Exxon Valdez Oil Spill
Restoration Project Annual Report

Diet Composition, Reproductive Energetics, and Productivity of Seabirds Damaged by the *Exxon Valdez* Oil Spill

Restoration Project 98163 G

Annual Report

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This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Study History: Restoration Project 98163 G is similar to the research described in the original proposal submitted as 95118-BAA. It is a component of the Alaska Predator Ecosystem Experiment Project (APEX), for which funding was first approved by the EVOS Trustee Council in April 1995. This research examines the effects of diet composition on the reproductive energetics and productivity of piscivorous seabirds in the northern Gulf of Alaska, using Pigeon Guillemots and Black-legged Kittiwakes as models. Component G works closely with other colony-based research that is part of APEX, including components E, F, J, and M, and provides data for Component Q of APEX (modeling factors limiting seabird recovery). In 1995, study sites for kittiwakes were breeding colonies at Shoup Bay, Eleanor Island, and Seal Island in Prince William Sound, and Gull Island, Chisik Island, and the Barren Islands in Lower Cook Inlet; study sites for guillemots were at Naked Island and Jackpot Island in PWS, and Kachemak Bay in Lower Cook Inlet. In 1996, field research continued with a shift in kittiwake study sites from Seal Island to North Icy Bay. In 1998, all study sites remained the same as in 1996 and 1997 with the exception of adding a Black-legged Kittiwake reference study site at Middleton Island in the northern Gulf of Alaska.

Abstract: A shift in marine trophic structure in the area affected by the *Exxon Valdez* oil spill (EVOS) may have hindered or prevented recovery of injured seabird resources, especially Pigeon Guillemots, Common Murres, and Marbled Murrelets. We studied energetic factors (diet composition, diet quality, meal size, meal delivery rate, adult daily energy expenditure) potentially constraining seabird productivity in the EVOS area, focusing on Pigeon Guillemots and Black-legged Kittiwakes as models of fish-eating seabirds. Energy density (kJ/g wet mass) varied widely within and between species of forage fish; schooling pelagic fishes had relatively high or low values, whereas nearshore demersal fishes were intermediate. Seabirds and other fish-eating predators can experience multi-fold differences in energy intake rates based solely on the types of fish consumed.

1998 was a mediocre or poor year for kittiwake nesting success at most APEX study colonies despite an apparent increase in proportion of after hatching year herring, capelin, and sand lance in the diets at most colonies. Low kittiwake productivity within the study area appeared to be linked to low availability of these species of forage fish within foraging range of nesting colonies early in the breeding season, but was not reflected in poor chick growth later in the breeding season. Similarly, 1998 also was a poor year for Pigeon Guillemot nesting success. Availability of high-quality schooling forage fish within foraging distance of guillemot colonies continues to be positively correlated with energy provisioning rates to guillemot nests, nestling growth rates, and overall productivity.

Key Words: energetics, energy, *Exxon Valdez* oil spill, fish, lipid, proximate composition, seabird, reproduction, trophic.

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EXECUTIVE SUMMARY

This restoration research project is a component of the APEX Project (Alaska Predator Ecosystem Experiment), which is investigating whether low food availability and quality contribute to the failure of some seabird and marine mammal populations to recover from the *Exxon Valdez* Oil Spill (EVOS). The basic premise of APEX is that a shift in marine trophic structure of the EVOS area has prevented recovery of injured seabird resources. Specifically, this research component of APEX addresses whether changes in diet quality may have constrained reproduction in Pigeon Guillemots (*Cepphus columba*), Common Murres (*Uria aalge*), and Marbled Murrelets (*Brachyramphus marmoratus*), all resources injured by the spill. The major hypothesis tested is that differences in the nutritional quality of forage fishes are a primary determinant of energy provisioning rates to seabird nestlings, which influence not only the growth and survival of young, but also other factors that regulate seabird populations (e.g., post-fledging survival and recruitment rates).

Pigeon Guillemots and Black-legged Kittiwakes (*Rissa tridactyla*) were the focal piscivorous seabirds studied during the 1998 breeding season. In cooperation with other APEX projects, we collected samples of nestling diets and measured nestling provisioning rates, growth rates, and nesting success in relation to diet. The two guillemot study sites in Prince William Sound (PWS) were located at Naked Island (an oiled site) and Jackpot Island (a non-oiled site), and were compared with guillemots nesting in Kachemak Bay (a reference site). The three study sites for kittiwakes in PWS were Eleanor Island (an oiled site), North Icy Bay (a non-oiled site), and Shoup Bay (a non-oiled site). The three kittiwake study sites for Lower Cook Inlet (LCI) were at Gull Island, Chisik Island, and the Barren Islands (all reference sites). Black-legged Kittiwakes also were studied on Middleton Island in the northern Gulf of Alaska where USGS biologists have been studying reproduction and behavior using a controlled experimental approach since 1996. In addition, forage fishes were collected using a variety of methods and analyzed in the lab to determine quality as seabird prey.

Forage fish exhibited a ten-fold difference in lipid content (% dry mass) and a five-fold difference in energy density (kJ/g wet mass) among individuals, such that predators could potentially experience large differences in foraging efficiency depending on prey choice (Anthony et al. unpubl. ms.). Schooling pelagic fishes tended to have either relatively high lipid content and energy density (e.g., Pacific herring *Clupea harengus*, capelin *Mallotus villosus*, and juvenile Pacific sand lance *Ammodytes hexapterus*) or low lipid content and energy density (e.g., juvenile walleye pollock *Theragra chalcogramma*, juvenile Pacific cod *Gadus macrocephalus*, and juvenile Pacific tomcod *Microgadus proximus*), whereas nearshore demersal fishes (e.g., blennies, gunnels, sculpins) had intermediate values. Interspecific variation in lipid content was the primary factor influencing energy density of forage fish, with variation in water content also contributing. Lipid content (% dry mass) was negatively correlated with water content (% wet mass) and positively correlated with protein content (% lean dry mass). Thus, in addition to higher energy density, high-lipid fish had higher nutritional value than low-lipid fish in part because of lower water content and higher protein content. Intraspecific differences in lipid content and energy density of forage fishes were related to size, sex, month, reproductive status, location, and year. Pelagic species maturing at a smaller size (e.g., capelin, sand lance, lanternfish (Myctophidae)) had higher and more variable energy densities than did pelagic or nearshore species maturing at a larger size (e.g., gadids, salmonids). Diet quality for some piscivorous seabirds in the EVOS area is sufficiently variable to affect prey selection.

The diets of Pigeon Guillemots at Naked Island and Kachemak Bay in 1998 were similar to each other but differed from that at Jackpot Island. As in recent years, near-shore demersal fishes were the dominant prey at Naked Island. Sand lance constituted ≤ 25% of prey items delivered at Kachemak Bay for the second year in a row in marked contrast to 1994 - 96 when sand lance dominated the diet. Pigeon Guillemot diets at Jackpot Island in 1998 contained a substantial proportion of Pacific herring, similar to 1994 - 1996 but in sharp contrast to 1997 when herring were notably absent from the diet.

In 1998, energy provisioning rates to Pigeon Guillemot nestlings were highest at Jackpot Island, intermediate at Naked Island, and lowest at Kachemak Bay. Naked Island experienced high nest predation in 1998 and so it is difficult to expand upon relationships among food resources, energy provisioning rates, and productivity at this site. Productivity and energy provisioning rates at Kachemak Bay were poor in 1998, reflecting the continued decline in the proportion of sand lance in the diet. Productivity and energy provisioning rates at Jackpot Island each increased slightly from 1997. Both productivity and energy provisioning rates, however, were still less than values measured in 1995. Energetics and productivity data from all three study sites continue to support the concept that Pigeon Guillemots require high energy provisioning rates to maintain productivity, and that all three components of energy provisioning rate (i.e., meal delivery rate, meal size, and energy density) are critical to their success.

Diets of Black-legged Kittiwakes in 1998 differed from those observed in 1997. The relative biomass of young-of-the-year (YOY) sand lance in the diet of Black-legged Kittiwakes decreased dramatically at all colonies except Eleanor. At the Shoup and Icy bay colonies, YOY sand lance was replaced by 1+ Pacific herring. In contrast the relative biomass of YOY sand lance increased in kittiwake diets at Eleanor Island, whereas the proportion of 1+ capelin declined markedly. Sand lance continued to be a primary prey item at all colonies in Lower Cook Inlet. The proportion of YOY sand lance declined and 1+ sand lance increased in the diet at each LCI colony in 1998 compared with 1997. Other notable diet shifts included a modest increase in the proportion of 1+ capelin and other osmeriids in the diet at the Barren Islands and Chisik Island.

Energy provisioning rates to Black-legged Kittiwake broods at Shoup and Icy bays in 1998 were similar to those observed in 1997. However, energy provisioning rates at Eleanor Island in 1998 decreased appreciably from the previous year. This decrease appeared to be due predominantly to a decline in average meal size. High levels of Peregrine Falcon predation at Eleanor Island in 1998 interfered with collection of chick meals later in the nesting season, when larger meals would have been more prevalent.

Productivity at Shoup Bay in 1998 was similar to 1997, reflecting the similarity in energy provisioning rates, while productivity at Icy Bay improved. In 1998, Icy Bay was the only kittiwake colony where energy provisioning rates exceeded 400 kJ / nest day. Energy provisioning rates at kittiwake colonies in LCI in 1998 were similar to those observed in 1997 and none of these colonies showed an improvement in productivity compared to 1997.

Despite the occurrence of prey items in the diet with relatively high energy density, energy provisioning rates and productivity only improved at Icy Bay in 1998 compared with 1997. Black-legged Kittiwakes in LCI initiated nesting later than usual and this may have been due to a lack of sufficient food resources early in the season. Black-legged Kittiwakes at Shoup Bay in 1998 continued to exhibit low meal delivery rates compared to years of higher productivity, suggesting individuals may have been travelling farther and allocating more time and energy to foraging to obtain prey. In contrast, Black-legged Kittiwakes at Icy Bay had higher feeding frequencies, higher energy provisioning rates, and higher productivity, despite similar diet composition to 1997. These data from LCI and PWS suggest that spatial and temporal availability of forage fish with high energy density may limit productivity of Black-legged Kittiwakes in the EVOS area.

