling chicks are within normal ranges observed in other studies. For example, in a 10-yr study of food consumption by Common Murre chicks at the Isle of May, Scotland (56.2° N), the average daily feeding frequency was 4.1 (±0.2 s.e.) meals/d (Harris and Wanless 1995). As in Cook Inlet, meals were comprised mostly of energy-rich species (sand lance *Ammodytes marinus*, herring *Clupea harengus*, sprat *Sprattus sprattus*). The 10-yr average daily food delivery during chick-rearing was estimated at 30 (±2 s.e.) g/d. The difference in daily food delivery between this study and ours (30 vs 26 g/d, respectively) is entirely due to the difference in estimate of average fish mass delivered (7.7g vs. 6.4 g, respectively). The difference may be real, however, since the mass of chicks at fledging age was also higher at the Isle of May (263 ±3.8g) than in Cook Inlet (227 ±6.5 g).

Similar murre CFR's have been observed elsewhere. Burger and Piatt (1990) reported an average CFR of 4.3 meals/d (range 3.7-4.9) during 4 years of study at Witless Bay, Newfoundland. In that study, total food intake averaged 57 g/d (range 45-66) owing to the much larger size of fish delivered (mean=13.3 g). Uttley et al. (1994) reported CFR's of 3.0 meals/d in a 'bad' food year at Sumburgh Head and 6.2 meals/d in a 'good' food year. Watanuki et al. (1992) estimated a CFR of 3.7 meals/d (19.5 hr day) for murres at Bluff. At the Gannett Islands, murre CFR's were 4.9 and 3.7 meals/d in 1982 and 1983, with corresponding chick departure weights of 231 and 246 g, respectively.

Adult attendance and discretionary time

Differences in size and quality of meals notwithstanding, self-respecting murre and kittiwake parents everywhere try to deliver about 4 meals/d to chicks. Murres forage only during the day and one adult of the pair almost always attends the nest-site to incubate the egg or guard the chick against predators (Cairns et al. 1987, Burger and Piatt 1990). Therefore a total of 14-16 h are available each day for off-duty murres to forage or engage in other activities. For murres under moderate to good food conditions, where foraging trips usually require a minimum of 2 h (above), this means that at least 8 h/d is invested in foraging; leaving 6-8 h for other activities. About 2-4 h of each day, adults are absent from nest sites, but not foraging for chicks (FTD's and CFR's calculated only from absences resulting in a meal delivery). We assume that during these absences, adults engage in self-maintenance activities, socialize or obtain meals for themselves (Cairns et al. 1987, Uttley et al. 1994). For the remaining hours of each day (ca. 4 h during incubation, 2.5 h during chick-rearing) off-duty murres can be found "loafing" at the nest site, using this "discretionary" time to attend the site with its mate (Fig. 14.4).

This overlap in time among mates attending the nest-site offers a time buffer that can be re-directed towards foraging when food supplies are scarce (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Zador and Piatt 1999). Discretionary co-attendance time has varied from about 2.4% to 40% of daylight hours among studies to date (Zador and Piatt 1999). Our study indicates that the relationship between discretionary time and food density is sigmoidal (Fig. 14.4, Table 14.1). During moderate to good food conditions in Cook Inlet, regression analysis suggested ($p<0.001$) asymptotic attendance at 76 bird-min/h during incubation and 71 bird-min/h during chick-rearing (Fig. 14.4). This corresponds to co-attendance of adults during 27% of daylight hours during incubation, and 18% of daylight hours during chick-rearing. Below threshold food densities (0.013 g/m^3, $p<0.001$), murres rapidly used up all their discretionary time on foraging trips of exponentially increasing duration (Fig. 14.4). It appears that discretionary time buffers were depleted during chick-rearing when foraging trips exceeded about 170 min.

As for murres, kittiwakes forage during the day and one adult of the pair usually attends the nest-site to incubate the egg or guard the chick against predators (Baird 1994). In contrast to murres, adult kittiwakes appear to have little or no discretionary time at high food densities that can be re-allocated to foraging when food is scarce (Fig. 14.5). During chick-rearing, some 16-18 h are available each day for activities of the off-duty adult. Under good food conditions, chick foraging trips usually required 3.3 h (above), meaning that at least 13 h/d were devoted to foraging trips that resulted in a chick meal; leaving at most 3-6 h for other activities. As in murres (above), adult kittiwakes may spend 2-4 h absent from nest sites for self-feeding or maintenance-- leaving just a little time for "loafing" at the nest-site. When foraging trips were more than 4 or 5 h-- often the case in Cook Inlet (Fig. 14.3)-- kittiwakes had no discretionary time at all. Indeed, adults were forced to abandon the chick altogether, leaving it vulnerable to predation (Fig. 14.5).

Roberts and Hatch (1993) noted similar behavior of kittiwakes at a food-deprived colony on Middleton Island. Adults co-attended nests less than 1% of the time, and rarely left nests unattended altogether during incubation and early chick-rearing; less than 10% of the time overall. The duration of foraging trips initiated when one adult remained on the nest (mean 3.8 h) versus when no adult remained on the nest (mean 1.7 h) strongly suggests that adult kittiwakes "strive to maintain continuous attendance with their chicks" even in the face of serious food shortages (Roberts and Hatch 1993). Similarly, at Sumburgh Head (Hamer et al. 1993), nests were almost never left unattended in 1991 (good food year, productivity 0.98 chicks/nest) whereas they were left unattended on 17% of observations during chick-rearing in 1990 (bad food year, productivity 0.0 chicks/nest).

Biological Parameters

In contrast to behavioral parameters (above)-- which all relate to the acquisition of energy-- the biological parameters that we studied all relate to the *disposition* of food energy obtained from foraging. In other words, physiological condition (chick growth, adult body condition) and reproductive output (laying, hatching and fledging success; clutch and brood size) exhibit a range of values that, for the most part, simply reflect how much food has been acquired. For this reason, relationships between biological parameters and food supply are straightforward: As long as some adequate (threshold) amount of food/energy is obtained, then metabolic demands for maintenance and growth are met, and reproduction is not limited by food. This has recently been demonstrated in a variety of experimental situations in the laboratory (Kitaysky et al. 1999, 2001; Romano 2000) and field (Jacobsen et al. 1995, Erikstad et al. 1997, Golet et al. 1998, Golet and Irons 1999, Gill 1999, Kitaysky et al. 1998, Kitaysky 1999, Harding et al. 2001).

However, the exact form of relationships between biological parameters and food supply in the wild has never been demonstrated. Further, we want to know how, or if, murres and kittiwakes can adjust their physiology or biology to compensate for low rates of food acquisition.

Chick growth rates

We observed few extreme low growth rates for kittiwake chicks in this study (Fig. 14.5). As food became scarce, adults abandoned nest-sites for extended periods (Fig. 14.5) and chicks were eaten by predators or fell out of their nests (as observed elsewhere; Hamer 1993, Roberts and Hatch 1993). Thus, starving or emaciated chicks quickly disappeared from samples, leaving us with no chicks to measure or only chicks with successful parents-- a bias also encountered in penguin studies (Williams and Croxall 1990). This was particularly true for *beta* chicks, which are often expelled by *alpha* chicks during early chick-rearing if food is scarce (Roberts and Hatch 1993). Consequently, we found no relationship between *beta* chick growth and food supply (Table 14.1).

