APPENDIX G

APEX: 95163 G

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 95163 G (formerly 95118-BAA)

Annual Report

Start-up Date: April 1995

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.

Daniel D. Roby[a]
John L. Ryder
Gail Blundell
Kathy R. Turco
Alex Prichard

Alaska Cooperative Fish and Wildlife Research Unit
and
Institute of Arctic Biology
University of Alaska Fairbanks
Fairbanks, Alaska 99775

[a] Present Address: Oregon Cooperative Wildlife Research Unit
Department of Fisheries and Wildlife
104 Nash Hall
Oregon State University
Corvallis, OR 97331-3803
(telephone: 503-737-1955)

SUMMARY

This restoration research project is a component of the APEX Project (Alaska Predator Ecosystem Experiment), which is investigating whether low food abundance contributes to the decline of seabird and marine mammal populations in the Exxon Valdez Oil Spill (EVOS) area. The basic premise of this research component is that a shift in diet quality may have constrained recovery of piscivorous seabirds injured by the spill: pigeon guillemots (*Cepphus columba*), common murres (*Uria aalge*), and marbled murrelets (*Brachyramphus marmoratus*). The major hypothesis to be 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, black-legged kittiwakes (*Rissa tridactyla*), and tufted puffins (*Fratercula cirrhata*) were the piscivorous species studied during the 1995 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 at (1) two guillemot breeding sites in Prince William Sound (PWS) (Naked Island, an oiled site, and Jackpot Island, an un-oiled site), and one in Kachemak Bay (a reference site); (2) three kittiwake colonies in PWS (Eleanor and Seal islands, both oiled sites, and Shoup Bay, an un-oiled site), and one on the Barren Islands (a reference site); and (3) one puffin colony in PWS (Seal Island, an oiled site), and one on the Barren Islands (a reference site). 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 was lipid content (% of dry mass). This varied from as much as 48% in some juvenile Pacific herring (*Clupea harengus*) to as low as 3% in some juvenile walleye pollock (*Theragra chalcogramma*). Average energy density (kJ/g wet mass) of age 1+ herring was 2.5 times greater than that of age 1+ pollock. Among the schooling forage fishes, sand lance (*Ammodytes hexapterus*) was second only to herring in lipid content and energy density, and capelin (*Mallotus villosus*) was third. Juvenile gadids (pollock, Pacific cod [*Gadus macrocephalus*], Pacific tomcod [*Microgadus proximus*]) were generally low in lipids and had the lowest energy densities of the sampled forage fishes. Nearshore demersal fishes (e.g., gunnels, pricklebacks, eelblennies, shannies), important prey of pigeon guillemots, were intermediate between herring and gadids in lipid content and energy density. The lipid content and energy density of herring, sand lance, and capelin, though generally high, were variable depending on age, sex, and reproductive status (pre- or post-spawning).

The diet of pigeon guillemots differed among the 3 study sites and was dominated by gadids and blennies at Naked Island, herring and blennies at Jackpot Island, and sand lance at Kachemak Bay. In 1995, growth performance of guillemot nestlings was highest at Kachemak Bay, lowest at Naked Island, and intermediate at Jackpot Island. In 1994, when herring were a large proportion of guillemot diets at Jackpot Island, growth performance of Jackpot Island nestlings was greater than at the other two sites. These trends are in agreement with measured energy densities for the dominant forage fish at the respective breeding sites. We hypothesize that recovery of pigeon guillemots at Naked Island (oiled site) is limited by low availability of high-quality, schooling forage fishes (specifically sand lance or herring), which are apparently crucial for maintaining high densities of breeding guillemots. Results from the first season of APEX field work support the hypothesis that breeding populations of pigeon guillemot in the EVOS area are constrained by the availability of high quality forage fishes.

The diet of black-legged kittiwakes also differed among the four study sites and was dominated by herring at Shoup Bay, Eleanor Island, Seal Island (PWS colonies), and capelin and sand lance at the Barren Islands. These three forage fish species had the highest lipid content and energy density of those schooling species sampled. Nestling regurgitations collected at all three PWS study sites had high average energy densities, but average energy density of nestling regurgitations from Shoup Bay was higher than that from Eleanor Island (sample sizes from Seal Island were small and did not differ significantly from either Shoup Bay or Eleanor Island), reflecting a higher quality diet at Shoup Bay. Shoup Bay kittiwakes also transported larger meals back to the colony to feed their nestlings, but they delivered meals less frequently than at Eleanor Island. These results support the independent observation that foraging trips by Shoup Bay kittiwakes lasted longer and extended further from the colony than did those of Eleanor Island kittiwakes (APEX Component 95163 E). Because of higher diet quality and larger chick meals, Shoup Bay kittiwakes provisioned energy to their nests at higher rates than Eleanor Island kittiwakes. Nestling growth rates were similar at the three PWS study sites, but the incidence of brood reduction was greater at Eleanor and Seal islands compared to Shoup Bay (APEX Component 95163 E). Productivity and nestling survival were fair-good at the four study colonies, a marked improvement over the early 1990s. Productivity of black-legged kittiwakes in the EVOS area appears limited by the availability of sand lance, herring, and capelin. Thus, results from the first season of APEX field work support the hypothesis that productivity of black-legged kittiwakes in the EVOS area is constrained by the availability of high quality forage fishes.

The diet of tufted puffin nestlings at Seal Island consisted mostly of juvenile prowfish, age 0+ herring, juvenile pink salmon, and 0+ pollock, in decreasing order of percent biomass of the diet. These forage fishes are found primarily in deeper water and are minor components of guillemot and kittiwake diets. Energy densities of prey averaged relatively low (2.6 kJ/g wet mass), and 0+ herring and pollock are also quite small. Consequently, large numbers of these prey must be supplied to meet nestling energy demands. Despite low quality diets, tufted puffin adults breeding on Seal Island were able to provision nestlings at a sufficient rate to support above average growth rates (APEX Component 95163 D). Tufted puffins nesting at Seal Island appear to be somewhat anomalous compared with other piscivorous seabirds nesting in Prince William Sound. Sand lance, capelin, or herring do not predominate in the diet, yet productivity and nestling growth rates are high. Seal Island is, however, a small puffin colony (c. 100 breeding pairs), and there is some evidence that puffin diets at other colonies in Prince William Sound (e.g., Naked Island, Agnes Island) are different. Also, the diet of puffin nestlings at Seal Island agrees well with availability, as indicated by forage fish surveys in that portion of the Sound.

In summary, results from the first season of field work support APEX Hypothesis 9, that productivity of pigeon guillemots and black-legged kittiwakes in the EVOS area is determined in part by differences in nutritional quality of forage fishes. By implication, the productivity of two other seabird species that were injured by the spill, common murre and marbled murrelet, 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 1991a). 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) or in a specialized pouch (e.g., auklets) 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, 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 (Myctophidae) and eulachon (*Thaleichthys pacificus*), 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 (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*), 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 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).

Three seabird species that were damaged by the *Exxon Valdez* oil spill (EVOS) are failing to recover at an acceptable rate: pigeon guillemot (*Cepphus columba*), common murre (*Uria aalge*), and marbled murrelet (*Brachyramphus marmoratus*). Damage from the spill to a fourth species of seabird, black-legged kittiwake (*Rissa tridactyla*), 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 and Stellar 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 Seal Island 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 a component of the Alaska Predator Ecosystem Experiment (APEX) Project (EVOS Projects 95163A-L), 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 hypotheses, and two of those specific hypotheses are the focus of this study:

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

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

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, is assumed to remain constant among breeding sites and years. This assumption may need to be tested in the future 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 1995 emphasized pigeon guillemots, black-legged kittiwakes, and tufted puffins and the primary study sites were in Prince William Sound: Naked Island (guillemots), Jackpot Island (guillemots), Eleanor Island (kittiwakes), Shoup Bay (kittiwakes), and Seal Island (puffins). Additional data on tufted puffins and black-legged kittiwakes nesting on the Barren Islands were available for comparison (APEX Components J and L). Also, comparative data for guillemots nesting in Kachemak Bay were available from a separate research project funded by the Coastal Marine Institute at the University of Alaska Fairbanks (Lawrence Duffy, PI).

