*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 97163 G

Annual Report

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

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**Study History:** Restoration Project 97163 G is similar to the research described in the original proposal submitted as 95118-BAA. It is a component of the Alaska Predator Ecosystem Experiment Project (APEX), for which funding was first approved by the EVOS Trustee Council in April 1995. This research examines the effects of diet composition on the reproductive energetics and productivity of piscivorous seabirds in the northern Gulf of Alaska, using pigeon guillemots and black-legged kittiwakes as models. Component G works closely with other colony based research that is part of APEX, including components E, F, J, and M, and provides data for Component Q of APEX (modeling factors limiting seabird recovery). In 1995, study sites for kittiwakes were breeding colonies at Shoup Bay, Eleanor Island, and Seal Island in Prince William Sound, and Gull Island, Chisik Island, and the Barren Islands in Lower Cook Inlet; study sites for guillemots were at Naked Island and Jackpot Island in PWS, and Kachemak Bay in Lower Cook Inlet. In 1996, field research continued with a shift in kittiwake study sites from Seal Island to North Icy Bay. In 1997, all study sites remained the same as in 1996.

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

1997 was a mediocre or poor year for kittiwake nesting success at most APEX study colonies, breaking the previous trend of higher kittiwake productivity associated with increasing availability of capelin, herring, and sand lance. Kittiwake productivity within the study area appears to be strongly linked to the availability of these three species of forage fish, which form schools nearshore and have high energy densities compared with most other forage fishes. Availability of high-quality schooling forage fish (sand lance, herring) within foraging distance of guillemot colonies was positively correlated with energy provisioning rates to guillemot nests, as well as nestling growth rates.

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

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## EXECUTIVE SUMMARY

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

Pigeon guillemots and black-legged kittiwakes were the focal piscivorous seabirds studied during the 1997 breeding season. In cooperation with other APEX projects, we collected samples of nestling diets and measured nestling provisioning rates, growth rates, and nesting success in relation to diet. The two guillemot study sites in Prince William Sound (PWS) were located at Naked Island (an oiled site) and Jackpot Island (an non-oiled site), and were compared with guillemots nesting in Kachemak Bay (a reference site). The three study sites for kittiwakes in PWS were Eleanor Island (an oiled site), North Icy Bay (a non-oiled site), and Shoup Bay (a non-oiled site). The three kittiwake study sites for Lower Cook Inlet (LCI) were at Gull Island, Chisik Island, and the Barren Islands (all reference sites). In addition, forage fishes were collected using a variety of methods and analyzed in the lab to determine quality as seabird prey.

Forage fish exhibited a ten-fold difference in lipid content (% dry mass) and a five-fold difference in energy density (kJ/g wet mass) among individuals, such that predators could potentially experience large differences in foraging efficiency depending on prey choice (see attached manuscript by Anthony et al.). Schooling pelagic fishes tended to have either relatively high lipid content and energy density (e.g., herring, capelin, sand lance) or low lipid content and energy density (e.g., pollock, cod, tomcod), whereas nearshore demersal fishes (e.g., blennies, sculpins) had intermediate values. Interspecific variation in lipid content was the primary factor influencing energy density of forage fishes, with variation in water content also contributing. Lipid content (% dry mass) was negatively correlated with water content (% wet mass) and positively correlated with protein content (% lean dry mass). Thus, high-lipid fish had higher nutritional value than low-lipid fish in part because of lower water content and higher protein content. Intraspecific differences in lipid content and energy density of forage fishes were related to size, sex, month, reproductive status, location, and year. Pelagic species maturing at a smaller size (e.g., capelin, sand lance, lanternfish) had higher and

more variable energy densities than did pelagic or nearshore species maturing at a larger size (e.g., gadids, salmonids). Diet quality for some piscivorous seabirds in the EVOS area is sufficiently variable to affect prey selection.

The diet of pigeon guillemots in 1997 was more similar among the three study sites than in previous years, and was dominated by blennies and sculpins (nearshore demersal fishes) at all three sites. Schooling forage fishes, however, were a significant component of guillemot diets at all three sites, mostly sand lance at Kachemak Bay and Naked Island, and mostly gadids at Jackpot Island. Notable was the near total absence of herring in the diets of Jackpot Island guillemots in 1997 (in contrast to 1994-96), while modest increases in the proportion of sand lance in the diet compared to 1996 occurred at Naked Island and Kachemak Bay.

In 1997, energy provisioning rates to guillemot nestlings were highest at Kachemak Bay, lowest at Naked Island, and intermediate at Jackpot Island. Results from 1997, the third field season of APEX, provide more support for the hypothesize that recovery of pigeon guillemots at Naked Island (an oiled site) is limited by availability of sand lance, which are apparently crucial for maintaining high densities of breeding guillemots in that region of Prince William Sound. 1997 results also support the general hypothesis that breeding populations of pigeon guillemot in the EVOS area are constrained by the availability of schooling forage fishes with relatively high lipid content and high energy density (i.e., sand lance, herring, or capelin).

The primary prey at most of the six APEX kittiwake study colonies in 1997 was young of the year sand lance. Two colonies in Prince William Sound were the exception; at the Shoup Bay colony herring were the most prevalent prey item and at Eleanor Island capelin were most prominant. Notable was the low incidence of capelin in kittiwake diets at the Barren Islands. Capelin, sand lance, and herring are three species of forage fish with high lipid content and energy density compared with other species sampled (see attached manuscript by Anthony et al.).

Energy provisioning rates to kittiwake broods were generally higher at Prince William Sound study sites than at Lower Cook Inlet study sites. Among PWS study sites, energy provisioning rates were highest at North Icy Bay, lowest at Eleanor Island, and intermediate at Shoup Bay. Compared to 1996, energy provisioning rates at Shoup Bay and Eleanor Island were lower in 1997, reflecting generally lower prey biomass in northeastern and central PWS. At kittiwake study sites in Lower Cook Inlet, energy provisioning rates were moderate at Gull Island, low at the Barren Islands, and very low at Chisik Island. The Chisik Island kittiwake colony completely failed in 1997, while the Barren Islands colony had a poor year with low nesting success. Compared with 1996, energy provisioning rates were lower at all LCI kittiwake study sites during 1997.

Results from 1997 provide more support for the importance of juvenile herring and, secondarily, sand lance for maintaining high energy provisioning rates and high breeding productivity at Prince William Sound kittiwake colonies. The results from the 1997 field season also underline the importance of capelin as a forage fish resource for kittiwakes and other piscivorous seabirds nesting in Lower Cook Inlet. Thus, results from the third season of APEX field work support the hypothesis that the productivity of black-legged kittiwakes in the EVOS area is limited by the availability of sand lance, herring, and capelin, all forage fishes with relatively high lipid content and high energy density compared with available 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 fish is particularly relevant to reproductive success because it is the primary determinant of the energy density of meals delivered to nestlings. Parent seabirds that transport chick meals in their stomachs (e.g., kittiwakes) normally transport meals that are close to the maximum load. Seabirds that transport chick meals as single prey items held in the bill (e.g., guillemots, murres, murrelets) experience additional constraints on meal size if optimal-sized prey are not readily available. Consequently, seabird parents that provision their young with fish high in lipids are able to support faster growing chicks that fledge earlier and with larger fat reserves (see annual report for APEX Component 97163 N). This is because the energy density of lipid is approximately twice that of protein and carbohydrate. Also, forage fish are generally very low in carbohydrate, and metabolism of protein as an energy source requires the energetically expensive process of excreting the resultant nitrogenous waste. 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 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 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 component G of the Alaska Predator Ecosystem Experiment (APEX) Project (EVOS Projects 97163 A-T), whose goal is to test the general hypothesis that a shift in the marine trophic structure of the EVOS area has prevented recovery of injured resources. APEX addresses 10 more specific working hypotheses, 5 of which (hypotheses 4, 7, 8, 9, 10) this component helps test and two of which are the focus of this study:

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

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

These two hypotheses address the two primary determinants of energy provisioning rates to nestling seabirds, which in turn have a direct bearing on fitness through variation in reproductive output. Another variable, parental investment, 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 1997 emphasized pigeon guillemots and black-legged kittiwakes.

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

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

Objective 2. To determine dietary parameters of pigeon guillemot and black-legged kittiwake chicks in the EVOS area, including:

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

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

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

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

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

## STUDY AREAS

Data collection from the field occurred in 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 1997 breeding season. These sites were identical to those seabird breeding sites that were used in 1996 and by other components of APEX.

Field work on pigeon guillemots was conducted at breeding colonies on Naked Island (oiled area), Jackpot Island (non-oiled area, both in PWS), and in Kachemak Bay (reference site). Approximately 500 guillemots nest along the shores of Naked Island (Sanger and Cody 1993), supporting a large proportion of the total breeding population of guillemots in PWS. The field camp in Cabin Bay served as the base camp for field studies of guillemots nesting on the western and northern shorelines of Naked Island (see annual report for APEX Component 97163 F by G. Golet). Naked Island has been the site of long term studies of guillemot reproductive ecology since 1979 by the U.S. Fish and Wildlife Service (Kuletz 1983).

Jackpot Island is a small island in southwestern PWS that supports the highest known breeding density of guillemots in the Sound (G. Sanger, D. L. Hayes, pers. comm.). Jackpot Island has been the site of intensive studies of guillemot nesting success since the 1994 field season and is located in a non-oiled portion of PWS. Kachemak Bay served as a third study site for guillemots. The breeding population of guillemots on the south shore of Kachemak Bay between Mallard Bay and Seldovia has been the site of intensive studies of guillemot breeding biology, diet, and productivity since 1994, first by UAF graduate student Alex Prichard, and then by M. Litzow and J. Piatt. Results in 1994-97 suggested that the guillemot prey base in parts of Kachemak Bay is largely sand lance, and is perhaps similar to the prey base at Naked Island 15-20 years ago. Consequently, the Kachemak Bay guillemot study site provides an excellent reference site for guillemot studies in PWS.

Field work on black-legged kittiwakes in PWS was conducted at three breeding colonies: (1) Shoup Bay in Port Valdez (non-oiled area), the largest kittiwake colony in PWS consisting of c. 6500 breeding pairs, (2) Eleanor Island in central

PWS near Knight Island (oiled area), with ca. 200 breeding pairs, and (3) North Icy Bay in south western PWS (non-oiled area), with ca. 500 breeding pairs. The Shoup Bay colony is the site of continuing long-term studies of kittiwake nesting ecology in PWS by the U.S. Fish and Wildlife Service; Eleanor Island and North Icy Bay have been selected as a sites for intensive study for comparison purposes (see annual report for APEX Component 97163 E by R. M. Suryan and D. B. Irons). In Lower Cook Inlet, kittiwake breeding colonies at the Barren Islands, Gull Island, and Chisik Island were monitored for diet and reproductive success (see annual reports for APEX Component 97163 J by D. G. Roseneau, A. B. Kettle, and G. V. Byrd and APEX Component 97163 M by J. Piatt et al.) .

## METHODS

### Field Data Collection

The research approach utilized a combination of sample/data collection in the field (in conjunction with other APEX components in PWS and LCI) and laboratory analyses of seabird diet and forage fish samples. A minimum of 40 active and accessible nests of each species were located and marked prior to hatching at each of the study colonies, and these nests were closely-monitored until the young fledged or the nesting attempt failed. Samples of forage fishes were collected concurrently with data on seabird reproduction during the 1997 breeding season.

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

Adult kittiwakes transport chick meals in the foregut, so chick diet samples consist of semi-digested food. Most kittiwake diet samples were collected when chicks regurgitated during routine weighing and measuring. Additional diet samples were collected by capturing adult kittiwakes as they returned to feed their young and encouraging them to regurgitate the contents of their esophagus. Fresh specimens of forage fishes used by kittiwakes were provided by trawl, cast net, dip net, and other methods through the cooperation of APEX Component 97163 A and others.

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

Proximate analysis of all samples was conducted by the third author (JAA) in the lab of the first author (DDR) at the Department of Fisheries and Wildlife, Oregon State University. Forage fish specimens and chick meals were reweighed on an analytical balance (± 0.1 mg), 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/isopropyl alcohol 7:2 (v:v) as the solvent system. Lean dry samples were then transferred from extraction thimbles to glass scintillation vials and ashed in a muffle furnace at 550°C in order to calculate ash-free lean dry mass (ca. 94 % protein) by subtraction. Energy density (kJ/g wet mass) and energy content of forage fishes and chick meals were calculated from their composition (% water, lipid, ash-free lean dry matter, and ash), using published energy equivalents of these fractions (Schmidt-Nielsen 1997: 171).

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

Active guillemot and kittiwake nests were checked every few days during the hatching period in order to determine hatching date. In the case of two-chick broods, siblings were marked soon after hatching so that individual growth rates could be monitored throughout the nestling period. Nestlings growth rates were determined by weighing and measuring chicks on a regular basis (every 3-5 days) throughout the nestling period. Nestling survival rates were calculated from the results of periodic nest checks, using the Mayfield method. During the fledging period, we attempted to check nests and weigh nestlings more frequently in order to more precisely determine fledging mass and age. Data on nestling body mass, wing chord, and primary feather length were separated by colony for each species.

Parental investment by adult kittiwakes raising broods was assessed by measuring daily energy expenditure (DEE) of breeding adults during the chick-rearing period. DEE was determined by measuring $CO_2$ production using the doubly-labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980, Roby and Ricklefs 1986). DEE of adult kittiwakes was measured at the Shoup Bay and North Icy Bay colonies in 1997, as representative of kittiwake colonies of different size, productivity, and food availability. Twenty-five nesting adults were injected with doubly-labeled water at each of these colonies.

Parent kittiwakes were captured at the nest with a noose pole and injected intraperitoneally with 0.9 ml of a mixture of deuterated (99.8 atom %) and oxygen-18 labeled (90 atom %) water ($D_2{}^{18}O$). These two isotopes are stable, so no permits for use of radioactive materials were necessary. Following injection, each adult was banded, weighed, measured, and marked with dye on the plumage for easy recognition on the colony. One hour after injection, when injected DLW had equilibrated with body water, a blood sample was collected from each adult by puncturing the brachial vein and collecting about 100 ul of blood in non-heparinized microhematocrit tubes, which were subjequently flame-sealed and kept refrigerated. Injected adults were then released and an attempt was made to recapture each adult at least once in the subsequent 48-hour period. Once recaptured, injected adults were reweighed and a second blood sample collected as described above. Isotope enrichments of blood samples were measured using mass spectrometry in the laboratory of Dr. Henk Visser (Centre for Isotope Research, University of Groningen, The Netherlands). Carbon dioxide production of each adult during each measurement interval was calculated using the equations of Lifson and McClintock (1966). DEE was calculated from CO2 production using an assumed RQ of 0.8 and an energetic equivalent of respired CO2 of 27.3 kJ/liter (Gessamen and Nagy 1988).

## RESULTS AND DISCUSSION

### Objective 1: Proximate Composition of Forage Fishes

Results and discussion related to this objective are presented in the attached manuscript: "Lipid content and energy density of forage fishes from the northern Gulf of Alaska" by J. A. Anthony, D. D. Roby , and K. R. Turco. This manuscript has been submitted for publication in the peer-reviewed, scientific journal *Canadian Journal of Fisheries and Aquatic Sciences.*

## Objective 2: Dietary Parameters of Nestling Seabirds

### Pigeon Guillemots

Forty-one pigeon guillemot chick meals (individual fish) were collected at Naked Island, 58 at Jackpot Island, and 47 at Kachemak Bay in 1997. Table 1-3 shows the species of fish collected as guillemot chick meals at the three sites, their average mass, and the percent of total prey biomass for each prey species at each site. 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. 1).

Taxonomic composition of guillemot nestling diets at Naked and Jackpot islands were more similar in 1997 than in any year since 1994, and consisted mostly of blennies and sculpins (Fig. 1). Guillemot diets on Jackpot Island diets were nearly devoid of juvenile herring, the dominant schooling forage fish in the diet in previous years, and instead the only schooling forage fishes that figured prominently in the diet were gadids (30.1% of prey biomass). Diets of guillemots on Naked Island included a significant proportion of sand lance (15.6% of prey biomass), a slight increase over 1995 and 1996. The proportion of sand lance in guillemot diets in Kachemak Bay appeared to decline in 1997, compared to previous years, but this was an artifact of including fewer nests in the sample where the parents were sand lance specialists (M. Litzow, pers. comm.)

Average mass of chick meals collected at Naked Island (9.7 g, sd = 4.41, n = 37) was considerably less than that of chick meals collected at Jackpot Island (17.1 g, sd = 11.19, n = 49), but only marginally less than meals collected in Kachemak Bay (12.3 g, sd = 6.71, n = 34). Feeding frequency (chick meals delivered/(nest day)) was similar at Jackpot Island (11.1 meals/(nest day), sd = 5.40, n = 55), Naked Island (12.2 meals/(nest day), sd = 5.78, n = 28), and Kachemak Bay (13.5 meals/(nest day), sd = 7.05, n = 63; Table 5). Consequently, the estimated mass of food delivered to guillemot nests at Jackpot Island (190 g/day) was more than that of guillemot nests at Naked Island (118 g/day), but similar to that of guillemot nests in Kachemak Bay (166 g/day).