With special efforts, we obtained repeated measures of some poorly-fed *alpha/singleton* chicks on Chisik Island in 1996 (11.1 g/d) and 1997 (14.4 g/d), allowing us to demonstrate a sigmoidal relationship between *alpha/singleton* chick growth rate and food supply (Fig. 14.5). Outside the extreme low values from Chisik Island, however, average *alpha/singleton* growth rates in all colony-years ranged between 14.5 and 19.8 g/d. Even when we include the extreme data, growth rates were not too variable (CV only 12.6%). The asymptotic rate of growth was 16.8 ±0.04 (s.e.) g/d ($p< 0.001$). Rates of kittiwake chick growth below the inflection point observed in this study (ca. 14g/d, Fig. 14.5) are unusual in Alaska (Murphy et al. 1991, Baird 1994, Suryan et al. 2000b) and at colonies in the Atlantic (Barrett and Runde 1980, Galbraith 1983, Barrett 1996)— suggesting that bias in sampling kittiwake chicks for growth measurements is a problem everywhere. Growth rates of less than 14 g/d were recorded for both *alpha* and *beta* chicks at the Middleton Tower colony, but only because predation was eliminated by the experimental set-up there (Gill 1999).

After initial attempts, we abandoned efforts to measure absolute murre chick growth rates because of the disturbance caused by us when capturing chicks in murre nesting areas. In many years we were able to capture murre chicks after they had fledged from nest-sites (either by capturing them on beaches as they made their way to the water, or on the water using small boats and dip-nets). However, murre chicks may fledge at a younger age in years of good food supply (Table 14.1; Uttley et al. 1994). By dividing chick body mass by wing length, it is possible to obtain an index of growth (i.e., body condition at fledging, Fig. 14.4) that is independent of age in larger chicks.

As for kittiwake chicks, the relationship between murre chick growth and food supply was sigmoidal, with an asymptotic ($p<0.001$) body condition index at 3.18 ±0.029 s.e. g/mm. Asymptotic indices were associated with absolute masses >209 g. The overall average chick body mass at fledging was 229 g (range of annual means 199-253 g). Chick body condition indices less than 3.0 were observed at Chisik only in 1998 (mass 199 g) and 1999 (mass 206 g); the colony-years of lowest food supply observed in this study. Over all colony-years (n=10) for which we have data, murre fledgling body condition was remarkably consistent (CV only 4.2%).

Based on fledgling masses and chick fledging age from study plots (average 20.2 d), we can estimate growth rates of about 9.7 to 13.2 g/d for murre chicks. Because growth continues throughout the 19-21 days in the nest (Gaston 1985), these rates are not much different than "maximum growth rates" of 8.6 to 15.7 g/d reported historically (Gaston 1985) for common murres. At the Isle of May, where murres appeared to be unlimited by food supply, Harris and Wanless (1995) reported a mean weight of chicks at day 21 (modal fledging age) of 263 ±3.8 g, and annual mean mass of 'large' chicks (immediately pre-fledging) ranged from 245 to 265 g (Harris and Wanless 1988). Mass of 'large' chicks (wing lengths > 60mm) at the Gannett Islands, Labrador, ranged from 231-246 g in the 1980's (Birkhead and Nettleship 1987) and from 223-233 g in the 1990's (Bryant et al. 1999). Lower growth rates (7-8 g/d) and similar final fledging masses (230-270 g) were observed for common and thick-billed murre chicks on Hornøya, Norway (Barrett et al. 1997). At Sumburgh Head, the mass of 'large' (wing length = 60 mm) chicks estimated from regression would be 256 g in the 'good' food year, and 212 g in the 'bad' food year (Uttley et al. 1994).

As for kittiwakes, there are few examples of extreme low growth rates in common murres. In contrast to the situation with kittiwakes, however, predation of unattended chicks is not a source of bias in assessing murre chick growth. Apparently, murres in Cook Inlet (and at Sumburgh Head, Uttley et al. 1994) maintained high chick growth rates in the face of declining food supplies by re-allocating discretionary time to foraging for chick meals. Only in the most extreme conditions (1998/99 at Chisik) did murre chicks appear to suffer from food deprivation. Similarly, common murre chick fledglings weighed only 204 g at Middleton Island (Hatch 1983), a site of persistent kittiwake breeding failure and presumably very poor food supplies (Gill 1999). The only other location where fledgling body masses of less than 210 g have been reported is at Vedøy, Norway (165 g, Røv et al. 1984; as reported in Harris and Wanless 1988). This was associated with an extreme case of long-term breeding failure of murre and puffin populations owing to a collapse of local herring stocks during the late 1970's (Anker-Nilssen 1997). Thus, it appears that extreme low growth rates in common murres are rarely observed in the wild because murres can buffer against declining food supplies over a wide range of conditions.

In summary, growth in both murre and kittiwake chicks is related to food density in a positive, sigmoidal fashion. This was predictable (Table 1.1). As long as chicks acquire adequate rations of food, they can grow at asymptotic rates. Excess rations are not assimilated by chicks (Romano 2000), and so growth rates are independent of food supply above the threshold (Fig. 14.5). Chick growth rates below threshold values indicate difficulty in acquiring food. However, low chick growth rate data are rarely recorded at kittiwake colonies where predation is common, nor at common murre colonies because adults can buffer chick feeding rates against moderate declines in food supply.

These results for kittiwakes and common murres stand in contrast to other seabird species for which reduced chick growth rates are commonly observed. For example, thick-billed murres-- which live mostly in Arctic habitats and face more extreme feeding conditions than common murres-- exhibit at least 2-fold geographic and temporal variability in fledgling mass (range 121-250 g; mean 181 ±39.4 g; CV=22%; Gaston 1985). Similarly, tufted puffins-- whose young are protected in burrows from predators-- exhibit 3-fold variability in chick growth rates (range 6.8-21.4 g/d; mean 15.2 ±4.5 g/d; CV=21%; Piatt et al. 1997).

Adult body condition

We found no relationship between adult body condition and food density for either murres or kittiwakes. This was true whether we used body condition data from stress studies (circles, Figs. 14.4, 14.5) or from collections for diet studies (squares, Figs. 14.4, 14.5) or combined data (Table 14.1, Figs. 14.4 and 14.5). Furthermore, variability in adult body condition was extremely low for both kittiwakes (CV = 7.5%) and murres (CV = 3.8%).

These results were not expected. We predicted a positive, non-linear relationship between adult body condition and food supply (Table 1.1) and it was reasonable to assume that body condition would be sensitive to variations in food supply (Monaghan et al. 1989, Hamer et al. 1991). Indeed, a variety of experimental studies-- where adult foraging effort is manipulated by increasing or decreasing clutch size of nesting seabirds-- have shown that adult body condition can be affected negatively by increasing workload (Johnsen et al. 1994, Jacobsen et al. 1995, Golet and Irons 1999).