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, black-legged kittiwake, and tufted puffin 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

Collection of data from the field occurred in Prince William Sound (Naked, Jackpot, Eleanor, and Seal islands, and Shoup Bay) and Lower Cook Inlet (south shore of Kachemak Bay and the Barren Islands) during the 1995 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 annual report for APEX Component 95163F by D. Lindsey Hayes). 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 was the site of intensive studies of guillemot nesting success during 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 by Alex Prichard, a UAF graduate student, of guillemot breeding biology and productivity during the 1994 and 1995 breeding seasons. 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. 1600 breeding pairs, (2) Eleanor Island in central PWS near Knight Island (oiled area), and (3) Seal Island, also in the oiled area of central PWS. Both of the latter are smaller colonies of about 200 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 annual report for APEX Component 95163 E by David B. Irons and Robert M. Suryan). 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 annual report for APEX Component 95163 M by John Piatt) .

About 550 tufted puffins were thought to breed on Big Smith Island, and another 160 on Little Smith Island (Sowls et al. 1978). However, preliminary surveys of tufted puffins nesting on these two islands revealed far fewer breeding pairs than earlier reports indicated. Consequently, the puffin field crew was moved to Seal Island where preliminary surveys suggested about 100 nesting pairs were using relatively accessible nest sites (see annual report for APEX Component 95163 D by J. Piatt). Additional data on puffin diets and nest success were obtained at the Barren Islands (see annual report for APEX Component 95163 J by David Roseneau).

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 1995 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 primarily by capturing adults in scraps of mist net as they entered the nest crevice with a chick meal held in their bill. A few guillemot chick meals were collected opportunistically when dropped meals were discovered in 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 chick meals in the stomach and esophagus, 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 mid-water trawl (APEX Component 95163 A).

Puffins frequently transport several fish at a time held in the bill when delivering meals to chicks. We used the puffin screening technique to acquire fresh samples of tufted puffin bill loads at the Seal Island colony. Screens were placed in a sample of active puffin nest burrows for a maximum of 3-hour periods, usually early in the morning when most chick meals are delivered. Care was taken to avoid screening burrows of chicks that were used to measure nestling growth rates.

Guillemot chick 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-pacs, 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 puffin bill loads were shipped frozen to Dr. Alan Springer's laboratory at the Institute of Marine Science, UAF, where the fourth author (KRT) sorted, identified, sexed, aged, measured, and determined reproductive status of specimens in preparation for proximate analysis. 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 Greg Golet.

Proximate analysis of all samples was conducted by the second author (JLR) in the lab of the first author (DDR) at the Institute of Arctic Biology, UAF. Forage fish specimens and chick meals were reweighed on an analytical balance (± 0.1 mg), 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 Soxtec HT-12 soxhlet apparatus and hexane/IPA 7:2 (v:v) as the solvent system. In cases where the dry mass of fish specimens was less than 2 g, specimens were combined to so as to achieve a sample mass for extraction of 2-3.5 g. Lean dry samples were then 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 chick meals were calculated from their composition (water, lipid, ash-free lean dry matter, and ash), using published energy equivalents of these fractions (Roby 1991).

Chick provisioning rates for pigeon guillemots, black-legged kittiwakes, and tufted puffins 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 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. Average meal size of tufted puffins was measured using the burrow screening technique. Bill loads dropped in front of the screen were washed clean, weighed, and either frozen for later proximate analysis or fed to the nestling. 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/day) was calculated as an estimate of energy provisioning rates (kJ/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. Nestlings 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 (sample sizes dictated by the availability of frozen specimens) were subjected to proximate analysis:

- 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 pallassii*)
- slender eelblenny (*Lumpenus fabricii*)
- padded sculpin (*Artedius fenestralis*)
- four horned sculpin (*Myoxocephalus quadricornis*)
- arctic shanny (*Stichaeus punctatus*)
- crescent gunnel (*Pholis laeta*)

The first six species represent dominant species of schooling fishes that are known to figure prominantly in diets of piscivorous seabirds in the EVOS area, while the last five species are representative of nearshore demersal fishes that commonly occur in the diet of pigeon guillemots.

Several patterns in the proximate composition of these forage fishes were revealed by inter-specific comparison (Fig. 1, Table 1). First, herring and sand lance had the highest lipid content (% dry mass) and, therefore, the highest energy density (kJ/g wet mass) of the species analyzed. Second, gadid species (pollock, cod, tomcod) consistently had the lowest lipid content and, consequently, the lowest energy density of the species analyzed. Capelin fell in the middle, but only spawned-out adult males were available for analysis, so it is likely that the proximate composition of pre-spawn adult capelin will be more similar to herring and sand lance than to gadids. Analysis of three capelin collected as guillemot chick meals (Table 3) support this supposition. There is a clear dichotomy in quality among the schooling forage fishes: gadids are generally low quality and other species are relatively high quality. No such dichotomy in quality was revealed among the nearshore demersal species (Fig. 1, Table 2), which tended to have higher lipid content and energy density than gadids, but lower than herring or sand lance.

Within-species comparisons of proximate composition revealed some age- and sex-related differences. The lipid content of herring increased dramatically from age class 0+ to older fish (Fig. 2). Lipid content, however, was highly variable (5-

48% of dry mass) even within an age class (Fig. 3), suggesting large variation in condition of herring from PWS. Some of this variation could be attributed to differences between sites in the average lipid content of herring (Fig. 2). The pattern of increasing lipid content with age was also evident in sand lance (Fig. 4), but was less pronounced than in herring. Also, variability in lipid content within an age class was less 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; Table 1).

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 forage and nearshore demersal fishes that were collected and analyzed in 1995 differed by a factor of up to 2.5. A parent seabird breeding in PWS could potentially increase its rate of energy provisioning to its brood by a factor of as much as 2.5 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

Pigeon Guillemots

Taxonomic composition of nestling diets were more similar between Naked and Jackpot islands in 1995 than they were in 1994 (Fig. 5). Jackpot Island diets continued to include a higher proportion of schooling forage fishes (especially Pacific herring), while Naked Island diets included a higher proportion of nearshore demersal fishes (pricklebacks, sculpins, gunnels).

Twenty-nine pigeon guillemots chick meals (individual fish) were collected at Naked Island and 27 at Jackpot Island. Table 3 shows the species of fish collected as chick meals at the two sites, their proximate composition, and their energy content. These samples of chick meals were generally representative of nestling diets at the respective study sites, as indicated by the species composition of fish observed being delivered to nests (Fig. 5). No chick meals were collected at Kachemak Bay.

Average mass of chick meals collected at Naked Island (14.7 g, sd = 7.9, n = 29) was less than that of chick meals collected at Jackpot Island (20.0 g, sd = 8.4, n = 27). Feeding frequency (chick meals delivered/(nest day)) was higher at Jackpot Island (16.5 meals/(nest day), n = 14) than at Naked Island (11.4 meals/(nest day), n = 31) or Kachemak Bay (10.8 meals/(nest day), n = 37; Fig. 6), even after means were adjusted for proportions of nests that contained 2-chick vs. 1-chick broods. Consequently, the estimated mass of food delivered to guillemot nests at Jackpot Island (330 g/day) was nearly twice that of guillemot nests at Naked Island (168 g/day).

The average energy density of chick meals collected at the two colonies was similar in 1995 (Table 3), despite the higher incidence of herring in the diet at Jackpot Island. The high lipid content of the capelin and sand lance chick meals collected at Naked Island and the low lipid content of the pollock and tomcod chick meals collected at Jackpot Island produced this result.

Black-legged Kittiwakes

Nestling meal sizes at Shoup Bay and Eleanor Island were estimated using both the average mass of chick regurgitations and the average mass increment from 2-hour periodic weighing of nestlings. Average mass of chick regurgitations from Shoup Bay (21.6 g, sd = 9.9, n = 86) was greater than that from Eleanor Island (12.4 g, sd = 9.3, n = 30; t = 4.60, $P < 0.001$). Average chick meal size based on periodic weighing was also greater at Shoup Bay (29.0 g, sd = 17.3, n = 37) than at Eleanor Island (21.3 g, sd = 12.3, n = 21; t = 1.78, $P = 0.08$).

