APPENDIX G

APEX: 96163G

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 96163 G

Annual Report

Start-up Date: April 1996

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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March 1997

STUDY HISTORY

Restoration Project 96163 G is similar to the research described in the original proposal submitted as 95118-BAA to be a component of the Alaska Predator Ecosystem Experiment Project (APEX), for which funding was first approved by the 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. Black-legged kittiwakes, pigeon guillemots, and tufted puffins were studied as bioindicators of the distribution and abundance of forage fishes to further understand the recovery of injured seabird resources. Study sites were at Shoup Bay, and Eleanor, Naked, Jackpot, and Seal islands in Prince William Sound and at Kachemak Bay, Gull, Chisik, and the Barren islands in Lower Cook Inlet. In 1996, this research continued without the tufted puffin component and with the shift from Seal Island to North Icy Bay for black-legged kittiwakes. To date, this project has produced new information advancing our knowledge of the comparative biochemical composition and physiological condition of forage fishes available to seabird, marine mammal, fish, and human predators; the influence of location, age, gender, and reproductive status on the nutritional quality of forage fishes; foraging strategy responses of breeding seabirds to shifts in prey availability; and the energetic consequences of foraging on different prey with different energy contents.

ABSTRACT

A shift in marine trophic structure of the *Exxon Valdez* oil spill (EVOS) area may have prevented recovery of injured seabird resources, especially pigeon guillemots, common murres, and marbled murrelets. We studied potential energetic factors (diet composition, diet quality, meal size, delivery rate) constraining seabird productivity in the EVOS area, focusing on pigeon guillemots and black-legged kittiwakes in oiled, non-oiled, and reference sites. Lipid content of fish prey in diets varied from 3% dry mass in juvenile walleye pollock to 48% in some juvenile herring. Seabirds can potentially experience a four-fold difference in energy intake based on fish quality. Guillemots preyed mostly on blennies and sculpins at Naked Island, herring at Jackpot Island, and sandlance and blennies at Kachemak Bay. Coincident with less sandlance in the diet, guillemot growth performance at Kachemak Bay declined in 1996 compared to 1995, and was not different than at Naked Island. Kittiwakes fed their young mostly herring and sandlance in Prince William Sound and sandlance and capelin in Lower Cook Inlet. Kittiwake growth and brood size were highest at Shoup Bay. Kittiwakes and guillemots require access to high-quality, schooling forage fishes to maintain high nesting densities.

KEY WORDS

energetics, energy, *Exxon Valdez*, fish, lipid, proximate composition, seabird, reproduction, trophic

EXECUTIVE SUMMARY

This restoration research project is a component of the Alaska Predator Ecosystem Experiment Project (APEX), which is investigating whether low food abundance and quality contributes 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 the 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 1995 and 1996 breeding season. In cooperation with other APEX projects, we collected samples of nestling meals and measured nestling growth rates, provisioning 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 one site in Kachemak Bay (a reference site). Three study sites for kittiwakes in PWS were located at Eleanor Island (an oiled site), North Icy Bay (a non-oiled site), and Shoup Bay (a non-oiled site), and were compared with three study sites in Lower Cook Inlet (LCI) at Gull, Chisik, and the Barren islands (all reference sites). In addition, forage fishes collected using a variety of methods were analyzed in the lab to determine quality as seabird prey.

The primary factor determining the energy density of forage fishes is lipid content (% dry mass); lipid has twice the energy density of protein and carbohydrates. The lipid content of forage fishes varied from a low of 3% dry mass in some juvenile walleye pollock (*Theragra chalcogramma*) to intermediate values of 22% in sand lance (*Ammodytes hexapterus*) and 37% in capelin (*Mallotus villosus*), to highs of 48% in some juvenile herring (*Clupea harengus pallasii*) and 52% in eulachon (*Thaleichthys pacificus*). Intraspecific variation in lipid content of forage fishes was related to location, age, gender, and reproductive status. Of those fishes present in the diets of kittiwakes and guillemots, herring, sand lance, and capelin had the highest energy density, nearshore demersal fishes (e.g., gunnels, pricklebacks, eelblennies, shannies) were intermediate, and gadids (e.g., walleye pollock, Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*)) were lowest in energy. Energy densities of fresh forage fishes ranged from 2.8 kJ/g wet mass in pollock, 6.3 kJ/g in sand lance, 7.4 kJ/g in capelin, to 10.0 kJ/g in eulachon and some herring. Consequently, piscivorous seabirds can experience a four-fold difference in energy intake based solely on the quality of forage fishes consumed.

The diets of guillemot nestlings were composed primarily of blennies and sculpins at Naked Island, herring at Jackpot Island, and sand lance and blennies at Kachemak Bay. The energy density of guillemot nestling diets was higher in Kachemak Bay than in Prince William Sound from 1994 through 1996. Coincident with less sand lance in the diet, guillemot growth

performance at Kachemak Bay was lower in 1996 compared with 1995. Unlike 1995, growth was not higher than at Naked Island. These results support the hypothesis that breeding guillemots in the EVOS area are constrained by the availability of high-quality forage fishes, especially sand lance.

Kittiwakes fed their young high energy schooling forage fishes, which were in decline and are now rebounding. In 1996, nestling diets were dominated by herring and sand lance in PWS and sand lance and capelin in LCI. The energy density of kittiwake nestling diets were higher at Shoup Bay than at Eleanor Island, and higher in 1996 than in 1995 for both sites. Shoup Bay kittiwakes also transported larger meals back to the colony to feed their chicks, when compared to those in the other study sites. Also, kittiwake growth performance and average brood size were higher at Shoup Bay than at Eleanor Island or North Icy Bay. Kittiwake parents at Shoup Bay selected higher quality prey and provided larger food loads for larger brood sizes and better growth rates for their chicks than parents at the other colonies in PWS and LCI. Our results support the hypothesis that breeding kittiwakes in the EVOS area are constrained by the availability of high quality forage fishes.

In summary, results from the 1996 season of field work support the APEX hypotheses structuring this project (4, 8, and 9). The species composition and abundance of fish used as prey by seabirds nesting in the EVOS area has changed. Kittiwakes and guillemots apparently require access to high quality, schooling forage fishes to maintain high nesting densities in the EVOS area. Productivity and size of forage species appear to change the energy potentially available for nesting seabirds. Changes in seabird reproductive productivity appear to reflect differences in forage fish abundance as measured in adult seabird foraging trip duration, brood meal size, and brood provisioning rates. Seabird reproductive productivity appears to be determined in part by differences in forage fish nutritional quality. By implication, the productivity of two other seabird species that were injured by the spill (specifically, common murres and marbled murrelets) may also be constrained by availability of high quality forage fishes.

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 fishes 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 brood meals in their stomachs (e.g., kittiwakes) or in a specialized pouch (e.g., auklets) normally transport meals that are close to the maximum load. Seabirds that transport brood meals as single prey items held in the bill (e.g., guillemots, murres, 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. 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. 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, lipids may constitute over 50% of dry mass (A. R. Place, unpubl. data; J. Piatt, unpubl. data; S. Payne, unpubl. data); 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; J. Piatt, unpubl. data). This means that a given fresh mass of lanternfishes or eulachon may have 3 to 4 times the energy content of the same mass of juvenile pollock or Pacific cod. By increasing the proportion of high-lipid fish in brood diets, parents can increase the energy density of brood meals in order to compensate for the low frequency of brood feeding (Ricklefs 1984, Ricklefs et al. 1985).

Three seabird species that were damaged by the *Exxon Valdez* oil spill 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 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 and Steller sea lions, 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 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 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, 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 (D. L. Hayes, unpubl. data). In contrast, guillemots breeding in Kachemak Bay continue to provision their young predominately with sand lance, and sand lance is particularly prevalent in the diet at breeding sites that support high densities of nesting guillemots (A. Prichard, unpubl. data).