Field studies of seabirds subjected to natural variation in food supply, however, rarely reveal any large effects on adult body condition. Indeed, for those single-colony studies where seasonal variability has been accounted for in sampling, variability in adult body condition among years was exceedingly low for great skuas *Catharacta skua* (CV = 0.9%, n=4 yr, Hamer et al. 1991), Arctic terns *Sterna paradisaea* (CV = 6.6%, n=4 yr, Suddaby and Ratcliffe 1997), yellow-nosed albatross *Diomedea chlororhynchos* (CV = 4.0%, n=4 yr, Weimerskirch et al. 2001), thick-billed murres (CV = 1.1%, n=5 yr, Bryant et al. 1999), common murres (CV = 0.6%, n=5 yr, Harris and Wanless 1988) and black-legged kittiwakes (CV = 4.8%, n=8 yr, Williams et al. 1998). In the case of the skuas, thick-billed murres and common murres, variability in body condition was so low as to baffle investigators, given that other measures indicated some marked changes in food supply had occurred. In the case of the terns, albatross and in a two year study of kittiwakes (Hamer et al. 1993), annual variation in adult body condition was often driven by one exceptional year, and otherwise body condition was not well correlated with food supply or indirect measures of food availability.

Taken together with our results, this suggests that body condition is strongly buffered against fluctuations in prey abundance. The reason for this seems clear: Survival of adults during the subsequent winter is correlated with adult body condition at the end of the breeding season (Jacobsen et al. 1995, Hamer et al. 1991, Golet et al. 1998) and adults should therefore be conservative in maintaining their own body condition. This behavior is to be expected in long-lived species which have the opportunity to breed over multiple years, and supports the basic prediction of life-history theory that parents should balance investment in their offspring against their own chance to reproduce in the future (Stearns 1992). Most breeding seabirds appear to maintain a safety margin above some threshold body mass at which they abandon breeding attempts altogether (Weimerskirch et al. 2001). We observed murres and kittiwakes near their limits in foraging ability, and near (murre) to total (kittiwake) failures in their ability to fledge chicks, but we never observed total abandonment of breeding effort. Collecting data on body condition of birds at or below thresholds of body condition may be difficult or impossible since these individuals would probably not remain at a colony to be captured.

Clutch size and laying success

Black-legged kittiwakes can lay up to three eggs whereas murres can lay only one egg. Kittiwakes build well-developed nests and it is relatively easy to assess what proportion of the population actually lay eggs after building nests (= laying success). In contrast, murres build no nest, and it is difficult to assess which birds attending crowded nesting areas are potential breeders. Thus, we have good data on variation in clutch size and laying success in kittiwakes, but none for murres.

Clutch size and laying success in kittiwakes were independent of food supply (Fig. 14.5, Table 14.1). On average, 69% of pairs that attempted to breed eventually laid eggs. For those that laid, the average clutch size was 1.49 ±0.18 s.d. eggs/nest. Laying success (CV = 28.7%) was more variable than clutch size (CV = 12.3%). There are at least two explanations for the lack of correspondence between these biological parameters and food supply. First, there was a gap in time between measurements: clutch size and laying success were measured in June while food supply was measured in late July - early August. We have no *a priori* reason to expect food supply (and secondarily kittiwake egg-production) in June to correlate with food supply in August, although we have weak evidence that this may be true. For example, the seine catch per effort of adult sand lance in Kachemak Bay tended (r^2=0.51, ns) to be high in August if it was high in June.

Alternatively, kittiwakes may have a programmed approach to egg-laying that is largely independent of food supply except under extreme conditions, i.e., when food supplies and nutrient reserves are so low as to preclude egg formation. Indeed, evidence from a variety of seabirds suggests that clutch size is maximized and that regulation of breeding effort occurs later by brood reduction or nest desertion (Sydeman et al. 1991, Monaghan et al. 1992, Hamer et al. 1993, Philips et al. 1996, Suddaby and Ratcliffe 1997). This may explain why, despite high variability in overall productivity among areas, kittiwake clutch size and laying success in Cook Inlet were similar to those observed during the same years (1995-1999) at several colonies in Prince William Sound (Suryan et al. 2000b; n= 15 colony-years, laying success = 78% [CV = 24.3%], mean clutch size = 1.66 ±0.19 s.d. eggs/nest [CV = 11.7%]); and throughout the Gulf of Alaska (Hatch 1990; n= 77 colony-years, laying success = 65% [CV = 33.7%]; for n = 91 colony-years, clutch size = 1.49 ± 0.23 s.d. [CV = 17.4%]).

Hatching, fledging and breeding success

Once the egg(s) have been laid, murres and kittiwakes are committed to a breeding effort. Incubation and guarding of the egg or chick is essential for survival of the offspring, and requires the presence of at least one adult. Not surprisingly, nest-attendance by at least one adult is among the least variable parameters for both murres (CV=0%) and kittiwakes (CV=7%) (Table 14.1). As predicted, hatching success and then fledging success in kittwakes were correlated with food supply (r^2=0.53 and 0.89, respectively) in a sigmoidal fashion (Fig. 14.5). Fledging success had the strongest relationship, presumably because is it was measured closer to the time period in which prey were sampled.

Despite the weak correlation between food supply and earlier events (laying, hatching), overall breeding success in kittiwakes was-- as predicted-- strongly correlated with food supply in sigmoidal fashion (Fig. 14.5, Table 14.1). Above the threshold prey density of 0.015 g/m^3, the upper asymptotic chick production was 0.46 chicks/pair. Below the threshold, the lower asymptotic chick production was 0.015 chicks/pair. Similarly, the best model to explain brood size at fledging was sigmoidal (Fig. 14.5), and suggests that as long as food supplies remained above threshold, kittiwakes could fledge 1.3 chicks/pair on average.

Contrary to predictions (Table 1.1), neither hatching, fledging nor breeding success in common murres was correlated with food supply (Fig. 14.4). Murres appeared to have trouble in only 2 years. In 1998 at Chisik Island and in 1999 at Gull Island, murres arrived at colonies with relatively high levels of corticosteroid stress hormones in their blood plasma (Kitaysky et al., in prep.) which suggests that they were stressed by lack of food even before they began to breed (Piatt et al. 1999, Kitaysky et al. 1999, 2000). On these two occasions, murres exhibited (Fig. 14.4) much lower than usual hatching success (52% vs. 70-90%), fledging success (<45% vs 64-92%), and consequently low overall breeding success (<30% vs. 53-81%).