The smaller chick meals delivered at Eleanor Island were more than compensated for by a higher frequency of chick meal deliveries. Nests on Eleanor Island received an average of 4.9 chick meal deliveries/day, while Shoup Bay nests received only 3.3 chick meals/day on average. Consequently, Eleanor Island nests received an estimated 105 g of food daily, compared with about 95 g of food daily at Shoup Bay nests. This despite a much higher prevalence of 2-chick broods at Shoup Bay compared to Eleanor Island.

Diet quality appears to be a key factor for Shoup Bay kittiwakes. Although the taxonomic composition of chick regurgitations from Shoup Bay and Eleanor Island were similar (herring, followed by sand lance, were the two dominant prey items at both sites), the average energy density of regurgitations from Shoup Bay (4.8 kJ/g wet mass, sd = 0.99, n = 85) was higher than regurgitations from Eleanor Island (4.2 kJ/g wet mass, sd = 0.85, n = 30; Table 4). Together with larger size, the higher energy density of Shoup Bay regurgitations resulted in a total energy content nearly twice that of Eleanor Island regurgitations (Table 4). Lipid content, and thus energy density, of chick regurgitations was high at both colonies (Table 4), reflecting the preponderance of high quality forage fishes (herring, sand lance) in the diet.

Tufted Puffins

Fourty-two puffin bill loads ranging from 1 to 11 fish were collected at Seal Island, and the average mass of these bill loads was 13.7 g (sd = 15.4, range = 0.7 - 73.9 g). The large range of bill load sizes probably reflects the inclusion of partial bill loads in the sample. Adult puffins transporting bill loads for nestlings do not always drop the entire load when they encounter a screen blocking the entrance to the nest burrow (J. Piatt, pers comm.). The largest "bill loads" may actually have consisted of two separate bill loads deposited at the screen by each parent. Consequently, there is some error associated with measuring chick meal size by using the puffin screening technique. Feeding frequency was reported as 4.9 meals/day (sd = 1.5, n = 21). These data suggest that on average puffin chicks raised on Seal Island in 1995 were fed about 67 g of food daily.

The diet of tufted puffin nestlings on Seal Island consisted primarily of juvenile prowfish (32% of biomass), juvenile herring (27%), juvenile pink salmon (20%), and juvenile pollock (12%). With the exception of herring, these species have small lipid reserves and low energy densities (Table 5). Out of 50 herring collected as part of bill loads, all but 3 were age class 0+ and consequently very small (0.6 - 5.5 g) and had low lipid contents (Table 5). High quality forage fish (1-2+ herring, 1-2+ sand lance) seem to be the exception in diets of tufted puffins nesting in Prince William Sound, at least based on the diets of Seal Island puffins. Larger sand lance and capelin constitute a greater proportion of the diet at the Barren Islands (Table 5; APEX Component 95163 J). The average energy density of puffin prey taxa at Seal Island is low (2.6 kJ/g wet mass), much lower than the average energy density of guillemot prey or kittiwake regurgitations.

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 (Naked and Jackpot islands, Kachemak Bay). 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. Figure 7 compares the slopes of these regression lines for the 3 guillemot study sites in 1994 and 1995. In 1994, the growth performance index for Jackpot Island was significantly greater than that for Naked Island or Kachemak Bay. In 1995, Jackpot Island and Kachemak Bay growth performance indices were higher than the Naked Island index.

Guillemot nestlings on Jackpot Island were fed larger meals more frequently compared with Naked Island guillemot nestlings in 1995. Although chick meal size was not measured at Kachemak Bay, most of the diet of guillemot chicks in Kachemak Bay consists of 1-2+ sand lance, a high quality diet for guillemot chicks.

While it is too early to conclude that inter-colony differences in growth performance indices are diet-related, the pattern is certainly suggestive.

Black-legged Kittiwakes

No significant differences were detected in growth rates of kittiwake chicks from Shoup Bay, Eleanor Island, or Seal Island colonies in 1995 (analyses based on comparing slopes of the linear phase of growth; APEX Component E). This is not surprising given the similarity in diets among the three sites. The average growth rate of kittiwake nestlings on the Barren Islands was significantly greater than at the PWS colonies, perhaps reflecting the preponderance of capelin and 1-2+ sand lance in the diet.

The lower incidence of brood reduction at Shoup Bay compared with Eleanor or Seal islands may reflect the somewhat higher quality of nestling diets at Shoup Bay.

Tufted Puffins

Growth rates of puffin nestlings during the linear phase (17.7 g/day) and survival to fledging age (>81%) were high in 1995 on Seal Island (APEX Component 95163 D). Despite low provisioning rates and low diet quality, Seal Island puffins experienced good reproductive success compared to many larger colonies in the Aleutians and off the Alaska Peninsula (J. Piatt, pers. comm.).

Tufted puffins nesting at Seal Island appear to be somewhat anomalous compared with other piscivorous seabirds nesting in Prince William Sound. Sand lance, capelin, or 1+ herring do not predominate in the diet, yet productivity and nestling growth rates are good compared with other puffin colonies in the Northern Gulf of Alaska. Seal Island is, however, a small puffin colony (about 100 breeding pairs), and there is some evidence that puffin diets at other colonies in Prince William Sound (e.g., Naked Island, Agnes Island) may differ. Also, the diet of puffin nestlings at Seal Island agrees well with availability, as indicated by forage fish surveys in that portion of the Sound.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

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). Measurements of these three parameters are available for guillemots breeding at Naked and Jackpot islands in PWS, kittiwakes breeding at Shoup Bay and Eleanor Island in PWS, and tufted puffins breeding at Seal Island in PWS. Measurements of these parameters and the resultant estimates of energy provisioning rates are presented in Table 6.

Several striking patterns emerge from Table 6. First, energy provisioning rates were apparently much higher (4-7X) for guillemots than for tufted puffins, even taking into account the larger average brood size of guillemots. This despite an apparently successful breeding season for puffins at Seal Island. It is possible that the estimate of energy provisioning rate for Seal Island puffins is too low, and the most plausible explanation for a low estimate is that the measurement of average bill load size is biased. The very small size of some bill loads collected at Seal Island in 1995 suggests that they represent only a fraction of the entire bill load. Even if average bill load size was underestimated by as much as a factor of 2-3, it is apparent that puffins provision their young at a considerably lower rate than guillemots. Puffins forage primarily in the pelagic zone, raise only 1-chick broods, and nestlings grow more slowly and fledge at an older age compared with guillemots. The estimates of energy provisioning rates presented here suggest that post-natal development in tufted puffins is energetically much more efficient than in guillemots. Given the more pelagic foraging habits of tufted puffins, it is puzzling that they appear to exercise little selection for prey quality; diet composition seems to be dictated primarily by availability. This may reflect nest site limitation as the primary constraint on the puffin breeding population at Seal Island. If this population is nest site-limited, then food may be readily available in proximity of the colony and selection for high quality prey may be less crucial for reproductive success.

Second, guillemots breeding at Jackpot Island are provisioning their young at a much higher rate than those breeding at Naked Island, due to larger meal sizes and higher feeding frequencies at Jackpot Island. These differences are apparently a consequence of the preponderance of schooling forage fishes in the diet of Jackpot Island guillemots. The difference in energy provisioning rates is associated with higher growth performance, higher nestling survival, and higher nesting density of guillemots at Jackpot Island compared with Naked Island. These differences were apparently even more pronounced in 1994.

Third, energy provisioning rates by kittiwakes were intermediate between those for guillemots and puffins. Diet quality was higher in kittiwakes than in either puffins or guillemots, and the high energy density of chick meals helped compensate for low feeding frequencies. Energy provisioning rates were somewhat higher at Shoup Bay, despite lower feeding frequencies than at Eleanor Island. Shoup Bay kittiwakes were able to provide their broods with larger and higher quality chick meals that more than compensated for lower feeding frequencies. The high energy density of kittiwake chick diets suggests that breeding adults are selecting prey based at least partly on quality.