INTRODUCTION

Reproductive success in seabirds is largely dependent on foraging constraints experienced by breeding adults. Previous studies on the reproductive energetics of seabirds have indicated that productivity is energy-limited, particularly during brood-rearing (Roby 1991). Also, the young of most seabird species accumulate substantial fat stores prior to fledging, an energy reserve that can be crucial for post-fledging survival in those species without post-fledging parental care (Perrins et al. 1973; but see Schreiber 1994). Data on foraging habitats, prey availability, and diet composition are critical for understanding the effects of changes in the distribution and abundance of forage fish resources on the productivity and dynamics of seabird populations.

The composition of forage fish is particularly relevant to reproductive success because it is the primary determinant of the energy density of meals delivered to nestlings. Parent seabirds that transport chick meals in their stomachs (e.g., kittiwakes) normally transport meals that are close to the maximum load. Seabirds that transport chick meals as single prey items held in the bill (e.g., guillemots, murres, and murrelets) experience additional constraints on meal size if optimal-sized prey are not readily available. Consequently, seabird parents that provision their young with fish high in lipids are able to support faster growing chicks that fledge earlier and with larger fat reserves (see annual report for APEX Component 98163 N). This is because the energy density of lipid is approximately twice that of protein and carbohydrate. Also, forage fish are generally very low in carbohydrate, and metabolism of protein as an energy source requires the energetically expensive process of excreting the resultant nitrogenous waste. Consequently, the metabolizable energy coefficient (proportion of ingested food energy that is usable by the bird) for diets high in lipids is significantly higher than low-lipid diets (see Annual report for APEX 98163N).

While breeding adults can afford to consume prey that are low quality (i.e., low-lipid) but abundant, reproductive success may depend on provisioning young with high quality (i.e., high-lipid) food items. If prey of adequate quality to support normal nestling growth and development are not available, nestlings either starve in the nest or prolong the nestling period and fledge with low fat reserves.

Forage fish vary considerably in lipid content, lipid:protein ratio, energy density, and nutritional quality. In some seabird prey, such as lanternfishes and eulachon (*Thaleichthys pacificus*), lipids may constitute over 50% of dry mass (Van Pelt et al. 1997; S. Payne, unpubl. data, Anthony et al., unpubl. ms.); while in other prey, such as juvenile walleye pollock and Pacific cod, lipids are frequently less than 5% of dry mass (J. Wejak, unpubl. data; Van Pelt et al. 1997; Anthony et al., unpubl. ms.). This means that a given fresh mass of lanternfish or eulachon may have 3-4 times the energy content of the same mass of juvenile pollock or Pacific cod. By increasing the proportion of high-lipid fish in chick diets, parents can increase the energy density of chick meals in order to compensate for the low frequency of chick feeding (Ricklefs 1984, Ricklefs et al. 1985; Lance and Roby, unpubl. ms.).

Three seabird species that were damaged by the *Exxon Valdez* oil spill (EVOS) are failing to recover at an acceptable rate: Pigeon Guillemot, Common Murre, and Marbled Murrelet. Damage from the spill to a fourth species of seabird, Black-legged Kittiwake, is equivocal, but recent reproductive failures of kittiwakes within the spill area may be due to longer term ecosystem perturbation related to the spill (D. B. Irons, pers. comm.). The status of Pigeon Guillemots and Marbled Murrelets in PWS and Lower Cook Inlet (LCI) has been of concern for nearly a decade due to declines in numbers of adults observed on survey routes (Laing and Klosiewski 1993, D. Zwiefelhofer, pers. comm.). All of these damaged or potentially damaged seabirds are piscivorous and rely to a greater or lesser extent on pelagic schooling fishes during the breeding season.

One prevalent hypothesis for the failure of these seabirds to recover is that changes in the abundance and species composition of forage fish resources within the spill area has resulted in reduced availability and quality of food for breeding seabirds. Concurrent population declines in some marine mammals, particularly harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubata*) have also been blamed on food limitation. Seabirds, unlike marine mammals, offer the possibility of directly measuring diet composition and feeding rates, and their relation to productivity. Thus the piscivorous seabirds breeding in PWS and LCI present an opportunity to assess the relationship between the relative availability of various forage fishes and the productivity of apex predators. Whether these changes in forage fish availability are related to or have been exacerbated by EVOS is unknown.

This study is relevant to EVOS Restoration Work because it is designed to develop a better understanding of how shifts in the diet of seabirds breeding in the EVOS area affect reproductive success. By monitoring the composition and provisioning rates of seabird nestling diets, prey preferences can be assessed. Measuring provisioning rates is crucial because even very poor quality prey may constitute an acceptable diet if it can be supplied at a high rate without substantially increased parental investment. Understanding the diet composition, foraging niche, and energetic constraints on seabirds breeding within the spill area will be crucial for designing management initiatives to enhance productivity in species that are failing to recover from EVOS. If forage fish that are high in lipids are an essential resource for successful reproduction, then efforts can be focused on assessing stocks of preferred forage fish and the factors that impinge on the availability of these resources within foraging distance of breeding colonies in the EVOS area. As long as the significance of diet composition is not understood, it will be difficult to interpret shifts in the utilization of forage fishes and develop a management plan for effective recovery of damaged species.

Guillemots are the most neritic members of the marine bird family Alcidae (i.e., murres, puffins, and auks), and like the other members of the family, capture prey during pursuit-dives. Pigeon guillemots are a well-suited species for monitoring forage fish availability for several reasons: (1) they are a common and widespread seabird species breeding in the EVOS area (Sowls et al. 1978); (2) they primarily forage within 5 km of the nest site (Drent 1965); (3) they raise their young almost entirely on fish; (4) they prey on a wide variety of fishes, including schooling forage fishes (e.g., sand lance, herring, pollock) and subtidal/nearshore demersal fishes (e.g., blennies, gunnels, sculpins; Drent 1965, Kuletz 1983); and (5) the one- or two-chick broods are fed in the nest until the young reach adult body size. Guillemots carry whole fish in their bills to the nest-site crevice to feed their young. Thus individual prey items can be identified, weighed, measured, and collected for composition analyses. In addition, there is strong evidence of a major shift in diet composition of guillemot pairs breeding at Naked Island. Sand lance were the predominant prey fed to young in the late 1970s (Kuletz 1983), but currently sand lance is a minor component of the diet (see annual report for APEX 98168 F). In contrast, guillemots breeding in Kachemak Bay provisioned their young predominately with sand lance in 1994 and 1995, and sand lance is particularly prevalent in the diet at breeding sites that support high densities of nesting guillemots (Prichard 1997).

Black-legged kittiwakes also breed abundantly in the spill area and rely largely on forage fish during reproduction. Unlike guillemots, kittiwakes are efficient fliers, forage at considerable distances from the nest, and capture prey at or near the surface. Although kittiwakes are highly colonial, cliff-nesting seabirds, they construct nests and can be readily studied at the breeding colony without causing substantial egg loss and chick mortality. Like guillemots, kittiwakes can raise one- or two-chick broods, and chicks remain in the nest until nearly adult size. Kittiwake breeding colonies at Shoup Bay, Eleanor Island, and North Icy Bay in PWS are easily accessible so that chicks can be weighed regularly without resorting to technical climbing. Kittiwake colonies at Gull Island, Chisik Island, and the Barren Islands in LCI are not as accessible as the PWS colonies, but acquiring sufficient data on reproductive performance for comparison with PWS colonies is feasible.

This study is component G of the Alaska Predator Ecosystem Experiment (APEX) Project (EVOS Projects 98163 A-T), whose goal is to test the general hypothesis that a shift in the marine trophic structure of the EVOS area has prevented recovery of injured resources.

APEX addresses 10 more specific working hypotheses, 5 of which (hypotheses 4, 7, 8, 9, 10) this component helps test and two of which are the focus of this study:

APEX Hypothesis 8: Changes in seabird productivity reflect differences in forage fish abundance, as measured in adult seabird foraging trips, chick meal-size, and chick meal delivery rates.

APEX Hypothesis 9: Seabird productivity is determined by differences in forage fish nutritional quality.

These two hypotheses address the two primary determinants of energy provisioning rates to nestling seabirds, which in turn have a direct bearing on fitness through variation in reproductive output. Another variable, parental investment, was assumed to remain constant among breeding sites and years. This assumption was tested for kittiwakes in 1997 and 1998 at Shoup Bay and North Icy Bay colonies by measuring parental energy expenditure rates during chick-rearing.

OBJECTIVES

The overall objective of this research is to determine the energy content and nutritional value of various forage fishes used by seabirds breeding in the EVOS area, and to relate differences in prey quality and availability to nestling growth performance and productivity of breeding adults. The research in 1998 emphasized Pigeon Guillemots and Black-legged Kittiwakes.

Objective 1. To determine the proximate composition of various forage fish species consumed by seabirds in the EVOS area as a function of size, sex, age class, and reproductive status, including:

a) lipid content
b) water content
c) ash-free lean dry matter (protein) content
d) energy density (kJ/g wet mass)

Objective 2. To determine dietary parameters of Pigeon Guillemot and Black-legged Kittiwake chicks in the EVOS area, including:

a) provisioning rate (meal size X meal delivery rate)
b) taxonomic composition of diets
c) biochemical composition of diets
d) energy density of diets

Objective 3. To determine the relationship between diet and the growth, development, and survival of seabird nestlings. Variables measured will include:

a) growth rates of total body mass
b) rates and patterns of wing and flight feather growth
c) fledgling body mass
d) fledging age

Objective 4. To determine the contribution of specific forage fish resources to the overall productivity of seabird breeding pairs and populations, including:

a) relative contribution of each forage fish species to overall energy intake of nestlings
b) gross foraging efficiency of parents
c) conversion efficiency of food to biomass in chicks
d) net production efficiency of the parent/offspring unit
e) estimates of population-level requirements for forage fish resources during brood-rearing

STUDY AREAS

Data collection from the field occurred in PWS (Naked, Jackpot, and Eleanor islands, and Shoup and North Icy bays), LCI (south shore of Kachemak Bay, Gull, Chisik, and the Barren islands), and Middleton Island during the 1998 breeding season. These sites, with the exception of Middleton Island, were identical to those seabird breeding sites that were used in 1996 and 1997 and by other components of APEX.