In other years, murres were apparently not limited by food during laying or hatching. Murres were able to compensate for extremely low food abundance during both incubation and chick-rearing by increasing the amount of discretionary time devoted to foraging (Fig. 14.4, see above "Behavioral Parameters"). In effect, murres were able to buffer their breeding success against a wide range of variation in prey abundance by foraging longer and farther from colonies during lean food years (Burger and Piatt 1990, Zador and Piatt 1999). In fact, it appears (Chapter 8) that some murres foraged beyond the 45 km zone around each colony that we surveyed to assess prey abundance, and this may have confounded our attempt to correlate breeding success with "local" food supply. In any case (Table 14.1), murre fledging success (CV = 28%) and breeding success (CV = 29%) were about 3 times less variable than kittiwake fledging success (CV = 81%) and breeding success (CV = 87%) because murres were able to behaviorally compensate for low food densities.

Obviously, murre breeding success cannot be *completely* independent of food supply. We may have failed to demonstrate a functional breeding response to variable food supply because the spatial scale of our sampling was too small, and because within the spatial range that murres operate, food supplies were simply never so low as to cause complete breeding failure. Functional response curves (above) for aggregation, foraging trip duration, and discretionary attendance all clearly indicate that murres-- like kittiwakes-- have a foraging threshold at about 0.013 g/m^3 of fish biomass. The difference between murres and kittiwakes is that under the same environmental circumstances, murres can exploit nearly 100 times more habitat than kittiwakes at the same distance from colonies, they can search nearly twice as much surface area than kittiwakes in the same time, and they have more time to forage (see "Foraging trip duration", above).

Consequently, while we frequently observed kittiwake breeding failures in Cook Inlet, we never observed total breeding failure in murres. Presumably, prey abundance was never so low throughout the entire study area that murres could not compensate to some degree. Perhaps if we could collect more data on murres during extremely poor food years (in the lower 10% of what we observed in our study), and at larger spatial scales, we could better resolve breeding response curves. With the data we have, however, we can assume that the breeding response of murres is sigmoidal (or a step-function) with a very low threshold for breeding failure. At the least, we can say that in the absence of disturbance (by humans, predation), breeding success of less than 0.4 chicks/pair in murres indicates limitation by food supply.

Our results are consistent with other studies. At Sumburgh Head, both murres (Uttley et al. 1994) and kittiwakes (Hamer et al. 1993) were examined simultaneously during a 'good' food year (1991) and a 'poor' food year (1990) that, by many measures, were similar to our best years at Gull Island and our worst years at Chisik Island, respectively. Murres exhibited high hatching success (76%, 72%) and fledging success (78%, 98%) in

1990 and 1991, respectively, and there was no significant difference in overall breeding success among years (59%, 70%; respectively). While kittiwakes showed little difference in hatching success (81%, 80%) between years, fledging success (0%, 85%) and overall breeding success (0%, 68%) were extremely different in 1990 and 1991, respectively.

No other simultaneous studies of murres, kittiwakes and food supply have been conducted. However, we can examine variability in breeding success of murres and kittiwakes from long-term (1975-1999) data collected throughout Alaska (Gulf of Alaska, Aleutians, Bering and Chukchi Seas) in a variety of monitoring and research programs (Hatch 1993, Dragoo et al. 2000). From these data (Fig. 14.6, Table 14.2), which include an extreme-- but natural-- range of environmental conditions for breeding (see Hatch 1993), we find that common murres (n=14 colonies, n=99 colony-years) have rarely had complete breeding failure (0 chicks/pair on only 4% of occasions), and on only 26% of occasions was breeding success indicative of limiting food supply (i.e., below 0.40 chicks/pair; see above). Remarkably, common murres were successful (>0.40 chicks/pair) about three-quarters of the time (Fig. 14.6) and variability in breeding success was quite low (CV = 40%) and similar to that observed in Cook Inlet (CV = 28%). In contrast, kittiwakes (n=17 colonies, n=235 colony-years) had complete failures (0 chicks/pair) 18% percent of the time, and showed signs of food limitation (breeding success < 0.46 chicks/pair; above) 77% of the time. On only 23% of occasions did kittiwakes appear to be un-restricted by food supply. Kittiwakes showed high levels of variability in breeding success in Cook Inlet (CV = 87%) and Alaska (CV = 110%).

A similar contrast in murre and kittiwake breeding success has been noted elsewhere (Table 14.2). Common murres observed during 54 colony-years at a variety of colonies in the North Atlantic (Birkhead 1976, Hedgren 1980, Birkhead and Nettleship 1987, Harris and Wanless 1988, unpubl. data; Burger and Piatt 1990, Bryant et al. 1999; J. Piatt, unpubl. data) averaged 0.75 ± 0.09 s.d. chicks/pair. Despite the span of years (1963-2001) and colonies (n=11), variability in breeding success was low (CV = 12%), with only one occasion where breeding success was less than 0.4 chicks/pair (0.26 chicks/pair, remaining values ranged from 0.52-0.88 chicks/pair). At the Isle of May, murres have never failed in 21 years of study (range 0.63 to 0.81 chicks/pair; Harris and Wanless, unpubl. data). Likewise, in 29 years of study at the Farallon Islands, California, common murres failed (<0.4 chicks/pair) only 3 times, all in association with strong ENSO events (Sydeman 2001, PRBO unpubl. data). Otherwise, breeding success ranged between 0.61 and 0.91 chicks/pair.

Kittiwake breeding success measured in the Atlantic during 143 colony-years (42 colonies, 1973-2001; Birkhead and Nettleship 1988, Harris and Wanless 1990, and unpubl. data; Hamer et al. 1993, Erikstad et al. 1995, Barrett 1996, and unpubl. data; Anker-Nilssen et al. 1997) averaged 0.77 ±0.39 chicks/pair and variability (CV = 53%) was more than 4 times greater than that observed in Atlantic murres (12%, Table 14.2). Indeed, it appears that under a wide range of conditions, kittiwake productivity is always more variable than murre productivity (Fig. 14.7). Furthermore, for both species, variability is high when productivity (and presumably food density) is low. This suggests that in "good times", high density prey aggregations are accessible by most colonies but in "bad times", prey aggregations are not just less abundant everywhere, they are patchy and accessible to only a few colonies.

Variability of seabird parameters in relation to food
Another informative way to look at the data collected over 15 colony-years in lower Cook Inlet is to examine variability in the different seabird parameters that we measured. For this purpose I calculated the ratio of maximum to minimum parameter values ("m/m Ratio") and coefficients of variation (CV's) for each parameter. In general, both measures of variability yielded similar results (Table 14.1) and parameters fell into categories of "low" (CV<20%), "medium" (20<CV<40%), and "high" (CV>40%) variability. It was not always possible to measure every parameter in all years, and so sample sizes are less than 15 in many cases, but usually more than 10 (Table 14.1). We always had some data from the "best" colony (Gull Island) and "worst" colony (Chisik Island), and so the calculated CV's should capture the range of natural variability in most cases.