The average energy density of chick meals collected at the Jackpot and Naked colonies were similar in 1997 (Table 5), despite the higher incidence of sand lance in the diet at Naked Island. The average energy density of chick meals from Kachemak Bay was higher than that of either of the PWS study sites. Estimated energy provisioning rates to guillemot broods was lowest at Naked Island, highest at Kachemak Bay, and intermediate at Jackpot Island (Table 5). Compared to previous years, energy provisioning rates at Naked Island declined, while rates at Kachemak Bay remained stable. Energy provisioning rates at Jackpot Island declined dramatically, due mostly to a decline in meal delivery rate, apparently due to the scarcity of herring within foraging distance of the colony.

### Black-legged Kittiwakes

Once again, the primary fishes in the diets of kittiwakes nesting at all 6 study colonies were sand lance, capelin, and herring (Table 4). The general pattern over all six study colonies of 1997 diets compared to 1996 diets was declines in herring and capelin and increases in sand lance (Fig. 2). Most of the sand lance in kittiwake diets in 1997 were small, young of the year fish, rather than adults (Table 4). The prevalence of 0+ sand lance in the diets of kittiwakes nesting at 4 of the 6 APEX study colonies suggests a general decline in the availability of herring and capelin. Sand lance continued to supply the vast majority of the diet at Gull Island in Kachemak Bay, despite the fact that over two-thirds of the biomass of the diet consisted of small, 0+ sand lance. There was a big decline in the incidence of herring in kittiwake diets from North Icy Bay, and herring were replaced mostly by 0+ sand lance. There was also a decline in the incidence of herring in diets of kittiwakes breeding at Eleanor Island, but there the herring was replaced primarily by capelin (Fig. 2). Juvenile walleye pollock were virtually absent from kittiwake diets in Prince William Sound, and were a very minor part of the diet in Lower Cook Inlet (Table 4).

Average nestling meal sizes at all six kittiwake study colonies were estimated from the average mass of whole chick and adult regurgitations. Estimated average mass of chick meals from all three PWS colonies was similar, but chick meals from Shoup Bay (22.7 g, n = 62) averaged greater than those from Eleanor Island (17.6 g, n = 55). Estimated average chick meal mass at the LCI colonies varied much more than in PWS. The Barren Islands had the largest average meal size, while Chisik Island had the lowest (Table 6). Gull Island, with intermediate chick meal size, was similar to that of Shoup Bay kittiwakes.

The smaller chick meals delivered at Eleanor Island were compensated for by a higher frequency of chick meal deliveries, so that broods at both Eleanor Island and Shoup Bay received about the same amount of food per day (69 g). Nests at North Icy Bay had the highest rate of chick meal deliveries (4.53 meals/(nest day)) of any of the 6 kittiwake study colonies. Consequently, North Icy Bay nests received an estimated 89 g of food daily, compared with about 81 g at Gull Island nests, 61 g at Barren Islands nests, and only 30 g at Chisik Island nests.

In 1997, diet quality was similar at all three kittiwake study colonies in PWS (Table 6). Energy density of diets at the three LCI kittiwake study sites were more variable, with the lowest energy density at the Barren Islands, highest energy density at Chisik Island, and intermediate energy density at Gull Island. The highest overall energy provisioning rates were recorded at the North Icy Bay colony, followed by Gull Island in Kachemak Bay, Shoup Bay and Eleanor Island in PWS, and finally Barren Islands and Chisik Island in LCI. Energy provisioning rates to kittiwake broods were generally lower in 1997, compared with 1996. The decline in energy provisioning rates was especially striking at the Shoup Bay colony, due mostly to longer foraging trips and a concommitant decline in meal delivery rates. This trend was apparently a reflection of lower availability of herring in northeastern PWS. Energy provisioning rates also declined from 1996 to 1997 at the Eleanor Island colony, but not nearly as drastically as at the Shoup Bay colony. The much longer foraging trips (and thus lower feeding frequency) observed at Eleanor Island in 1997 compared to previous years was partly balanced by larger chick meal size and higher diet quality.

## Objective 3: Diet and Productivity

### Pigeon Guillemots

Nesting productivity of guillemots at Naked Island was lower in 1997 than in 1995 or 1996, in agreement with lower estimated energy provisioning rates in 1997. In contrast, the productivity of guillemots at Jackpot Island was much higher in 1997 than in 1996, when mink predation caused total nesting failure. But compared to 1995, productivity at Jackpot Island was lower in 1997, in agreement with lower estimated energy provisioning rates and the scarcity of herring in 1997 compared with 1995. The productivity at Kachemak Bay was similar in 1997 and 1996, in agreement with similar energy provisioning rates in the two years.

### Black-legged Kittiwakes

The productivity of kittiwake study colonies in 1997 was generally lower than in 1996, in agreement with lower energy provisioning rates in 1997. Productivity at the North Icy Bay colony was higher in 1997 than in 1996, in agreement with high energy provisioning rates in 1997 (highest of all kittiwake study colonies). The productivity of the Shoup Bay colony was markedly lower in 1997 compared with 1996, in agreement with lower energy provisioning rates. The higher incidence of brood reduction and nest failure at the Shoup Bay colony compared with previous years apparently reflected the scarcity of juvenile herring within foraging distance of the Shoup Bay colony. The Chisik Island kittiwake colony failed completely, in association with extremely low energy provisioning rates. The Barren Islands colony had considerably lower productivity in 1997 compared with 1996, apparently due to reduced availability of both capelin and sand lance.

## Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

The average guillemot prey size at Jackpot Island in 1997 continued to be higher than at Naked Island, despite the absence of juvenile herring in the Jackpot Island diets. Diet quality (energy density of chick meals) has remained fairly constant within each study colony, but diet quality at Kachemak Bay has been consistently higher than at Prince William Sound sites. Availability of schooling forage fish, especially sand lance, within foraging distance of the colony is positively correlated with nestling growth rates, fledging weights, and chick survival (see manuscript by Golet et al. under APEX Component F). The higher proportion of schooling forage fish in guillemot diets is associated with higher prey provisioning rates to broods. Thus the local availability of schooling forage fish (sand lance at Naked Island and Kachemak Bay, herring at Jackpot Island) appears to be closely linked to productivity of guillemot nesting pairs.

As part of a pilot study investigating energy expenditure rates of adult kittiwakes feeding young, we measured field metabolic rates using the doubly labeled water technique at two colonies in Prince William Sound during 1997: Shoup Bay and Icy Bay. Preliminary results indicate a trend toward higher energy expenditure rates by adults feeding young at Shoup Bay compared with Icy Bay, although the difference was not significant (Table 7). Sample sizes and statistical power, however, will increase considerably once lab analyses are completed. The combination of higher average daily energy expenditure and lower water turnover rates of adult kittiwakes nesting at Shoup Bay suggests that the foraging efficiency of Shoup Bay kittiwakes was lower than that of North Icy Bay kittiwakes in 1997. Lower foraging efficiency at Shoup Bay is consistent with lower productivity, lower energy provisioning rates, and lower apparent availability of alternative prey at Shoup Bay compared with Icy Bay in 1997.

The trend established in the first two years of APEX of higher kittiwake productivity associated with increasing availability of sand lance, capelin, and herring was broken in 1997, a mediocre or poor year at most APEX study colonies. In Prince William Sound, productivity of the inland colony at Shoup Bay seems to be largely dependent on availability of herring, while Eleanor Island and Icy Bay can potentially prey switch to capelin and/or sand lance. Declining availability of capelin in the vicinity of the Barren Islands was reflected in declining kittiwake productivity there. Gull Island appears to be entirely dependent on local availability of sand lance. Kittiwake productivity within the study area appeared to be strongly linked to the availability of three species of forage fish: Pacific sand lance, Pacific herring, and capelin. These three species form schools nearshore and have high energy densities compared with most other forage fishes.

If herring does not rebound in PWS and capelin does not rebound in LCI, 1998 may be even poorer than 1997 for productivity of kittiwakes at the six study colonies. The relatively high availability of young of the year sand lance at most kittiwake study colonies is a potential source of optimism for productivity in 1998. But high sea surface temperatures associated with the 1997-98 El Niño may lower survival and reduce availability of sand lance, capelin, and herring to seabird predators in 1998 breeding season.

## CONCLUSIONS

### Objective 1: Proximate Composition of Forage Fishes

- Please see Conclusions Section of the attached manuscript "Lipid content and energy density of forage fishes from the northern Gulf of Alaska."

### Objective 2: Dietary Parameters of Nestling Seabirds

#### Pigeon Guillemots

- Nearshore demersal fishes (blennies & sculpins) were the bulk of guillemot diets at all three study sites in 1997.

- Herring was virtually absent in diets at Jackpot Island, in marked contrast to previous years.

- Energy provisioning rates declined at Naked Island (due mostly to declining prey size), and declined dramatically at Jackpot Island, apparently due to low availability of juvenile herring.

- Average quality (energy density) of the diet in Kachemak Bay continued to be higher than either of the Prince William Sound study sites.

#### Black-legged Kittiwakes

- Herring and capelin declined and young of the year sand lance increased in kittiwake diets in 1997, compared with 1996.

- Energy provisioning rates to kittiwake broods were generally lower in 1997 than in 1996, apparently related to lower foraging efficiency on 0+ sand lance.

- Energy provisioning rates at Shoup Bay declined dramatically from 1996, due mostly to longer foraging trips and a concommitant decline in meal delivery rates, coincident with lower availability of herring.

- At Lower Cook Inlet colonies, energy provisioning rates were lowest at Chisik Island, highest at Gull Island, and intermediate at the Barren Islands

### Objective 3: Diet and Productivity

#### Pigeon Guillemots

- Productivity was lower at Naked Island in 1997 than in 1995 or 1996, in agreement with lower energy provisioning rates in 1997.

- Productivity at Jackpot Island was lower in 1997 than in 1995, in agreement with lower energy provisioning rates in 1997.

- Productivity at Kachemak Bay was similar in 1997 to 1996, in agreement with similar energy provisioning rates in the two years.

**Black-legged Kittiwakes**

- Productivity was generally lower at kittiwake study colonies in 1997 compared to 1996, in agreement with lower energy provisioning rates and higher reliance on 0+ sand lance as prey in 1997.

- Productivity at Shoup Bay was markedly lower in 1997 compared with 1996, in agreement with lower energy provisioning rates and lower availability of herring.

- The Barrens Island colony had poor nesting success and the Chisik Island colony failed completely, in association with very low energy provisioning rates.

## Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

**Pigeon Guillemots**

- Diet quality has remained fairly constant within each study colony, but diet quality at Kachemak Bay has been consistently higher than at Prince William Sound sites.

- Higher proportion of schooling forage fishes (sand lance, herring) in guillemot diets is associated with higher prey provisioning rates to broods.

- Availability of schooling forage fish (sand lance, herring) within foraging distance of the colony is positively correlated with nestling growth rates, fledging weights, and chick survival.

**Black-legged Kittiwakes**

- A pilot study measuring adult daily energy expenditure indicated lower foraging efficiency by parents feeding young at Shoup Bay compared with North Icy Bay, consistent with lower productivity and lower energy provisioning rates at Shoup Bay compared with Icy Bay in 1997.

- Generally lower productivity of kittiwake colonies in 1997 reflected greater reliance on small, 0+ sand lance as a food source.

- Productivity of the large inland colony at Shoup Bay in Prince William Sound seems dependent on availability of juvenile herring.

- Productivity of the Barren Islands colony in Lower Cook Inlet seems dependent on availability of capelin.

- The trend established in the early years of APEX of higher kittiwake productivity associated with increasing availability of sand lance, capelin, and herring was broken in 1997, a mediocre or poor year at most APEX study colonies.

- Kittiwake productivity within the study area appears to be strongly linked to the availability of three species of forage fish: Pacific sand lance, Pacific herring, and capelin. These three species form schools nearshore and have high energy densities compared with most other forage fishes.

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Table 1. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to pigeon guillemot broods at Jackpot Island, Prince William Sound in 1997.

| Species | Number of Prey Items | Average Mass (g) | % Total Biomass of Prey |
|---|---|---|---|
| Walleye pollock | 4 | 35.7 | 17.1 |
| Crested sculpin | 5 | 26.7 | 15.9 |
| Snake prickleback | 4 | 30.5 | 14.6 |
| Daubed shanny | 6 | 14.2 | 10.1 |
| Crescent gunnel | 11 | 6.9 | 9.1 |
| Pacific tomcod | 3 | 23.4 | 8.4 |
| Slender eelblenny | 5 | 12.8 | 7.6 |
| Pacific cod | 2 | 19.2 | 4.6 |
| Northern ronquil | 3 | 11.2 | 4.0 |
| Great sculpin | 2 | 26.7 | 3.7 |
| Ribbed sculpin | 1 | 18.8 | 2.3 |
| Pacific sand lance | 1 | 13.4 | 1.6 |
| White-barred gunnel | 1 | 6.6 | 0.8 |
| Capelin | 1 | 3.1 | 0.4 |

Table 2. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to pigeon guillemot broods at Naked Island, Prince William Sound in 1997.

| Species | Number of Prey Items | Average Mass (g) | % Total Biomass of Prey |
|---|---|---|---|
| Crescent gunnel | 5 | 12.6 | 17.7 |
| Slender eelblenny | 5 | 11.4 | 16.0 |
| Pacific sand lance | 9 | 6.2 | 15.6 |
| Spiny-nosed sculpin | 2 | 14.1 | 7.9 |
| Chum salmon | 2 | 14.0 | 7.8 |
| Grunt sculpin | 3 | 9.1 | 7.7 |
| Rock sole | 2 | 11.2 | 6.3 |
| Northern ronquil | 2 | 9.7 | 5.4 |
| Rough-spined sculpin | 2 | 7.2 | 4.0 |
| Capelin | 2 | 6.2 | 3.5 |
| Great sculpin | 1 | 12.6 | 3.5 |
| Squid | 1 | 8.3 | 2.3 |
| Pacific tomcod | 1 | 7.8 | 2.2 |

Table 3. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to pigeon guillemot broods at Kachemak Bay, Lower Cook Inlet in 1997.

| Species | Number of Prey Items | Average Mass (g) | % Total Biomass of Prey |
|---|---|---|---|
| Slender eelblenny | 7 | 18.8 | 32.8 |
| Tidepool sculpin | 4 | 12.4 | 12.3 |
| Pacific sand lance | 7 | 5.5 | 9.5 |
| Crescent gunnel | 4 | 9.2 | 9.1 |
| Ribbed sculpin | 2 | 15.1 | 7.5 |
| Rock sole | 2 | 13.3 | 6.6 |
| Red Irish lord | 1 | 22.8 | 5.7 |
| Great sculpin | 1 | 20.9 | 5.2 |
| Four-horned sculpin | 1 | 18.4 | 4.6 |
| Daubed shanny | 1 | 15.6 | 3.9 |
| Arctic shanny | 1 | 5.0 | 1.2 |
| High cockscomb | 1 | 4.8 | 1.2 |
| Spiny-nosed sculpin | 1 | 1.7 | 0.4 |

Table 4. Taxonomic composition of the diet (% prey biomass) of black-legged kittiwake nestlings at six study colonies in the northern Gulf of Alaska during the 1997 breeding season (YOY = young of year).

| | Sand Lance | | Herring | | Capelin | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Location | YOY | Older | YOY | Older | YOY | Older | Gadids | Euphausiids | Other |
| Prince William Sound | | | | | | | | | |
| Shoup Bay | 19.0 | 7.3 | 17.4 | **26.2** | 3.1 | 5.7 | --- | --- | 21.3 |
| Eleanor Island | 21.2 | 10.9 | 12.6 | 15.1 | 1.5 | **29.6** | --- | --- | 9.2 |
| North Icy Bay | **36.7** | 8.1 | 8.6 | 15.7 | 5.5 | 14.4 | 1.1 | 3.2 | 6.8 |
| Lower Cook Inlet | | | | | | | | | |
| Barren Islands | **34.9** | 13.4 | 0.1 | 6.1 | 0.8 | 25.6 | 0.5 | 14.3 | 4.3 |
| Gull Island | **69.1** | 16.1 | --- | 10.4 | --- | 1.3 | 2.1 | 1.1 | --- |
| Chisik Island | **51.0** | 17.5 | --- | 10.3 | --- | --- | 6.6 | --- | 14.6 |

Table 5. Average feeding frequency, meal size, energy density, and estimated energy provisioning rates to pigeon guillemot broods at three study sites in the northern Gulf of Alaska, 1995-1997.

| Location /Year | Feeding Frequency (meals/nest day) | Meal Size (g) | Energy Density (kJ/g wet mass) | Energy Provisioning Rate (kJ/nest day) |
|---|---|---|---|---|
| Naked Island | | | | |
| 1995 | 11.4 | 14.7 | 4.4 | **737** |
| 1996 | 12.0 | 14.2 | 4.4 | **750** |
| 1997 | 12.2 | 9.7 | 4.2 | **497** |
| Jackpot Island | | | | |
| 1995 | 16.6 | 20.0 | 4.2 | **1,394** |
| 1996 | ? | 10.7 | 4.5 | **?** |
| 1997 | 11.1 | 17.1 | 4.1 | **778** |
| Kachemak Bay | | | | |
| 1995 | ? | ? | 5.2 | **?** |
| 1996 | 14.2 | 11.4 | 5.1 | **826** |
| 1997 | 13.5 | 12.2 | 5.0 | **824** |