Field work on Pigeon Guillemots was conducted at breeding colonies on Naked Island (oiled area), Jackpot Island (non-oiled area, both in PWS), and in Kachemak Bay (reference site). Approximately 500 guillemots nest along the shores of Naked Island (Sanger and Cody 1993), supporting a large proportion of the total breeding population of guillemots in PWS. The field camp in Cabin Bay served as the base camp for field studies of guillemots nesting on the western and northern shorelines of Naked Island (see annual report for APEX Component 98163 F by G. Golet). Naked Island has been the site of long term studies of guillemot reproductive ecology since 1979 by the U.S. Fish and Wildlife Service (Kuletz 1983).

Jackpot Island is a small island in southwestern PWS that supports the highest known breeding density of guillemots in the Sound (G. Sanger, D. L. Hayes, pers. comm.). Jackpot Island has been the site of intensive studies of guillemot nesting success since the 1994 field season and is located in a non-oiled portion of PWS. Kachemak Bay served as a third study site for guillemots. The breeding population of guillemots on the south shore of Kachemak Bay between Mallard Bay and Seldovia has been the site of intensive studies of guillemot breeding biology, diet, and productivity since 1994, first by UAF graduate student A. Prichard, and then by M. Litzow and J. Piatt. Results in 1994-96 suggested that the guillemot prey base in parts of Kachemak Bay is largely sand lance, and is perhaps similar to the prey base at Naked Island 15-20 years ago. Consequently, the Kachemak Bay guillemot study site provides an excellent reference site for guillemot studies in PWS.

Field work on Black-legged Kittiwakes in PWS was conducted at three breeding colonies: (1) Shoup Bay in Port Valdez (non-oiled area), the largest kittiwake colony in PWS consisting of c. 8000 breeding pairs, (2) Eleanor Island in central PWS near Knight Island (oiled area), with ca. 200 breeding pairs, and (3) North Icy Bay in south western PWS (non-oiled area), with ca. 500 breeding pairs. The Shoup Bay colony is the site of continuing long-term studies of kittiwake nesting ecology in PWS by the U.S. Fish and Wildlife Service. Eleanor Island and North Icy Bay have been selected as sites for intensive study for comparison purposes (see annual report for APEX Component 98163 E by R. M. Suryan and D. B. Irons). In Lower Cook Inlet, kittiwake breeding colonies at the Barren Islands, Gull Island, and Chisik Island were monitored for diet and reproductive success (see annual reports for APEX Component 98163 J by D. G. Roseneau, A. B. Kettle, and G. V. Byrd and APEX Component 98163 M by J. Piatt et al.) In addition, a kittiwake colony on Middleton Island in the northern Gulf of Alaska was chosen to directly examine the effects of food availability on daily energy expenditure. Approximately 250 pairs of kittiwakes nest on an artificial structure on Middleton Island and have been under the influence of a supplementary feeding experiment since 1996 (Hatch pers. comm.).

METHODS

Field Data Collection

The research approach utilized a combination of sample/data collection in the field (in conjunction with other APEX components in PWS and LCI) and laboratory analyses of seabird diet and forage fish samples. A minimum of 40 active and accessible nests of each species were located and marked prior to hatching at each of the study colonies, and these nests were closely-monitored until the young fledged or the nesting attempt failed. Samples of forage fishes were collected concurrently with data on seabird reproduction during the 1998 breeding season.

Fresh samples of forage fishes used by guillemots were collected for determination of species composition and proximate composition of the diet. Guillemot diet samples were collected opportunistically when dropped fish were encountered during nest checks or by capturing adults in scraps of mist net as they entered the nest crevice with a chick meal held in their bill. Supplemental samples of fishes fed to guillemot chicks were collected using beach seines and minnow traps deployed in guillemot foraging areas and by netting specimens at low tide during spring tide series.

Adult kittiwakes transport chick meals in the foregut, so chick diet samples consist of semi-digested food. Most kittiwake diet samples were collected when chicks regurgitated during routine weighing and measuring. Additional diet samples were collected by capturing adult kittiwakes as they returned to feed their young and encouraging them to regurgitate the contents of their esophagus. Fresh specimens of forage fishes used by kittiwakes were provided by trawl, cast net, dip net, and other methods through the cooperation of APEX Component 98163 A and others.

Guillemot chick meals, kittiwake regurgitations, and fresh fish samples were weighed (± 0.1 g) in the field on battery-powered, top-loading balances, placed in whirl-paks, and immediately frozen in small, propane-powered freezers that were maintained at each of the study sites. Samples of fresh forage fish, guillemot chick meals, and kittiwake regurgitations were shipped frozen to the lab of Dr. Alan Springer and Kathy Turco at the Institute of Marine Science, UAF, where the third author (KRT) sorted, identified, sexed, aged, measured, and determined reproductive status of specimens in preparation for proximate analysis.

Proximate analysis of all samples was conducted in the lab of the first author (DDR) under the direction of the second author (PGRJ) at the Department of Fisheries and Wildlife, Oregon State University. Forage fish specimens and chick meals were reweighed on an analytical balance (± 0.1 mg) and dried to constant mass in a convection oven at 60°C to determine water content. Lipid content of dried samples was determined by solvent extraction for a minimum of ten hours using a soxhlet apparatus and hexane/isopropyl alcohol 7:2 (v:v) as the solvent system. Lean dry samples were then transferred from extraction thimbles to glass scintillation vials and ashed in a muffle furnace at 600°C for 12 hours in order to calculate ash-free lean dry mass (ca. 94 % protein) by subtraction. Energy density (kJ/g wet mass) and energy content of forage fishes and chick meals were calculated from their composition (% water, lipid, ash-free lean dry matter, and ash), using published energy equivalents of these fractions (Schmidt-Nielsen 1997: 171).

Chick provisioning rates for Pigeon Guillemots and Black-legged Kittiwakes at each of the study sites were determined by monitoring active nests to determine meal delivery rates (meals/day) throughout the 24 h period (dawn to dusk watches). Average meal mass was determined for guillemots using the sample of individual prey items collected at nest sites. Average meal mass for Black-legged Kittiwakes was estimated from average mass of regurgitations recovered from chicks that had just been fed and from adults that had just returned to the colony from foraging trips. These data were supplemented with data on meal size from a few colonies using the periodic weighing technique. Nestlings were weighed in a sample of nests at 2-hour intervals during concurrent watches to determine meal delivery rates. The mass increment between weighings of chicks that were fed was corrected for mass loss between weighings and feedings by adding the average of mass loss in the previous 2-hour period and mass loss in the subsequent 2-hour period to the observed mass increment. This corrected mass increment was used as an estimate of meal size. The product of average meal size (g) and average meal delivery rate (meals/day) was used as an estimate of average quantity of food delivered to a nest daily by a pair of adults (g/(nest day)). The taxonomic and proximate composition of the diet was used to calculate average energy density of chick diets for each species at each site. Finally, the product of average energy density of chick diets (kJ/g wet mass) and average quantity of food delivered (g/(nest day)) was used as an estimate of energy provisioning rates (kJ/(nest day)) for each species at each site.

Active guillemot and kittiwake nests were checked every few days during the hatching period in order to determine hatching date. In the case of two-chick broods, siblings were marked soon after hatching so that individual growth rates could be monitored throughout the nestling period. Nestling growth rates were determined by weighing and measuring chicks on a regular basis (every 3-5 days) throughout the nestling period. Nestling survival rates were calculated from the results of periodic nest checks, using the Mayfield method.

During the fledging period, we attempted to check nests and weigh nestlings more frequently in order to more precisely determine fledging mass and age. Data on nestling body mass, wing chord, and primary feather length were separated by colony for each species.

Parental investment by adult kittiwakes raising broods was assessed by measuring daily energy expenditure (DEE) of breeding adults during the chick-rearing period. DEE was determined by measuring CO_2 production using the doubly-labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980, Roby and Ricklefs 1986, Speakman 1997). DEE of adult kittiwakes was measured at the Shoup Bay and North Icy Bay colonies in 1997 and 1998, as representative of kittiwake colonies of different size, productivity, and food availability. Twenty-five nesting adults were injected with doubly-labeled water during the chick-rearing period at each of these colonies. DEE of adult kittiwakes feeding young also was measured at Middleton Island in 1998. Eighty kittiwakes were injected with DLW over 6 days; 40 were birds that received ad libidum supplemental feeding three times / day and 40 were birds that did not receive supplemental feeding.

Parent kittiwakes were captured at the nest with a noose pole and injected intraperitoneally with 0.9 ml (Shoup and Icy bays) or 0.4 ml (Middleton Island) of a mixture of deuterated (99.8 atom %) and oxygen-18 labeled (90 atom %) water ($D_2{}^{18}O$). These two isotopes are stable, so no permits for use of radioactive materials were necessary. Following injection, each adult was banded, weighed, measured, and marked with dye on the plumage for easy recognition on the colony. One hour after injection, when injected DLW had equilibrated with body water, a blood sample was collected from each adult by puncturing the brachial vein and collecting about 100 ul of blood in non-heparinized microhematocrit tubes, which were subsequently flame-sealed and kept refrigerated. Injected adults were then released and an attempt was made to recapture each adult at least once in the subsequent 48-hour period at Shoup and Icy bays or once in the subsequent 24-hour period at Middleton Island. Once recaptured, injected adults were reweighed and a second blood sample collected as described above. Isotope enrichments of blood samples were measured using mass spectrometry in the laboratory of Dr. Henk Visser (Centre for Isotope Research, University of Groningen, The Netherlands). Carbon dioxide production of each adult during each measurement interval was calculated using the equations of Speakman (1997). DEE was calculated from CO_2 production using an assumed RQ of 0.8 and an energetic equivalent of respired CO_2 of 27.3 kJ/liter (Gessamen and Nagy 1988).