The CV in forage fish biomass (as measured hydroacoustically) among all years and colonies was 80%. This corresponded to about a 20-fold difference in mean forage fish abundance between low and high extremes. If fluctuations in prey abundance have a strong influence on any foraging or breeding parameters, then variability in those parameters should be similar to variability in prey abundance. On the other hand, if seabirds are able to buffer against fluctuations in prey abundance, then we expect variability in some seabird parameters to be less than the variability observed in food supply. Finally, by ranking the seabird parameters from most variable to least variable for murres and kittiwakes we can highlight (Fig. 14.8) some similarities and differences in the way each species responds to variability in prey abundance:

Similarities among species:
1) Variability in density of adults at sea was of similar magnitude (>70%) to variability in forage fish biomass (80%).
2) Adults minimized variability in time spent guarding the egg or chick at the nest site.
3) Adult birds minimized variability in their own body condition.
4) Variability in parameters relating to chick development (condition index, growth rate, age of fledging) was low to moderate.
5) Variability in food acquisition parameters (trip duration, chick feeding rate) was moderate.
6) Variability in early breeding parameters was lower than later breeding parameters (clutch size < laying success < hatching success < fledging success).

Differences among species:
1) Fledging and overall breeding success in kittiwakes was of similar magnitude to variability in forage fish biomass, whereas these parameters were only moderately variable in murres.
2) Discretionary time (available for re-direction to foraging effort) during incubation and chick-rearing was highly variable in murres. Kittiwakes had no discretionary time in most years.

Response of seabirds to prey: Summary and conclusions

We had two main objectives in this study. First, we wanted to establish the form and strength of seabird responses to changes in prey abundance. Second, we wanted to assess the range of variability in those responses.

Form of response

We predicted that-- as in other vertebrates (Holling 1965, Murdoch and Oaten 1975, Piatt 1990)-- murres and kittiwakes would likely exhibit non-linear foraging relationships with food supply. The aggregative response of murres and kittiwakes was, in fact, sigmoidal and bird density at sea was strongly correlated with prey density around each colony (Table 14.1). In recent years, breeding success in several seabird species has been shown to be a curvilinear function of food density (Arctic skua, Philips et al. 1996; Atlantic puffin, Anker-Nilssen et al. 1997; Arctic tern, Suddaby and Ratcliffe 1997), and we demonstrated a similar relationship for black-legged kittiwakes. Common murres did not exhibit such a relationship because breeding success was buffered by increased foraging effort in the face of declining food supply. In accord with Cairns' (1987) predictions, however, we demonstrated for the first time that other parameters such as discretionary ("loafing") time, foraging trip duration and chick growth rate in common murres also varied in curvilinear fashion with prey density. We also found curvilinear relationships between food density and hatching success, fledging success, chick feeding rate and brood size in black-legged kittiwakes.

The non-linearity of functional relationships is wide-spread in predator-prey systems (Holling 1965, Hassell et al. 1977) and it contributes to the stability of predator and prey populations (Steele 1974, Murdoch and Oaten 1975). A more readily apparent consequence of the sigmoidal response is that it introduces "on-off" dynamics into many of the seabird parameters we choose to measure. If prey density is above threshold, the parameter of study (e.g., fledging success) is high ("on"). Below threshold, it is low ("off"). Prey densities can vary over quite a wide range, but if they always remain above (or below) threshold, then there will be no apparent relationship between predators and their food supply (e.g., at a colony of murres that appeared to be unlimited by food supply in the 1980's, Harris and Wanless 1988, 1995). In contrast, marked differences in predator biology can be observed in only 2 years of study if one happens to observe conditions on both sides of a prey threshold (e.g., murres at Sumburgh Head, Monaghan et al. 1994, Uttley et al. 1994). Whatever the circumstances, it is imprudent to interpret the effects of food supply on seabird biology without knowledge of basic functional relationships (Furness and Camphuysen 1997). In particular, we must be cautious in using seabirds as "monitors of the marine environment" if we do not know the form of response for parameters we use to infer change (Cairns 1987). Finally, the effects of non-linear predator-prey dynamics are likely to "trickle up" through food webs. As a changing environment affects prey populations, we ought to expect dramatic non-linear (Steele 1974) changes in predator populations (e.g., Anderson and Piatt 1999) rather than smooth linear transitions in community composition.

Although multi-species, ecosystem management is a stated goal of fisheries organizations (Botsford et al. 1997), management of predatory and forage fish populations in order to sustain marine mammals or birds is still largely a conceptual exercise. Estimates of total food requirements of colonial seabirds and marine mammals have been available for decades (Furness and Tasker 1997), but only recently have there been attempts to include forage considerations in fish population assessment models (Stephenson 1997). Management of forage fish populations will ultimately require knowledge of the form of predator responses to prey density (Steele 1974) and the thresholds of prey density needed to support different predator populations (Piatt and Methven 1992, Byrd et al. 1997, Furness and Tasker 1997). We can now propose, for example, that forage fish densities of about 0.015 g/m^3 or higher are needed to support healthy murre and kittiwake populations in Alaska (and probably elsewhere). In lieu of acoustic survey data, we can also suggest approximate minimum CPUE values for beach seine (100 forage fish/set) and mid-water trawl (300 forage fish/km trawled) sampling, below which seabirds would have trouble breeding. At present, there are no other comparable data published on the minimum prey density requirements of marine birds or mammals.

In addition to hypothesizing curvilinear relationships, Cairns (1987) further suggested that different seabird parameters would have differing thresholds to prey density. For example, Cairns proposed that as prey density declined, chick growth rate would diminish somewhat before any effect on breeding success would be observed. As prey densities fell further, breeding success would diminish before effects on adult survival were observed. The basic supposition was that birds would sequentially adjust activity budgets, loafing time, chick growth, and then breeding success, before prey density fell enough to affect their own survival. The main point of Cairn's hypothesis was that because different parameters should be sensitive to different thresholds of prey density, we can use different seabird parameters as graduated indicators of food abundance over a wide range of food supplies.

Our results do not support this hypothesis. Statistical estimation of thresholds (inflection points) in all our sigmoidal response curves (Table 14.1) suggest that thresholds were very similar in all but one response(see below), occupying a very narrow (1/2000) range of prey densities (0.008 to 0.015 g/m^3) within the spectrum observed during 15 colony-years of acoustic surveys (0.003 to 0.07 g/m^3). Why should prey density thresholds for aggregation (COMU, BLKI), chick feeding (BLKI), chick growth (COMU, BLKI), hatching success (BLKI), fledging success (BLKI), brood size (BLKI), overall breeding success (BLKI) and discretionary time (COMU) all be the same? Probably because there is only *one* physical threshold, and that is the fish school density above which seabirds can successfully acquire food energy at a rate that is sufficient to support daily metabolic demands (Piatt 1990). As noted earlier, it is the *acquisition* of energy that sets the pace for all subsequent activities that involve the *disposition* of energy.