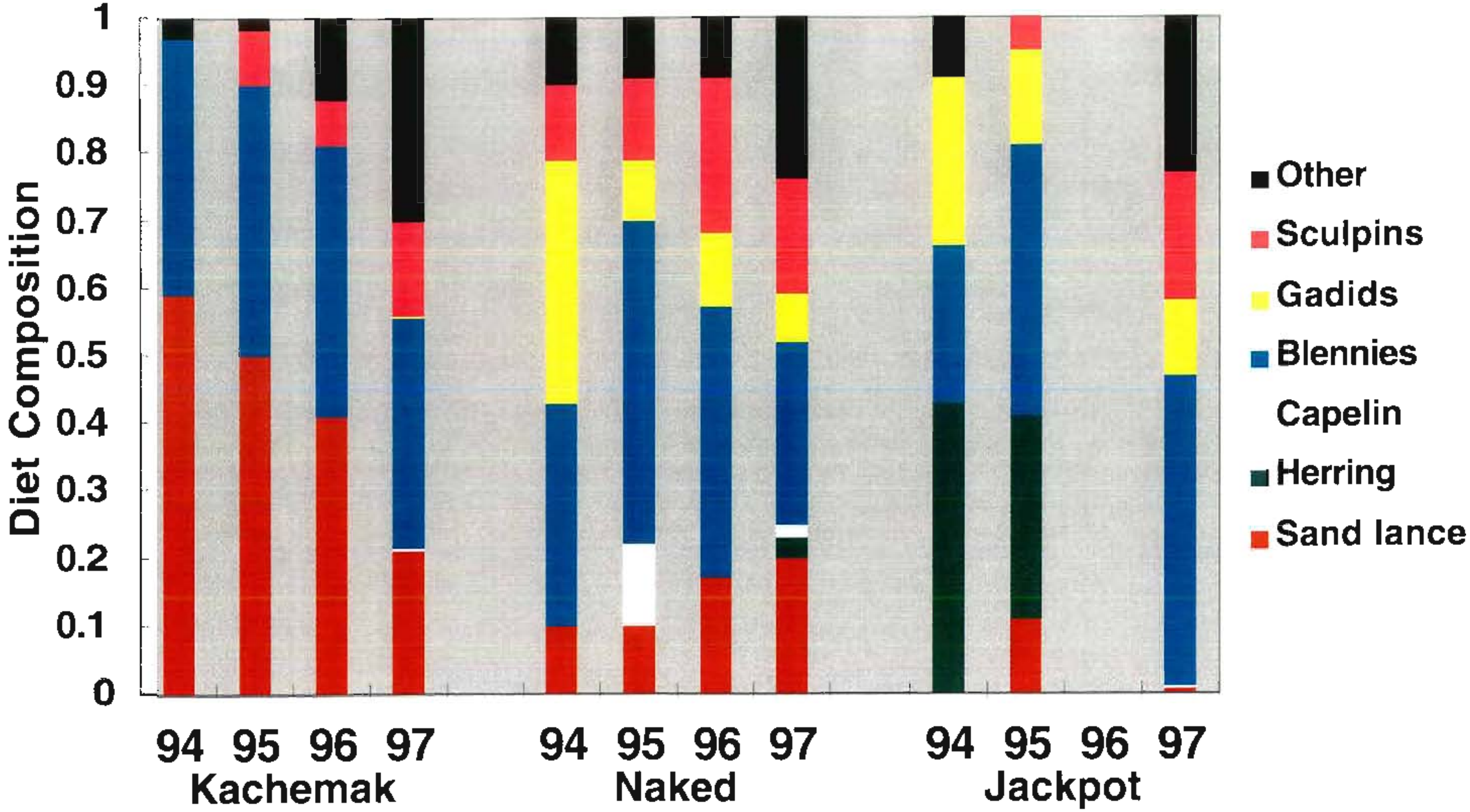
Table 6. Average feeding frequency, meal size, energy density, and estimated energy provisioning rates to black-legged kittiwake broods at six study sites in the northern Gulf of Alaska, 1995-1997.

| Location /Year | Feeding Frequency (meals/nest day) | Meal Size (g) | Energy Density (kJ/g wet mass) | Energy Provisioning Rate (kJ/nest day) |
|---|---|---|---|---|
| Shoup Bay | | | | |
| 1995 | 3.3 | 29.0 | 4.8 | **463** |
| 1996 | 4.3 | 30.6 | 4.7 | **618** |
| 1997 | 3.03 | 22.7 | 4.9 | **337** |
| Eleanor Island | | | | |
| 1995 | 4.9 | 21.3 | 4.2 | **441** |
| 1996 | 4.6 | 23.1 | 3.8 | **404** |
| 1997 | 3.94 | 17.6 | 4.5 | **312** |
| North Icy Bay | | | | |
| 1996 | ? | 24.5 | 4.5 | **?** |
| 1997 | 4.53 | 19.7 | 4.6 | **410** |
| Barren Islands | | | | |
| 1996 | 2.4 | ? | 4.0 | **?** |
| 1997 | 1.96 | 30.6 | 4.0 | **240** |
| Gull Island | | | | |
| 1996 | 4.7 | 17.2 | 4.9 | **396** |
| 1997 | 3.53 | 23.0 | 4.6 | **373** |
| Chisik Island | | | | |
| 1996 | 2.8 | 24.4 | 3.4 | **232** |
| 1997 | 2.75 | 11.0 | 5.1 | **154** |

Table 7. Preliminary results from doubly labeled water experiment to measure daily energy expenditure of free-ranging adult kittiwakes at two Prince William Sound colonies in 1997 (Shoup Bay and North Icy Bay colonies).

| | Body Mass (g) | Total Body Water (%) | Daily Energy Expenditure (kJ/d) | Water Flux Rate (g/d) |
|---|---|---|---|---|
| Shoup Bay Colony (n = 10) | | | | |
| **Mean** | **394.7** | **61.89** | **937.95** | **196.06** |
| SD | 22.62 | 2.386 | 178.48 | 51.687 |
| North Icy Bay Colony (n = 10) | | | | |
| **Mean** | **374.9** | **62.94** | **821.36** | **215.645** |
| SD | 31.18 | 1.516 | 201.197 | 59.959 |

# Pigeon Guillemot Diets in the Northern Gulf of Alaska



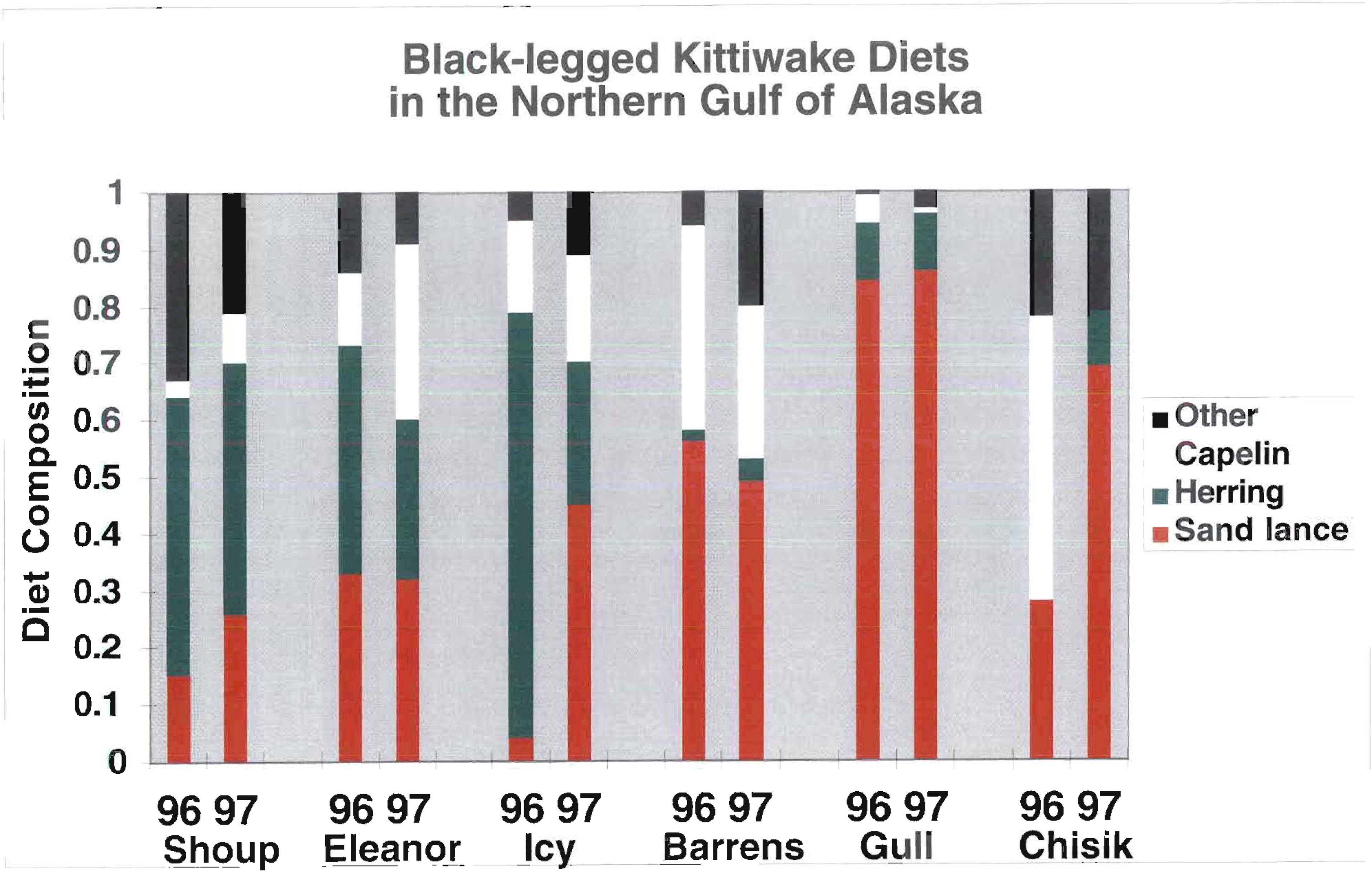

Black-legged Kittiwake Diets
in the Northern Gulf of Alaska
Diet Composition
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
96 97
Shoup
96 97
Eleanor
96 97
Icy
96 97
Barrens
96 97
Gull
96 97
Chisik
Other
Capelin
Herring
Sand lance

Fig. 2.

# Lipid content and energy density of forage fishes from the northern Gulf of Alaska

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Running Title: Composition of Forage Fishes

## Abstract

Piscivorous predators can experience multi-fold differences in energy intake rates based solely on the types of fishes consumed. We estimated energy density (kJ/g) of 1,311 fish from 32 species by proximate analysis for lipid, water, ash-free lean dry matter, and ash contents and evaluated factors contributing to its variation. Lipid content was the primary determinant of energy density, ranging from 2 to 61% dry mass and resulting in a 5-fold difference in energy density of individuals (2.0-10.8 kJ/g wet mass). Energy density varied widely within and between species. Schooling pelagic fishes had relatively high or low values, whereas nearshore demersal fishes were intermediate. Pelagic species maturing at a smaller size had higher and more variable energy density than pelagic or nearshore species maturing larger. High-lipid fishes had less water (% wet mass) and more protein (% lean dry mass) than low-lipid fishes. In some forage fishes, size, month, reproductive status, or location contributed significantly to intraspecific variation in energy density. Differences in quality may affect diet selection of breeding seabirds especially, as they must transport food for their young from foraging area to nest site.

## Introduction

Adult, juvenile, and larval fishes provide the bulk of the diet for many seabirds, marine mammals, and predacious fishes. In subarctic marine environments, food for fish stocks fluctuate on annual and decadal scales (Beamish and Bouillon 1995), influencing forage fish abundance and condition throughout predator life cycles and affecting predator productivity (Braun and Hunt 1983; Furness and Barrett 1985;

Springer et al. 1986). Timing of seasonal reproduction for predators is closely associated with food supply, because of relatively high energy demands for courtship, gamete production, incubation or gestation, lactation, and other post-natal care of young (Perrins 1970; Lockyer 1987). The distribution and abundance of some marine predators are strongly influenced by forage fish concentrations (Brown and Nettleship 1983; Furness and Barrett 1985; Payne et al. 1986). Declines in fish populations can lead to declines in predator populations, such as the reductions in seabirds, sea lions, and seals following a decrease in juvenile walleye pollock (*Theragra chalcogramma*) in Alaska (Springer 1992).

As prey vary in resource value, optimally foraging predators must integrate this variability in simultaneously balancing costs and benefits to optimize short-term survival and long-term reproductive fitness (Stephens and Krebs 1986). Predators rely on prey availability to satisfy nutritional and energy requirements (Murphy 1994), but can compensate to some extent through adjustments in prey quality (Ricklefs 1979). We defined prey quality as lipid content and energy density (kJ/g). Energy density of lipid is about twice that of protein and carbohydrate (Schmidt-Nielsen 1997: 171). Lipid content differs considerably among fishes (Clarke and Prince 1980), which are generally low in carbohydrate and high in protein. Protein metabolism as an energy source is energetically expensive compared with lipid and carbohydrate metabolism (Schmidt-Nielsen 1997). A diet high in lipid provides sufficient metabolizable energy for maintenance so dietary protein can be allocated to tissue synthesis and growth in young predators (Roby 1991). Differences in lipid content could influence adult predator survival or productivity.

Seabird productivity is frequently energy-limited (Perrins et al. 1973; Drent and Daan 1980; Roby 1991). Birds have higher energy requirements than other vertebrates, after normalizing for body size. High power requirements of flight impose high mass-specific metabolic rates and birds can only meet their metabolic needs from stored reserves for short periods (Walsberg 1983; Blem 1990). Central place foragers optimize their energy delivery rate to the nest by increasing meal size or energy content (Orians and Pearson 1979). As seabirds must transport food to the nest to feed their young, power requirements of flight limit transport capacity (Ricklefs 1984; Ricklefs et al. 1985; Roby 1991). Seabirds would be expected to select prey based on energy density.

Few studies have investigated the energy content and nutritional value of forage fishes, despite their importance as food for many marine predators. Commercially-harvested forage species (e.g., capelin [*Mallotus villosus*], Pacific herring [*Clupea harengus pallasi*]) have received some attention (Jangaard et al. 1967; Nevenzel et al. 1969; Winters 1970; Jangaard 1974; Sidwell et al. 1974; Montevecchi and Piatt 1984; Holdway and Beamish 1984). Non-commercial forage fishes have been neglected, especially nearshore demersal species (Krzynowek and Murphy 1987; Hislop et al. 1991). Limited research has been published on the bioenergetics of fishes in Alaskan waters (Harris et al. 1986; Paul et al. 1996). Two recent publications investigated the proximate composition of forage fishes from the Gulf of Alaska (Payne et al. in press; Van Pelt et al. 1997), but these studies relied on a limited number of species and small sample sizes.

We examined the biochemical composition of forage fishes from Prince William Sound (PWS) and Lower Cook Inlet (LCI) in the northern Gulf of Alaska (NGOA) with the largest samples to date of species, individuals, sampling sites, and life history stages. The major hypotheses tested were: (1) differences in proximate composition (i.e., lipid, water, ash-free lean dry matter, and ash contents) and energy density of forage fishes from NGOA are sufficient to influence prey selection by predators; (2) inter- and intraspecific differences in energy density are determined primarily by differences in lipid content; and (3) factors such as size, sex, month, reproductive status, location, and year result in substantial intraspecific differences in lipid content and energy density. If the range in quality of forage fishes is sufficient to influence predator selection of prey, the availability of higher quality fishes would be expected to influence diet quality, survival, productivity, and demography of piscivorous predators.

## Methods

We defined forage fishes as species commonly consumed by higher trophic levels and subdivided these taxa further into pelagic schooling (i.e., dwelling in schools) and nearshore demersal fishes (i.e., bottom-dwelling in lower intertidal and subtidal zones). This study focused on seabird prey and our sample is limited to fish < 300 mm standard length. Of 32 species (N = 1,312 fish), 18 were represented by sample sizes greater than five individuals (Appendix 1).

Fishes were collected in Prince William Sound (PWS) and Lower Cook Inlet (LCI), northern Gulf of Alaska (NGOA), with additional samples of eulachon (*Thaleichthys pacificus*) from Lynn Canal, southeastern Alaska. PWS was divided into three regions: northeastern (Valdez Arm, Port Fidalgo, Port Gravina), central (Naked, Block, Eleanor, northern Knight, Smith, and Seal islands), and southwestern (Knight Island Passage, Icy, and Whale bays; Montague, Jackpot and Chenega islands).

Fresh samples were collected by mid-water trawl, beach seine, cast net, dip net, minnow trap, and turning over rocks at low tide during the seabird breeding season (May through September) in 1995 and 1996. Small sample sizes were supplemented with whole fish that pigeon guillemots (*Cepphus columba*) or tufted puffins (*Fratercula cirrhata*) delivered to their nestlings. Guillemot chick meals were collected by capturing adults in mist nets or by picking up fish dropped near the nest. Puffin chick meals were collected by placing screens over burrow nest entrances, which caused some adults to drop their bill load of fish. Disturbance of the colonies was minimized.

Some samples were frozen at -20 °C immediately; others were kept in a cooler (< 10 °C) or propane freezer (-8 °C) before storage at -20 °C. In the laboratory, samples were partially thawed, weighed on an analytical balance (± 0.1 mg) to determine wet mass, and measured for standard length (± 1 mm). Fish were identified to the lowest taxonomic level possible.