RESULTS AND DISCUSSION

Objective 1: Proximate Composition of Forage Fishes

Analysis of proximate composition of forage fishes continued during 1998. Approximately 63 Pigeon Guillemot and 178 Black-legged Kittiwake chick meals were collected and analyzed for the 1998 field season. Notable additions to the prey species analyzed include surf smelt (*Hypomesus pretiosus*) from Chisik Island, euphausiid spp. from Icy Bay, salmon eggs from PWS Black-legged Kittiwake colonies, and a time series of surf smelt from LCI. Results and discussion from analyses completed prior to the

1998 field season represent the majority of these analyses and are presented in the manuscript attached to last years annual report: "Lipid content and energy density of forage fishes from the northern Gulf of Alaska" by J.A. Anthony, D.D. Roby, and K.R. Turco. This manuscript has been submitted to the peer-reviewed Journal of Experimental Marine Biology and Ecology.

Objective 2: Dietary Parameters of Nestling Seabirds

Pigeon Guillemots

Sixty-three Pigeon Guillemot chick meals were collected from the colonies at Jackpot Island, Naked Island, and Kachemak Bay during 1998 (Table 1). Nineteen fish species were identified in the diet and the number of prey species collected at each study area appeared similar (Table 2). However, 13 prey species were unique to a single study area and only two prey species (slender eelblenny *Lumpenus fabricii* and ribbed sculpin *Triglops pingeli*) were collected at all three Pigeon Guillemot study sites. Tables 3-5 show the taxonomic composition, average item mass, and the percent of the total biomass for each prey species at each site.

Pigeon Guillemot nestling diets assessed during day-long nest watches are used to determine the proportion of the total deliveries represented by each prey species or forage-fish group. These are hereafter referred to as meal delivery rate (MDR) diets and appear in Figure 1. MDR diets differed from chick meal collection diets at two sites in 1998 (compare Tables 3-5 with Figure 1). For example, at Jackpot Island, Pacific herring were under-represented and gadids over-represented in the collection diet. Similarly, at Kachemak Bay, gadids and blennies were under-represented and sculpins over-represented in the collection diet. However, as all meals collected at Kachemak Bay were discards, the collection diet may not be entirely accurate. Diet as determined from collections and MDR appeared similar at Naked Island in 1998. These differences demonstrate the importance of collecting both types of diet data.

As in previous years, blennies, crescent gunnels (*Pholis laeta*), and various sculpins (Cottidae) continued to comprise a large proportion of the number of items delivered to the nests of Pigeon Guillemots at all three study areas (Figure 1). This consistent pattern among years at all study areas likely reflects the relative availability of these items near nest sites. Despite the relative importance of these nearshore demersal fishes to nestling diets at all nesting areas in 1998, some differences in diet composition among the three study areas did occur this year. For example, Naked Island and Kachemak Bay diets were the most similar, consisting primarily of nearshore demersal fishes. Sand lance continued to comprise a smaller proportion of the diet at these two sites. However, the Jackpot Island diet differed from these two locations; here, Pacific herring was the most dominant prey item numerically, although nearshore demersals continued to be important. Annual shifts in diets within nesting areas were inconsistent. Diet composition at Kachemak Bay and Naked Island in 1998 was similar to that observed in 1997. The most notable aspect of each of these diets is the relatively low proportion of schooling fish in the diet, especially at Kachemak Bay where sand lance were more prevalent in 1994 - 1996. In contrast, the diet at Jackpot Island in 1998 differed substantially from that of 1997. Pacific herring, which were an important item in the diet of Jackpot Island guillemots in 1994 and 1995, rebounded considerably.

The average mass of chick meals collected at each of the three sites in 1998 appeared similar to values obtained in 1997 (Table 6). Chick meals at Jackpot Island tended to be the largest while those at Kachemak Bay and Naked Island were somewhat smaller (about half the mass of those at Jackpot Island) and similar to each other. Meal size at Jackpot Island and Kachemak Bay in 1998 appeared similar to previous years. Meals collected at Naked Island in 1998, although similar to 1997 in size, still showed an approximate 35% decrease from the first two years of the study.

Feeding frequency also appeared similar among the three study sites, ranging from 11.1 to 13.1 meals delivered per nest day (Table 6). These values and their ranking among sites were similar to 1997. The total amount of food delivered to nests, however, did not appear to be similar among the three study sites in 1998. As in previous years, higher food delivery rates to nests were observed at Jackpot Island (237 g/day) than at Naked Island (130 g/day) or Kachemak Bay (117 g/day). Furthermore, the amount of food delivered to Kachemak Bay nests in 1998 appeared to decrease from 1997 (197 g/day), and although the daily amount of food delivered to Naked Island increased between 1997 and 1998, it was still less than the amount measured in 1995 and 1996 (~165 g/day).

Diet quality in 1998 (as determined by average energy density of collected prey items) was similar among study sites (Table 6). Compared to 1997, however, the average energy density decreased slightly at Kachemak Bay, increased slightly at Naked Island, and remained similar at Jackpot Island. Energy provisioning rates also increased at Jackpot Island and Naked Island but decreased substantially at Kachemak Bay. The increase at Jackpot Island appears to be due to an increase in mean meal size (possibly due to more herring being delivered as opposed to blennies; Table 3) while at Naked Island it appears due to increases in both delivery rate and increased energy density of food. The decrease in EPR at Kachemak Bay was due primarily to a decrease in delivery rate. However, as all of the meals collected at Kachemak Bay nests in 1998 were discards, it is difficult to assess the reliability of the average energy density value used to calculate energy provisioning rate.

Black-legged Kittiwakes

A total of 118 adult and 60 whole chick meals were collected from the six Black-legged kittiwake colonies in PWS and LCI (Table 7). The average number of species / meal ranged from 1.0 to 1.4 at all colonies (Table 8). As in previous years, Pacific herring, Pacific sand lance, and capelin made up the majority of the diet and accounted for 41.1%, 27.3%, and 19.0% of the biomass, respectively, when data were pooled among all six colonies. Pacific herring were more common in meals collected at PWS colonies while at LCI colonies sand lance and capelin were more common (Figure 2). Sand lance, Pacific herring, and capelin combined for the lowest proportion of biomass in the diet

(79%) at Shoup Bay. Shoup Bay kittiwake diets also had the greatest number of species in collected meals.

Diets at each colony in 1998 appeared to shift from those observed in 1997 (Figure 3). In general, PWS colonies experienced an increase in the proportion of 1+ Pacific herring and a decrease in the proportion of YOY sand lance in the diet. The proportion of older sand lance in the diets at Shoup and Icy bays appeared to remain similar in 1998, however. Unlike Shoup and Icy bays, the kittiwakes at Eleanor Island experienced a large increase in the proportion of YOY sand lance in the diet while the proportion of 1+ capelin decreased dramatically. In LCI, all colonies experienced a dramatic decrease in the proportion of YOY sand lance in the diet. Chisik and the Barrens had substantial increases in the proportion of 1+ osmeriids (i.e., capelin and unidentified osmeriids, the latter appears in the 'other' category of Fig. 3), while kittiwakes at Gull Island experienced a dramatic increase in 1+ sand lance. Euphausiid spp., which appeared to be an important part of the diet at the Barrens in 1997, did not occur in the diet in 1998 at any colonies in LCI. Adult meals containing euphausiid spp. were, however, collected at Icy Bay. Additionally, one regurgitation with longfin smelt (*Spirinchus dilatus*) were collected from both Icy Bay and Eleanor Island.

Average nestling meal sizes at all six Black-legged Kittiwake colonies were estimated from the average mass of whole chick and adult regurgitations (Table 9). Unlike 1997, mean meal size in PWS varied more than in LCI. Chick meals collected in 1998 compared with 1997 appeared to decrease in size at Eleanor, the Barrens, and Gull and appeared to remain similar at the other three colonies. Meals at Shoup Bay (24.4 g, n = 59) appeared to be larger than at all other colonies, while meals at Eleanor (~ 10.0g, n =15) appeared to be smaller than those at other colonies. This pattern may have been due to the prevalence of 1+ herring in the diet at Shoup Bay and YOY sand lance in the diet at Eleanor Island (Figure 3). Meal sizes at the other four colonies appeared similar (range 15.6 g - 18.9 g).

As in 1997, feeding frequencies in 1998 appeared to be higher at Icy Bay than at any of the other colonies (Table 9). Additionally, the feeding frequency at Icy Bay appeared to be slightly higher in 1998 than in 1997 while average meal sizes at Icy Bay were similar in 1997 and 1998, resulting in a slight increase in the amount of food delivered to nestlings to ~ 90 g / nest day. Feeding frequencies appeared to be similar between kittiwakes nesting at Eleanor and Gull islands during 1998. Because of differences in average meal sizes at each colony, however, the amount of food delivered to nestlings differed (~ 45g / nest day at Eleanor and ~ 65 g / nest day at Gull). Amount of food delivered to kittiwake nests in the barrens remained similar between 1997 and 1998 (~ 65 g / day) as feeding frequency increased but meal size decreased. The decrease in meal size may be due in part to small sample sizes of meals in 1997 (n = 11) and two meals in 1997 with large amounts of euphausiids (37 g and 40 g). None the less, it still appears that meal size decreased in 1998. Feeding frequency for kittiwakes at Shoup Bay did not change from 1997. These birds had the lowest feeding frequency of any colony during 1998, although lower feeding frequencies may have been partially offset by larger meal sizes. This resulted in ~ 75 g of food being delivered / nest day at Shoup, a slightly higher value than observed in LCI but lower than observed at Icy Bay.

Diet quality (as determined from energy density of collected meals) at Shoup and Icy bays during 1998 remained similar to values observed in 1997 (Table 9). Energy density of meals at Eleanor Island, however, appeared to decrease from 1997. This led to a greater range in mean energy density values at the three PWS colonies. At LCI colonies, energy density values appeared to be less divergent than in 1997.

Energy provisioning rates appeared to remain similar at 4 colonies (Shoup Bay, Icy Bay, Barren Islands, and Gull Island) and decrease at one (Eleanor Island; Table 9). Energy provisioning rates were not available for Chisik Island due to total colony failure. As in 1997, the energy provisioning rate was highest at Icy Bay. All 1998 energy provisioning rate values are, however, still lower than those observed during 1995 and 1996 at Shoup Bay. Feeding frequencies appear to be limiting energy provisioning rates at Shoup Bay and the Barrens, while meal size appears to have limited energy provisioning rates at Gull this year. The extreme drop in energy provisioning rate at Eleanor was due to smaller meal sizes which were likely due to wide-spread nest predation and a decrease in sampling effort during the latter portions of the breeding season, when larger meals and a shift in diet to capelin likely would have been observed. In 1998, energy provisioning rate was > 400 kJ/nest day only at Icy Bay.