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 one component of the APEX Project, working in conjunction with EVOS Projects 95163A-P, to test the overall hypothesis that a shift in the marine trophic structure of the EVOS area has prevented recovery of injured resources and 12 more specific hypotheses related to this. The three specific hypotheses of this study are:

1. Productivity and size of forage species change the energy potentially available for seabirds (APEX Hypothesis 4).

2. Changes in seabird reproductive productivity reflect differences in forage fish abundance as measured in adult seabird foraging trips, brood-meal size, and brood-provisioning rates (APEX Hypothesis 8).

3. Seabird reproductive productivity is determined in part by differences in forage fish nutritional quality (APEX Hypothesis 9).

These 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, is assumed to remain constant among breeding sites and years. This assumption will be tested in 1997 and 1998 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 1996 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 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 Prince William Sound (Naked, Jackpot, and Eleanor islands, and Shoup and North Icy bays) and Lower Cook Inlet (south shore of Kachemak Bay, Gull, Chisik, and the Barren islands) during the 1996 breeding season. These sites were identical to those seabird breeding sites that were used 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 APEX Component 96163 F). 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 1994 and is located in a non-oiled portion of PWS. Kachemak Bay served as a third study site for guillemots. Since 1994, the breeding population of guillemots on the south shore of Kachemak Bay (from Mallard Bay in the northeast to Seldovia in the southwest) has been studied intensively. Results in 1994 suggested that the guillemot prey base in 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. 6500 breeding pairs, (2) Eleanor Island in central PWS near Knight Island (oiled area) with c. 200 breeding pairs, and (3) North Icy Bay in southeast PWS and a non-oiled area with c. 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, and Eleanor Island has been selected as a site for intensive study for comparison purposes (see APEX Component 96163 E). In Lower Cook Inlet, kittiwake breeding colonies at the Barren Islands (high productivity), Gull Island (moderate productivity), and Chisik Island (low productivity) were monitored for diet and reproductive success (see APEX Component 96163 M) .

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 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 1996 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 by capturing adults in scraps of mist net as they entered the nest crevice with a chick meal held in their bill and opportunistically when dropped meals were discovered in or near nest crevices. 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 brood meals in the stomach and esophagus, so 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 mid-water trawl (APEX Component 96163 A).

Puffin bill loads from the Barren Islands were also used as a source of prey samples. Guillemot brood meals, kittiwake regurgitations, puffin bill loads, 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 brood meals, puffin bill loads, and kittiwake regurgitations were shipped frozen to Dr. A. Springer's laboratory at the Institute of Marine Science, UAF, where K. Turco sorted, identified, sexed, aged, measured, and determined reproductive status of specimens in preparation for proximate analysis. Some kittiwake regurgitations were shipped frozen to the University of California Santa Cruz, where the semidigested material was sorted and identified to species to the extent possible by G. Golet.

Proximate analysis of all samples was conducted by the first author and Heather Zollinger in the second author's laboratory at the Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, OSU. Forage fish specimens and brood 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 using a soxhlet apparatus and 7:2 hexane/isopropyl alcohol (v:v) as the solvent system. Lean dry samples were transferred from extraction thimbles to glass scintillation vials and ashed in a muffle furnace at 550°C in order to calculate ash-free lean dry mass (protein) by subtraction. Energy density (kJ/g wet mass) and energy content of forage fishes and brood meals were calculated from their composition (water, lipid, ash-free lean dry matter, and ash), using published energy equivalents of these fractions (Schmidt-Nielsen 1990).

Brood provisioning rates for pigeon guillemots and black-legged kittiwakes at each of the study sites were determined by monitoring active nests for meal delivery rates (meals/ nest day) throughout the 24 hour 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 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 brood diets for each species at each site. Finally, the product of average energy density of brood diets (kJ/g wet mass) and average quantity of food delivered (g/nest day) was calculated as an estimate of energy provisioning rates (kJ/nest day) for each species at each site.

Active guillemot and kittiwake nests were checked daily or every other day 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 (known-age, in most cases) on a regular basis (every three days, if possible) 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 weigh nestlings every other day 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.

Breeding adult guillemots and kittiwakes that were captured at the nest were weighed, measured, and banded for future identification.

RESULTS AND DISCUSSION

Objective 1: Proximate Composition of Forage Fishes

Specimens of the following forage fish taxa (and two invertebrates) were subjected to proximate analysis in 1995 and 1996:

Schooling fishes:
juvenile walleye pollock (*Theragra chalcogramma*)
juvenile Pacific cod (*Gadus macrocephalus*)
juvenile Pacific tomcod (*Microgadus proximus*)
Pacific sand lance (*Ammodytes hexapterus*)
capelin (*Mallotus villosus*)
Pacific herring (*Clupea harengus pallasii*)
Pacific sandfish (*Trichodon trichodon*)
eulachon (*Thaleichthys pacificus*)
lanternfish (Myctophidae)
Pacific salmon (*Onchorhynchus* spp.)
lingcod (*Ophiodon elongatus*)
prowfish (*Zaprora silenus*)
surf smelt (*Hypomesus pretiosus*)
kelp greenling (*Hexagrammos decagrammus*)

Nearshore demersal fishes:
crescent gunnel (*Pholis laeta*)
slender eelblenny (*Lumpenus fabricii*)
snake prickleback (*Lumpenus sagitta*)
daubed shanny (*Lumpenus maculatus*)
black prickleback (*Xiphister atropurpureus*)
northern ronquil (*Ronquilus jordani*)
crested sculpin (*Blepsias bilobus*)
silverspotted sculpin (*Blepsias cirrhosus*)
four horned sculpin (*Myoxocephalus quadricornis*)
plain sculpin (*Myoxocephalus jaok*)
padded sculpin (*Artedius fenestralis*)
ribbed sculpin (*Triglops pingeli*)
roughspine sculpin (*Triglops macellus*)
slim sculpin (*Radulinus asprellus*)
tidepool sculpin (*Oligocottus maculosus*)
arctic shanny (*Stichaeus punctatus*)

Other:
shrimp (*Pandalus* spp.)
dover sole (*Microstomus pacificus*)
rex sole (*Glyptocephalus zachirus*)
squid (unknown species)

Several patterns in the proximate composition of these forage fishes were revealed by interspecific comparison (Figure 1). First, lanternfishes and eulachon had the highest lipid content, and therefore the highest energy density (kJ/g wet mass) of the forage fishes analyzed. Herring, sand lance, and capelin had the highest values for forage fishes observed in the diets of seabirds in this study. Gadid species (pollock, cod, tomcod) and prowfish consistently had the lowest lipid content and, consequently, the lowest energy density. There is a clear dichotomy in quality among the schooling forage fishes: gadids are generally low quality and herring, sand lance, and capelin are relatively high quality. No such dichotomy in quality was revealed among the nearshore demersal species (Figure 1). Nearshore demersal fishes (blennies, sculpins, pricklebacks) were intermediate in energy density.

Intraspecific comparisons of proximate composition revealed differences related to age, location, gender and reproductive status. The lipid content of herring increased dramatically from age class 0+ to older fish (Figure 2). Lipid content was highly variable within an age class, which was suggestive of wide variation in the condition of juvenile herring from PWS. Some of this variation could be attributed to differences between collection sites in the average lipid content of herring (Figure 2). Variability in lipid content within an age class was less pronounced in sand lance compared to herring. Surprisingly, the lipid content of 1+ sand lance was somewhat greater than in 2+ sand lance. Female 2+ sand lance had higher lipid content and higher energy density than male 2+ sand lance. Juvenile pollock exhibited a different pattern of lipid content as a function of age: 0+ pollock had slightly higher lipid content than 1+ or 2+ pollock (but lower than 0+ herring or sand lance).