Young-of-the-year allocate energy differently than older juvenile and adult fishes (Love 1970). Species with documented size-age relations were divided into their size-age classes (Smoker and Pearcy 1970; Dick and Warner 1982; Hatch and Sanger 1992; L. Haldorson [University of Alaska, 11120 Glacier Highway, Juneau, AK 99801], personal communication). Young-of-the-year capelin were < 80 mm standard length for females and < 90 mm for males, reflecting known sex differences in growth rate (Hatch and Sanger 1992). Species without documented size-age relations were divided into 'small' and 'large' size-classes at 100 mm for pelagic species and 80 mm for nearshore demersal species (Appendix 1). Small fish appeared to approximate young-of-the-year adequately and large fish were either all juveniles (e.g., walleye pollock, Pacific tomcod [*Microgadus* *proximus*], Pacific cod [*Gadus macrocephalus*]) or included juveniles and adults (e.g., capelin, Pacific sand lance [*Ammodytes hexapterus*], Pacific herring).

Sex was determined by external morphology or internal examination of gonads for a subsample of mature pelagic fish. Reproductive status was assigned by examining ovaries or testes and classifying gonadal development into resting (Stage 1; gonads < 0.5 body length in a light pink, thread-like strand), developing (Stage 2; gonads > 0.5 body length), ripe (Stage 3; gonads extended nearly entire length of abdominal cavity in a turgid sac), running (Stage 4; similar to stage 3 but contents spontaneously emerged with light pressure), and spent (Stage 5; gonads shrunken with some contents visible).

Water content was determined by drying each fish to constant mass in a convection oven at 60 °C. Chick meals were not included in analyses involving wet mass, because these fish may have been desiccated before collection. Each fish was ground and homogenized thoroughly with mortar and pestle before extraction. Samples < 2 g dry mass collected in 1995 were pooled to attain a sample mass of 2-3.5 g for lipid extraction, whereas those collected in 1996 were analyzed individually. Total lipids were extracted from dried samples with a soxhlet apparatus and a solvent system of 7:2 hexane:isopropyl alcohol (v:v). This solvent system is relatively non-toxic; extracts most complex lipids, such as structural lipids (e.g., phospholipids, sterols), as well as neutral lipids (storage forms such as triacylglycerols and wax esters); and does not extract non-lipids (Radin 1981). Carbohydrate content was assumed to be negligible (< 0.6%; Sidwell et al. 1974; Stansby 1976; Craig et al. 1978). The samples, now dry and lean, were transferred to glass scintillation vials and incinerated in a muffle furnace at 550 °C for 12 h. Ash content is the portion remaining, mostly mineral from skeletal material.

Protein is estimated by ash-free lean dry matter (AFLDM; 94% protein; Montevecchi et al. 1984). We express AFLDM content as % lean dry mass, because this measure is independent of water and lipid content.

Energy density (kJ/g) of wet mass and dry mass were calculated from proximate composition with published energy equivalents for these fractions (Schmidt-Nielsen 1997:171). The energy equivalent of lipid is 39.3 kJ/g. The energy equivalent of protein depends on the efficiency of the metabolic pathway used by the consumer. Birds excrete uric acid as their primary nitrogenous waste, so we used the energy equivalent of protein for uricotelic vertebrates (17.8 kJ/g).

Unless otherwise noted, 'lipid content' refers to % dry mass and 'energy density' refers to kJ/g wet mass. Energy density based on wet mass is relevant in assessing relative prey quality for breeding seabirds, because fish are transported back to the nest in this form. Expressing energy density based on dry mass is appropriate for interspecific comparisons (Table 1, Appendix 2), because it minimizes effects related to variation in water content from desiccation (Montevecchi and Piatt 1984).

Data were analyzed with Statview (Abacus Concepts, Berkeley, CA 94704). All proportional data underwent arcsin transformation. The level of statistical significance was $\alpha = 0.05$ for all tests.

## Results

### Interspecific Variation in Proximate Composition

### Lipid Content

Forage fishes exhibited a 10-fold difference in mean lipid content, ranging from 5% dry mass in Pacific tomcod to 50% in eulachon (Fig. 1). Most species averaged 10-25% lipid (Appendix 2).

When only large fish (> 100 mm or > 80 mm) were analyzed, mean lipid content ranged from 3% in tomcod to 50% in eulachon (Fig. 1; analysis of variance, $F_{17,805} = 42.9$, $P < 0.01$). Based on lipid content, five groups were discernable among the 18 species represented by more than 5 individuals (Fig. 1; analysis of variance with Bonferroni-Dunn multiple comparison, $F_{4,822} = 179$, $P < 0.01$). Adult eulachon and lanternfish (Myctophidae) had the highest mean lipid contents. Pacific herring was next, followed by a group of Pacific sand lance, capelin, and Pacific sandfish (*Trichodon trichodon*). The fourth group was predominantly nearshore demersal fishes, such as slender eelblenny (*Lumpenus fabricii*), arctic shanny (*Stichaeus punctatus*), snake prickleback (*Lumpenus sagitta*), crescent gunnel (*Pholis laeta*), and northern ronquil (*Ronquilus jordani*); but also included a few pelagic fishes, namely surf smelt (*Hypomesus pretiosus*) and prowfish (*Zaprora silenus*). Low-lipid fishes were in the fifth group, composed of tidepool sculpin (*Oligocottus maculosus*), Pacific cod, pink salmon (*Oncorhynchus gorbuscha*), walleye pollock, and Pacific tomcod.

Mean lipid content of small fishes (< 100 mm or < 80 mm) ranged from 5% in tomcod to 18% in capelin (Appendix 2; analysis of variance, $F_{11,276} = 19.3$, $P < 0.01$). Species high in lipid as adults generally were lower in lipid as young-of-the-year.

Capelin had the highest lipid content of small fishes, despite a wide range with some individuals containing only 1-2% lipid. Young-of-the-year capelin and sand lance had relatively high lipid contents compared to other small fishes, and were high-lipid as adults. Young-of-the-year herring had only moderate lipid content, despite high lipid content in older fish.

### Water Content

Mean water content of wet mass ranged from 62% in lanternfish to 84% in prowfish (Appendix 2) and was correlated negatively with lipid content for large fishes ($R = -0.73$, $P < 0.01$). Eulachon was an outlier, with a much higher water content of wet mass (71%) than expected for its high lipid content (50%).

Mean water content of lean mass for large fishes varied from 73% in lanternfish to 85% in prowfish (analysis of variance, $F_{17,742} = 54.4$, $P < 0.01$), reflecting the degree of hydration of muscle and other lean tissue. The correlation between water content (% lean mass) and lipid content was not significant.

### Ash-free Lean Dry Matter Content

Mean AFLDM content of lean dry mass differed from 79% in tidepool sculpin to 89% in sand lance and surf smelt (Appendix 2; analysis of variance, $F_{17,794} = 33.3$, $P < 0.01$). Most fish averaged 86-88% AFLDM. Lipid content was correlated positively with AFLDM content of lean dry mass ($R = 0.43$, $P < 0.02$). Therefore, high-lipid fish tended to have a higher protein content of lean dry tissue than did low-lipid fish. No relation between AFLDM content (% lean dry mass) and water content (% lean mass) was apparent. Ash content of lean dry mass is the inverse of AFLDM content of lean dry mass.

### Energy Density

Large forage fishes exhibited a 3-fold difference in mean energy density, ranging from 3.0 kJ/g wet mass in prowfish to 8.5 kJ/g in lanternfish (Fig. 2; analysis of variance, $F_{17,797} = 22.7$, $P < 0.01$). Energy density for most species averaged 4-6 kJ/g. Individual forage fish exhibited a 5-fold difference in energy density, ranging from 2.0 kJ/g to 10.8 kJ/g (Appendix 1).

Based on energy density, four groups were apparent in the 18 species represented by more than 5 individuals (analysis of variance with Bonferroni-Dunn multiple comparison, $F_{3,811} = 120$, $P < 0.01$). Adult lanternfish and eulachon had the highest mean energy densities (Fig. 2), associated with very high lipid contents. Herring and sand lance were next, followed by a group of capelin, sandfish, slender eelblenny, crescent gunnel, arctic shanny, snake prickleback, and surf smelt. Lowest mean energy densities were in the group of northern ronquil, tidepool sculpin, pink salmon, cod, pollock, tomcod, and prowfish.

Energy density of small fish differed significantly among species (analysis of variance, $F_{10,266} = 29.8$, $P < 0.01$). Young-of-the-year sand lance had the highest mean energy density (5.1 kJ/g), while small prowfish had the lowest (2.8 kJ/g; Appendix 2).

### Proximate Composition as it Relates to Energy Density

Lipid content was the primary determinant of energy density, explaining 83% of interspecific variation (forward stepwise multiple regression partial $r^2 = 0.83$, $P < 0.01$). Variation in water content of lean mass explained an additional 14% of the variation in energy density (partial $r^2 = 0.14$, $P < 0.01$). Thus, interspecific differences in energy density of forage fishes were explained almost entirely by variation in lipid content and water content of lean mass (multiple $r^2 = 0.97$, $P < 0.01$). Ash content (or conversely, AFLDM content) of lean dry mass did not explain a significant proportion of the variance, apparently due to little variance among species.

## Intraspecific Variation in Proximate Composition

Variation in quality differed among species. Pelagic schooling fishes tended to have higher intraspecific variance than nearshore demersal species (variance ratio F-test, F = 0.097, $P < 0.01$). Lipid content of capelin was extremely variable in both young-of-the-year (2-39%) and older fish (3-51%). Herring exhibited a similarly large 6-fold variation in lipid content of young-of-the-year (5-32%) and 10-fold variation in older fish (5-55%). Sand lance had a 4-fold difference in lipid content for young-of-the-year (8-35%), which was greater than for older fish (14-35%). Less intraspecific variability was apparent in other species, such as a 2-fold difference in walleye pollock, with 5-9% in small fish and 3-10% in large fish. Arctic shanny (≥ 80 mm) varied little, with lipid content ranging from 12-18%.

### Size

Pelagic species maturing at a smaller size were more variable in quality than pelagic or nearshore species maturing at a larger size. Size differences in lipid content were detected within our 300-mm size constraint. In some species, standard length and lipid content were correlated positively (Fig. 3a-d, Appendix 2): herring (R = 0.73, $P < 0.01$), pre-spawning sand lance (R = 0.25, $P < 0.01$), pre-spawning capelin (R = 0.24, $P < 0.01$), padded sculpin (R = 0.72, $P < 0.01$), sandfish (R = 0.85, $P < 0.01$), and surf smelt (R = 0.76, $P < 0.05$). In contrast, size and lipid content were correlated negatively in tomcod

(Fig. 3e; R = - 0.44, $P < 0.05$). For other species, size and lipid content were not correlated (e.g., walleye pollock [Fig. 3f], Pacific cod).

Herring demonstrated an especially dramatic increase in lipid content from young-of-the-year to older fish (Fig. 3a; analysis of variance, $F_{1,288} = 163$, $P < 0.01$). The largest herring in our sample (140-300 mm) averaged almost twice the lipid content of 100-140 mm size-class and three times that of the < 100 mm size-class (Mean ± SE: 38% ± 1.6, 25% ± 0.7, and 10% ± 0.5, respectively; $F_{2,287} = 129$, $P < 0.01$).

Hatch and Sanger (1992) defined age-classes for female capelin as < 80 mm for young-of-the-year, 80-100 mm for age $1^+$, 101-114 mm for age $2^+$, and > 114 mm for age $3^+$. Age-classes for males were defined as < 90 mm for young-of-the-year, 90-109 mm for age $1^+$, 110-119 mm for age $2^+$, and > 119 mm for age $3^+$. In pre-spawning capelin (Fig. 3c), lipid content increased from 18% ± 1.8 for young-of-the-year to 25% ± 1.5 for $1^+$ capelin to 32% ± 2.4 for $2^+$ capelin, and decreased again to 21% ± 2.1 for $3^+$ capelin (analysis of variance, $F_{3,133} = 11.8$, $P < 0.01$).

### Sex

Only Pacific sand lance demonstrated significant differences in lipid content between the sexes (Table 1a). Female sand lance had higher lipid content (23.2% ± 3.7) than did males (20.6% ± 4.9; analysis of variance, $F_{1,212} = 24.5$, $P < 0.01$), with concomitant higher energy density (5.79 kJ/g vs. 5.25 kJ/g; $F_{1,211} = 40.7$, $P < 0.01$).

## Month

Quality was highest in June for capelin and sand lance, the only two species with adequate sample size over time. Lipid content of older capelin decreased significantly from June through September (Fig. 4; analysis of variance, $F_{3,146} = 23.2$, $P < 0.01$), such that energy density in June (6.7 kJ/g ± 0.60) steadily decreased from July (5.3 kJ/g ± 1.6) through August (4.0 kJ/g ± 0.88) to a low in September (3.7 kJ/g ± 0.87; $F_{3,146} = 23.2$, $P < 0.01$).

Lipid content of older sand lance declined steadily from June through September (Fig. 4; analysis of variance, $F_{3,309} = 24.4$, $P < 0.01$). Reflecting changes in lipid content, energy density decreased from June (5.6 kJ/g ± 0.09) through September (4.9 kJ/g ± 0.10; $F_{3,308} = 13.1$, $P < 0.01$).

Young-of-the-year sand lance in PWS decreased in lipid content from June to July, but increased again in August (Fig. 4; analysis of variance, $F_{2,31} = 6.80$, $P < 0.01$). The AFLDM content of lean dry mass increased from June (87% ± 0.5) through August (90% ± 0.7; $F_{2,30} = 5.72$, $P < 0.01$). Thus, energy density was highest in June (6.5 kJ/g ±0.11), decreased in July (4.8 kJ/g ± 0.15) and increased again in August (5.3 kJ/g ± 0.19; $F_{2,31} = 9.39$, $P < 0.01$).

## Reproductive Status

Lipid content varied with reproductive status in species reaching maturity within our 300-mm size constraint. In capelin, lipid content was highest for resting and developing stages of reproduction (Table 1b). Ripe, running, and spent capelin had significantly lower lipid content than did those in resting and developing stages (analysis of variance, $F_{4,88} = 7.42$, $P < 0.01$). Thus, energy density for resting and developing capelin was higher than ripe, running, and spent capelin ($F_{4,88} = 5.11$, $P = 0.01$). The AFLDM content of lean dry mass was significantly higher for resting, developing, and ripe capelin compared to those in running and spent stages ($F_{4,84} = 6.38$, $P < 0.01$).

In sand lance, lipid content decreased from resting to ripe fish (Table 1a) for both females (analysis of variance, $F_{2,102} = 11.5$, $P < 0.01$) and males ($F_{2,91} = 27.6$, $P < 0.01$). Therefore, energy density decreased significantly from resting to ripe in both females ($F_{2,101} = 4.26$, $P < 0.02$) and males ($F_{2,91} = 10.4$, $P < 0.01$). Resting female sand lance had lower AFLDM content of lean dry mass than did developing and ripe females ($F_{2,102} = 8.43$, $P < 0.01$). Resting and developing males had higher AFLDM content of lean dry mass than ripe males ($F_{2,91} = 3.81$, $P < 0.03$).

### Location

Considerable variation in lipid content within size-classes of Pacific herring was attributable to location within PWS (analysis of variance, $F_{8,264} = 30.9$, $P < 0.01$). Differences were most pronounced in 100-140 mm herring, because the composition among locations of fish < 100 mm and > 140 mm were similar. Herring (100-140 mm) from northeastern PWS had significantly higher lipid content (29% ± 0.1) than those from central (24% ± 1.3) or southwestern PWS (21% ± 1.3; $F_{2,181} = 11.1$, $P < 0.01$). Consequently, energy density of herring (100-140 mm) was higher in northeastern PWS (6.3 kJ/g ± 0.15) than either central (5.2 kJ/g ± 0.19) or southwestern PWS (4.8 kJ/g ± 0.15; $F_{2,178} = 24.8$, $P < 0.01$). Energy density of herring (100-140 mm) from central PWS was marginally higher than from southwestern PWS ($P = 0.047$).

Pacific herring (> 140 mm) from PWS had higher lipid content than those from LCI (41% ± 1.9 vs. 32% ± 2.7; analysis of variance, $F_{1,38} = 9.90$, $P < 0.01$), which resulted in higher energy density (8.1 kJ/g ± 0.33 vs. 6.9 kJ/g ± 0.42; $F_{1,37} = 6.04$, $P < 0.02$).

### Year

Pacific herring (100-175 mm) from PWS had higher energy density in 1995 (6.3 kJ/g ± 0.22) than in 1996 (5.6 kJ/g ± 0.13; analysis of variance, $F_{1,204} = 6.91$, $P < 0.01$). Among the three regions, southwestern PWS had the highest quality herring in 1995 (Fig. 5), much higher than this region in 1996 for both lipid content ($F_{1,71} = 15.8$, $P < 0.01$) and energy density ($F_{1,69} = 22.3$, $P < 0.01$). In contrast, the northeastern region had the highest quality herring in 1996, with less variance in lipid content between the two years than in southwestern (variance ratio F-test, $F = 0.36$, $P < 0.01$) and central PWS (variance ratio F-test, $F = 1.72$, $P < 0.03$).

### Proximate Composition as it Relates to Energy Density

Variation in lipid content explained most of the intraspecific variation in energy density in most forage fishes (Table 2a, b, d). Variation in water content of lean mass contributed a large proportion of the residual variation in energy density in many species (Table 2b, d). For a few species with high water content of lean mass, such as eulachon at 82% (Appendix 2) and prowfish at 85%, variation in water content of lean mass explained more of the variation in energy density than did lipid content (Table 2c). In a few species, ash content (or AFLDM content) of lean dry mass explained a significant proportion (1-5%) of the intraspecific variation in energy density (Table 2d).