Objective 3: Diet and Productivity

Pigeon Guillemots

Nesting productivity of Pigeon Guillemots in 1998 was mediocre to poor at all three study sites. Mink nest predation was the primary cause of poor productivity at Naked Island, although prior to much of the predation chick growth rates appeared to be poor also. These results are in agreement with the low energy provisioning rates observed at Naked Island in 1998. In fact, energy provisioning rates at Naked Island were substantially lower in 1997 and 1998 when compared to 1995 and 1996, although even those energy provisioning rates were low compared to 1995 at Jackpot Island. Productivity of Pigeon Guillemots at Kachemak Bay also was low in 1998, continuing a trend of lowered productivity over the past two years. Similarly, energy provisioning rate at Kachemak Bay in 1998 also was substantially lower than that observed in 1997 and slightly lower than that observed in 1996. Productivity and chick growth rates of Pigeon Guillemots at Jackpot Island in 1998 were similar to those observed in 1997 and greater than those observed at Kachemak Bay and Naked Island in 1998. Similarly, energy provisioning rates at Jackpot Island in 1998 were similar to those observed in 1997 yet substantially higher than those observed at the other two study sites in 1998. Neither productivity nor energy provisioning rates at Jackpot Island have returned to levels observed in 1995 or 1994.

Black-legged Kittiwakes

The productivity of Black-legged Kittiwakes in 1998 was poor at all colonies except Icy Bay despite the prevalence of older Pacific herring, sand lance, and capelin in the diet at each colony. Productivity at Icy Bay in 1998 was the highest recorded over the past few years at any of the study colonies and energy provisioning rates there appear slightly higher than last year. In contrast, productivity at the other five colonies in 1998 was similar to or lower than 1997 levels, although predation was at least partly responsible for lower productivity at Eleanor Island. Similarly, energy provisioning rates at these five colonies also were similar to or lower than those observed in 1996 or 1997, suggesting food resources may be limiting productivity despite the presence of high quality prey in the diet at each colony (Table 9, Figure 3). Delayed nest initiation at Gull Island and the Barren Islands, longer foraging trips at Shoup Bay, lower feeding frequencies at Shoup Bay and Chisik Island, lower meal sizes at Eleanor, Gull, and Chisik islands, and lower forage fish densities from surveys all suggest that availability of high quality prey items may have been limited temporally and spatially in 1998. Furthermore, a comparison of energy provisioning rates and productivity at Black-legged Kittiwakes colonies in PWS and LCI since 1995 suggest a positive correlation between the two metrics and indicate that productivity usually appears to be poor for Black-legged Kittiwakes at these colonies when energy provisioning rates drop below 400 kJ / nest day.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

As in 1997, the average Pigeon Guillemot prey size at Jackpot Island in 1998 continued to be higher than at Naked Island or Kachemak Bay. Diet quality appeared to improve at Naked Island and Jackpot Island in 1998; unfortunately, a small sample size of collected meals from Kachemak Bay in 1998 prohibits a sound comparison of energy density values among all colonies. An increased proportion of 1+ Pacific herring in the diet at Jackpot Island compared to last year contributed to the increase in energy density and energy provisioning rates at that colony in 1998. The importance of schooling fish in the diet is further supported by the return of 1+ Pacific herring in the diets of Black-legged Kittiwakes at Shoup and Icy bays. Furthermore, Black-legged Kittiwakes in LCI appeared to be opportunistic and continued to make use of a variety of high energy osmeriids as well as 1+ sand lance. It appears that although such high quality prey items are essential for good/high productivity, mere presence of these items in the diet does not insure high productivity. Other factors, such as sufficient availability near colonies early in the breeding season, affect productivity via the interaction with breeding phenology and feeding frequency. These relationships continue to highlight the importance of collecting an array of data at multiple time and space scales.

In an effort to further improve our understanding of relationships between foraging and breeding biology of seabirds in the northern Gulf of Alaska, we investigated daily energy expenditure (DEE) of Black-legged Kittiwakes in 1997 and 1998. We used doubly-labeled water to measure field metabolic rates of adults with chicks at Shoup and Icy bays in 1997 and 1998. Our objective was to determine if DEE varied among colonies within years or within colonies among years. We also sought to determine if there was a relationship between DEE and either productivity or energy provisioning rate. Furthermore, we examined DEE of Black-legged Kittiwakes at Middleton Island in 1998. Although not located in PWS, Middleton Island provides a unique opportunity to directly examine the role of food availability on DEE. Here, a manipulative experiment has been underway since 1996 with a treatment group of nests receiving ad libidum supplemental food three times / day and a control group of nests receiving no supplemental food each day. We hypothesized that the treatment group would exhibit lower DEE than the control group. We also hypothesized that the treatment group at Middleton would exhibit lower DEE than Black-legged Kittiwakes at Shoup or Icy bays.

Figure 4 shows the distribution of DEE values for Black-legged Kittiwakes at each colony. Despite having only half of the DEE analyses completed from Shoup and Icy bays in 1998, an ANOVA still revealed a significant difference among many of the colony-by-year groups. Kittiwakes at Icy Bay in 1998 had a higher mean DEE than kittiwakes in any of the other groupings and the fed kittiwakes at Middleton Island had a lower mean DEE than kittiwakes in any of the other groupings. There were no other pairwise comparisons that were significantly different. This pattern suggests a convex relationship where DEE and productivity are lower when food availability is low (Shoup Bay 1997 & 1998, Icy Bay 1997), DEE and productivity rise as food availability improves (Icy Bay 1998), and DEE decreases but productivity remains stable or increases as food becomes super abundant (Middleton fed birds). These relationships may become clearer in 1999 when we plan on measuring DEE in conjunction with direct observations of foraging behavior.

CONCLUSIONS

Objective 1: Proximate Composition of Forage Fishes

- Please see manuscript "Lipid content and energy density of forage fishes from the northern Gulf of Alaska" attached to the 1997 annual report.

Objective 2: Dietary Parameters of Nestling Seabirds

Pigeon Guillemots

- As in 1997, nearshore demersal fishes (blennies, gunnels, and sculpins) provided the majority of the biomass in Pigeon Guillemot diets at all three study sites.

- Herring rebounded at Jackpot Island in 1998, with the overall diet appearing more similar to that observed in 1994 - 1996.

- Sand lance did not rebound at Kachemak Bay and continued to comprise a smaller proportion of the diet than observed in 1994 - 1996.

- Energy provisioning rates increased at Jackpot Island (due mostly to an increase in Pacific herring and average energy density of prey) and Naked Island (increase in feeding frequency and energy density). In contrast, energy provisioning rates decreased drastically at Kachemak Bay (sharp drop in feeding frequency).

Black-legged Kittiwakes

- In 1998, 1+ Pacific herring rebounded at Shoup and Icy bays while the proportion of 1+ capelin and osmeriids increased at Chisik Island and the Barrens.

- Young of the year sand lance accounted for less biomass in the diets at all colonies in 1998 compared with 1997, except at Eleanor Island. Despite the relatively high availability of young of the year sand lance at most colonies in 1997, there was not an increase in the biomass of 1+ sand lance in the diets at most colonies in 1998 (with the exception of Gull Island).

- At each colony except Icy Bay, energy provisioning rates in 1998 did not improve and remained < 400 kJ/day. As in 1997, Icy Bay had higher EPRs than all other colonies. EPR at Icy Bay was still less than that observed in 1996 at Shoup Bay, however.

- The diets observed in 1998 appeared to differ from those observed in 1997 at all colonies. Most colonies saw an increase in 1+ schooling fish (Pacific herring in PWS, capelin, unidentified osmeriids, and sand lance in LCI). The exception to this was Eleanor Island, where young of the year sand lance dominated the diet.

Objective 3: Diet and Productivity

Pigeon Guillemots

- Productivity was similar at Jackpot Island in 1998 compared to 1997, in agreement with similar energy provisioning rates between the two years. Productivity was still substantially lower, however, than that observed in 1994.
- Productivity at Kachemak Bay was lower in 1998 than 1997, in agreement with lower energy provisioning rates in 1998.
- Productivity at Naked Island was poor in 1998 due to nest predation by mink.

Black-legged Kittiwakes

- Only at Icy Bay was productivity high in 1998 and improved compared to 1997; energy provisioning rates continued to be > 400 kJ / nest day at Icy Bay.
- Productivity in 1998 at Eleanor Island was low due to nest predation by peregrine falcons.
- Productivity in 1998 at all other colonies was lower than in 1997, in agreement with declines in energy provisioning rates at each colony.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

Pigeon Guillemots

- Diet quality improved at Jackpot Island in 1998 concurrent with a return of Pacific herring to the diet; this forage fish species was noticeably absent in 1997.
- Diet quality remained similar at Kachemak Bay and Naked Island, with low proportions of schooling fish in the diet at both sites. The proportion of sand lance in the diets at Kachemak Bay guillemots remained lower than 1994 - 1996.
- Higher proportions of schooling forage fish in the diet was associated with higher energy provisioning rates to chicks.

Black-legged Kittiwakes

- Despite the appearance of generally high quality fish in the diet at each colony, productivity in 1998 remained low at all colonies but Icy Bay. Young of the year sand lance comprised smaller proportions of the diet at each colony in 1998, except at Eleanor Island.
- A variety of other data suggest that, although present in the diet, sufficient quantities of high quality prey may not have been available early enough in the season or near enough to most colonies (with the exception of Icy Bay) to maintain high productivity. This was supported by higher nest failure rates during incubation
- Colonies in LCI relied on capelin and unidentified osmeriids to compliment sand lance in the diet.
- As with last year, the trend in the early years of APEX of higher Black-legged Kittiwake productivity associated with increasing availability of sand lance, capelin, and Pacific herring was not restored, with productivity remaining poor at all colonies except Icy Bay.
- Doubly-labeled water studies of adult kittiwake energetics from PWS and Middleton Island indicated that DEE of Black-legged Kittiwakes may be highest at intermediate levels of food availability.

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LITERATURE CITED

Asbirk, S. 1979. The adaptive significance of the reproductive pattern in the black guillemot, *Cepphus grylle*. Vidensk. Meddr. dansk naturh. Foren. 141:29-80.