The observed inter- and intra-specific differences in lipid content of forage fishes reflect differences in life history as they influence reliance on stored energy reserves for survival or reproduction. For example, sand lance spawn in the fall (Dick and Warner 1982), and adults, especially females, presumably deposit lipid reserves during summer for later investment in gametes. Juvenile pollock, however, feed year-round and selection has favored allocation of assimilated energy to rapid somatic growth over storage of lipid during the juvenile period.

The energy densities for those schooling and nearshore demersal fishes that were collected and analyzed in 1995 and 1996 differed by a factor of up to four. A parent seabird breeding in PWS could potentially increase its rate of energy provisioning to its brood by a factor of as much as four by selecting prey based on quality, given similar availability. Such an increase in energy provisioning rate could dramatically enhance fitness.

Objective 2: Dietary Parameters of Nestling Seabirds

Data collected in 1996 built on the data set that began in 1995 to broaden our understanding of how seabirds compensate prey availability, diet quality, prey selection, meal size, and feeding frequency to maximize energy provisioning rates to the brood. The patterns are beginning to appear in the second year of this four-year field study: the importance of certain high-quality schooling forage fishes, the flexibility of meal size in response to shifting prey availability, and the trade-off between increasing feeding frequency and meal size. Pigeon guillemots and black-legged kittiwakes have demonstrated different foraging strategies to deal with reproducing under shifting conditions of food availability and quality.

Pigeon Guillemots

Pigeon guillemots have a diverse diet, composed of poorly-known nearshore demersal fishes, as well as relatively well-known schooling forage fishes. Blennies and sculpins were the primary prey of nestlings at Naked Island in 1996 (Figure 3), whereas the proportion of gadids has decreased since 1994. At Kachemak Bay, nestlings were fed mostly sand lance and blennies in 1996, but the proportion of sand lance in the diet decreased from 1995. Pacific herring and gunnels were the main prey for nestlings at Jackpot Island in 1996, although sample size was small due to intense nest predation by a mink and a resultant high rate of nest failure. The proportion of schooling forage fishes in 1996 diets was greatest at Jackpot Island (46%), followed by Kachemak Bay (36%) and Naked Island (21%).

One hundred and one pigeon guillemot brood meals, composed of individual fish, were collected in 1996: 73 at Naked Island, 25 at Kachemak Bay, and 3 at Jackpot Island. These samples were generally representative of nestling diets at the respective study sites, as indicated by the species composition of fish observed delivered to the nest by adults (Figure 3). The average mass of brood meals collected from Naked Island was similar in 1995 and 1996 (Table 1). Sample size of brood meals at Jackpot Island was small in 1996, so no estimate of average meal size could be made. In 1995 and 1996, average meal size at Naked Island was smaller than at Jackpot Island in 1995. The average mass of brood meals collected at Kachemak Bay (11.4, s.d. = 7.9, $n = 25$) was slightly less than at Naked Island (14.2, s.d. = 11.6, $n = 73$; $t = 4.02$, one-tailed, $p = 0.09$).

Diet quality appears to be an important factor influencing energy provisioning rates to pigeon guillemot nestlings. The average energy density of brood meals was similar at Naked and Jackpot islands in both 1995 and 1996 (Table 1). An increase in the proportion of sand lance in guillemot diets at Naked Island from 1995 to 1996 may have been compensated by a decrease in capelin. At Jackpot Island, energy density of brood meals was moderate in both years, despite a high incidence of herring in the diet. This is apparently due to geographical differences in lipid content of juvenile herring; herring from northeast PWS had higher lipid content and energy density than herring from southwest or central PWS. Brood meals at Kachemak Bay had higher average energy densities than the other sites in 1994, 1995, and 1996, due to the high proportion of sand lance in the diet. The average energy density of guillemot brood meals from Kachemak Bay declined in 1996, coincident with a decline in the proportion of sand lance in the diet.

Guillemot feeding frequency (brood meals delivered per nest day) was highest at Jackpot Island (1995), intermediate at Kachemak Bay (1996), and lowest at Naked Island (1995, 1996; Table 1). The feeding frequency at Naked Island was similar in 1995 and 1996 (means adjusted for proportions of nests containing one- and two-chick broods). Consequently, the estimated mass of food delivered to guillemot nests at Jackpot Island (330 g/nest day, 1995) were almost twice those at Naked Island (170 g/nest day, 1996) or Kachemak Bay (162 g/nest day, 1996).

Energy provisioning rates (kJ/nest day) can be estimated from measurements of feeding frequency (meals/nest day), meal size (g wet mass), and energy density of meals (kJ/g wet mass). Energy provisioning rates for guillemots were almost twice as high at Jackpot Island (1,394 kJ/nest day, 1995) than at Naked Island (750 kJ/nest day, 1996) and Kachemak Bay (826 kJ/nest day, 1996; Table 1). Limited data for 1996 suggests that feeding frequency was about 17.6 meals/nest day at Jackpot Island, which was similar to 1995. If the small sample of meal size data was representative, the energy provisioning rate at Jackpot Island (847 kJ/nest day, estimated for 1996) would be slightly higher than Naked Island (1995, 1996) and Kachemak Bay (1996). If the 1996 meal size data from Jackpot Island were biased low and average meal size was closer to 20.0 grams (as observed in 1995), then the energy provisioning rate at Jackpot Island in 1996 would be about twice as high as the other two study sites (1,584 kJ/nest day). Guillemots nesting at Kachemak Bay provisioned their young with energy at a higher rate than at Naked Island. They compensated for low average meal size and moderate feeding frequency with high energy density of prey. At Naked Island, where the energy density of brood meals was moderate, guillemots delivered moderate-sized fishes at a lower feeding frequency compared to the other two sites. Consequently, energy provisioning rates to broods at Naked Island were lower than at the other two study sites.

Black-legged Kittiwakes

In 1996, the diet of black-legged kittiwake nestlings in PWS was composed primarily of herring and sand lance (Figure 4). Capelin supplemented the diet, more so in the central and southwestern portions of the Sound. Some kittiwakes at Eleanor Island also consumed salmon smolts, while others at Shoup Bay fed on offal from fish processors. In comparison with 1995, nestling diets at Shoup Bay showed a small increase in herring and a small decrease in sand lance and capelin. At Eleanor Island, nestlings were fed less herring and more salmon smolts in 1996 compared to 1995. Sand lance and capelin figured prominently in kittiwake diets from LCI (Figure 4). Kittiwake nestlings at Gull Island fed their young sand lance, supplemented with herring. The sample size for kittiwake diets from Chisik Island was very small. At the Barren Islands, sand lance was more important than capelin in 1996, which was a reversal from the diet composition in 1995.

By filling the esophagus and stomach with forage fishes, black-legged kittiwake parents can maximize meal size for their nestlings and potentially increase the efficiency of foraging trips. Different average meal sizes among colonies contributed to intercolony differences in energy provisioning rates (Table 2). Shoup Bay in 1995 provides the best example of a kittiwake colony where large meal size compensated for longer foraging trips. In 1996, meal size at Shoup Bay was larger than at any other kittiwake colony, while meal size at North Icy Bay, Chisik Island, and Eleanor Island was moderate. Gull Island had the smallest average meal size. Meal sizes were similar at Shoup Bay and Eleanor Island in both 1995 and 1996 (Table 3).

Parent kittiwakes in PWS and LCI fed their broods food with average energy densities of 3 to 5 kJ/g wet mass (Table 2). Average energy densities of brood regurgitations were higher at Gull Island, Shoup Bay, and North Icy Bay than at Eleanor, Chisik, and the Barren islands. The energy density of kittiwake regurgitations was higher at Shoup Bay than at Eleanor Island, and higher in 1996 than in 1995 at both sites (Table 3). Shoup Bay diets had a predominance of herring with high average lipid contents, compared to a more diverse diet of herring, sand lance, capelin, and salmon smolt at Eleanor Island.