CONCLUSIONS

Objective 1

1. Juvenile herring and sand lance had the highest average energy densities
2. Gadids (pollock, cod, tomcod) had the lowest average energy densities
3. Age 0+ fish had lower energy densities than older conspecifics for herring and

sand lance, the reverse was true for gadids
4. Adult female sand lance had higher energy densities than males

Objective 2

1. Provisioning rates of energy to guillemot nestlings were higher at Jackpot Island and Kachemak Bay than at Naked Island
2. Provisioning rates of energy to kittiwake nestlings were higher at Shoup Bay than at Eleanor Island
3. Diet quality and provisioning rates of energy to puffin nestlings at Seal Island were lower than for either guillemot nestlings or kittiwake nestlings

Objective 3

1. Guillemot growth performance and nestling survival was apparently correlated with estimated energy provisioning rates
2. Kittiwake growth was similar at PWS study sites, and diet and energy provisioning rates were similar as well
3. Puffin nestlings at Seal Island were fed a low quality diet, but quantity was sufficient to support good growth rates

Objective 4

1. Guillemots may require access to high quality forage fish (herring, sand lance) to maintain high nesting densities in the EVOS area
2. Productivity of kittiwakes in the EVOS area appears to depend on availability of high quality forage fishes (sand lance, capelin, herring)
3. In Prince William Sound, juvenile herring and adult sand lance are the primary energy sources for piscivorous seabirds
4. 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 1995 breeding season. We wish to gratefully acknowledge the assistance and contributions of: APEX Project Manager David C. Duffy, NMFS Program Coordinator Bruce Wright, APEX Administrative Assistant Annette Nelson; APEX PIs Dave Irons, Lindsey Hayes, John Piatt, Lew Haldorson, Ken Coyle, Dave Roseneau, Bill Ostrand, and Paul Anderson; field crews at Shoup Bay (Kirk Lenington [leader], Jared Gerstein, Cynthia Restrepo, Sean Wolfe), Eleanor Island (Rob Suryan [leader], Kyle Payton, John Ryder, Teresa Sauer), Naked Island (Lindsey Hayes [leader], Dom Malenfant, Ted Spencer, Dave Tessler), Jackpot Island (Gail Blundell [leader], Darcie Ziel), Seal Island (Laird Henkel, Kriss Neuman), Kachemak Bay (Alex Prichard [leader], Matt Kopec, John Shook, Mike Litzow), and Barren Islands (Arthur Kettle [leader]); personnel with Region 7 Migratory Bird Management Office, U.S. Fish and Wildlife Service: (Debbie Flint, Steve Kendall, Bert Pratte, and Kent Wohl); personnel with the Alaska Science Center, National Biological Service (Tom Van Pelt); personnel of the School of Fisheries and Ocean Sciences, University of Alaska Fairbanks (Alan Springer, Kathy Turco); 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); and personnel with the Alaska Department of Fish and Game in Cordova. The following PIs on other EVOS-funded projects provided valuable assistance: Evelyn Brown (SEA Project), Kathy Frost (Marine Mammal Project), 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.

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LIST OF FIGURES

Table 1. Proximate composition of schooling forage fishes from the EVOS area, 1995 (std. dev. in parentheses).

Species, age	N	Sex	Location	Date	Fresh Mass (g)	% Water	% Lipid (dry mass)	% AFLDM (dry mass)	Energy Content (kJ/fish)	Energy Density (kJ/g wet mass)
Herring, 0+	49	?	S. Graveyard	7/16'	3.19 (0.56)	77.6 (0.10)	9.7 (0.9)	81.0 (0.8)	12.5 (2.85)	4.0 (2.85)
Herring, 1+	25	?	Naked I.	7/16'	13.2 (3.97)	77.9 (2.60)	22.3 (9.0)	64.1 (8.0)	62.2 (24.9)	4.4 (0.97)
Herring, 1+	30	M	Pt. Gravina	8/11'	18.5 (5.10)	67.7 (3.35)	29.1 (6.9)	62.8 (5.9)	129.8 (53.3)	7.1 (1.40)
Herring, 2+	4	?	Jackpot	7/25'	36.9 (13.3)	74.2 (3.00)	31.5 (8.2)	58.7 (7.0)	225.0 (110.0)	5.8 (1.11)
Sandlance, 0+	27	?	Naked I.	7/16'	1.86 (0.53)	78.4 (0.68)	12.1 (1.5)	78.8 (0.7)	6.6 (2.30)	4.2 (0.30)
Sandlance, 0+	9	?	Naked I.	8/16'	1.59 (0.51)	77.1 (1.33)	14.9 (2.8)	76.5 (2.2)	7.2 (2.60)	4.4 (0.30)
Sandlance, 0+	36	?	Block I.	8/10-12'	2.04 (0.40)	76.0 (1.43)	17.9 (3.0)	78.4 (8.6)	10.2 (2.64)	4.9 (0.28)
Sandlance, 1+	10	?	Block I.	7/13'	9.36 (0.78)	71.4 (1.10)	27.7 (2.8)	65.1 (2.5)	59.3 (6.90)	6.3 (0.40)
Sandlance, 1+	10	?	Block I.	8/10'	9.32 (0.67)	72.2 (1.50)	25.7 (4.3)	67.0 (3.3)	56.0 (6.12)	6.0 (0.58)
Sandlance, 2+	6	F	Block I.	7/13-8/10'	16.1 (3.94)	73.8 (1.50)	21.7 (3.5)	71.0 (3.2)	83.4 (21.1)	5.3 (0.30)
Sandlance, 2+	5	M	Block I.	7/13-8/10'	13.6 (2.08)	75.6 (1.00)	17.5 (1.7)	73.9 (1.9)	64.3 (7.47)	4.8 (0.21)
Capelin, adult	10	M	Naked I.	8/3'	21.9 (1.53)	79.2 (1.50)	13.0 (6.8)	77.4 (5.2)	82.6 (14.4)	3.8 (0.66)
Pollock, 0+	87	?	Naked/Seal I	8/1-8/10'	1.16 (0.40)	79.3 (1.5)	7.7 (0.8)	80.5 (0.8)	4.1 (1.48)	3.5 (0.26)
Pollock, 2+	14	?	E.Graveyard	8/5'	33.1 (7.2)	78.2 (1.1)	5.9 (2.4)	80.7 (1.8)	120.0 (31.3)	3.6 (0.29)
Tomcod, 0+	13	?	Naked I.	7/16-28'	2.11 (0.66)	81.7 (6.6)	5.8 (0.6)	78.9 (2.1)	6.2 (2.0)	2.8 (0.1)
Pac. Cod, 0+	38	?	Naked I.	7/16-8/16'	3.1 (1.7)	83.2 (1.2)	6.0 (1.1)	80.2 (0.9)	8.9 (5.1)	2.8 (0.1)
Pac. Cod, 1+	5	?	Kachemak B.	7/15'	13.2 (2.8)	77.0 (1.7)	4.4 (0.5)	79.2 (0.8)	44.9 (13.2)	3.4 (0.4)

Table 2. Proximate composition of nearshore demersal fishes of Prince William Sound, 1995 (std. dev. in parentheses)

Species	**N**	**Fresh Mass (g)**	**% Water**	**% Lipid** (dry mass)	**% AFLDM** (dry mass)	**Energy Content** (kJ/fish)	**Energy Density** (kJ/g wet mass)
Crescent Gunnel	10	11.6 (2.2)	74.2 (1.5)	13.2 (4.5)	74.8 (2.4)	52.4 (9.4)	4.8 (0.6)
Slender Eelblenny	14	8.2 (2.9)	76.8 (1.0)	15.6 (2.6)	73.3 (2.5)	36.0 (14.6)	4.4 (0.3)
Arctic Shanny	19	6.4 (3.0)	75.7 (1.2)	14.4 (3.4)	73.5 (1.3)	28.5 (13.8)	4.5 (0.5)
Padded Sculpin	21	8.3 (4.2)	78.7 (1.6)	9.8 (3.8)	73.2 (2.6)	30.1 (19.7)	3.6 (0.5)
Four-horned Sculpin*	7	1.5 (0.6)	81.5 (2.3)	8.6	74.8	4.5	3.0

* individual fish pooled for proximate analysis

Table 4. Proximate composition and energy content of black-legged kittiwake chick regurgitations from three colonies in Prince William Sound (std. dev. in parentheses).