The behavior that results in threshold patch foraging is well described. First, the rate at which predators capture prey is a non-linear function of prey density within the patch (Holling 1965, Murdoch and Oaten 1975). In low density patches, the physical dispersal of prey limits the rate at which predators can capture and consume them. As prey density increases, so does the rate of capture. At moderate to high prey patch densities, however, capture rate levels off because of a saturation effect: there is a physical limit to how quickly predators can capture, handle, consume and digest prey. In seeking to maximize daily food intake, most predators and all higher vertebrates will avoid patches with low capture rates and actively seek out patches with a higher probability of asymptotic capture rates (Goss-Custard 1970, Green 1980, Lima 1983, Piatt 1990). Thus, thresholds are set behaviorally by a predator during its' search for food, and it follows that subsequent behavior and biology will be calibrated to the same threshold. We might also have predicted that murres and kittiwakes would have different foraging thresholds owing to differences in body size and total metabolic demand (Piatt 1990, Furness and Camphuysen 1997)-- but they did not. It may be that thresholds are determined by mass-specific metabolic demands, which are remarkably similar for murres and kittiwakes (see above, "Foraging trip duration").

With respect to aggregation, discretionary time, chick growth and foraging trip duration, murres responded functionally over the same range of prey densities as kittiwakes. It appears, however, that murres did buffer fledging and breeding success against low prey densities by increasing foraging time budgets. In this one instance, a time-budget buffer effectively lowered the threshold for breeding success in murres. We were unable to statistically resolve this threshold, however, because we lacked sufficient data at extreme low densities, and probably also because our study areas were not large enough to include all the potential foraging area for murres (see above, "Hatching, fledging and breeding success"). In any case, this "time-buffered threshold" is different than the more commonly described "patch density threshold" above. In this one case, then, Cairn's hypothesis is correct. A failure in murre breeding success would indicate much lower food supplies than a failure or decline in any other parameter we measured.

Variability

One of the main reasons for initiating this study was to examine natural variability in seabird biology within the geographic area affected by the *Exxon Valdez* oil spill. We are interested in two aspects of variability. First, is food supply a major source of variability in seabird parameters we measured? Second, which parameters are most sensitive to changes in food supply?

Variability in bird density at sea (CV>70%) reflected variability in prey density (CV=80%), and murre and kittiwake dispersion was well-explained by food dispersion ($r^2 > 0.70$, Table 14.1). This suggests that adult murres and kittiwakes track the abundance and distribution of prey schools at the spatial scale of measurement (1000's km^2). In turn, this tracking *sets the baseline variability* for all other parameters (Table 14.1) because variability in prey acquisition (including foraging trip duration, chick-feeding rate) depends on success in tracking the prey, and, in turn, all other parameters (body condition, reproductive success) vary with the rate of prey acquisition.

Murres and kittiwakes had to cope with a 20-fold variation in food density between colony-years of study. Both species were able to buffer against fluctuations in food supply to different degrees and in different ways. Both species appeared to minimize effects of variability on their own body condition first, and then on the condition (growth) of chicks. Foraging behaviors (trip duration, frequency) were moderately variable, indicating some ability to buffer foraging effort against extreme changes in food supply. Some parameters (clutch size, guarding of chick) appeared relatively insensitive to food supply, suggesting that if conditions are good enough to initiate breeding that these parameters will be maintained at relatively fixed levels.

Kittiwakes and murres differed most with respect to breeding success. Kittiwake fledging and breeding success were strongly correlated with food supply, and slightly more variable (CV=81-87%). Murre breeding success was poorly correlated with food, and less than half as variable (CV = 29%). However, the background variability in food supply is largely captured in murre discretionary time (CV =66%), used by murres to buffer breeding success.

These results are entirely consistent with life-history theory (Stearns 1992) which predicts that in long-lived animals that reproduce over many years, there is a trade-off between investment in the current year's reproductive effort and subsequent adult survival. When food is limiting during a breeding season, adults should always take care of themselves first-- and if necessary, even abandon their chicks-- because adults can always attempt to reproduce again in subsequent years. The importance of maintaining adult body condition is very clear, given the strong linkage between body condition and survival in seabirds (Erikstad et al. 1998, Golet et al. 1998, Weimerskirch et al. 2001). After taking care of themselves, it follows that adults would minimize variation in chick growth and condition, which is linked with survival to breeding age (Sagar and Horning 1998, Weimerskirch et al. 2000).

It is not clear whether murres and kittiwakes can actively buffer variability in foraging trip duration or chick feeding rate. There parameters are moderately variable in both murres and kittiwakes, but it may simply be that there is a limited range of possible values that these parameters can take. Below a certain level of effort (ca. 2-3 chick meals/day), chicks would fail and the reproductive effort would end. Delivery rates above 4 meals/day are probably unnecessary. Similarly, there is an upper limit to the number of hours available for foraging in each day, and this sets a limit on the number of possible trips (see above, "Foraging trip duration"). It may be that in other taxa such as the procelliformes-- which forage over many days-- foraging trips can be much more variable (e.g., Weimerskirch et al. 2001).

Finally, variability in kittiwake breeding success is only slightly higher than the background variability in food supply. The difference may simply be due to measurement error, or it may reflect that fact that other factors such as weather and predation can also influence kittiwake breeding success (Barrett and Runde 1980, Hamer et al. 1993, Hatch et al. 1994). In any case, kittiwake breeding success appears to be very sensitive to fluctuations in food supply. This parameter should therefore prove to be a reliable indicator of variability in the marine environment (e.g., Aebischer et al. 1990). In contrast, murre breeding success tells us little about food supplies (except under extreme circumstances), whereas murre time-budgets are almost as sensitive as kittiwake breeding success to prey fluctuations. Given that murres (spp.) are probably *the* most widely monitored seabirds in the Northern Hemisphere (Gaston and Jones 1998), it is time to re-evaluate the utility of measuring breeding success in this species. At the very least, it is time to add time-budgets to the repertoire of parameters we routinely measure at murre colonies (Cairns 1987).

Can Seabirds Recover from Effects of the EVOS?

The immediate impact of the *Exxon Valdez* oil spill included a substantial loss of adult common murres (Piatt et al. 1990). Other species to experience population declines or reduced productivity following the spill included Black-legged Kittiwakes, Marbled Murrelets and Pigeon Guillemots (Spies et al. 1996). Populations of most seabirds had still not recovered five years after the spill (Spies et al. 1996). Models suggested that it could take decades for murre populations to fully recover to stable age distributions *if* environmental conditions were favorable (Ford et al. 1982, Piatt et al. 1990). However, evidence accumulated during the 1990's that environmental conditions were *not* favorable to seabirds in years following the oil spill. A "regime shift" had occurred in the Gulf of Alaska (GOA) during the late 1970's, apparently resulting in marked changes in seabird diets, and a lowering of reproductive success and population size in some marine bird and mammal populations (Piatt and Anderson 1996, Francis et al. 1998).

This new information raised several questions: To what degree were seabirds affected by natural changes in the GOA environment before the spill? Could effects of the spill be separated from natural variability? In light of the regime shift, what was the current status of seabird populations in the GOA, and, could current conditions limit recovery of seabirds from effects of the spill? This study was initiated to answer some of these questions for seabirds in lower Cook Inlet, and particularly the Barren Islands, where bird populations were hit hardest by the spill (Piatt and Ford 1996).