Feeding frequencies (brood meals delivered per nest day) were highest at Gull Island and Eleanor Island, intermediate at Shoup Bay, and lowest at Chisik and the Barren islands (Table 2; means adjusted for proportions of nests that contained one- and two-chick broods). Intercolony differences in the rates of food delivery to broods were driven by meal size and/or feeding frequency. The estimated rate of food delivery to kittiwake nests at Shoup Bay (132 g/nest day) and Eleanor Island (106 g/nest day) were greater than at Gull Island (81 g/nest day) and almost twice that at Chisik Island (68 g/nest day). Delivery rates at Shoup Bay were a third higher in 1996 than in 1995, while delivery rates were about the same at Eleanor Island each year. Shoup Bay had a lower average food delivery rate than Eleanor Island in 1995 (96 vs. 104 g/nest day), and a higher rate in 1996 (132 vs. 106 g/nest day).

Energy provisioning rates, calculated from the product of meal size, energy density, and feeding frequency, were highest at Shoup Bay, intermediate at Eleanor and Gull islands, and lowest at Chisik Island (Table 2). Energy provisioning rates to nestlings were higher at Shoup Bay than at Eleanor Island in 1996, but provisioning rates were similar at the two colonies in 1995 (Table 3). Energy provisioning rates were higher at Shoup Bay in 1996 than in 1995. Energy was provisioned to broods at Shoup Bay at a rate more than twice that at Chisik Island. The estimated energy provisioning rate at Gull Island was comparatively low, however, because average meal size was low. Based on foraging trip durations (APEX Component 96163 E), the feeding frequency at North Icy Bay was estimated at about 4 meals/nest day. This frequency would produce an energy provisioning rate of 441 kJ/nest day, lower than at Shoup Bay and higher than at Eleanor Island. Average meal size at the Barren Islands would have to be around 40 grams for an energy provisioning rate similar to Eleanor and Gull islands, colonies with similar productivity to the Barren Islands. Limited data on meal size at the Barren Islands suggest that this estimate may be larger than the meals actually delivered.

Objective 3: Diet and Nestling Growth and Survival

Pigeon Guillemots

Data on body mass of nestling guillemots were plotted as a function of wing length for each of the study sites. By taking the square root of body mass and the square root of the log of wing length, this relationship was linearized and homogeneity of variance was achieved. The slope of the resultant least squares regression line can serve as an index to growth performance of nestlings over the entire pre-fledging period.

The growth performance of guillemot nestlings at Naked Island in 1996 was similar to 1995 (Figure 5). Growth performance at Kachemak Bay declined from 1995 to 1996, coincident with a lower proportion of sand lance in the diet. Growth at Kachemak Bay was not significantly different than at Naked Island in 1996. Nest predation by a mink at Jackpot Island resulted in no successful fledging from that colony, and a limited data set for nestling growth.

Growth performance of guillemot nestlings paralleled patterns in energy provisioning rates, determined by energy density, feeding frequency, and meal size. Slightly more energy was delivered to Kachemak Bay nestlings than those at Naked Island in 1996, and the growth index was slightly greater. The average energy provisioning rate at Kachemak Bay was lower in 1996 than at Jackpot Island in 1995, and the growth performance index was lower as well. Inter-colony differences in the growth performance index appear to be related to the quality of diets provisioned to nestlings.

Black-legged Kittiwakes

Nestling growth performance was similar among kittiwake colonies in 1996 (Figure 6). Gull Island growth performance was similar to those of the PWS colonies, and Chisik Island growth was lower than at the Barren Islands. A combination of herring and sand lance in the diets in PWS and mostly sand lance at Gull Island in LCI provided the energy density to support high growth rates. Breeding adults at Chisik Island were unable to provision their young with sufficient energy to support growth rates as high as at the other colonies, but some chicks did survive to fledging.

Kittiwake nesting productivity was highest at the Shoup Bay colony in 1996. This colony demonstrated the highest nestling growth performance, lowest incidence of brood reduction, and a high productivity (0.73 fledglings/nest). Breeding adults at Shoup Bay fed their nestlings a higher quality diet and larger brood meals, although the range and duration of foraging trips were high compared to other colonies. Confronted with low food availability, kittiwakes at Chisik Island had the lowest nesting success, with low growth performance, more single chick broods, and low productivity (0.05 fledglings/ nest).

Kittiwakes nesting at North Icy Bay provisioned their young with high-quality prey, although herring in southwestern PWS have a lower energy density than in the northeastern region where Shoup Bay kittiwakes forage. Nonetheless, the energy density of the diet at North Icy Bay was high; meal size was fairly large; and the estimated energy provisioning rate was intermediate between Shoup Bay and Chisik Island. Associated with this foraging strategy, growth performance was low to intermediate, brood size was low, and productivity was low (0.28). High laying success (87% of nest structures with ≥ 1 egg) and mean clutch size (≥ 1.73 eggs) suggest loss of eggs and chicks (see APEX Component 96163 E) to predation, disease, or another factor.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

Energy provisioning rates were higher for pigeon guillemots than for black-legged kittiwakes in 1995 and 1996. Guillemots provisioned their young with energy (average: 788 to 986 kJ/day) at about twice the rate for kittiwakes (average: 413 kJ/day) in both years. Yet, these two species have similar average brood sizes. Several factors may contribute to this pattern. Guillemots forage close to the colony and capture prey during pursuit dives, so they can prey on fishes throughout the water column. Kittiwakes forage at considerable distances from the colony and capture prey at or near the surface.

Growth rates of nestlings paralleled the patterns in energy provisioning rates. The growth rates for guillemot nestlings (average = 21 g/day, Naked Island) were higher than for kittiwakes (average = 17 g/day, Shoup Bay). Guillemot nestlings fledged at a higher mass (456 g, Naked Island) than kittiwakes (396 g, Shoup Bay), despite similar fledging ages. This leads to the inference that the mass specific metabolic rate for guillemot nestlings is higher than kittiwakes, and their maintenance costs are likely higher. Guillemot nestlings appear to be less efficient in growth, as their average energy provisioning rate was about twice those for kittiwakes.

Guillemots in the EVOS area fed their nestlings schooling forage fishes and nearshore demersal fishes. Kittiwakes fed primarily on high-quality, schooling forage fishes during chick-rearing. Diet quality was higher for kittiwake nestlings than for guillemots, and the high energy density of brood meals helped compensate for low feeding frequencies. The high energy density of kittiwake chick diets suggests that breeding adults are selecting prey based at least partly on quality. In support of this, energy provisioning rates at Shoup Bay were close to those for guillemots. High energy provisioning rates are associated with higher growth performance, which would be expected to lead to higher survival and, in turn, to higher nesting densities.

The species composition and abundance of fishes consumed by seabirds breeding in the EVOS area has changed over time. The prevalence of herring, sand lance, and capelin in kittiwake and guillemot diets coincides with rebounding populations of these species since the early 1990s. Both guillemots and kittiwakes in the northern Gulf of Alaska apparently require access to these high-quality, schooling forage fishes to maintain high nesting densities. Juvenile herring and adult sand lance were the primary energy sources for piscivorous seabirds in PWS, whereas sand lance and capelin were important in LCI. By implication, the productivity of common murres and marbled murrelets, injured by the spill and slow to recover, may also be constrained by availability of high quality forage fishes.

CONCLUSIONS

Objective 1: Proximate Composition of Forage Fishes

- Myctophids and eulachon had the highest energy densities of sampled forage fishes (Figure 1).
- Herring, capelin, and sand lance had the highest average energy densities of those forage fishes found in seabird diets (Figure 1).
- Pollock, Pacific tomcod, and prowfish had the lowest average energy densities of sampled forage fishes (Figure 1).
- Nearshore demersal fishes (blennies, sculpins) had intermediate energy densities (Figure 1).
- Differences in location, age, gender, and reproductive state lead to intraspecific differences in energy density of forage fishes (Figure 2).
    - Herring from northeastern Prince William Sound had higher energy densities than in the central or southwestern Sound, demonstrating regional differences in lipid content.