Location	N	% water (field)	% lipid (dry mass)	% AFLDM (dry mass)	Energy Density (kJ/g dry mass)	Energy Density (kJ/g wet mass)	Energy Content (kJ)
Shoup Bay	**86**	**75.7** (3.3)	**17.3** (7.0)	**72.6** (6.4)	**19.7** (1.7)	**4.84** (0.99)	**104.1** (53.1)
Seal Island	**14**	**76.5** (2.4)	**14.9** (5.5)	**74.3** (5.7)	**19.1** (1.3)	**4.50** (0.73)	**64.8** (32.3)
Eleanor Island	**30**	**77.7** (2.6)	**13.6** (7.6)	**75.7** (7.0)	**18.8** (1.8)	**4.23** (0.85)	**53.8** (47.4)

Table 5. Proximate composition and energy content of fish fed to nestling tufted puffins in the EVOS area, 1995 (std. dev. in parentheses).

Species/Age	N:	% water (field)	% lipid (dry mass)	% AFLDM (dry mass)	Energy Density (kJ/g wet mass)	Energy Content (kJ)
SEAL ISLAND						
Prowfish, 1+	10	86.9 (1.0)	11.0 (2.8)	75.4 (2.3)	2.25 (0.23)	42.4 (25.8)
Pink Salmon, 1+	5	82.3 (1.1)	5.3 (0.7)	82.5 (0.9)	2.92 (0.83)	59.5 (19.1)
Capelin (spwn.male)	1	81.3	9.8	76.6	3.31	71.7
Herring, 1+	1	72.7	36.4	55.8	6.49	211.2
Herring, 0+	35	84.1 (2.7)	6.5 (0.8)	78.6 (0.8)	2.62 (0.30)	4.8 (2.1)
Pollock 0+	45	85.5 (2.3)	5.8 (1.0)	78.5 (0.7)	2.23 (0.22)	2.8 (0.9)
Sand lance, 0+	3	79.7 (3.9)	15.5	71.9	3.82	3.9 (1.1)
ALL SPECIES					2.64 (0.85)	13.0 (27.9)
NAKED ISLAND						
Sand lance, 0-1+	18	74.4 (2.6)	17.1 (1.1)	72.0 (1.3)	5.30 (0.95)	14.1 (3.6)
AGNES ISLAND						
Pollock, 1+	1	81.9	5.5	76.6	2.81	50.5
Prowfish, 1+	1	88.0	9.8	75.0	1.99	19.3
Prowfish, 2+	1	87.5	9.2	74.4	2.02	47.4
ALL SPECIES					2.29 (0.45)	39.1 (17.2)
BARREN ISLANDS						
Pink Salmon, 1+	4	77.1 (0.9)	4.9 (0.8)	84.1 (1.1)	3.80 (0.18)	79.4 (39.8)
Prowfish, 1+	1	83.0	11.2	74.5	2.94	33.6
Sand lance, 2+	3	67.6 (2.0)	35.0 (1.9)	57.0 (2.1)	7.56 (0.59)	97.3 (12.0)
Capelin, 1+	6	77.0 (2.7)	6.0 (2.3)	78.2 (0.6)	3.58 (0.01)	10.9 (2.5)
ALL SPECIES					4.78 (1.95)	51.0 (43.6)

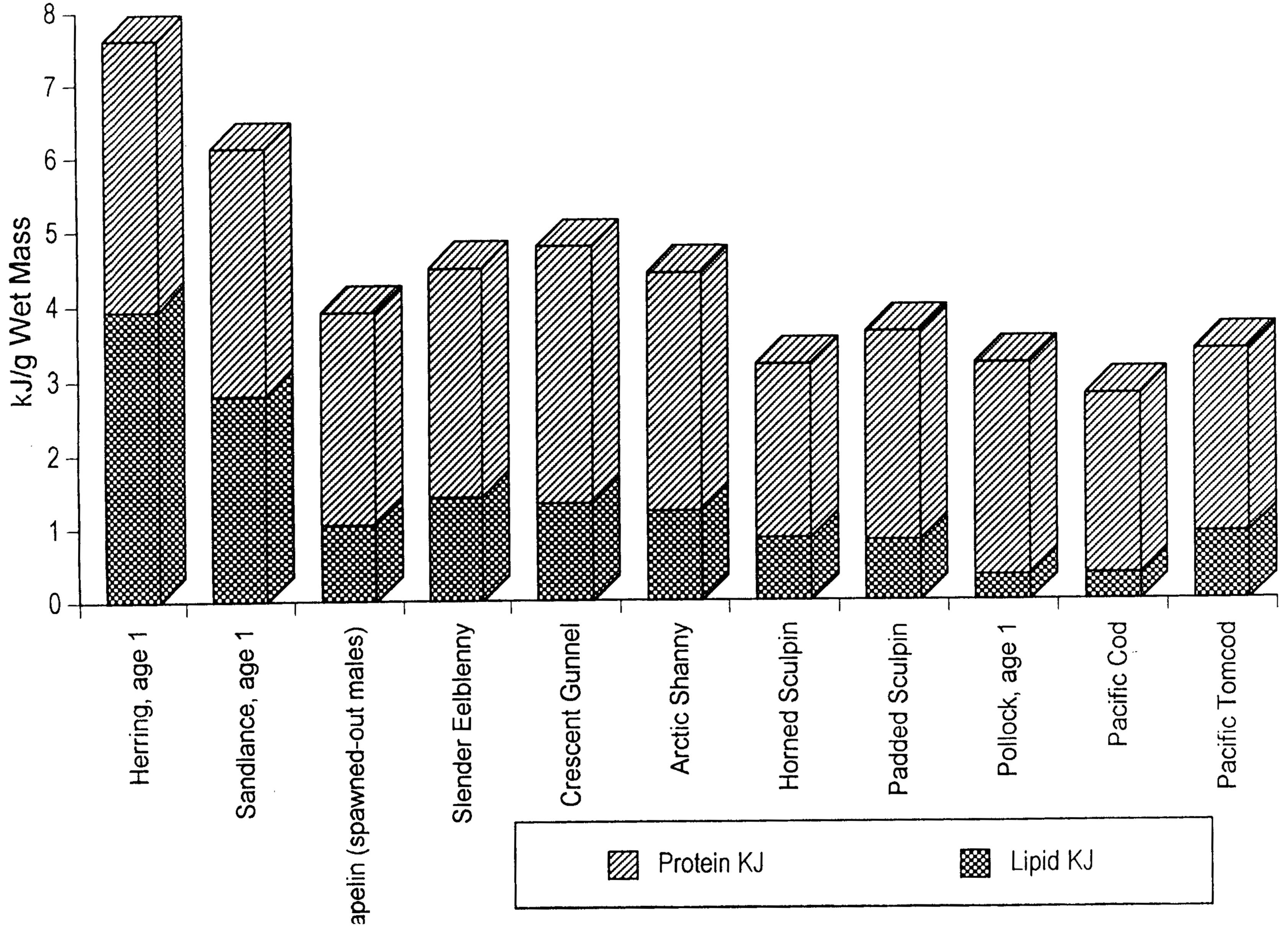
Table 6. Calculations for energy provisioning rates to nests for three species of piscivorous seabirds in the EVOS area, 1995 (std. dev., sample size in parentheses)

Species/Location	Feeding Frequency (meals/(nest day))	Meal Size (g wet mass)	Energy Density (kJ/g wet mass)	Energy Provisioning Rate (kJ/(nest day))
PIGEON GUILLEMOT				
Jackpot I.	**16.6** (4.2, 14)	**20.0** (8.4, 27)	**3.73** (1.53, 27)	**1,238**
Naked I.	**11.4** (4.4, 31)	**14.7** (7.9, 29)	**4.00** (0.74, 28)	**670**
BLACK-LEGGED KITTIWAKE				
Shoup Bay	**3.3** (0.7, 10)	**29.0** (17.3, 37)	**4.84** (0.99, 85)	**463**
Eleanor I.	**4.9** (1.7, 9)	**21.3** (12.3, 21)	**4.23** (0.85, 30)	**441**
TUFTED PUFFIN				
Seal I.	**4.9** (1.5, 21)	**13.7*** (15.4, 42)	**2.64** (0.85, 42)	**177**

* may be biased low; see text

Fig. 1.