Many forage fishes demonstrated a close correlation between water content (% wet mass) and energy density (kJ/g wet mass). Thus, water content is a cost- and time-

Table 4. Relative contributions of factors influencing intraspecific variation in lipid content (% dry mass) and energy density (kJ/g wet mass) in forage fishes from the northern Gulf of Alaska, 1995-1996. Adjusted regression coefficients ($r^2$) were the result of a forward stepwise multiple regression on indicator variables within species. All probabilities were $P < 0.05$.

| Species | | Size small-large | Month | Sex | Reproductive status | Location NGOA[a] | Location PWS[b] | Year |
|---|---|---|---|---|---|---|---|---|
| | Multiple $r^2$ | Partial $r^2$ | Partial $r^2$ | Partial $r^2$ | Partial $r^2$ | Partial $r^2$ | Partial $r^2$ | Partial $r^2$ |
| Pacific sand lance: | | | | | | | | |
| Lipid content | 0.37 | 0.01 | 0.29 | 0.05 | 0.02 | - | - | - |
| Energy density | 0.43 | - | 0.02 | 0.11 | - | 0.26 | - | 0.04 |
| Pacific herring: | | | | | | | | |
| Lipid content | 0.38 | 0.38 | - | - | - | - | - | - |
| Energy density | 0.31 | 0.27 | 0.01 | - | - | - | - | 0.03 |
| Capelin: | | | | | | | | |
| Lipid content | 0.35 | - | 0.17 | - | 0.18 | - | - | - |
| Energy density | 0.23 | - | 0.10 | - | 0.13 | - | - | - |
| Walleye pollock: | | | | | | | | |
| Lipid content | 0.15 | 0.14 | - | - | - | - | - | - |
| Energy density | 0.24 | 0.24 | - | - | - | - | - | - |

[a] Location in the northern Gulf of Alaska is either Prince William Sound or Lower Cook Inlet.

[b] Location in Prince William Sound is either northeastern, central, or southwestern regions.

efficient way to estimate species-specific energy density in lieu of proximate analysis or bomb calorimetry (Table 3).

### Relative Contributions of Factors Influencing Quality

Size and month were the most influential factors contributing to intraspecific variation in lipid content and energy density, with notable contributions from sex, reproductive status, and location (Table 4). Reproductive status was confounded with month. Location within PWS and year did not explain much of the variation in lipid content or energy density.

Relative contributions of these factors to intraspecific variation in quality varied among forage fish species. Most of the variation in lipid content and energy density in sand lance was explained by month and sex (Table 4). The effect of location (PWS vs. LCI) on energy density was significant primarily because of differences between locations in AFLDM content of lean dry mass. Size contributed most to the intraspecific variation in lipid content and energy density for herring and pollock, whereas month and reproductive status were most influential for capelin.

It is noteworthy that less than 50% of the intraspecific variation in quality was explained by the potentially influential factors of size, sex, month, reproductive status, location in NGOA, location in PWS, and year. Any residual, unexplained variation in lipid content and energy density was assumed to be primarily related to individual variation in condition.

## Discussion

The biochemical composition of forage fishes varied considerably both within and among species in NGOA, reflecting wide variability in prey quality for higher trophic levels. Piscivorous seabirds and other marine predators could enhance their energy intake rates by foraging on particular species or by keying in on size, sex, month, reproductive status, or location when foraging on a particular species of fish. By selecting for prey quality,within the context of relative prey availability, piscivorous predators can potentially increase their own fitness and the productivity of the population.

## Differences in Fish Quality

Differences in the quality of forage fishes were sufficient to influence prey selection by predators (hypothesis 1). Seabirds, marine mammals, and predacious fishes could experience a 10-fold difference in lipid content (% dry mass) and a 5-fold difference in energy density (kJ/g wet mass), based on prey choice. Increased energy intake rate through prey selection would be especially important to seabirds raising young, which have limited transport capacity (e.g., size of bill or foregut; Ricklefs 1984; Ricklefs et al. 1985; Roby 1991) and high energy cost of transport (Walsberg 1983; Blem 1990). In addition to increasing energy provisioning rates to the brood, parents selecting high-energy prey can potentially adjust their time and energy costs of reproduction by making fewer trips between foraging areas and nest site, foraging farther from the colony, raising more young per nesting attempt, raising young with larger fat reserves, and/or reducing parental investment to enhance their own survival (Ashmole 1971; Drent and Daan 1980; Ricklefs 1984; Laugksch and Duffy 1986; Obst 1986). Seabird parents that provision their young with high-lipid fish raise faster growing nestlings that fledge earlier and have larger fat reserves, attributes that increase their chance of pre- and post-fledgling survival (Ricklefs 1979; Ricklefs 1983; Massias and Becker 1990).

A clear dichotomy in quality was found among pelagic forage fishes between high-lipid (e.g., lanternfish, eulachon, Pacific herring, Pacific sand lance, capelin) and low-lipid species (e.g., walleye pollock, Pacific cod, Pacific tomcod). Some similarities existed among species from the same taxonomic family: osmerids (e.g., eulachon, capelin, surf smelt) tended to be high-lipid (30% ± 18% for fish ≥ 100 mm); gadids (e.g., pollock, cod, tomcod) were low-lipid (6% ± 2%); and stichaeids (e.g., arctic shanny, slender eelblenny, snake prickleback), a family of nearshore demersal fishes, were intermediate (14% ± 2%). Other families were not well represented in our sample. We demonstrated that pelagic fishes varied considerably in their lipid content and energy density, whereas nearshore demersal species were consistently intermediate.

Pelagic species attaining maturity at a smaller size (e.g., sand lance, capelin) had higher and more variable energy density than did species reaching maturity at a size larger than our upper limit of 300 mm (e.g., gadids). Size-related differences in lipid content among pelagic fishes result from changes in allocation of energy for maintenance, growth, reproduction, and storage with maturity. Some species attaining reproductive maturity at a smaller size invest relatively less energy in growth and invest in reproduction earlier than fishes reaching maturity at a larger size. Young organisms allocate a higher proportion of assimilated energy to growth. Rapid weight gain early in life requires more protein than does normal protein turnover in adults, such that older fish store more energy as lipid (Harris et al. 1986).

## Variation in Energy Density from Proximate Composition

Lipid content was the primary determinant of variation in energy density of forage fishes both within and between species (hypothesis 2). Lipid content explained 83% of the variation among species in energy density and water content of lean mass explained an additional 14%. Variation in ash content of lean dry mass (or conversely, AFLDM content) did not explain a significant proportion of the variation in energy density among species, but did explain 1-5% of the intraspecific variation in some species. Variation in water content of lean mass explained the majority of intraspecific variation in energy density for a few fishes with high water content of lean tissue (i.e., prowfish, eulachon).

## Factors Influencing Intraspecific Variation in Energy Density

Piscivorous predators can potentially increase energy intake by selecting prey within species for such factors as size, sex, month, reproductive state, location, and year to enhance lipid content and energy density (hypothesis 3). In this study, size and month were most influential to variation in lipid content and energy density, with notable effects from sex, reproductive status, and location. Similar-sized conspecifics in NGOA had generally similar lipid content and energy density, based on comparisons between this study, Van Pelt et al. (1997), and Payne et al. (in press). As size of fish and month of collection were comparable among these studies, any differences within species are probably related to effects of sex, reproductive status, location, or year.

### Size

Pelagic fishes that mature at a smaller size were more variable in quality than pelagic or nearshore species that mature at a larger size. We observed increasing lipid content with increasing size for many species (e.g., herring, sand lance, padded sculpin), supporting increased allocation of energy to storage with maturity. Lipid content was correlated negatively with size for some species (e.g., tomcod). Other fishes showed no correlation between size and lipid content (e.g., walleye pollock, cod).

In organisms with high juvenile mortality, selection favors rapid growth to adult size (Calow and Townsend 1981). Juveniles allocate their energy to somatic growth to increase locomotive efficiency, predator evasion, and food procurement. Once an organism is large enough to reduce predation pressure, selection favors maintaining an energy reserve, especially if life expectancy is long compared to the periods of food scarcity and reproduction (Calow and Townsend 1981).

### Sex

We detected differences in quality between the sexes only in Pacific sand lance, in which females had higher lipid content and energy density than males. Females appear to invest more in biochemical changes associated with reproduction; however, males compensate to some extent with a greater investment in reproductive behaviors and reproductive structures (Love 1970). Our sampling period corresponded to the progression of sand lance toward spawning in mid-autumn (Dick and Warner 1982). Many species were collected when the gonads were inactive, when sex differences would not be expected (Love 1970). We may not have detected differences between the sexes in other species due to different timing of reproduction or small sample sizes. In Newfoundland, Montevecchi and Piatt (1984) found sex differences in the composition of capelin only during the spawning period.

### Month and Reproductive Status

Productivity in the Gulf of Alaska pulses with bimodal phytoplankton blooms in spring (April-May) and autumn (September-October) that, after a short time lag, support high densities of zooplankton that further serve as food for planktivorous fishes (Cooney and Coyle 1988). Many animals perform energetically expensive activities (e.g., reproduction, larval release) during these periods of food abundance (Love 1970). Monthly differences in intraspecific lipid content and energy density appear to reflect fluctuations in reliance on stored energy reserves and procured nutrients for survival, growth, and reproduction. Fish allocating most of their energy to somatic growth or reproduction in spring and summer must shift to increasing lipid storage to survive overwinter (Love 1970).

Capelin in Alaska are thought to spawn nearshore from late May to early June (Warner and Shafford 1979 in Dick and Warner 1982), after the spring bloom, followed by offshore movement before or around the autumn bloom. Our results support commencement of spawning in May, as many capelin in our sample were already spent in July (when we first identified reproductive stage). Also, a small sample of spent males was collected as early as 26 May in 1996. Our data suggest spawning extends through September, as the proportion of spent capelin continued to increase throughout the summer.

Capelin have adapted to productivity cycles by fasting when resources are low during overwintering and spawning and feeding on the blooms during pre-spawning and post-spawning (Winters 1970). The highest lipid content in capelin was recorded in June and decreased dramatically with advancing reproductive stage throughout the summer, in concordance with prey availability and investment in reproductive structures and behaviors. For example, lipid content of resting capelin decreased by 30% between July and August (34% ± 11 vs. 23% ± 14), followed by a more than 50% decline by September (10% ± 6).

Sand lance use a different reproductive strategy than capelin by spawning mid-autumn, before or during the bloom. Sand lance had the highest lipid content in June. We observed ripe sand lance as early as July and as late as September. The incidence of ripe sand lance in our sample increased throughout the summer, corresponding to a steady decline in lipid content. Sand lance appear to increase investment in reproduction, rather than energy storage, as autumn approaches. These differences in reproductive strategies between sand lance and capelin reflect differences in life history, as they influence reliance on stored energy reserves for survival or reproduction.

### Location

Geographic variation in lipid content and energy density was evident in some forage fishes. Location effects probably resulted from relative abundance and possibly from the nutritional quality of zooplankton prey. Herring provided an exceptional example of the influence of geographic location on lipid content and energy density, both within PWS and between PWS and LCI. Herring in the size range of 100-140 mm, presumably the $1^+$ age class, exhibited the greatest geographic variation in composition. After controlling for year effect, herring in the northeastern portion of PWS were higher in lipid than those from the rest of PWS. The northeastern portion of PWS has low exchange with the NGOA (Royer 1979) and may have a more stable, larger population of zooplankton. Consequently, higher densities of calanoid copepods in the northeastern portion of PWS may provide more food for zooplanktivores, such as herring (Cooney et al. 1996). Regional differences in prey availability apparently result in differences in body growth (Ware 1985) and lipid reserves.

### Year

Most forage fishes did not exhibit annual differences in composition. Differences between 1995 and 1996 in energy density of herring suggested that the availability and/or quality of their food may have been better in 1995. Juvenile herring (100-175 mm) from southwestern PWS in 1995 had about 25% higher lipid content than those from northeastern PWS and more than twice the lipid content of those from central PWS. These regional differences were no longer apparent in 1996. In 1996, herring from southwestern PWS had the lowest lipid content, herring from northeastern PWS had the highest lipid content, and there was less regional variation in lipid content compared with 1995.

## Implications for Piscivorous Predators

Birds appear to be able to select prey based on composition of macronutrients and micronutrients to satisfy their nutritional and energy requirements (Murphy 1994). Differences in prey quality can clearly alter energy provisioning rates to seabird young (Ricklefs 1984; Ricklefs et al. 1985; Roby 1991; Lance 1996), implying that seabirds may select prey based on energy density. Given the high lipid content and energy density of lanternfish and eulachon, it seems reasonable that seabirds would select these taxa. These fishes are consumed by seabirds and marine mammals in Alaska (Fritz et al. 1993; Lance 1996), but are not prevalent in seabird diets in the study area. Lanternfish are meso-pelagic and eulachon are bathy-pelagic fishes, both living mostly beyond the continental shelf (Parks and Zenger 1979). Lanternfish become available to predators only during their vertical migration to the surface at night to prey on plankton (Fast 1960), while juvenile eulachon remain at depth until age $3^{+}$, when these anadromous fish migrate to rivers to spawn (Barraclough 1964). Instead, herring, sand lance, and capelin, the three next most energy-dense species, are available to predators nearshore and in shallow water. These three species are the primary prey of piscivorous seabirds in Alaska (Springer 1991; Hatch et al. 1993).

Seabirds apparently select prey based on species. As the intraspecific variation in quality of forage fishes demonstrate is as much as 10-fold, it is also potentially advantageous for piscivorous predators to select for characteristics within species. Selection of forage fish based on month or size would have the greatest potential effect on energy density of the diet, while selection based on sex, reproductive status, or location would also enhance diets of some forage fish species.

A predator could potentially increase energy density of the diet while foraging on sand lance, capelin, or herring by selecting prey larger than 100 mm standard length. Predators foraging on sand lance could enhance dietary energy density by selecting females and those in a resting stage of reproduction. Predators consuming capelin should select for resting and developing stages of reproduction. Feeding on capelin early in the summer and switching to sand lance later would increase energy intake rates, if availability were equal. Predators feeding on herring could enhance energy density of the diet by selecting prey in certain regions of PWS, but the regions supporting the highest quality herring apparently differ among years.

Proximate composition and energy density of prey can be integrated with prey selection, predator metabolic requirements, and predator abundance in bioenergetics models to understand how ecosystem shifts influence marine trophic structure. The NGOA ecosystem appears to be undergoing a shift in the composition and abundance of forage fish species. The incidence of Pacific sand lance, Pacific herring, and capelin in seabird diets has fluctuated (Hatch et al. 1993; Oakley and Kuletz 1996; Piatt and Anderson 1996), coincident with population fluctuations of these forage fishes (Anderson et al. 1994). These species have high energy densities compared to the juvenile pollock that are apparently declining in the pelagic zone (Anderson et al. 1994). The range in quality of forage fishes is sufficient to influence predator selection of prey, such that the availability of higher quality fishes would be expected to influence productivity of piscivorous predators.

## Conclusions

- Forage fishes exhibited a ten-fold difference in lipid content (% dry mass) and a five-fold difference in energy density (kJ/g wet mass) among individuals, such that predators could potentially experience large differences in foraging efficiency depending on prey choice.
- Schooling pelagic fishes tended to have either relatively high or low lipid content and energy density, whereas nearshore demersal fishes had intermediate values.
- Interspecific variation in lipid content was the primary factor influencing energy density of forage fishes, with variation in water content also contributing.

- Lipid content (% dry mass) was negatively correlated with water content (% wet mass) and positively correlated with protein content (% lean dry mass). Thus, high-lipid fish had higher nutritional value than low-lipid fish, because of lower water content (% wet mass), higher protein content, and lower ash content (% lean dry mass).
- Intraspecific differences in lipid content and energy density of forage fishes were related to size, sex, month, reproductive status, location, and year. Size and month were the factors with the most influence, with contributions from sex, reproductive status, and location. Pelagic species maturing at a smaller size had higher and more variable energy densities than did pelagic or nearshore species maturing at a larger size.

- Diet quality for some piscivorous seabirds is sufficiently variable to affect prey selection. Additional studies are needed to examine the relative importance of food quality and quantity for survival and productivity of seabirds.

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## Figure Captions

Figure 1. Lipid and ash-free lean dry matter (AFLDM) contents (% dry mass) of forage fishes (≥ 100 mm) from the northern Gulf of Alaska in 1995 and 1996. Ash content (% dry mass) comprises the unmarked proportion, as the three constituents sum to 100%. Error bars represent two standard errors about the mean or roughly the 95% confidence interval. Species connected with lines above the bar graph have no significant difference in lipid content among species (Univariate ANOVA with Bonferroni-Dunn multiple comparisons tests). Sample sizes are indicated above each bar.

Figure 2. Relative contributions of lipid content and AFLDM content toward total energy density (kJ/g wet mass) of forage fishes (≥ 100 mm) from the northern Gulf of Alaska, 1995 and 1996. Error bars represent two standard errors about the mean or roughly the 95% confidence interval. Species connected with lines above the bar graph have no significant difference in energy density among species (Univariate ANOVA with Bonferroni-Dunn multiple comparisons tests). Sample sizes are indicated above each bar.