- Age 1+ and 2+ herring and sand lance had higher energy densities than conspecific age 0+ fish.

Objective 2: Dietary Parameters of Nestling Seabirds

- Guillemots fed their young mostly blennies and sculpins at Naked Island, herring at Jackpot Island, and sand lance and blennies at Kachemak Bay in 1996 (Figure 3).
- The energy density of guillemot nestling diets was higher in Kachemak Bay than in Prince William Sound from 1994 through 1996 (Table 1).
- Kittiwakes fed mostly on herring and sand lance in Prince William Sound and sand lance and capelin in Lower Cook Inlet (Figure 4).
- In 1996, herring was the dominant prey item for kittiwakes breeding in Prince William Sound and sand lance was dominant in Lower Cook Inlet (Figure 4).
- The energy density of kittiwake nestling diets was higher at Shoup Bay than at Eleanor Island, and higher in 1996 than in 1995 for both sites (Table 2).

Objective 3: Diet and Nestling Growth and Survival

- Guillemot growth performance at Kachemak Bay declined in 1996 compared with 1995, and was not significantly higher than at Naked Island (Figure 5).
- The lower growth performance of guillemots at Kachemak Bay in 1996 was coincident with less sand lance in the diet, compared to 1995 (Figure 5).
- Kittiwake growth performance was higher at Shoup Bay than at Eleanor Island or North Icy Bay (Figure 6), coincident with herring of higher quality in the diet.
- Kittiwakes in Prince William Sound had higher productivity in 1996 compared with 1995, coincident with more herring, capelin, and sand lance in the diet - all high quality forage fishes.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

- The species composition and abundance of fish used as prey by seabirds nesting in the EVOS area has changed. The prevalence of herring, capelin, and sand lance in seabird diets has increased, corresponding to rebounding populations of these forage fishes since the early 1990s.
- Guillemots apparently require access to high quality, schooling forage fishes (herring, sand lance) to maintain high nesting densities in the EVOS area.

- Productivity of kittiwakes in the EVOS area also appears dependent on availability of high quality forage fishes (herring, sand lance, capelin).

- In Prince William Sound, juvenile herring and adult sand lance are the primary energy sources for piscivorous seabirds.

- Outside the Sound, sand lance and capelin are the primary energy sources for piscivorous seabirds in the EVOS area.

ACKNOWLEDGMENTS

This study would not have been possible without the close cooperation of other APEX PIs and the hard work of many of the individuals supported by APEX projects during the 1996 breeding season. We wish to gratefully acknowledge the assistance and contributions of: APEX Project Manager Dave Duffy, NMFS Program Coordinator Bruce Wright; APEX PIs Dave Irons, Lindsey Hayes, John Piatt, Lew Haldorson, Ken Coyle, Dave Roseneau, Bill Ostrand, and Paul Anderson; field crews at Shoup Bay (Terry Sauer, Chris Kuntsch, Max Kaufman), Eleanor Island (Rob Suryan, John Ryder, Jeb Benson, James Weldy), Naked Island (Lindsey Hayes, Ted Spencer, Mark Russell, Bryan Duggan), Jackpot Island (Pam Seiser, Cynthia Restrepo), Kachemak Bay (Mike Litzow, April Nielsen), and Barren Islands (Arthur Kettle); personnel with Region 7 Migratory Bird Management Office, USFWS: (Debbie Flint, Steve Kendall, Bert Pratte, and Kent Wohl); personnel with the Alaska Science Center, USGS-BRD (Tom Van Pelt); personnel of the School of Fisheries and Ocean Sciences, University of Alaska Fairbanks (Alan Springer, Kathy Turco); Greg Golet of the University of California Santa Cruz; personnel of the Oregon Cooperative Wildlife Research Unit, OSU (Bob Anthony, Melani Bonnichsen); personnel of the Department of Fisheries and Wildlife (Ellen Holsberry, Lori Hurt, LaVon Mauer, Jan Mosley); personnel of the Alaska Cooperative Fish and Wildlife Research Unit, UAF (Norma Mosso, Jim Reynolds, Judy Romans, Kathy Pearse, Joy Heimgartner); personnel of the Institute of Arctic Biology Business Office (Mel Hughes, Marty Conner, Jean James, Ted Inman, and Genelle Tilton). The following PIs on other EVOS-funded projects provided valuable assistance: Evelyn Brown (SEA Project), Kathy Frost (Marine Mammal Project), Dave McGuire, Terry Bowyer, Larry Duffy, and Leslie Holland-Bartels (Nearshore Vertebrate Predators Project), Kathy Kuletz (Marbled Murrelet Project), and A. J. Paul (SEA Project). To all these individuals and many more, we express our sincere appreciation.

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.

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.

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.

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. 1991. 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.

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.

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.

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Table 2. Feeding frequency, meal size, and energy density in determining energy provisioning rates to black-legged kittiwake nestlings in the northern Gulf of Alaska, 1996.

Table 3. Feeding frequency, meal size, and energy density in determining energy provisioning rates to black-legged kittiwake nestlings at Shoup Bay and Eleanor Island, 1995 - 1996.