Energy density (protein KJ, lipid KJ) of forage fishes in Prince William Sound, Alaska



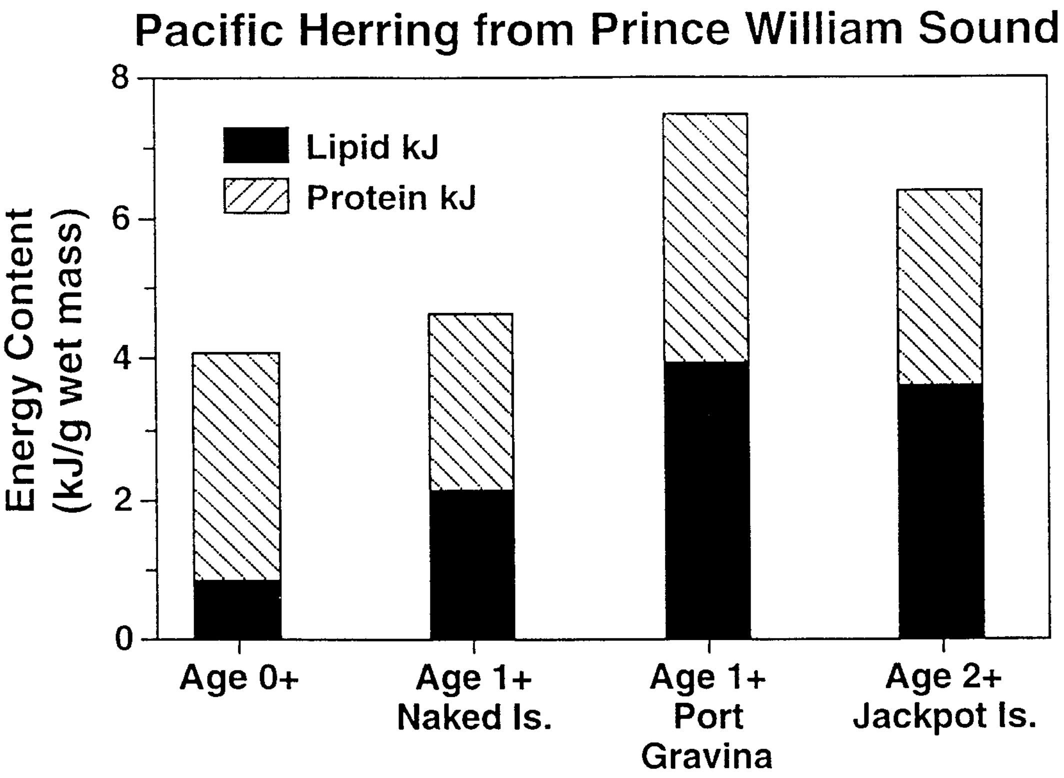

Pacific Herring from Prince William Sound
Energy Content (kJ/g wet mass)
0
2
4
6
8
Lipid kJ
Protein kJ
Age 0+
Age 1+ Naked Is.
Age 1+ Port Gravina
Age 2+ Jackpot Is.

Fig. 3

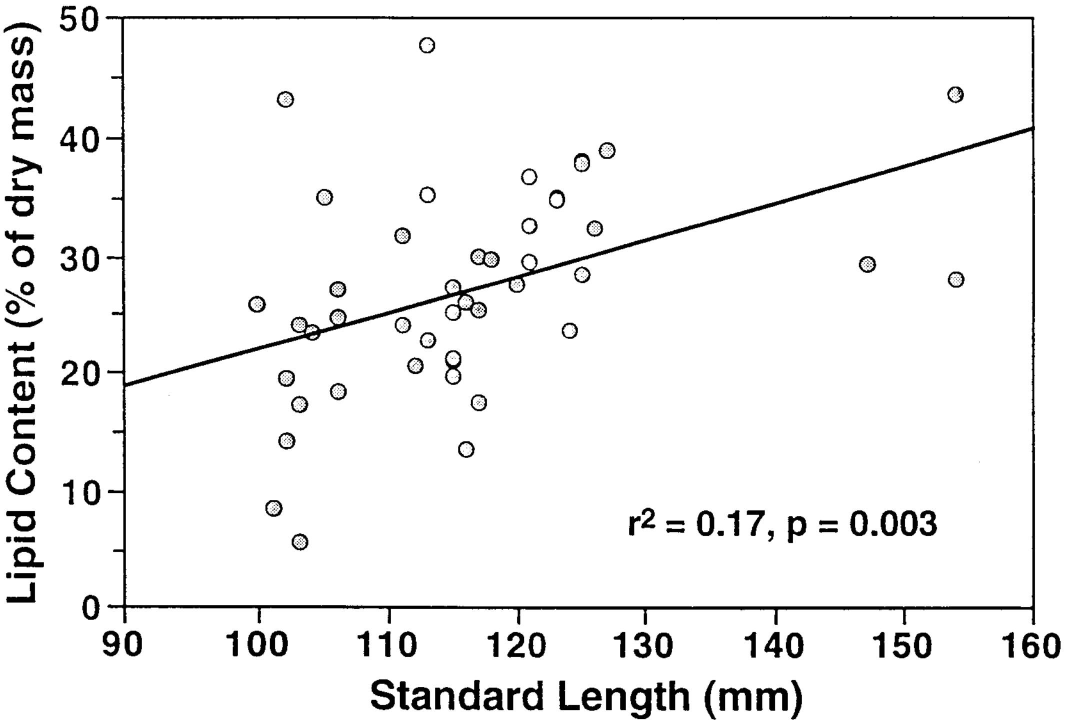

Lipid Content (% of dry mass)
0
10
20
30
40
50
90
100
110
120
130
140
150
160
Standard Length (mm)
$r^2 = 0.17$, $p = 0.003$