Population status of seabirds in Cook Inlet

Our study was designed to provide contrasting data from a "food-poor" colony (Chisik), where murre and kittiwake populations were known to have been declining at rates of 4-9% per annum for the past 30 years (Fig. 14.9), and a "food-rich" colony (Gull) where murre and kittiwake populations grew at rates of 9% per annum at some point during the past 25 years. Kittiwakes increased rapidly on Gull Island during the 1980's, but populations leveled off in the1990's and remained at the same level throughout the course of our study. Evidence suggests that this was due entirely to saturation of nesting habitat on the island. In the absence of nest-site limitation, we believe that kittiwakes would still be increasing at the rate observed prior to the plateau, and at a rate similar to that observed for murres (which are not yet limited by nesting habitat). Trends at the Barren Islands were unknown prior to the EVOS oil spill, but both murres and kittiwakes exhibited modest increasing trends during the past decade (Fig. 14.9).

Productivity in kittiwakes (Fig. 14.10) parallels population trends. Kittiwakes have failed chronically at Chisik for more than 30 years, averaging 0.05 chicks/pair during that time, and only 0.02 chicks/pair during this study (1995-1999). Kittiwakes averaged 0.44 chicks/pair at Gull Island since 1984, and 0.48 chicks/pair during this study. This is higher average productivity than has been observed at any other colony in Alaska except Cape Lisburne, where populations have been increasing for the past 20 years (Dragoo et al. 2000). Productivity is more variable at the Barrens, averaging 0.29 chicks/pair during the past decade, and 0.43 chicks/pair during this study (Fig. 14.10).

In contrast, murre productivity does not correlate with population trends. Despite having markedly different population trends at the 3 colonies (Fig. 14.9), breeding success was high on Chisik (0.56 chicks/pair), Gull (0.54 chicks/pair) and the Barren islands (0.72 chicks/pair) during this study (Fig. 14.2). There are no prior historical data for murres except from the Barrens in 1989-1993 (Nysewander et al. 1993, Roseneau et al. 1994, Boersma et al. 1995). When included, these data suggest an average productivity of 0.54 chicks/pair at the Barrens during the past 12 years.

Results from Chisik beg the question: How can murres reproduce successfully and yet experience population declines of 9% per annum? A similar question has been asked about murres in the Shetlands, which continued to have high breeding success even as numbers at colonies declined in apparent response to a crash in food stocks (Furness and Camphuysen 1997). These questions may be addressed by a study on adult seabird survival, also funded by the EVOS Trustee Council (Restoration Project 01338). Analysis of data collected in 2001 is still under way. Adding results from this study, we can now assess population trends, adult survival and productivity for murres and kittiwakes on Gull and Chisik islands. From these we can estimate recruitment and immigration if we assume that about 40% of juveniles survive to breed (a high-end estimate, Hudson 1985).

Preliminary results (Piatt 2001) suggest that there are marked differences in population parameters of murres on Gull and Chisik islands (Table 14.3). On Chisik, annual adult mortality (8.0% pa) may largely account for the population decline (-8.9% pa), leaving a 0.9% pa decline to be explained by emigration. If 40% of juveniles actually survived to breed, then recruitment (11% pa) would have to balanced by a much larger rate of emigration (12% pa). However, survival of chicks is likely to be much lower if chicks are underweight (Hatch 1983, Sagar and Horning 1998)-- as they frequently are at Chisik (Fig. 14.2). Furthermore, recruitment at a declining murre colony is likely to be less than 20% (Hudson 1985) and possibly less than 5% (Hatchwell and Birkhead 1991). Thus, recruitment at Chisik may, in fact, be neglible. With modest emigration, and a fairly high adult mortality rate, this would explain how murres can maintain such high breeding success and yet experience serious population declines. In contrast, the high rate (9.1% pa) of murre population increase at Gull Island can be explained by a low rate (4% pa) of adult mortality that is more than offset by high rates of recruitment and immigration (Table 14.3).

Kittiwake population parameters appear more straightforward (Table 14.3). At Chisik, recruitment has to be virtually zero because productivity is negligible. Thus, the population decline (-4.3% pa) is explained entirely by adult mortality (7% pa), offset slightly by immigration. At Gull Island, a much higher adult mortality rate (18% pa) is balanced by much higher levels of productivity, recruitment and immigration. The differences in survival and productivity between Gull and Chisik seem to support the hypothesis that long-lived seabirds trade off the costs of reproduction with adult survival (Erikstad et al. 1998, Golet et al. 1998).

Population parameter indices

How do we compare the health of seabird populations among the islands in Cook Inlet, or among regions in Alaska? We have already seen that for each species, any one parameter we choose to examine can provide biased inferences about population status depending on whether it is correlated with fluctuations in food supply, linear or non-linear in response to changes in prey density, and highly variable or relatively constant in the face of environmental change.

One way to assess and compare the performance of seabirds at colonies in Cook Inlet is to examine the deviation of parameter values from average at all three colonies (Fig. 14.11). For example, the average breeding success of kittiwakes in 15 colony-years (3 colonies in 1995-1999) of study was 0.312 chicks/pair. Success of kittiwakes at the Barrens was lower than this in 2 years of study, and higher in 3 years. Success was higher than average in all 5 years at Gull Island, and much lower than average in all 5 years at Chisik. Similarly, we calculated deviations from average in other parameters (e.g., attendance, feeding rate, growth rate, fledging success, etc.), standardized the deviations, and arbitrarily ranked them from largest to smallest at each colony so that we could compare them all together (Fig. 14.11). In total, we can compare 266 parameter deviations (20 species-parameters by year, colony).

This provides a holistic assessment of how well seabirds were doing at each colony during the years of our study. Analysis reveals (Fig. 14.11) that, in respect to all the parameters measured, birds at Gull Island do better than average most of the time (mean deviation = +0.24), while those at Chisik do poorly most of the time (mean deviation = -0.37). At the Barrens, measured parameters were above average slightly more often than they were below average (mean deviation = +0.09).

Judging from the range of parameter values we observed at Chisik and Gull islands, and in comparing these with values obtained in studies conducted elsewhere under a wide range of conditions (e.g., Hamer et al. 1993, Uttley et al. 1993, Monaghan et al. 1994, Dragoo et al. 2000, Gill 1999, Suryan et al. 2000b, etc.), it is clear that Chisik and Gull exemplify the extremes of failing and thriving colonies, respectively, in Alaska. Consequently, this analysis provides a calibration for seabird performance at the Barren Islands and suggests that murres and kittiwakes there are doing modestly well. This conclusion is corroborated by data on population trends (Fig. 14.9).

Indeed, there is a strong correlation between our parameter indices of population health and population trends (Fig. 14.12). This relationship seems intuitively reasonable. Our parameter indices integrate a suite of values that include behavioral, physiological and biological measurements. The combination of these parameters-- and many more unmeasured parameters-- is ultimately what determines whether a population will increase or decrease. Similarly, population trend represents an integration of *all* factors influencing population biology.