Figure 3. Relation between standard length (mm) and lipid content (% dry mass) of some forage fishes sampled in the northern Gulf of Alaska in 1995 and 1996: (a) Padded sculpin, (b) Pacific herring, (c) Pacific sand lance, (d) Capelin, with spent fish indicated by solid symbols, (e) Pacific tomcod, and (f) Walleye pollock. Scale differs among graphs.

Figure 4. Monthly differences in lipid content (% dry mass) of capelin and Pacific sand lance from the northern Gulf of Alaska, 1995 and 1996. Error bars represent two standard errors about the mean or roughly the 95% confidence interval.

Figure 5. Relative contributions of lipid and AFLDM toward total energy density (kJ/g wet mass) of Pacific herring from Prince William Sound, Alaska, in 1995 and 1996. Error bars represent two standard errors about the mean or roughly the 95% confidence interval. Sample sizes are indicated above each bar.

Table 1. Proximate composition of the sexes and reproductive stages of (a) Pacific sand lance and (b) capelin from the northern Gulf of Alaska, collected from May through September in 1995 and 1996. Standard error is presented with means.

| Species | n | Water<br>% lean mass | Lipid<br>% dry mass | AFLDM<br>% lean dry mass | Energy density<br>kJ/g dry mass | Energy density<br>kJ/g wet mass |
|---|---|---|---|---|---|---|
| (a) Pacific sand lance: | | | | | | |
| Female | 112 | 76.2 ± 1.9 | 23.2 ± 3.7 | 88.1 ± 1.3 | 20.6 ± 0.88 | 5.79 ± 0.54 |
| Resting | 39 | 77.7 ± 0.3 | 25.2 ± 0.7 | 87.4 ± 0.2 | 20.8 ± 0.15 | 5.59 ± 0.09 |
| Developing | 51 | 75.7 ± 0.2 | 22.7 ± 0.4 | 88.3 ± 0.1 | 20.6 ± 0.11 | 5.91 ± 0.07 |
| Ripe | 15 | 75.3 ± 0.3 | 20.4 ± 0.7 | 88.3 ± 0.2 | 19.9 ± 0.18 | 5.71 ± 0.12 |
| Male | 104 | 77.2 ± 2.0 | 20.6 ± 4.9 | 87.5 ± 1.1 | 19.9 ± 1.20 | 5.25 ± 0.73 |
| Resting | 36 | 77.8 ± 0.3 | 24.3 ± 0.8 | 87.5 ± 0.2 | 20.7 ± 0.20 | 5.43 ± 0.09 |
| Developing | 37 | 76.5 ± 0.3 | 19.9 ± 0.7 | 87.6 ± 0.1 | 19.7 ± 0.18 | 5.38 ± 0.15 |
| Ripe | 23 | 78.2 ± 0.3 | 16.6 ± 0.5 | 87.0 ± 0.2 | 19.0 ± 0.14 | 4.65 ± 0.08 |
| (b) Capelin: | | | | | | |
| Sexes Combined | | | | | | |
| Resting | 40 | 80.4 ± 0.8 | 32.8 ± 2.0 | 88.0 ± 0.8 | 22.4 ± 2.71 | 5.85 ± 0.24 |
| Developing | 12 | 80.2 ± 0.4 | 32.4 ± 3.5 | 88.1 ± 0.3 | 22.4 ± 2.96 | 5.86 ± 0.43 |
| Ripe | 10 | 79.4 ± 0.4 | 19.8 ± 2.8 | 89.0 ± 0.3 | 19.6 ± 1.83 | 4.83 ± 0.19 |
| Running | 6 | 80.6 ± 0.5 | 15.6 ± 4.2 | 86.6 ± 0.7 | 18.4 ± 1.51 | 4.03 ± 0.42 |
| Spent | 30 | 81.1 ± 0.3 | 18.7 ± 2.8 | 86.8 ± 0.4 | 19.3 ± 3.59 | 4.38 ± 0.32 |

Table 2. Relative contributions of lipid, water, and AFLDM content to intraspecific variation in energy density of forage fishes from the northern Gulf of Alaska, 1995-1996. Adjusted regression coefficients ($r^2$) were the result of a forward stepwise multiple regression within species. All probabilities were $P < 0.01$.

| | | Lipid<br>% dry mass | Water<br>% lean mass | AFLDM<br>% lean dry mass |
|---|---|---|---|---|
| Species | Multiple $r^2$ | Partial $r^2$ | Partial $r^2$ | Partial $r^2$ |
| (a) Lipid only: | | | | |
| Arctic shanny | 0.98 | 0.98 | 0 | 0 |
| (b) Lipid and water: | | | | |
| Surf smelt | 0.99 | 0.97 | 0.02 | 0 |
| Capelin | 0.95 | 0.94 | 0.01 | 0 |
| Pacific sandfish | 0.94 | 0.83 | 0.11 | 0 |
| Pacific tomcod | 0.55 | 0.28 | 0.27 | 0 |
| (c) Water and lipid: | | | | |
| Eulachon | 0.94 | 0.17 | 0.77 | 0 |
| Prowfish | 0.85 | 0.34 | 0.51 | 0 |
| (d) Lipid, water, and ash: | | | | |
| Pacific herring | 0.95 | 0.87 | 0.07 | 0.01 |
| Pacific sand lance | 0.94 | 0.78 | 0.15 | 0.01 |
| Crescent gunnel | 0.95 | 0.74 | 0.17 | 0.04 |
| Walleye pollock | 0.79 | 0.46 | 0.28 | 0.05 |
| Pacific cod | 0.90 | 0.73 | 0.15 | 0.02 |

Table 3. Simple linear regression equations predicting energy density (kJ/g wet mass; Y) from water content (% wet mass; X) for forage fishes sampled in the northern Gulf of Alaska. Size classes were combined. All probabilities were $P < 0.01$.

| Species | Sample size | Regression equation | $r^2$ |
|---|---|---|---|
| Capelin | 152 | Y = 32.2 - 36.1 X | 0.97 |
| Crescent gunnel | 36 | Y = 18.8 - 19.3 X | 0.58 |
| Eulachon | 33 | Y = 28.7 - 30.0 X | 0.97 |
| Lingcod | 11 | Y = 17.8 - 18.3 X | 0.77 |
| Pacific cod | 18 | Y = 20.5 - 21.7 X | 0.83 |
| Pacific herring | 277 | Y = 32.4 - 36.8 X | 0.95 |
| Padded sculpin | 12 | Y = 33.7 - 39.1 X | 0.92 |
| Pacific tomcod | 19 | Y = 20.1 - 22.1 X | 0.48 |
| Pink salmon | 49 | Y = 18.2 - 18.7 X | 0.86 |
| Prowfish | 24 | Y = 16.6 - 16.4 X | 0.74 |
| Pacific sand lance | 278 | Y = 24.4 - 26.2 X | 0.80 |
| Pacific sandfish | 37 | Y = 25.3 - 27.6 X | 0.36 |
| Slender eelblenny | 22 | Y = 23.5 - 25.2 X | 0.80 |
| Walleye pollock | 45 | Y = 17.9 - 18.3 X | 0.70 |

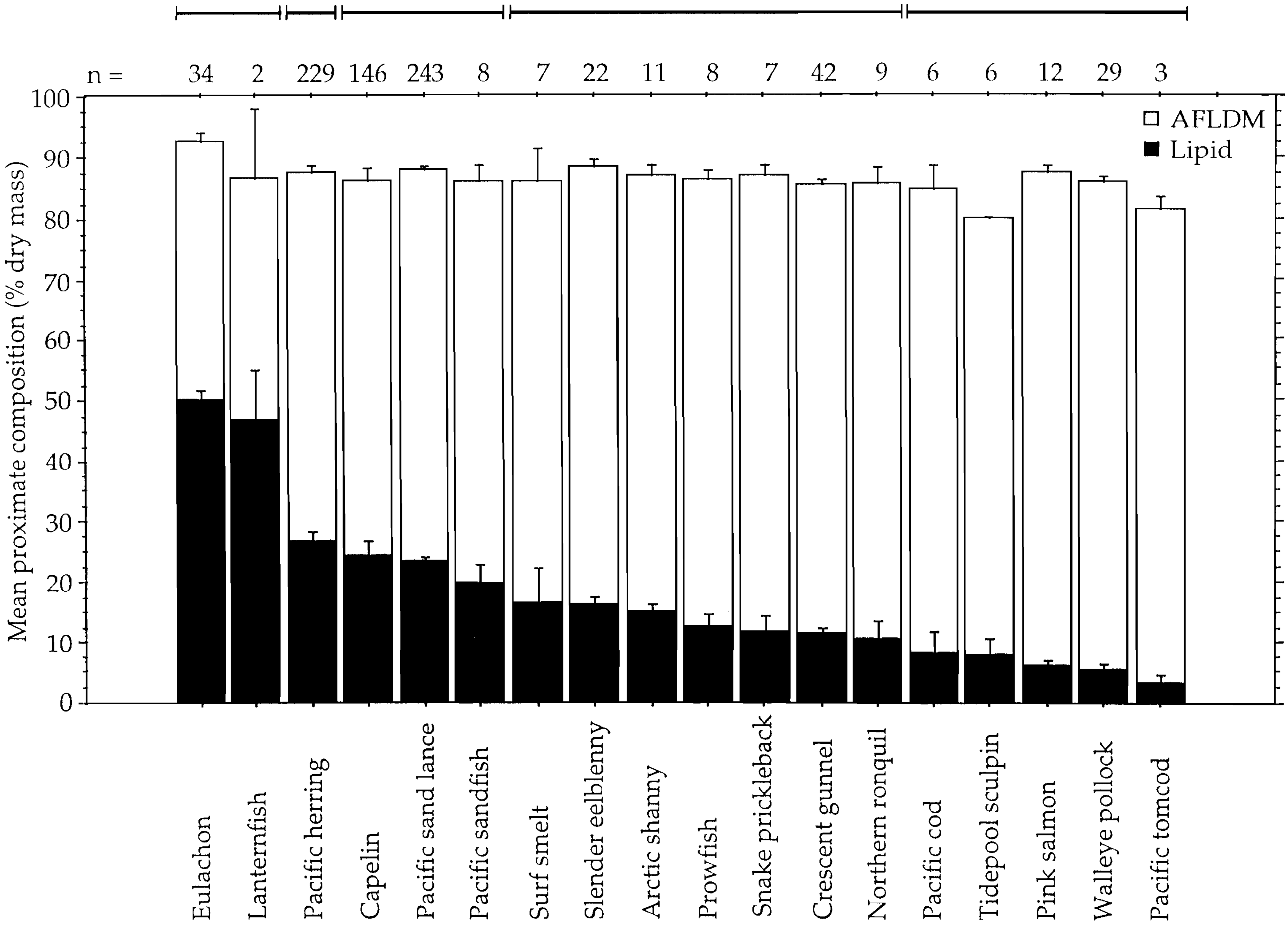

n =
34
2
229
146
243
8
7
22
11
8
7
42
9
6
6
12
29
3
Mean proximate composition (% dry mass)
0
10
20
30
40
50
60
70
80
90
100
□ AFLDM
■ Lipid
Eulachon
Lanternfish
Pacific herring
Capelin
Pacific sand lance
Pacific sandfish
Surf smelt
Slender eelblenny
Arctic shanny
Prowfish
Snake prickleback
Crescent gunnel
Northern ronquil
Pacific cod
Tidepool sculpin
Pink salmon
Walleye pollock
Pacific tomcod

FIG. 1

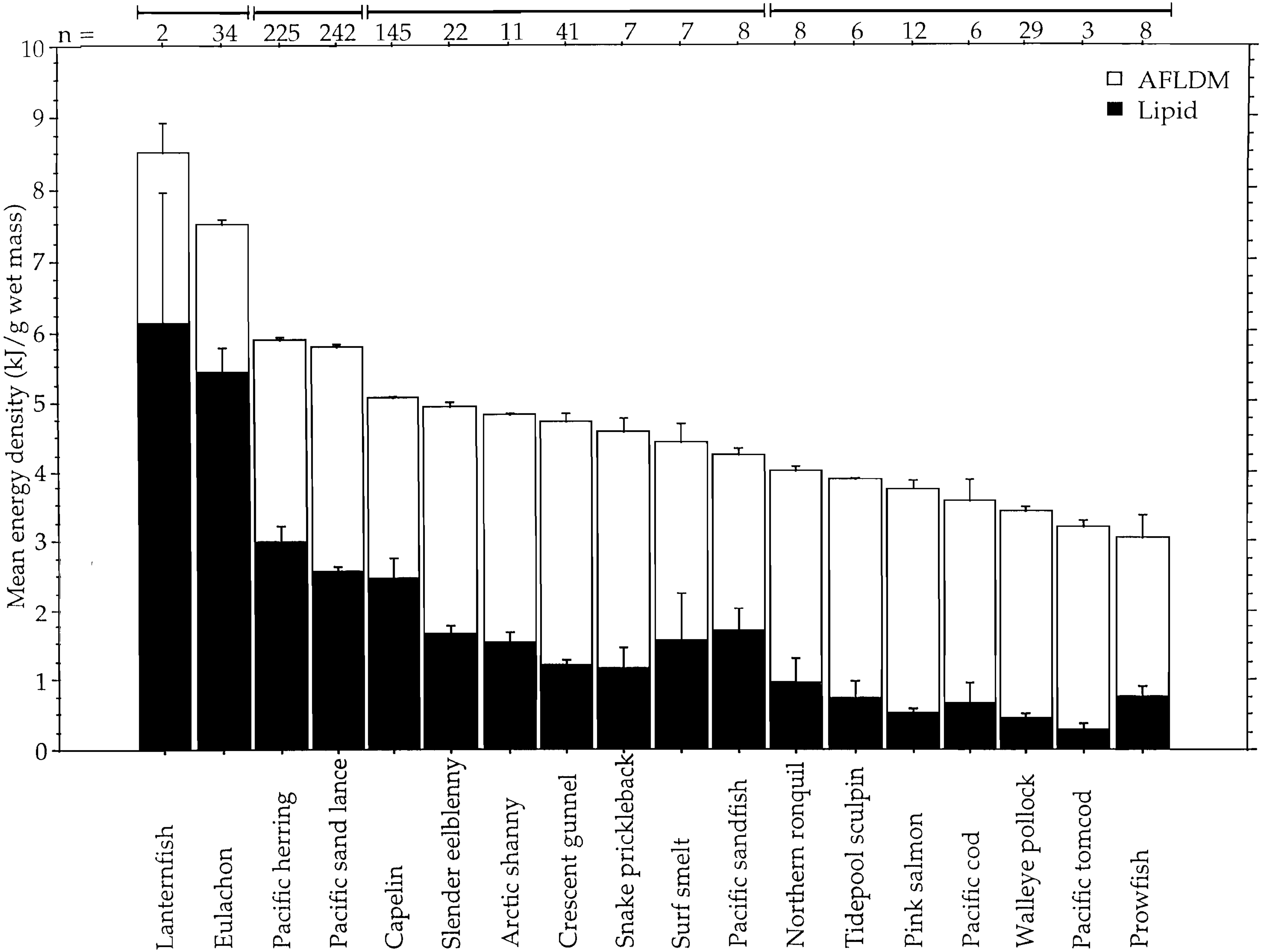
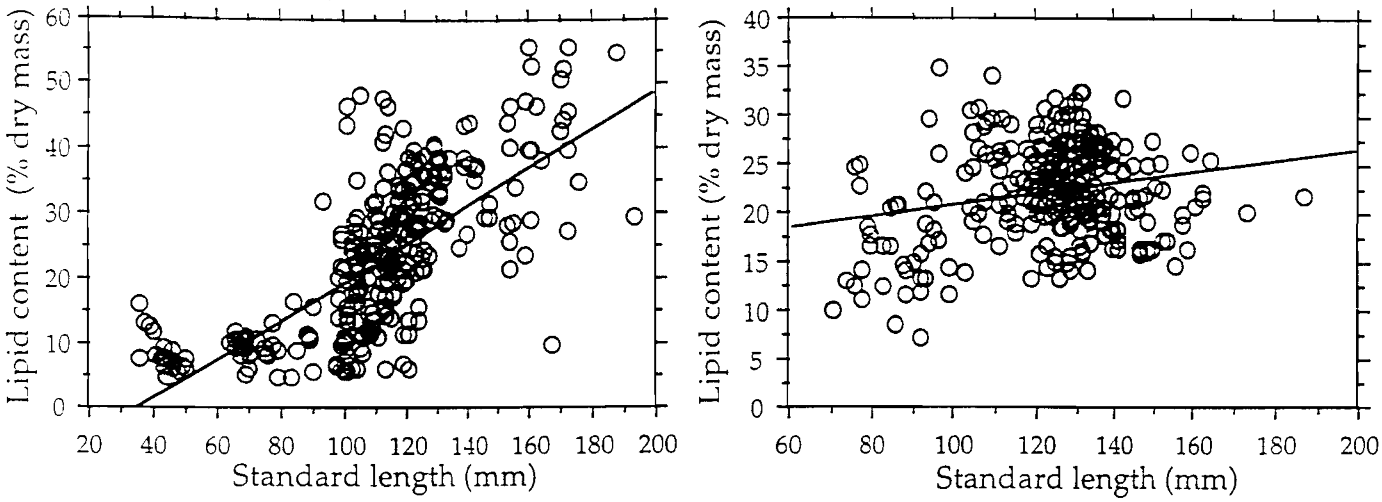
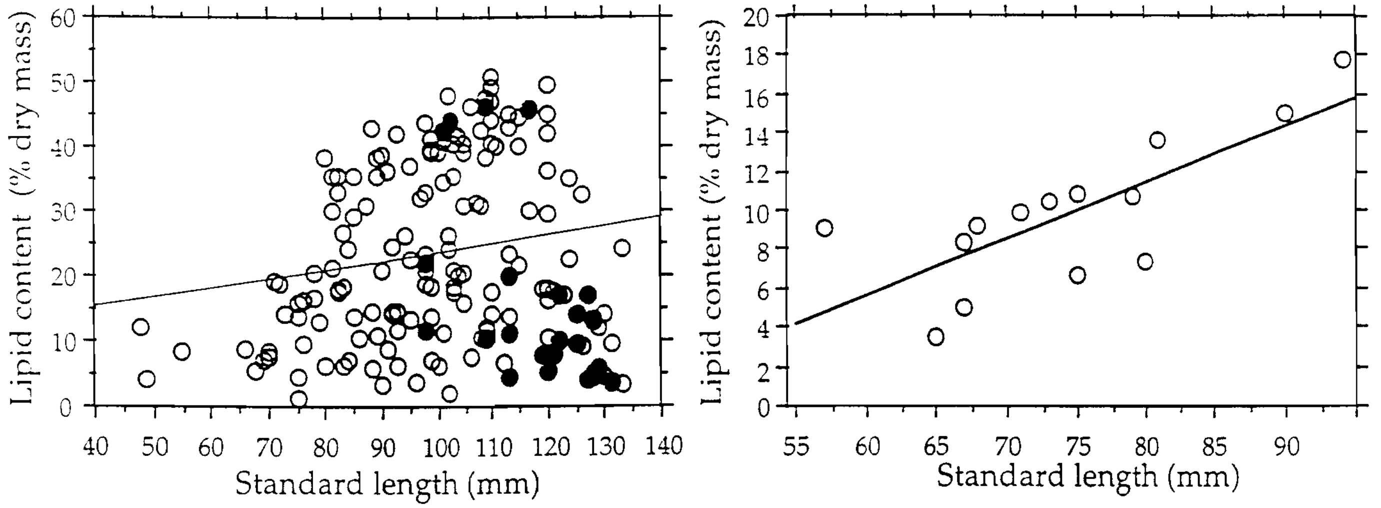