Fig. 4

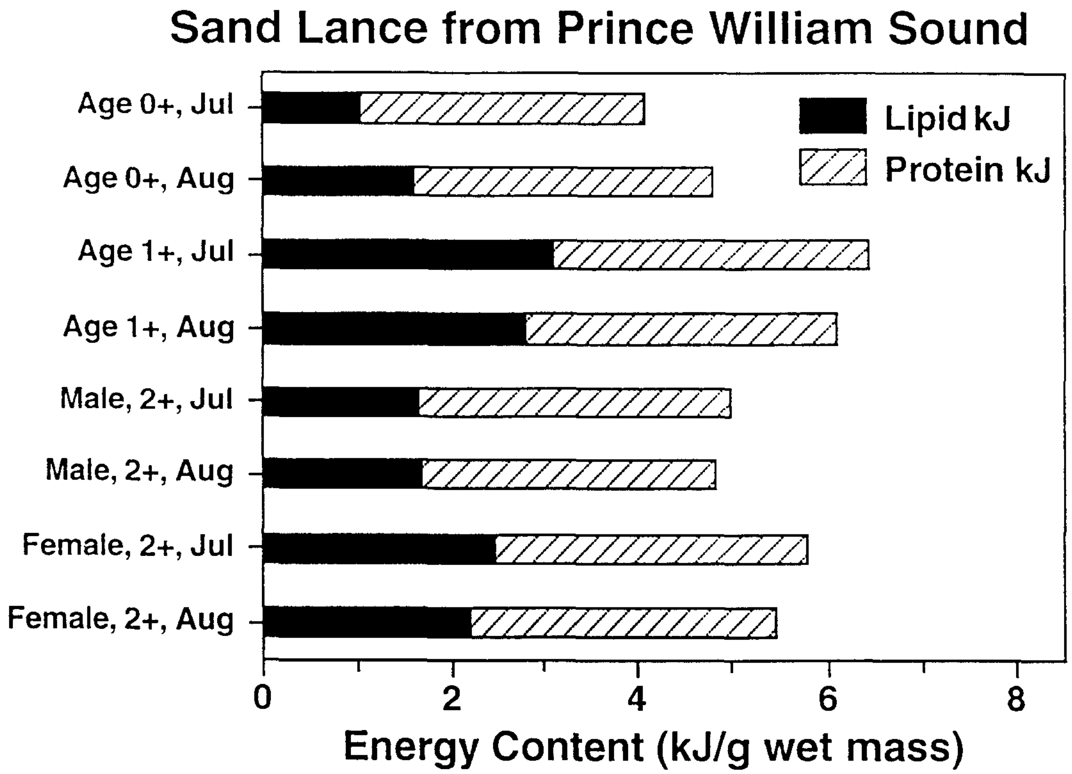

Sand Lance from Prince William Sound
Age 0+, Jul
Age 0+, Aug
Age 1+, Jul
Age 1+, Aug
Male, 2+, Jul
Male, 2+, Aug
Female, 2+, Jul
Female, 2+, Aug
Lipid kJ
Protein kJ
0
2
4
6
8
Energy Content (kJ/g wet mass)

Fig. 5

Pigeon Guillemot Diets in Kachemak Bay and Prince William Sound (Jackpot Island and Naked Island), Alaska

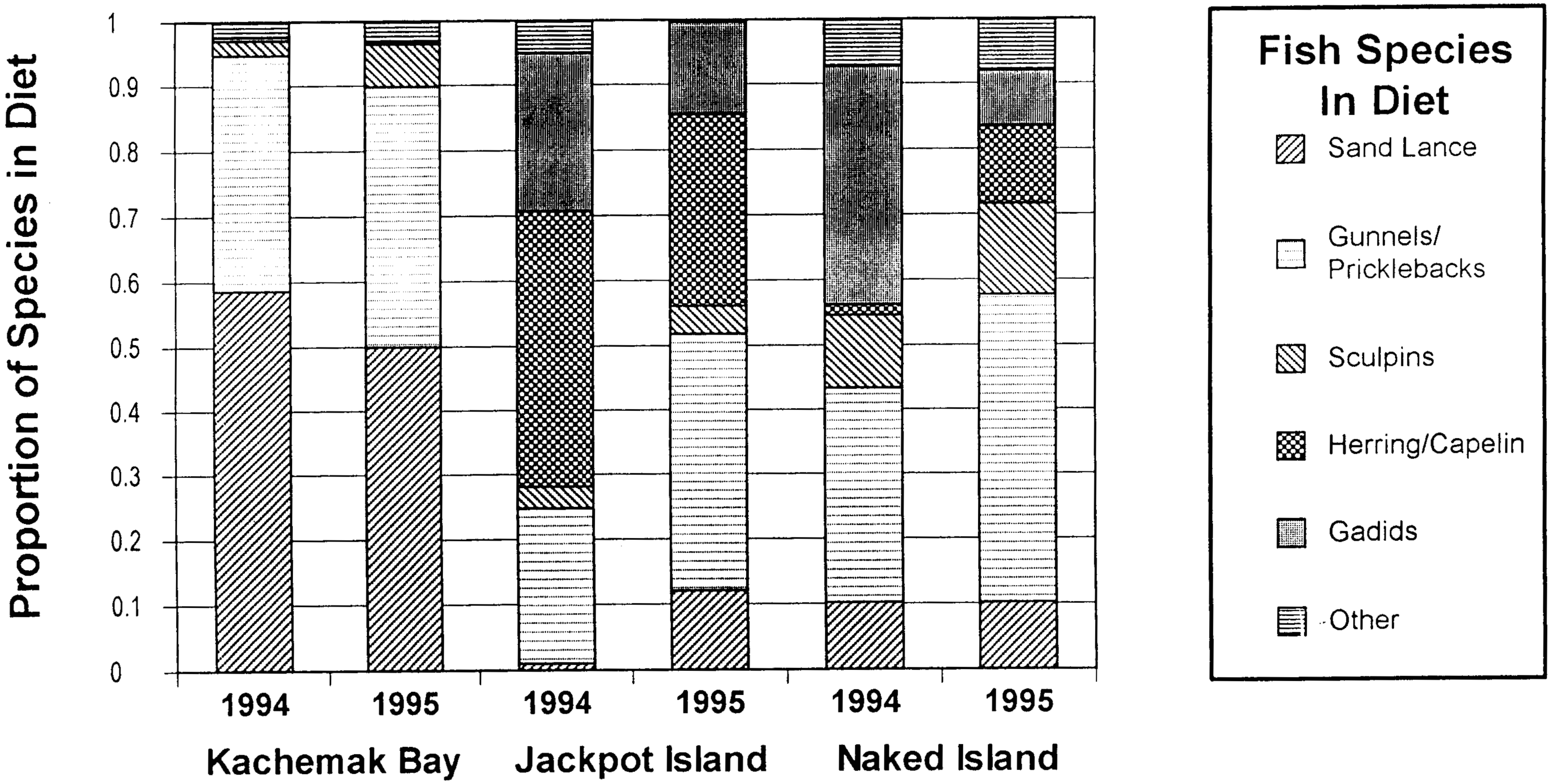


Fig. 6

Prey Delivery Rates to Guillemot Nests in Kachemak Bay and Prince William Sound (Jackpot Island, Naked Island), Alaska