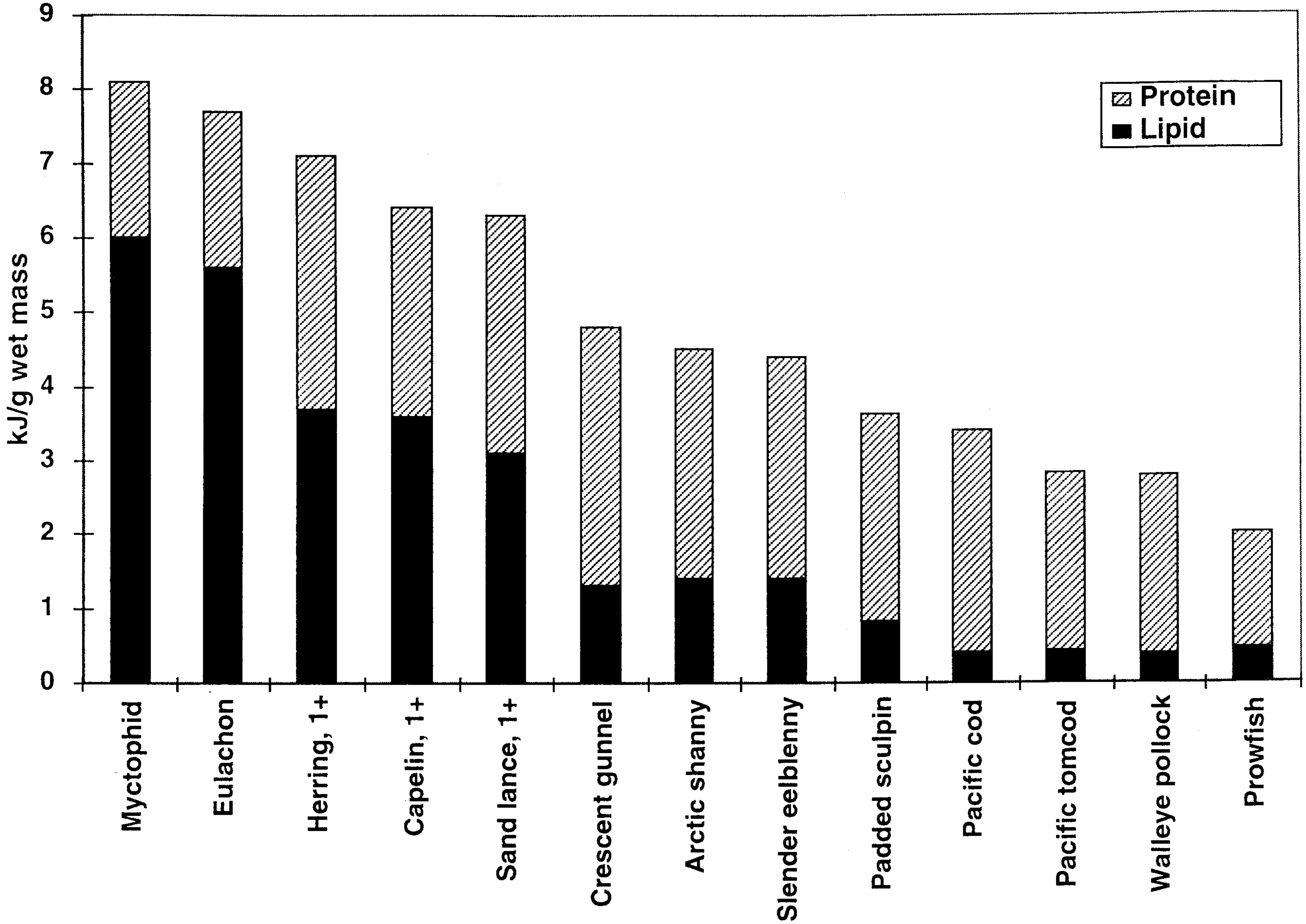

Figure 1. Energy density (kJ/g wet mass) and relative energy content in lipid vs. protein for forage fishes sampled in the northern Gulf of Alaska in 1995 and 1996.

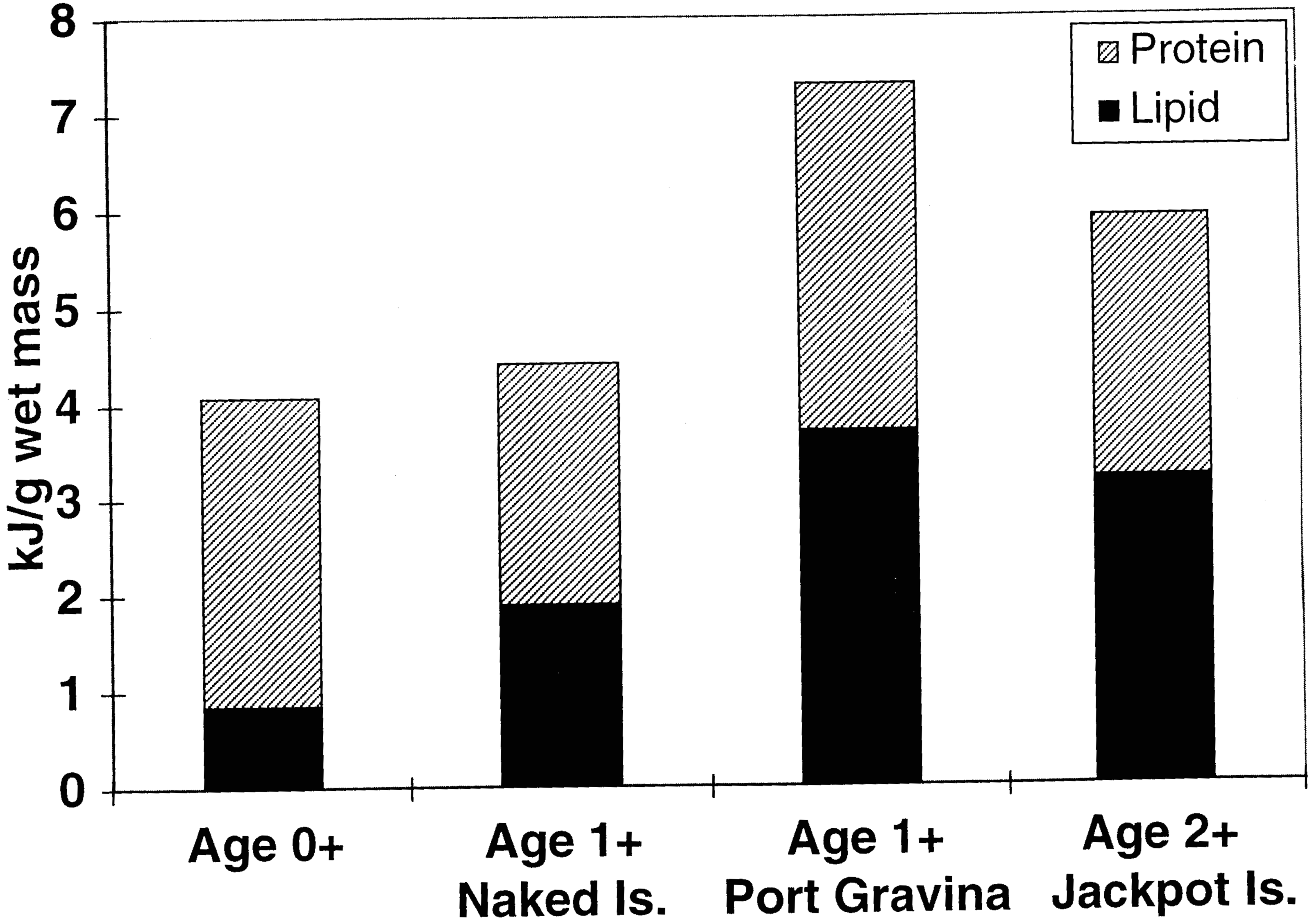

Figure 2. Energy density (kJ/g wet mass) and relative energy content in lipid vs. protein for Pacific herring sampled in the northern Gulf of Alaska in 1995 and 1996. Nutritional quality varies with location and age.