n =
2
34
225
242
145
22
11
41
7
7
8
8
6
12
6
29
3
8
AFLDM
Lipid
Mean energy density (kJ/g wet mass)
0
1
2
3
4
5
6
7
8
9
10
Lanternfish
Eulachon
Pacific herring
Pacific sand lance
Capelin
Slender eelblenny
Arctic shanny
Crescent gunnel
Snake prickleback
Surf smelt
Pacific sandfish
Northern ronquil
Tidepool sculpin
Pink salmon
Pacific cod
Walleye pollock
Pacific tomcod
Prowfish

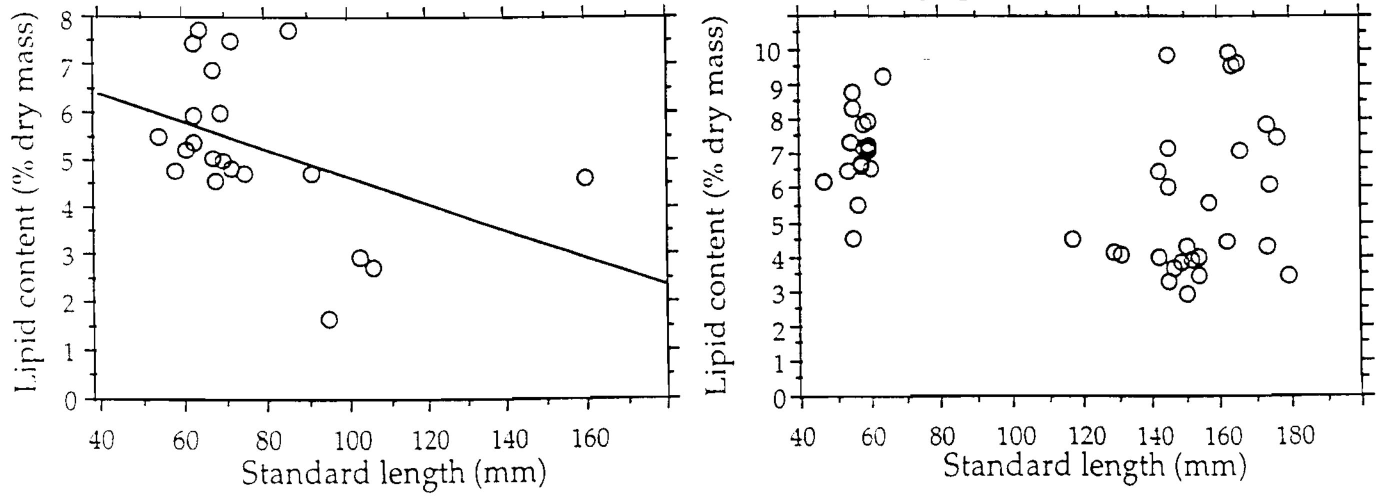
FIG. 2


(a) Pacific herring

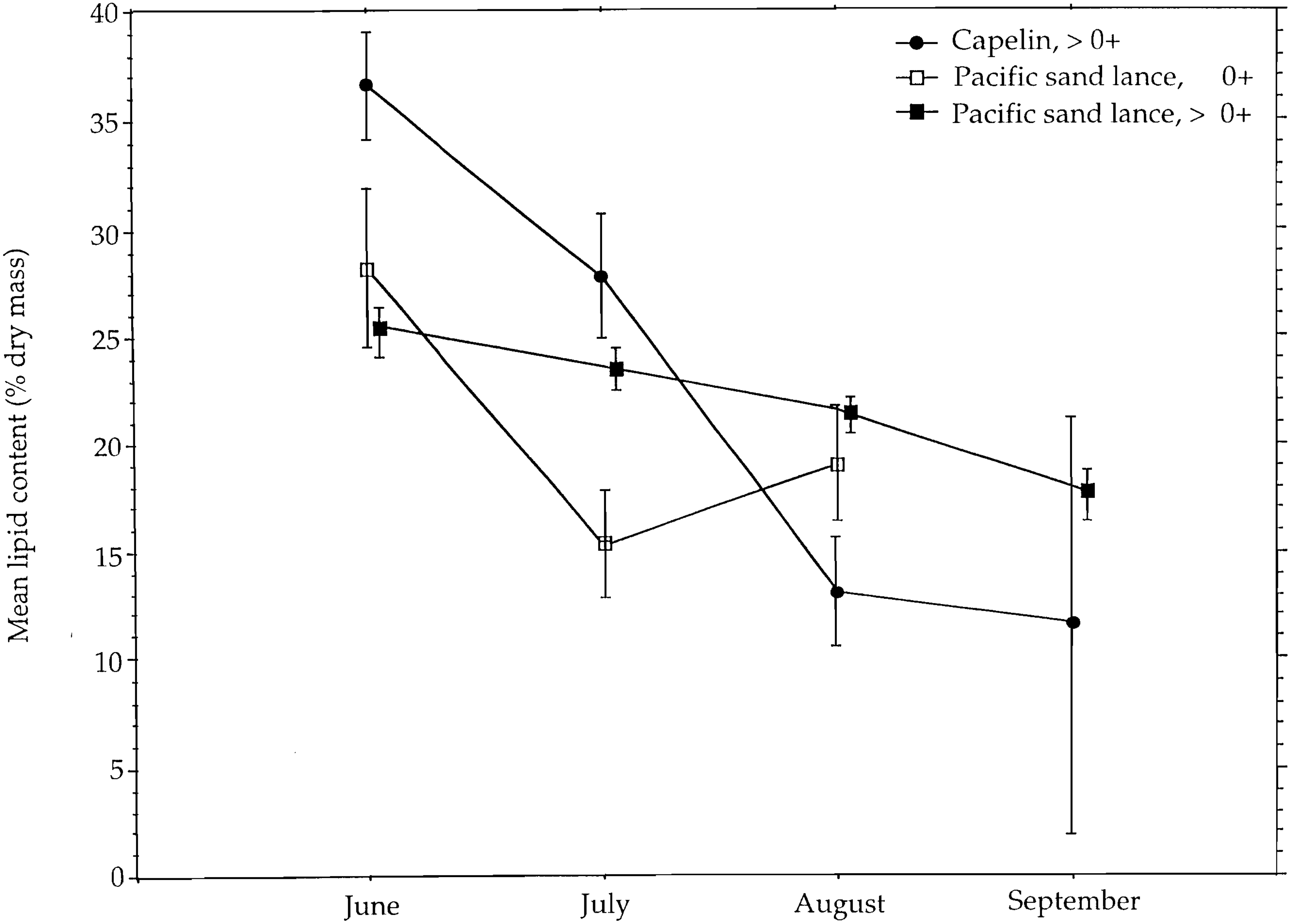
(b) Pacific sand lance


(c) Capelin

(d) Padded sculpin


(e) Pacific tomcod

(f) Walleye pollock



Mean lipid content (% dry mass)
40
35
30
25
20
15
10
5
0
June
July
August
September
● Capelin, > 0+
□ Pacific sand lance, 0+
■ Pacific sand lance, > 0+

FIG. 4

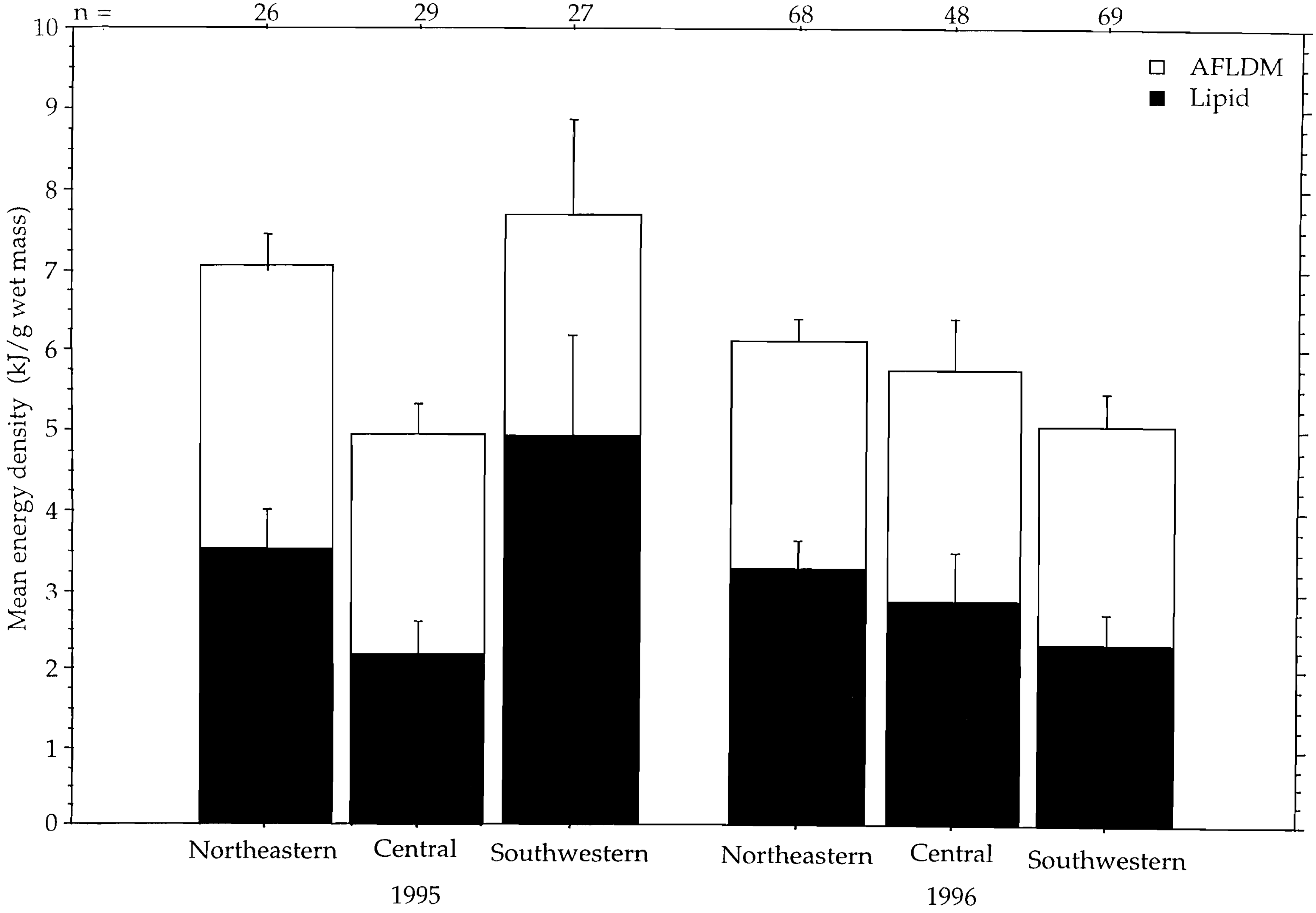

n =
26
29
27
68
48
69
10
9
8
7
6
5
4
3
2
1
0
Mean energy density (kJ/g wet mass)
☐ AFLDM
■ Lipid
Northeastern
Central
Southwestern
1995
Northeastern
Central
Southwestern
1996

FIG. 5

Appendix 1. Size of forage fish samples for proximate analysis. Ranges are presented in parentheses with means.

| Species | | n | Sex | Size class | Size-Age class | Standard length (mm) | Wet mass (g) |
|---|---|---|---|---|---|---|---|
| Armor-head sculpin | *Gymnocanthus galeatus* | 1 | - | ≥ 80 | large | 109 | 20.9 |
| Arctic shanny | *Stichaeus punctatus* | 11 | - | ≥ 80 | large | 95 (76 - 112) | 9.04 (6.38 - 12.7) |
| Black prickleback | *Xiphisteratro purpureus* | 3 | - | ≥ 80 | large | 174 (124 - 215) | 17.8 (4.59 - 24.8) |
| Capelin | *Mallotus villosus* | 32 | F | ≥ 80 | $> 0^+$ | 103 (83 - 121) | 8.15 (3.68 - 13.1) |
| Capelin | | 1 | M | < 90 | $0^+$ | 82 | 4.70 |
| Capelin | | 73 | M | ≥ 90 | $> 0^+$ | 114 (95- 133) | 13.0 (6.12 - 23.5) |
| Capelin | | 31 | - | < 80 | $0^+$ | 71 (48 - 79) | 2.27 (0.82 - 3.27) |
| Capelin | | 41 | - | ≥ 80 | $> 0^+$ | 94 (80 - 126) | 5.55 (2.19 - 13.3) |
| Crescent gunnel | *Pholis laeta* | 42 | - | ≥ 100 | large | 140 (103 - 186) | 10.4 (3.44 - 28.1) |
| Crested sculpin | *Blepsias bilobus* | 2 | - | ≥ 80 | large | 87 (84 - 90) | 20.2 |
| Daubed shanny | *Lumpenus maculatus* | 2 | - | ≥ 80 | large | 127 (120 - 134) | 7.21 (6.43 - 7.98) |
| Dover sole | *Microstomus pacificus* | 1 | - | ≥ 80 | large | 105 | 10.8 |
| Eulachon (Hooligan) | *Thaleichthys pacificus* | 10 | F | ≥ 100 | $> 0^+$ | 155 (141 - 173) | 28.4 (20.5 - 35.5) |
| Eulachon | | 14 | M | ≥ 100 | $> 0^+$ | 162 (151 - 174) | 31.0 (24.5 - 39.1) |
| Eulachon | | 10 | - | ≥ 100 | $> 0^+$ | 178 (138 - 202) | 44.0 (19.0 - 84.2) |
| Flatfish | unknown species | 2 | - | < 80 | small | 69 (68 - 70) | 5.49 (5.06 - 5.92) |
| Flatfish | | 2 | - | ≥ 80 | large | 87 (83 - 91) | 11.9 (8.48 - 15.4) |
| Great sculpin | *Myoxocephalus polyacanthocephalus* | 1 | - | ≥ 80 | large | 105 | 17.8 |

Appendix 1. Continued.