Anthony, J.A., D. D. Roby, and K. R. Turco. Unpubl. ms. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Sumitted to J. Exp. Mar. Biol. Ecol.

Ashmole, N. P. 1971. Seabird ecology and the marine environment. Pp. 223-286 in D. S. Farner and J. R. King (eds.), Avian Biology, Vol. 1. Academic Press, New York.

Barrett, R. T., T. Anker-Nilssen, F. Rikardsen, K. Valde, N. Rov, and W. Vader. 1987. The food, growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980-1983. Ornis Scand. 18: 73-83.

Birt-Friesen, V. L., W. A. Montevecchi, D. K. Cairns, and S. A. Macko. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70:357-367.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911-917.

Clarke, A. in press. Seabirds. in R. G. Ackman (ed.), Marine Biogenic Lipids. Chemical Rubber Co.

Dick, M. H., and I. M. Warner. 1982. Pacific sand lance, *Ammodytes hexapterus* Pallas, in the Kodiak island group, Alaska. Syesis 15:43-50.

Dragoo, D. E. 1991. Food habits and productivity of kittiwakes and murres at St. George Island, Alaska. Unpubl. M.S. thesis, University of Alaska, Fairbanks. 104 pp.

Drent, R. H. 1965. Breeding biology of the pigeon guillemot, *Cepphus columba*. Ardea 53:99-159.

Ellis, H. I. 1984. Energetics of free-ranging seabirds. Pp. 203-234 in G. C. Whittow and H. Rahn (eds.), Seabird Energetics. Plenum Press, New York.

Flint, E. N., G. L. Hunt, Jr., and M. A. Rubega. 1990. Time allocation and field metabolic rate in two sympatric kittiwake species. Acta XX Congressus Internationalis Ornithologici, Supplement, pp. 426-427. (Abstract).

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt, Jr. In press. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In The status, ecology and conservation of marine birds of the North Pacific, K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey (eds.). Can. Wildl. Serv. Spec. Pub., Ottawa.

Hislop, J. R. G., M. P. Harris, and J. G. M. Smith. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J. Zool., Lond. 224: 501-517.

Hunt, G. L., Jr., B. Burgeson, and G. A. Sanger. 1981a. Feeding ecology of seabirds in the eastern Bering Sea. Pp. 629-647 in D. W. Wood and J. A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources. Vol. 1, U.S. Gov. Printing Office, Washington, D.C.

Hunt, G. L., Jr., Z. Eppley, B. Burgeson, and R. Squibb. 1981b. Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands, 1975-1979. Environ. Assess. Alaskan Contin. Shelf, Ann. Rep. Princ. Investig. NOAA Environ. Res Lab., Boulder, CO 12: 1-258.

Kuletz, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. M.S. Thesis, Univ. of California, Irvine. 79 pp.

Laing, K. K., and S. P. Klosiewski. 1993. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Bird Study No. 2. Final Report. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska.

Lance, B. K., and D. D. Roby. Unpubl. ms. Diet and postnatal growth in Red-legged and Black-legged Kittiwakes: an interspecies fostering experiemnt. Submitted to The Auk.

Massias, A., and P. H. Becker. 1990. Nutritive value of food and growth in common tern *Sterna hirundo* chicks. Ornis Scand. 21: 187-194.

Montevecchi, W. A., and J. Piatt. 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comp. Biochem. Physiol. 78A: 15-20.

Montevecchi, W. A., R. E. Ricklefs, I. R. Kirkham, and D. Gabaldon. 1984. Growth energetics of nestling gannets (*Sula bassanus*). Auk 101: 334-341.

Oakley, K. 1981. Determinants of the population size and distribution of the pigeon guillemot (*Cepphus columba*) at Naked Island, Prince William Sound, Alaska. M.S. Thesis, Univ. of Alaska, Fairbanks. 65 pp.

Oakley, K., and K. J. Kuletz. ms. Population, reproduction and foraging ecology of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Bird Study Number 9. Final Report. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska.

Obst, B. S., K. A. Nagy, and R. E. Ricklefs. 1987. Energy utilization in Wilson's Storm-petrel (*Oceanites oceanicus*). Physiol. Zool.

Prichard, A.K. 1997. Evaluation of Pigeon Guillemots as bioindicators of nearshore ecosystem health. Unpubl. M.S. thesis, Univ. Alaska Fairbanks. 93p.

Prince, P. A., and C. Ricketts. 1981. Relationships between food supply and growth in albatrosses: an interspecies chick fostering experiment. Ornis Scand. 12: 207-210.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292 in R. A. Paynter (ed.), Avian Energetics. Publ. Nuttall Ornithol. Club, No. 15.

Ricklefs, R. E. 1979. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. 54: 269-290.

Ricklefs, R. E. 1983a. Some considerations on the reproductive energetics of pelagic seabirds. Studies in Avian Biology No. 8: 84-94.

Ricklefs, R. E. 1983b. Avian postnatal development. Pp. 1-83 in D. S. Farner, J. R. King, and K. C. Parkes (eds.), Avian Biology, Vol. 7. Academic Press, New York.

Ricklefs, R. E. 1984. Meal sizes and feeding rates of Christmas Shearwaters and Phoenix Petrels on Christmas Island, Central Pacific Ocean. Ornis Scand. 15: 16-22.

Ricklefs, R. E., S. C. White, and J. Cullen. 1980a. Postnatal development of Leach's Storm-petrel. Auk 97: 768-781.

Ricklefs, R. E., S. C. White, and J. Cullen. 1980b. Energetics of postnatal growth in Leach's Storm-petrel. Auk 97: 566-575.

Ricklefs, R. E., C. H. Day, C. E. Huntington and J. B. Williams. 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. J. Anim. Ecol. 54: 883-898.

Ricklefs, R. E., A. R. Place, and D. J. Anderson. 1987. An experimental investigation of the influence of diet quality on growth in Leach's Storm-Petrel. Am. Nat. 130: 300-305.

Roby, D. D. 1989. Chick feeding in the diving petrels *Pelecanoides georgicus* and *P. urinatrix exsul*. Antarctic Science 1: 337-342.

Roby, D. D. 1991a. Diet and postnatal energetics in two convergent taxa of plankton-feeding seabirds. Auk 108: 131-146.

Roby, D. D., and R. E. Ricklefs. 1986. Energy expenditure in adult Least Auklets and diving petrels during the chick-rearing period. Physiol. Zool. 59: 661- 678.

Sanger, G. A., and M. B. Cody. 1993. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. Draft Final Report, Restoration Project 93034, U.S. Fish and Wildlife Service, Anchorage, AK.

Sargent, J. R. 1976. The structure, metabolism and function of lipids in marine organisms. Pp. 149-212 in D. C. Malins and J. R. Sargent (eds.), Biochemical and Biophysical Perspectives in Marine Biology, Vol. 3. Academic Press, London.

Shea, R. E., and R. E. Ricklefs. 1985. An experimental test of the idea that food supply limits growth in a tropical pelagic seabird. Am. Nat. 126: 116-122.

Simons, T. R., and G. C. Whittow. 1984. Energetics of breeding Dark-rumped Petrels. Pp. 159-181 in G. C. Whittow and H. Rahn (eds.), Seabird Energetics. Plenum Press, New York.

Sowls, A. L., S. A. Hatch, and C. J. Lensink. 1978. Catalog of Alaskan seabird colonies. U.S. Dept. Interior, Fish and Wildlife Service, FWS/OBS-78/78.

Speakman, J.R. 1997. Doubly Labelled Water. Theory and Practice. Chapman and Hall, London.

Springer, A. M. 1992. A review: walleye pollock in the North Pacific--how much difference do they really make? Fish. Oceanogr. 1: 80-96.

Springer, A. M., and G. V. Byrd. 1988. Seabird dependence on walleye pollock in the southeastern Bering Sea. Pp. 667-677 in International symposium on the biology and management of walleye pollock. Lowell Wakefield Fish. Symp. 7, Alaska Sea Grant Rep. 89-1.

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

Walsberg, G. E. 1983. Avian ecological energetics. Pp. 161-220 in D. S. Farner and J. R. King (eds.), Avian biology, Vol. 7. Academic Press, New York.

Wanless, S., and M. P. Harris. 1992. Activity budgets, diet and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May. Bird-Study 39: 145-154.

LIST OF TABLES

LIST OF FIGURES

Table 1. Number of meals collected at Pigeon Guillemot nests from adults, chicks, and discards at three study sites in the northern Gulf of Alaska, July - August 1998.

	Jackpot Island	Kachemak Bay	Naked Island	All sites
Sampling Effort				
No. nests	20	4	12	36
Collection days	17	3	12	32
Dates	7/15 - 8/10	7/10 - 8/01	7/07 - 8/03	7/07 - 8/10
Meals Collected				
No. adult meals	12	0	6	18
No. chick meals	5	0	0	5
No. discard meals	14	13	13	40
Total meals	31	13	19	63

Table 2. Number of items of each prey species collected at Pigeon Guillemot nests at three study sites in the northern Gulf of Alaska, July - August 1998.

Species	# sites	Jackpot Island	Kachemak Bay	Naked Island
Crested Sculpin	1	1	0	0
Great Sculpin	1	0	3	0
Ribbed Sculpin	3	1	1	2
Rough-spined Sculpin	1	2	0	0
Unknown Sculpin	1	0	1	0
Red Irish Lord	1	0	2	0
Northern Ronquil	2	5	0	1
Crescent Gunnel	2	4	0	3
Arctic Shanny	1	0	2	0
Daubed Shanny	1	0	0	2
Snake Prickleback	1	2	0	0
Slender Eelblenny	3	1	1	1
Flatfish	1	0	0	1
Rock Sole	1	0	0	1
Ling Cod	1	0	0	3
Pacific Cod	1	3	0	0
Walleye Pollock	1	4	0	0
Pacific Herring	2	8	0	1
Sand Lance	2	0	3	4
Species richness	19	10	7	10

Table 3. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to Pigeon Guillemot broods at Jackpot Island, Prince William Sound, Alaska, July - August 1998.