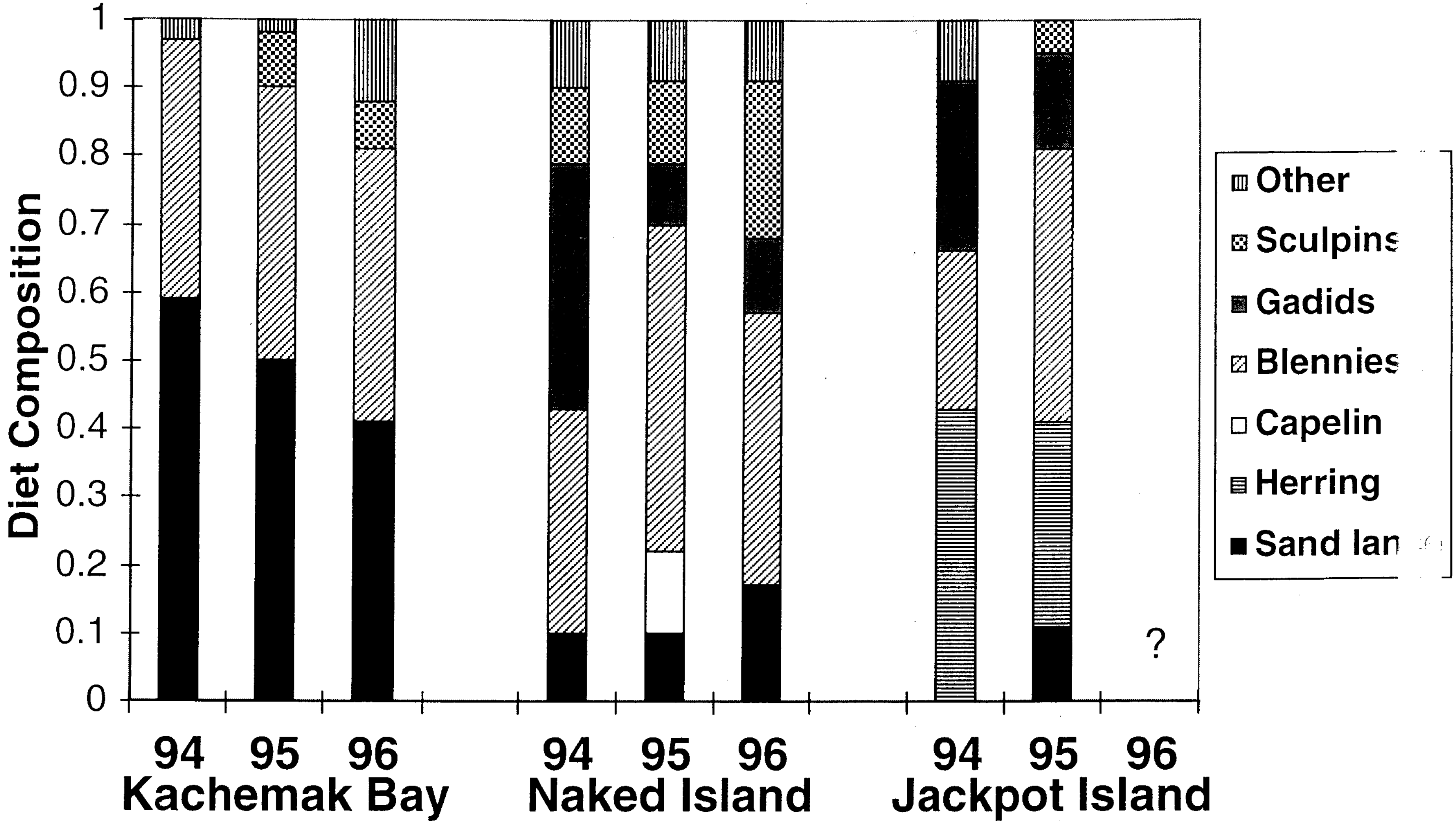

Figure 3. Diet composition of nestling pigeon guillemots in the northern Gulf of Alaska, 1994 - 1996.

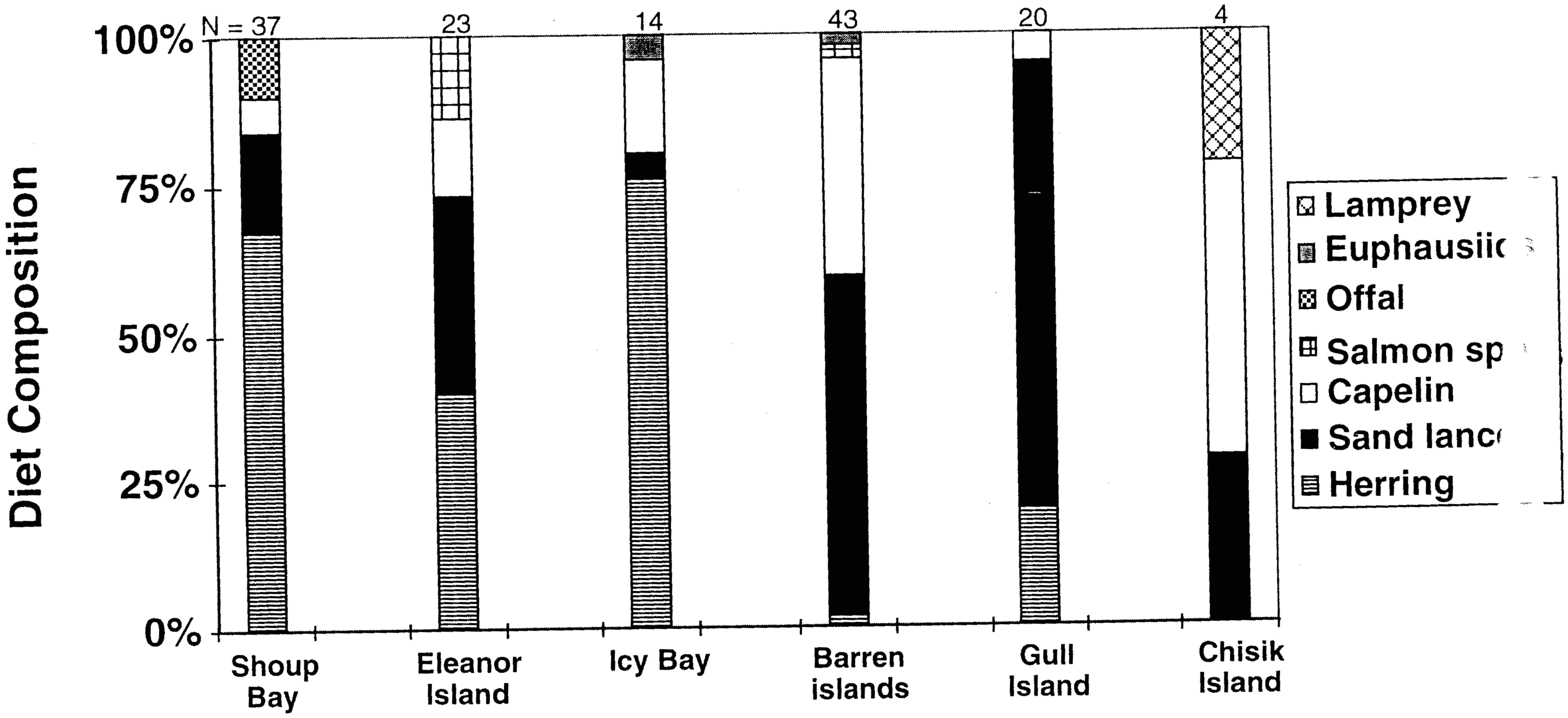

Figure 4. Diet composition of nestling black-legged kittiwakes in the northern Gulf of Alaska, 1996.