So why measure dozens of species-parameters throughout summer when simply counting birds on plots for 4-6 weeks will provide an indication of population health? One major reason is that because, in the future at least, measuring both parameter indices and population trend would allow us to distinguish between anthropogenic and natural impacts on seabird populations-- something we could not do following the *Exxon Valdez* oil spill (Piatt and Anderson 1996). For example, if studies of murres at a colony yielded a parameter index of +0.25 but population trends were stable or decreasing, this would indicate that populations were not being limited by food supply, but rather by something that was removing large numbers of breeding birds from the population, such as gill-net mortality, oil pollution, or hunting.

The parameter index also offers an instantaneous measure of health of seabird populations, whereas population trend data, by definition, needs to be collected over many years to establish a trend. One year's sampling may be all that is needed to assess the status of populations (e.g., parameter indices for 1995-1999 at Chisik were always negative, ranging from -0.24 to -0.62; whereas at Gull they were always positive, ranging from +0.19 to +0.29). In contrast, census data can be highly variable among consecutive years, and may need to be collected for a decade or longer to establish trends (e.g, Dragoo et al. 2000). Finally, census information will be misleading if study plots used for census purposes become saturated with breeding birds, or breeding habitat on a colony is saturated (as we found on Gull Island).

Data provided in this study can now be used as a baseline to assess the status of other seabird colonies in Alaska. We know that data collected at Chisik, Gull and the Barren islands feature an extreme range of parameter values that reflect prey densities below and above threshold values. One could visit any murre or kittiwake colony once, collect data on a variety of parameter values (not necessarily all of the parameters we measured), and calculate standardized deviations from averages using data collected at that colony and data provided here in Chapters 8 and 9. From this exercise it should be possible to determine whether the health of the colony in question is above or below average.

Conclusion

Gull and Chisik islands support relatively small seabird colonies (1000's of birds) that apparently were little affected by the *Exxon Valdez* oil spill. Their population dynamics reflect meso-scale habitat characteristics that differ somewhat from the Barren islands, which contain orders-of-magnitude more breeding birds (10,000's of birds). Evidence suggests that ecological conditions and food supplies for seabirds in the eastern half of lower Cook Inlet will support modest population growth and allow recovery from losses incurred from the oil spill. Indeed, given the rates of increase observed at Gull and the Barren islands in the years since the spill, populations should have already recovered to numbers observed prior to the spill (assuming a ca. 35% decline in Cook Inlet populations pre- and post-spill; Piatt and Anderson 1996). However, declines at Cook Inlet colonies may have accounted for only about 10% of the total mortality in the Gulf of Alaska (Piatt and Anderson 1996), and it is not clear whether conditions in lower Cook Inlet are typical of elsewhere in the Gulf of Alaska.

In the absence of quantitative data on food supplies, one way to answer that question is to compare seabird parameter indices from Cook Inlet to those gathered in other areas of Alaska. Unfortunately, the full suite of parameters measured in our studies has rarely been surveyed at other colonies. However, one parameter that has been widely reported is breeding success of Black-legged Kittiwakes (Table 14.2). We have established that kittiwake breeding success exhibits a strong, sigmoidal response to prey density (see above, "Hatching, fledging, and breeding success"). We can conclude from that analysis that kittiwake breeding success above 0.46 chicks/pair represents asymptotic reproduction *unlimited* by food supply, while breeding success below 0.015 chicks/pair represents asymptotic reproduction under conditions of *severe food deprivation*. Breeding success that ranges between 0.015 and 0.46 chicks/pair represents reproduction that is *limited to some degree* by food supplies that hover around the threshold.

Using these criteria, we can indirectly assess the status of food supplies for seabirds in Alaska by examining the historical breeding success of kittiwakes over time and space (Fig. 14.13; data from Hatch 1993, Dragoo et al. 2000). Prior to the regime shift that occurred in the late 1970's (Francis et al. 1998), kittiwake productivity in both the Gulf of Alaska and Bering Sea was very similar: only a small proportion (5-6%) of colony-years of production were food deprived, a large proportion (38-40%) were unlimited by food, and slightly more than half (55-56%) were limited to some degree by food supply. After the regime shift, but mostly prior to the *Exxon Valdez* oil spill in 1989, there was a marked change in kittiwake productivity (Fig.14.13). The frequency of food-deprived production in the 1980's increased 6-fold (to 37%) in the Gulf of Alaska, while the frequency of unlimited production declined by half (to 17%). A similar, but less pronounced, shift occurred in the Bering Sea. In the 1990's, there was a significant improvement in feeding conditions in the Gulf of Alaska: Whereas the frequency of unlimited production remained the same (at 17%), food-deprived production decreased (to 30%) while food-limited production increased (to 54%). By comparison, however, conditions in Cook Inlet had improved substantially more than the Gulf as a whole (in which Cook Inlet data are included). Of 24 colony-years of production in the 1990's, 29% were unlimited by food, 50% were limited to some degree, and 29% were unlimited. Conditions in the Bering Sea improved even more than in the GOA.

In summary, this analysis supports the hypothesis that a regime shift in the late 1970's reduced food availability to seabirds in the 1980's and 1990's, resulting in widespread population declines, lower breeding success, and mass mortality events (Piatt and Anderson 1996, Francis et al. 1998). The evidence further suggests that there was a slight improvement in feeding conditions in the 1990's and that conditions in Cook Inlet are better than those in the Gulf as a whole. In general, however, current (to 1999) conditions continue to be depressed compared to the 1970's. While seabirds in Cook Inlet colonies may have already recovered numerically to pre-spill levels, it is still not clear whether conditions elsewhere in the Gulf of Alaska would have supported similar rates of recovery during the 1990's.

Future Prospects
We can shed some light on the potential for future seabird recovery by examining historical data on small-mesh trawl catches in the Gulf of Alaska (Anderson and Piatt 1999). A shift in ocean climate during the late 1970's triggered a reorganization of community structure in the Gulf of Alaska ecosystem, as evidenced in changing catch composition on long-term (1953-1997) small-mesh trawl surveys. Forage species such as pandalid shrimp and capelin declined and never recovered because of recruitment failure and predation. Total trawl catch biomass declined by more than 50% and remained low through the 1980s. In contrast, recruitment of high trophic-level groundfish improved during the 1980s, yielding a > 250% increase in catch biomass during the 1990s. This trophic reorganization apparently occurred at the expense of piscivorous sea birds and marine mammals.

Analyses of long-term climate data reveal significant cycles in North Pacific climate, including those due to El Nino events (5-7 year cycle) and those to decadal-scale shifts in the position and intensity of the Aleutian Low pressure cell in winter. The recent 'warm regime', which has not favored forage fish and seabirds, has now exceeded in duration any previous decadal-scale warm cycle event on record. It is predicted that we should return to a 'cold regime' again in the very near future (Ware 1995, Francis et al. 1998). If so, then one can reasonably predict that ecological conditions will return to those that favor seabirds in the Gulf of Alaska. In turn, this would undoubtedly hasten the recovery of seabirds from damages incurred from the *Exxon Valdez* oil spill.

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