Species	Number of prey items	Average mass g	% Total biomass of prey
Pacific Herring	8	18.19	23.75
Walleye Pollock	4	35.13	22.93
Pacific Cod	3	41.38	20.26
Northern Ronquil	5	12.29	10.03
Rough-spined Sculpin	2	21.50	7.02
Snake Prickleback	2	15.10	4.93
Crescent Gunnel	4	6.82	4.45
Crested Sculpin	1	26.75	4.36
Ribbed Sculpin	1	7.47	1.22
Slender Eelblenny	1	6.42	1.05

Table 4. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to Pigeon Guillemot broods at Kachemak Bay, lower Cook Inlet, Alaska, July - August 1998.

Species	Number of prey items	Average mass (g)	% Total biomass of prey
Red Irish Lord	2	17.66	25.80
Great Sculpin	3	11.76	25.78
Pacific Sand Lance	3	6.61	14.48
Slender Eelblenny	1	18.90	13.81
Ribbed Sculpin	1	16.72	12.21
Unknown Sculpin	1	6.25	4.57
Arctic Shanny	2	2.28	3.34

Table 5. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to Pigeon Guillemot broods at Naked Island, Prince William Sound, Alaska, July - August 1998.

Species	Number of prey items	Average mass (g)	% Total biomass of prey
Crescent Gunnel	3	11.90	18.96
Pacific Sand Lance	4	8.11	17.24
Ribbed Sculpin	2	13.78	14.64
Daubed Shanny	2	11.62	12.34
Ling Cod	3	5.97	9.52
Slender Eelblenny	1	15.89	8.44
Pacific Herring	1	14.33	7.61
Rock Sole	1	14.17	7.52
Flatfish	1	5.99	3.18
Northern Ronquil	1	1.03	0.55

Table 6. Average feeding frequency, meal size, energy density, and energy provisioning rates to Pigeon Guillemot broods at three study sites in the northern Gulf of Alaska, 1995 - 1998.

Location / Year	Feeding frequency (meals/nest day)[1]	Meal size (g)	Energy density (kJ / g wet mass)	Energy provisioning rate (kJ / nest day)[2]
Jackpot Island				
1995	13.8	20.0	4.2	1158
1996	?	?	?	?
1997	12.7	17.1	4.1	890
1998	12.0	19.8	4.2	997
Kachemak Bay				
1995	?	?	5.2	?
1996	10.9	11.4	5.1	634
1997	16.2	12.2	5.0	989
1998	11.1	10.5	4.5	532
Naked Island				
1995	11.4	14.7	4.4	737
1996	11.6	14.2	4.4	725
1997	11.2	9.7	4.0	434
1998	13.1	9.9	4.4	570

[1] Nest days are 16 hour observation periods.
[2] Energy provisioning rate = feeding frequency * meal size * energy density.

Table 7. Number of regurgitated meals collected at Black-legged Kittiwake nests from adults and chicks (whole = complete chick meals, random = partial chick meals) at six colonies in the northern Gulf of Alaska, June - August 1998.

	Adult	Whole	Random	Total
Eleanor Island	10	5	18	33
Icy Bay	25	11	50	86
Shoup Bay	17	42	182	241
Barren Islands	23	2	0	25
Chisik Island	16	0	0	16
Gull Island	27	0	76	103
Total	118	60	326	514

Table 8. Mean (± 1 s.e.) number of prey species / chick meal in regurgitations collected from Black-legged Kittiwakes at six colonies in the northern Gulf of Alaska, June - August 1998.

	Adult	Chick
Eleanor	1.4 (0.16)	1.2 (0.20)
Icy	1.2 (0.52)	1.2 (0.40)
Shoup	1.1 (0.24)	1.4 (0.54)
Barrens	1.3 (0.66)	1.0 (0.00)
Chisik	1.4 (0.81)	--
Gull	1.1 (0.42)	--

Table 9. Average feeding frequency, meal size, energy density, and energy provisioning rates to Black-legged Kittiwake broods at six colonies in the northern Gulf of Alaska, 1995 - 1998.

Location / Year	Feeding frequency (meals/nest day)	Meal size (g)	Energy density (kJ / g wet mass)	Energy provisioning rate (kJ / nest day)
Shoup Bay				
1995	3.3	29.0	4.8	463
1996	4.3	30.6	4.7	618
1997	3.0	22.7	4.9	337
1998	3.0	24.4	4.7	344
Eleanor Island				
1995	4.9	21.3	4.2	441
1996	4.6	23.1	3.8	404
1997	3.9	17.6	4.5	312
1998	4.6	10.5	4.0	193
North Icy Bay				
1996	?	24.5	4.5	?
1997	4.5	19.7	4.6	410
1998	5.1	20.5	4.4	460
Barren Islands				
1996	3.2	20.8	4.0	266
1997	2.2	30.6	4.0	269
1998	3.5	18.9	4.5	297
Gull Island				
1996	4.7	17.2	4.9	396
1997	3.5	23.0	4.6	373
1998	4.1	15.6	5.4	345
Chisik Island				
1996	2.8	24.4	3.4	232
1997	2.7	11.0	5.1	154
1998	Failed	15.9	4.5	?

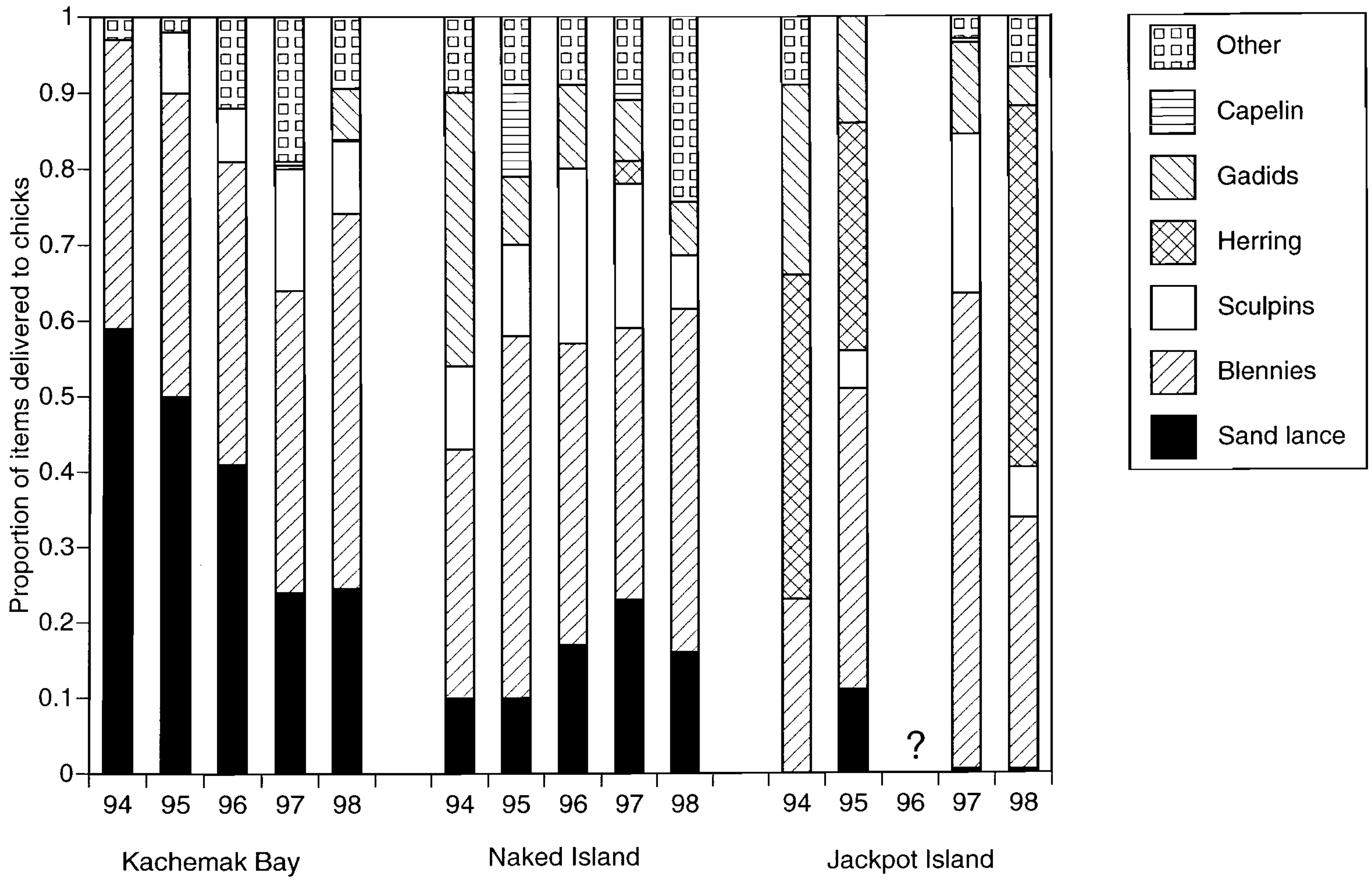
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion of items delivered to chicks
94
95
96
97
98
94
95
96
97
98
94
95
96
97
98
?
Kachemak Bay
Naked Island
Jackpot Island
Other
Capelin
Gadids
Herring
Sculpins
Blennies
Sand lance