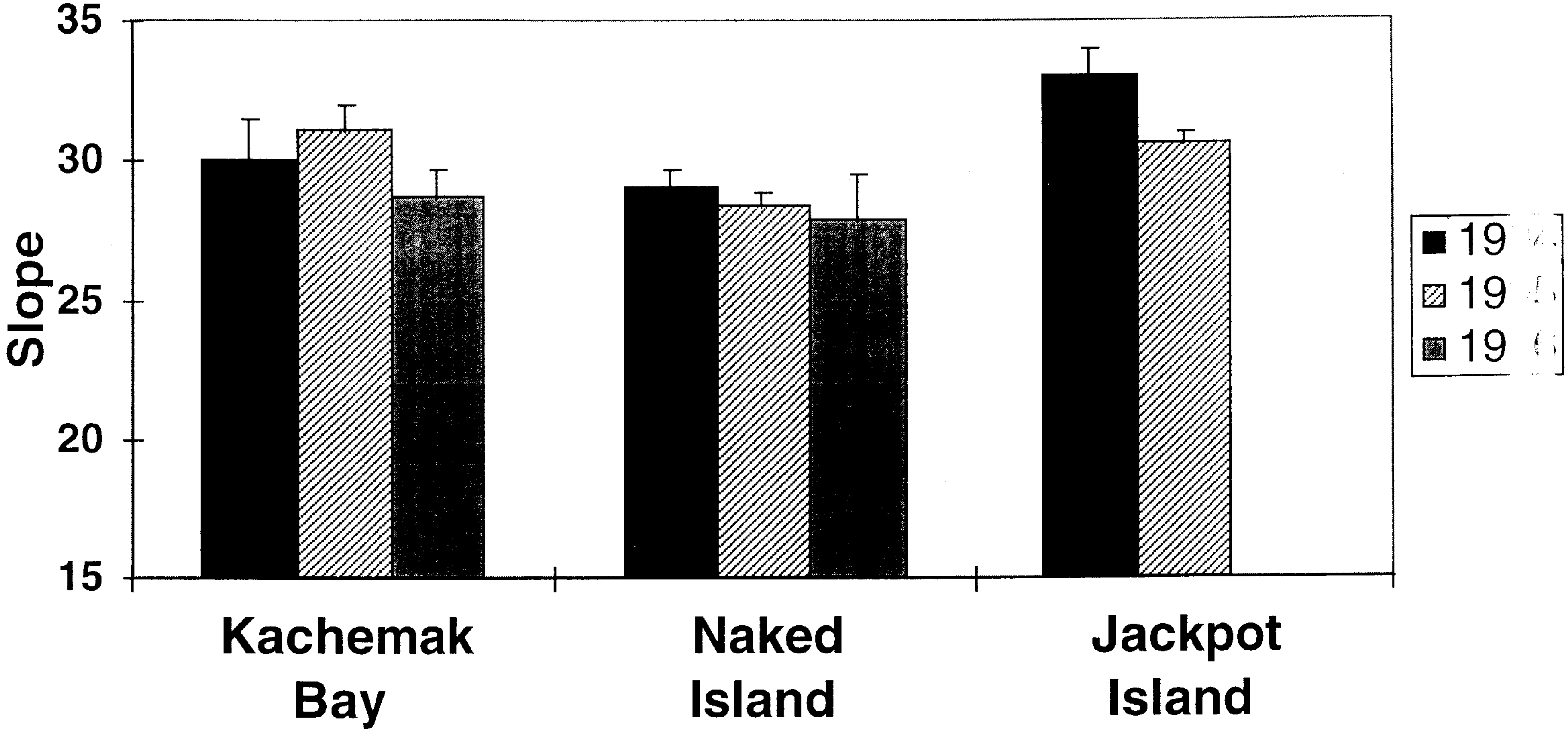

Figure 5. Index to growth performance for pigeon guillemot nestlings at three sites from 1994 through 1996. The growth performance index is the slope of the least squares regression line for the square root of body mass vs. the square root of the natural log of wing length.

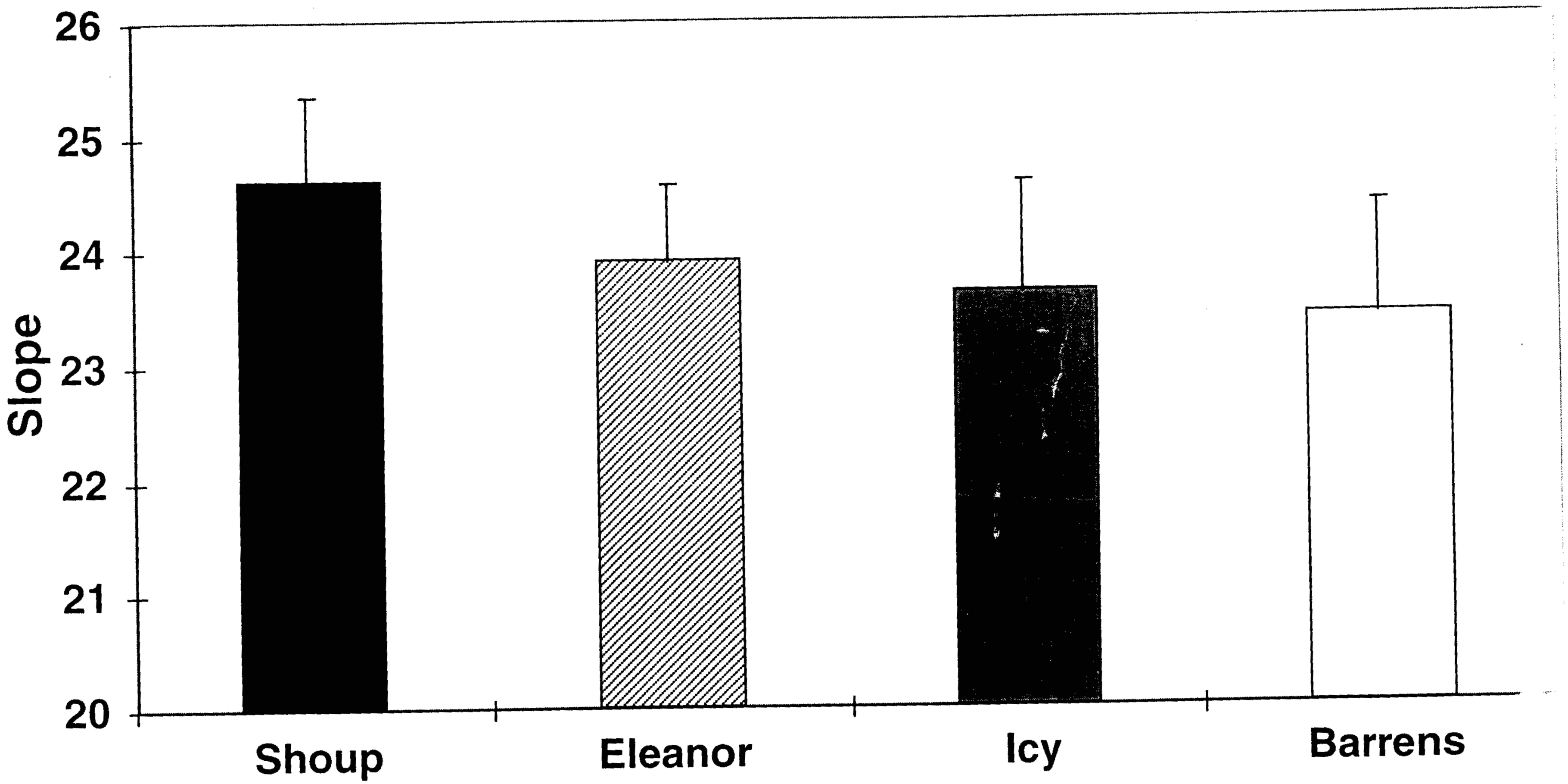

Figure 6. Index to growth performance for black-legged kittiwake nestlings at four sites, 1996. The growth performance index is the slope of the least squares regression line for the square root of body mass vs. the squar root of the natural log of wing length

Table 1. Feeding frequency, meal size, and energy density in determining energy provisioning rates to pigeon guillemot nestlings in the northern Gulf of Alaska, 1994-1996.

	Meal Size (g wet mass)	Energy Density (kJ/g wet mass)	Feeding Frequency (meals/nest day)	Energy Provisioning Rate (kJ/nest day)
Naked Island				
1994	?	4.0	?	?
1995	**14.7**	**4.4**	**11.4**	**737**
1996	**14.2**	**4.4**	**12.0**	**750**
Jackpot Island				
1994	?	4.5	?	?
1995	**20.0**	**4.2**	**16.6**	**1,394**
1996	**10.7**	**4.5**	**?**	**?**
Kachemak Bay				
1994	?	5.5	?	?
1995	**?**	**5.2**	**?**	**?**
1996	**11.4**	**5.1**	**14.2**	**826**

Table 2. Energy Provisioning Rates to Black-legged Kittiwake Nestlings in the Northern Gulf of Alaska, 1996.

	Meal Size (g wet mass)	Energy Density (kJ/g wet mass)	Feeding Frequency (meals/nest day)	Energy Provisioning Rate (kJ/nest day)
Shoup Bay	**30.6**	**4.7**	**4.3**	**618**
Eleanor Island	**23.1**	**3.8**	**4.6**	**404**
North Icy Bay	**24.5**	**4.5**	**?**	**?**
Barren islands	**?**	**4.0**	**2.4**	**?**
Gull Island	**17.2**	**4.9**	**4.7**	**396**
Chisik Island	**24.4**	**3.4**	**2.8**	**232**

Table 3. Energy Provisioning Rates to Black-legged Kittiwake Nestlings in the Northern Gulf of Alaska, 1995-1996.

	Meal Size (g wet mass)	Energy Density (kJ/g wet mass)	Feeding Frequency (meals/nest day)	Energy Provisioning Rate (kJ/nest day)
Shoup Bay				
1995	29.0	4.8	3.3	463
1996	30.6	4.7	4.3	618
Eleanor Island				
1995	21.3	4.2	4.9	441
1996	23.1	3.8	4.6	404