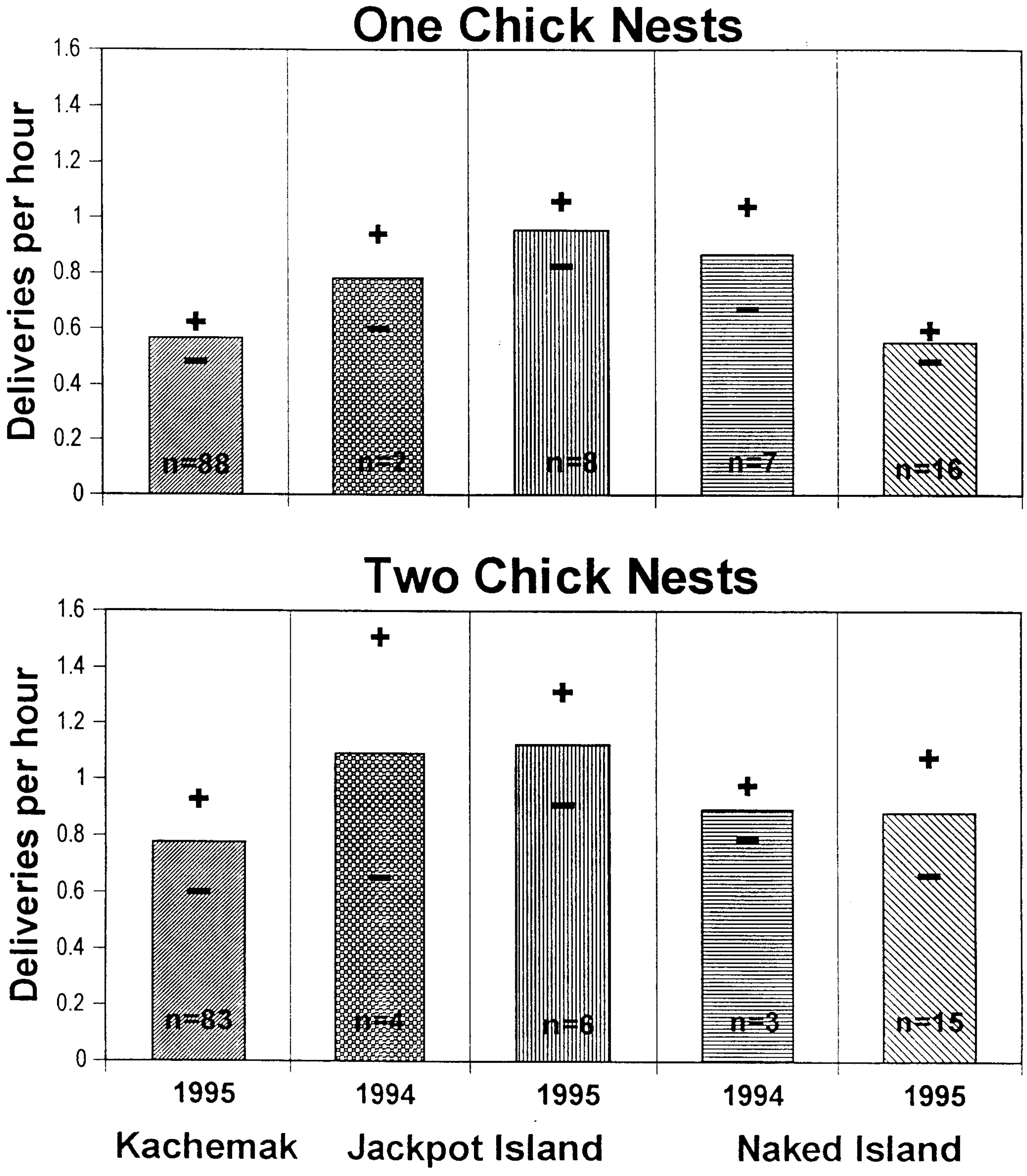
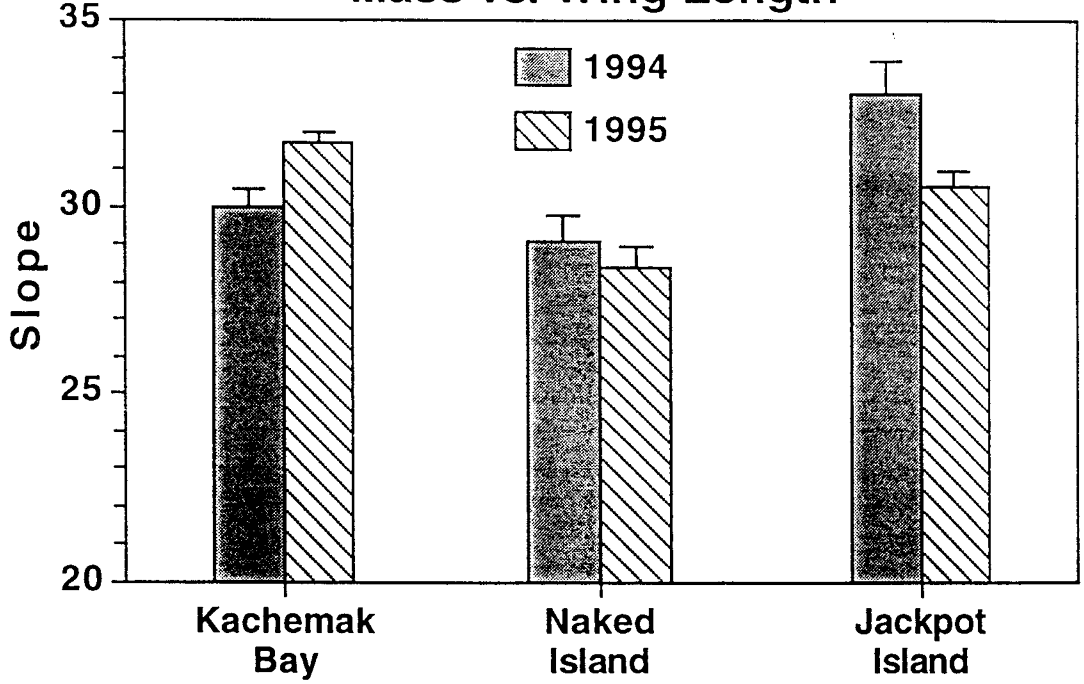


Fig 7

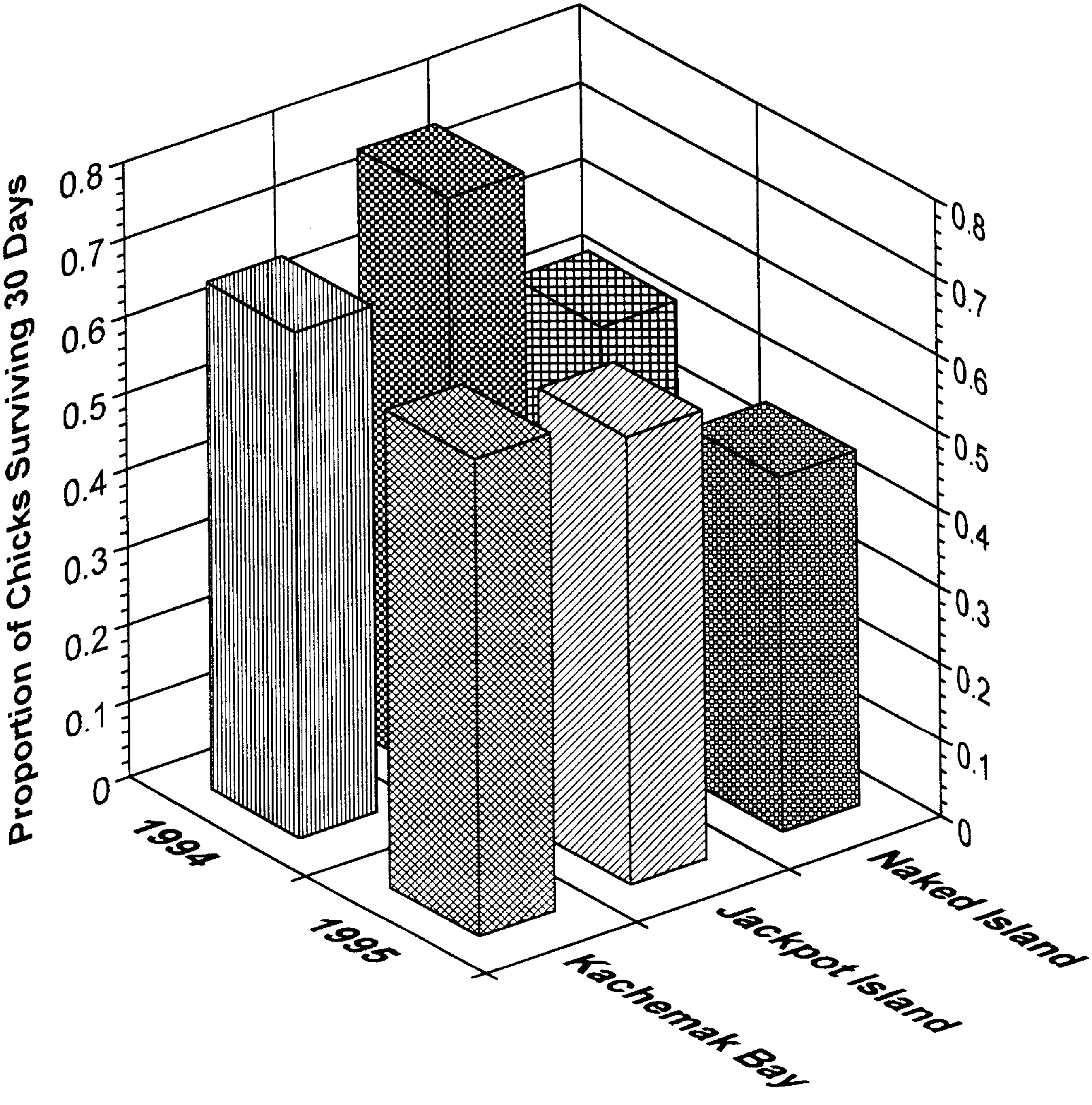


Guillemot Growth Performance
Mass vs. Wing Length

Fig. 8

Nestling Survival

Kachemak Bay and Prince William Sound (Jackpot Island, Naked Island), Alaska



Chick survival for first 30 days of nestling period (Mayfield Method)