Figure 1

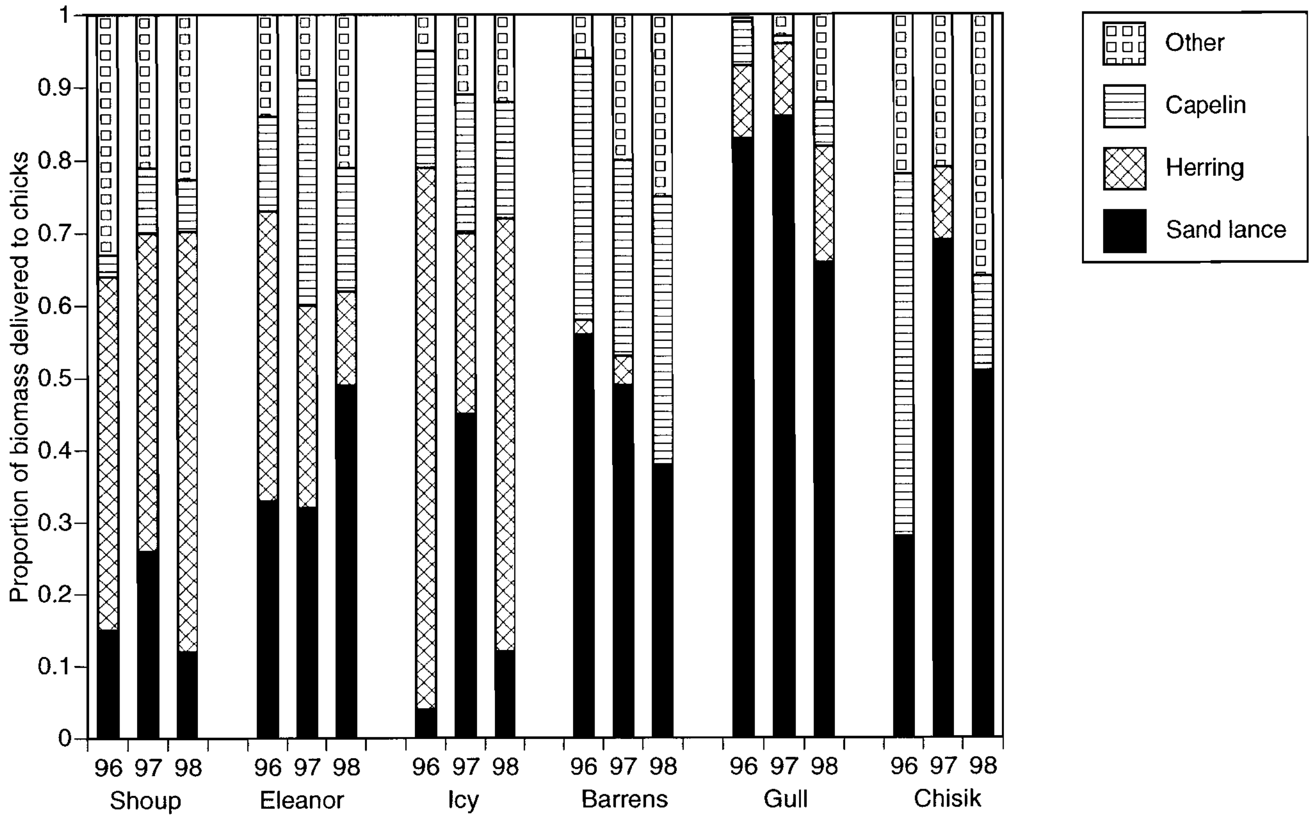
Proportion of biomass delivered to chicks
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
96 97 98
Shoup
96 97 98
Eleanor
96 97 98
Icy
96 97 98
Barrens
96 97 98
Gull
96 97 98
Chisik
Other
Capelin
Herring
Sand lance

Figure 2

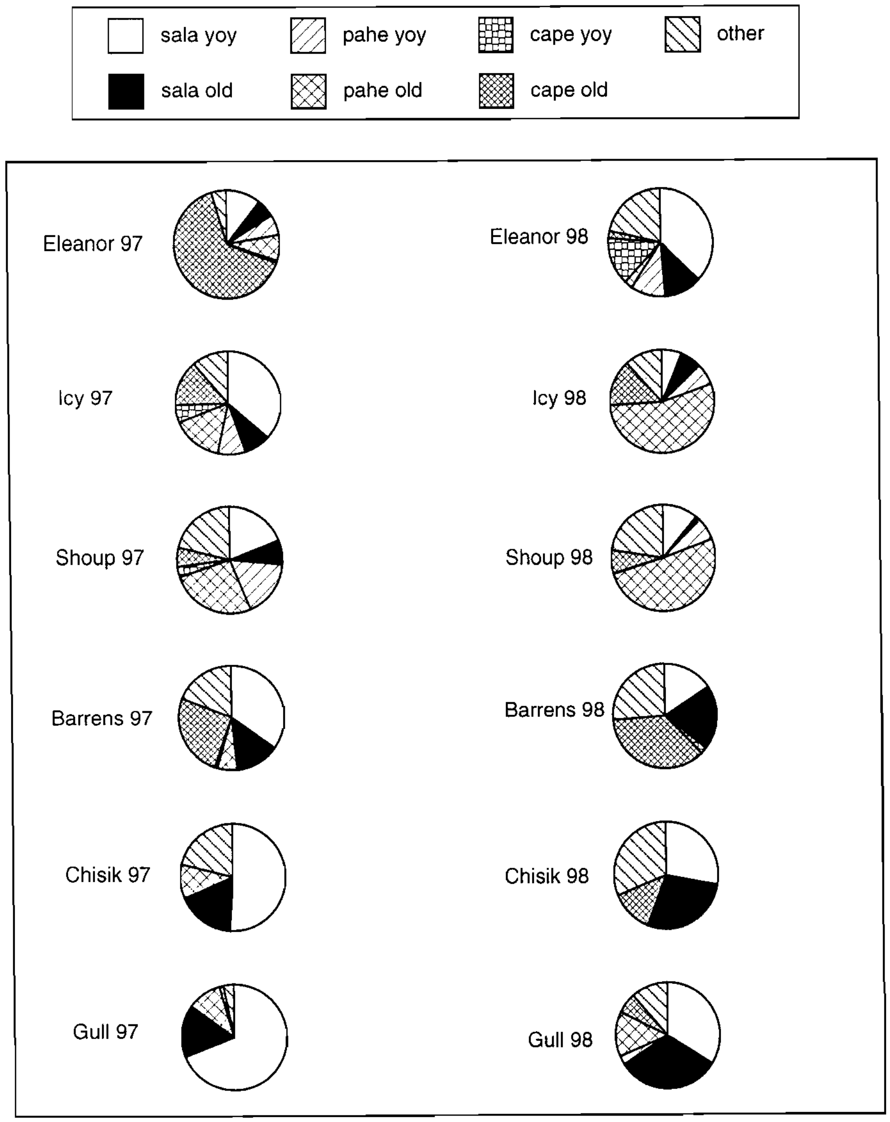
sala yoy
pahe yoy
cape yoy
other
sala old
pahe old
cape old
Eleanor 97
Eleanor 98
Icy 97
Icy 98
Shoup 97
Shoup 98
Barrens 97
Barrens 98
Chisik 97
Chisik 98
Gull 97
Gull 98

Figure 3

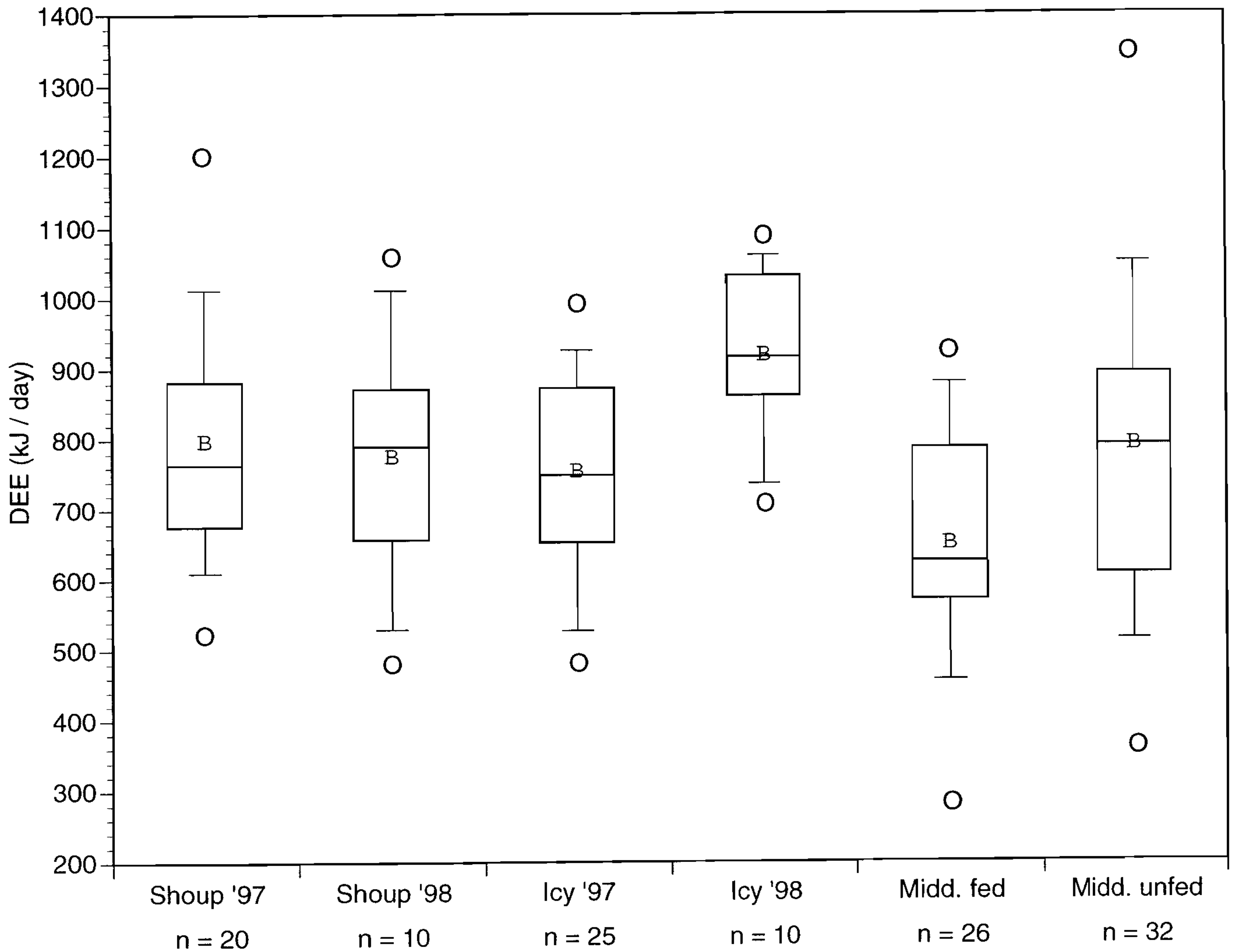
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
DEE (kJ / day)
B
Shoup '97
n = 20
Shoup '98
n = 10
Icy '97
n = 25
Icy '98
n = 10
Midd. fed
n = 26
Midd. unfed
n = 32

Figure 4.