| Species | | n | Sex | Size class | Size-Age class | Standard length (mm) | Wet mass (g) |
|---|---|---|---|---|---|---|---|
| High cockscomb | *Anoplarchus purpurescens* | 1 | - | ≥ 80 | large | 120 | 10.5 |
| Horned sculpin | *Myoxocephalus quadricornis* | 2 | - | < 80 | small | 60 (40 - 79) | 9.16 (9.16 - 9.16) |
| Lanternfish | Family Myctophidae | 2 | - | | > $0^+$ | 55 (37 - 73) | 2.02 (0.33 - 3.7) |
| Lingcod | *Ophiodon elongatus* | 12 | | ≥ 100 | large | 77 (69 - 89) | 2.87 (1.72 - 4.27) |
| Northern ronquil | *Ronquilus jordani* | 8 | - | ≥ 80 | large | 114 (85 - 160) | 13.5 (4.16 - 37.4) |
| Pacific cod | *Gadus macrocephalus* | 15 | - | < 100 | $0^+$ | 73 (58 - 86) | 3.88 (3.28 - 4.46) |
| Pacific cod | | 5 | - | ≥ 100 | > $0^+$ | 121 (111- 136) | 15.4 (11. 9 - 23.1) |
| Pacific herring | *Clupea harengus pallasii* | 15 | F | ≥ 100 | > $0^+$ | 170 (155 - 194) | 66.0 (48.2 - 102) |
| Pacific herring | | 11 | M | ≥ 100 | > $0^+$ | 151 (111 - 173) | 46.7 (9.70 - 76.1) |
| Pacific herring | | 63 | - | < 100 | $0^+$ | 67 (37 - 99) | 3.52 (0.35 - 11.4) |
| Pacific herring | | 203 | - | ≥ 100 | > $0^+$ | 118 (100- 160) | 19.1 (6.93 - 49.1) |
| Pacific sand lance | *Ammodytes hexapterus* | 98 | F | ≥ 100 | > $0^+$ | 134 (111 - 188) | 10.7 (6.00 - 26.5) |
| Pacific sand lance | | 2 | M | < 100 | $0^+$ | 95 (93 - 96) | 2.77 (2.73 - 2.81) |
| Pacific sand lance | | 75 | M | ≥ 100 | > $0^+$ | 131 (114 - 158) | 10.1 (5.26 - 19.5) |
| Pacific sand lance | | 37 | - | < 100 | $0^+$ | 86 (70 - 99) | 2.56 (1.21 - 3.71) |
| Pacific sand lance | | 70 | - | ≥ 100 | > $0^+$ | 122 (103 - 174) | 7.84 (3.70 - 25.1) |
| Pacific sandfish | *Trichodon trichodon* | 30 | - | < 100 | small | 68 (57 - 97) | 4.74 (2.35 - 14.8) |
| Pacific sandfish | | 8 | - | ≥ 100 | large | 106 (100 - 112) | 20.3 (17.5 - 22.3) |

Appendix 1. Continued.

| Species | | n | Sex | Size class | Size-Age class | Standard length (mm) | Wet mass (g) |
|---|---|---|---|---|---|---|---|
| Pacific tomcod | *Microgadus proximus* | 20 | - | < 100 | $0^+$ | 69 (54 - 95) | 2.90 (1.21 - 6.79) |
| Pacific tomcod | | 3 | - | ≥ 100 | $> 0^+$ | 123 (103 - 160) | 14. 4 (7.80 - 25.0) |
| Padded sculpin | *Artedius fenestralis* | 10 | - | < 80 | small | 70 (57 - 79) | 8.69 (7.77 - 9.80) |
| Padded sculpin | | 4 | - | ≥ 80 | large | 86 (80 - 94) | 13.4 (8.36 - 18.5) |
| Pink salmon | *Oncorhynchus gorbuscha* | 37 | - | < 100 | $0^+$ | 85 (57 - 98) | 7.49 (3.40 - 11.6) |
| Pink salmon | | 9 | - | ≥ 100 | $> 0^+$ | 112 (102 - 135) | 14.5 (10.6 - 19.5) |
| Plain sculpin | *Myoxocephalus jaok* | 1 | - | < 80 | small | 75 | 5.69 |
| Prowfish | *Zaprora silenus* | 15 | - | < 100 | small | 70 (53 - 87) | 7.88 (2.75 - 17.6) |
| Prowfish | | 8 | - | ≥ 100 | large | 107 (100 - 118) | 20.6 (11.6 - 33.0) |
| Red irish lord | *Hemilepidotus hemilepidotus* | 1 | - | ≥ 80 | large | 97 | 21.9 |
| Red salmon | *Oncorhynchus nerka* | 5 | - | < 100 | $0^+$ | 72 (65 - 77) | 3.72 (2.93 - 4.58) |
| Rex sole | *Glyptocephalus zachirus* | 3 | - | ≥ 80 | large | 138 (129 - 150) | 17.9 (15.5 - 22.0) |
| Ribbed sculpin | *Triglops pingeli* | 1 | - | < 80 | small | 71 | 5.28 |
| Ribbed sculpin | | 5 | - | ≥ 80 | large | 120 (107 - 160) | 9.53 (7.16 - 12.8) |
| Rough spine sculpin | *Triglops macellus* | 2 | - | ≥ 80 | large | 112 (107 - 116) | 9.57 (5.96 - 13.2) |
| Searcher | *Bathymaster signatus* | 1 | - | ≥ 80 | large | 139 | 25. 9 |
| Silverspotted sculpin | *Blepsias cirrhosus* | 1 | - | ≥ 80 | large | 83 | 8.64 |
| Slender eelblenny | *Lumpenus fabricii* | 22 | - | ≥ 100 | large | 156 (113 - 295) | 15.4 (6.70 - 43.0) |
| Slender sculpin | *Cottus tenuis* | 1 | - | ≥ 80 | large | 80 | 2.7 |

Appendix 1. Continued.

| Species | | n | Sex | Size class | Size-Age class | Standard length (mm) | Wet mass (g) |
|---|---|---|---|---|---|---|---|
| Snake prickleback | *Lumpenus sagitta* | 7 | - | ≥ 80 | large | 208 (142 - 272) | 22.5 (6.99 - 47.6) |
| Spotted snailfish | *Liparis callyodon* | 1 | - | < 100 | small | 94 | 15. 8 |
| Surf smelt | *Hypomesus pretiosus* | 5 | M | < 100 | small | 118 (106 - 131) | 17.2 (10.4 - 23.7) |
| Surf smelt | | 2 | - | ≥ 100 | large | 105 (101 - 108) | 10.1 (9.64 - 10.6) |
| Tidepool sculpin | *Oligocottus maculosus* | 1 | - | < 80 | small | 44 | 1.06 |
| Tidepool sculpin | | 6 | - | ≥ 80 | large | 120 (110 - 130) | 28.3 (18.0 - 38.0) |
| Walleye pollock | *Theragra chalcogramma* | 17 | - | < 100 | $0^+$ | 57 (47 - 64) | |
| Walleye pollock | | 27 | - | ≥ 100 | $> 0^+$ | 154 (117 - 179) | 29.0 (16.6 - 47.0) |

Appendix 2. Proximate composition of forage fishes from the northern Gulf of Alaska, collected from May through August 1995-1996. Energy content (kJ/fish) is the product of wet mass (g) and energy density (kJ/g wet mass). Standard error is presented with means.

| Species | Size class (mm) | n | Wet mass (g) | Water % lean mass | Lipid % dry mass | AFLDM % lean dry mass | Energy density (kJ/g dry mass) | Energy density (kJ/g wet mass) |
|---|---|---|---|---|---|---|---|---|
| Armor-head sculpin | ≥ 80 | 1 | 20.9 | 77.1 | 16.1 | 82.1 | 18.6 | 4.77 |
| Arctic shanny | ≥ 80 | 11 | 9.04 ± 0.76 | 76.4 ± 0.20 | 15.1 ± 0.60 | 85.4 ± 0.40 | 18.7 ± 0.16 | 4.79 ± 0.08 |
| Black prickleback | ≥ 80 | 3 | 17.8 ± 6.62 | 75.7 ± 3.30 | 6.75 ± 1.20 | 81.8 | 16.3 ± 0.52 | 4.11 ± 0.35 |
| Capelin | < 100 | 32 | 2.34 ± 0.13 | 80.3 ± 0.20 | 17.7 ± 1.80 | 88.5 ± 0.30 | 19.1 ± 0.50 | 4.17 ± 0.21 |
| Capelin | ≥ 100 | 146 | 9.85 ± 0.46 | 80.3 ± 0.10 | 24.3 ± 1.20 | 87.5 ± 0.20 | 20.5 ± 0.28 | 5.04 ± 0.13 |
| Crescent gunnel | ≥ 80 | 42 | 10.4 ± 0.59 | 76.0 ± 0.20 | 11.5 ± 0.40 | 84.7 ± 0.30 | 17.7 ± 0.14 | 4.69 ± 0.08 |
| Crested sculpin | ≥ 80 | 2 | 18.1 ± 2.14 | 83.9 ± 0.10 | 16.9 ± 1.30 | 84.8 ± 0.02 | 19.2 ± 0.31 | 3.54 ± 0.13 |
| Daubed shanny | ≥ 80 | 2 | 7.21 ± 0.78 | 77.1 ± 1.20 | 16.5 ± 1.30 | 84.6 ± 0.70 | 18.9 ± 0.53 | 4.83 ± 0.07 |
| Dover sole | ≥ 80 | 1 | 10.8 | 82.5 | 5.60 | 82.6 | 16.1 | 2.86 |
| Eulachon | ≥ 100 | 34 | 34.1 ± 2.06 | 82.3 ± 0.30 | 50.0 ± 0.80 | 88.2 ± 0.20 | 27.2 ± 0.19 | 7.49 ± 0.19 |
| Flatfish | < 80 | 2 | 5.49 ± 0.43 | 79.4 ± 0.30 | 8.60 ± 0.20 | 83.3 ± 1.10 | 16.5 ± 0.23 | 3.61 ± 0.004 |
| Flatfish | ≥ 80 | 2 | 11.9 ± 3.46 | 78.8 ± 0.50 | 10.9 ± 0.70 | 84.0 ± 0.04 | 17.2 ± 0.30 | 3.95 ± 0.17 |
| Great sculpin | ≥ 80 | 1 | 17.8 | 77.6 | 3.80 | 77.0 | 14.3 | 3.22 |
| High cockscomb | ≥ 80 | 1 | 10.5 | 76.7 | 9.40 | 84.0 | 17.2 | 4.28 |
| Horned sculpin | < 80 | 2 | 9.16 | 81.3 | 8.50 ± 0.10 | 80.2 ± 1.60 | 16.4 ± 0.29 | 3.48 ± 0.30 |

Appendix 2. Continued.

| Species | Size class (mm) | n | Wet mass (g) | Water % lean mass | Lipid % dry mass | AFLDM % lean dry mass | Energy density (kJ/g dry mass) | Energy density (kJ/g wet mass) |
|---|---|---|---|---|---|---|---|---|
| Lanternfish | ≥ 100 | 2 | 2.02 ± 1.68 | 73.4 ± 1.80 | 46.3 ± 4.40 | 86.5 ± 3.50 | 25.3 ± 0.70 | 8.49 ± 0.70 |
| Lingcod | < 100 | 12 | 2.87 ± 0.26 | 77.9 ± 0.40 | 10.1 ± 0.60 | 86.0 ± 0.30 | 17.0 ± 0.14 | 3.98 ± 0.14 |
| Northern ronquil | ≥ 80 | 8 | 13.5 ± 3.28 | 78.7 ± 0.20 | 10.7 ± 1.50 | 83.9 ± 0.30 | 17.5 ± 0.36 | 3.98 ± 0.17 |
| Pacific cod | < 100 | 15 | 3.88 ± 0.17 | 79.1 ± 0.20 | 8.05 ± 0.80 | 85.0 ± 0.30 | 17.1 ± 0.22 | 3.65 ± 0.08 |
| Pacific cod | ≥ 100 | 6 | 15.4 ± 2.07 | 80.4 ± 1.20 | 8.10 ± 1.70 | 83.9 ± 0.30 | 16.8 ± 0.36 | 3.54 ± 0.19 |
| Pacific herring | < 100 | 63 | 3.52 ± 0.46 | 79.2 ± 0.10 | 10.5 ± 0.80 | 86.6 ± 0.30 | 17.8 ± 0.17 | 3.69 ± 0.07 |
| Pacific herring | ≥ 100 | 229 | 23.5 ± 1.08 | 78.0 ± 0.10 | 26.8 ± 0.70 | 86.3 ± 0.10 | 21.3 ± 0.19 | 5.84 ± 0.11 |
| Pacific sandfish | < 100 | 30 | 4.74 ± 0.60 | 80.1 ± 0.20 | 11.0 ± 0.60 | 85.0 ± 0.20 | 17.1 ± 0.18 | 3.55 ± 0.06 |
| Pacific sandfish | ≥ 100 | 8 | 20.3 ± 0.69 | 82.0 ± 0.30 | 19.8 ± 1.50 | 83.8 ± 0.20 | 19.5 ± 0.35 | 4.23 ± 0.17 |
| Pacific sand lance | < 100 | 39 | 2.58 ± 0.13 | 76.5 ± 0.30 | 17.3 ± 0.90 | 88.9 ± 0.40 | 20.0 ± 0.29 | 5.06 ± 0.12 |
| Pacific sand lance | ≥ 100 | 242 | 9.69 ± 0.22 | 76.4 ± 0.10 | 23.4 ± 0.30 | 88.1 ± 0.10 | 20.6 ± 0.07 | 5.74 ± 0.04 |
| Pacific tomcod | < 100 | 20 | 2.90 ± 0.35 | 80.3 ± 0.20 | 5.59 ± 0.40 | 83.2 ± 0.20 | 15.8 ± 0.17 | 3.04 ± 0.06 |
| Pacific tomcod | ≥ 100 | 3 | 14.4 ± 5.36 | 79.4 ± 0.04 | 3.43 ± 0.60 | 82.5 ± 0.60 | 15.3 ± 0.38 | 3.16 ± 0.11 |
| Padded sculpin | < 80 | 10 | 8.69 ± 0.42 | 77.8 ± 0.10 | 8.36 ± 0.80 | 81.0 ± 0.30 | 16.5 ± 0.24 | 3.82 ± 0.08 |
| Padded sculpin | ≥ 80 | 4 | 13.4 ± 2.27 | 77.3 ± 0.20 | 13.5 ± 2.20 | 81.7 ± 0.50 | 17.9 ± 0.62 | 4.37 ± 0.23 |
| Pink salmon | < 100 | 37 | 7.49 ± 0.35 | 79.9 ± 0.20 | 7.28 ± 0.40 | 86.2 ± 0.20 | 16.8 ± 0.10 | 3.41 ± 0.04 |
| Pink salmon | ≥ 100 | 9 | 14.5 ± 0.94 | 78.5 ± 0.50 | 6.35 ± 0.50 | 87.4 ± 0.20 | 16.9 ± 0.09 | 3.73 ± 0.10 |
| Plain sculpin | < 80 | 1 | 5.69 | 78.7 | 6.60 | 78.2 | 17.9 | 3.24 |

Appendix 2. Continued.

| Species | Size class (mm) | n | Wet mass (g) | Water % lean mass | Lipid % dry mass | AFLDM % lean dry mass | Energy density (kJ/g dry mass) | Energy density (kJ/g wet mass) |
|---|---|---|---|---|---|---|---|---|
| Prowfish | < 100 | 16 | 7.88 ± 1.11 | 85.4 ± 0.40 | 13.7 ± 1.00 | 84.5 ± 0.40 | 18.1 ± 0.23 | 2.84 ± 0.07 |
| Prowfish | ≥ 100 | 8 | 20.6 ± 2.81 | 85.2 ± 0.70 | 12.7 ± 1.00 | 84.5 ± 0.50 | 18.1 ± 0.29 | 3.01 ± 0.15 |
| Red salmon | < 100 | 5 | 3.72 ± 0.28 | 77.6 ± 0.70 | 11.9 ± 1.20 | 88.2 ± 0.10 | 17.8 ± 0.34 | 4.35 ± 0.28 |
| Red irish lord | ≥ 80 | 1 | 21.9 | 76.3 | 5.90 | 79.8 | 15.7 | 3.85 |
| Rex sole | ≥ 80 | 3 | 17.9 ± 2.07 | 0 | 3.60 ± 0.20 | 81.4 ± 0.70 | 15.4 ± 0.32 | 3.02 ± 0.21 |
| Ribbed sculpin | ≥ 80 | 5 | 9.53 ± 1.19 | 76.2 ± 0.40 | 16.7 ± 2.20 | 77.7 ± 3.00 | 17.9 ± 1.06 | 4.80 ± 0.43 |
| Rough spine sculpin | ≥ 80 | 2 | 9.57 ± 3.61 | 75.2 ± 0.20 | 17.6 ± 8.20 | 83.4 ± 2.00 | 19.0 ± 2.15 | 5.26 ± 0.83 |
| Searcher | ≥ 80 | 1 | 25.9 | 78 | 11.8 | 85.8 | 17.9 | 4.24 |
| Silverspotted sculpin | ≥ 80 | 1 | 8.64 | 81 | 6.60 | 78.1 | 15.5 | 3.05 |
| Slender eelblenny | ≥ 80 | 22 | 15.4 ± 2.07 | 77.2 ± 0.20 | 16.3 ± 0.60 | 86.6 ± 0.20 | 19.2 ± 0.14 | 4.90 ± 0.08 |
| Slender sculpin | ≥ 80 | 1 | 2.70 | 74.7 | 11.2 | 77.6 | 16.2 | 4.29 |
| Snake prickleback | ≥ 80 | 7 | 22.5 ± 5.37 | 76.3 ± 0.70 | 11.6 ± 1.40 | 84.9 ± 0.60 | 18.0 ± 0.44 | 4.55 ± 0.18 |
| Spotted snailfish | < 100 | 1 | 15.8 | 79.5 | 4.50 | 83.9 | 15.7 | 3.28 |
| Surf smelt | ≥ 100 | 7 | 15.2 ± 2.29 | 78.3 ± 0.40 | 16.5 ± 2.90 | 88.6 ± 0.30 | 18.8 ± 0.69 | 4.39 ± 0.35 |
| Tidepool sculpin | < 80 | 1 | 1.06 | 0 | 11.6 | 79.7 | 15.5 | 4.75 |
| Tidepool sculpin | ≥ 80 | 6 | 28.3 ± 2.63 | 76.5 ± 0.30 | 7.76 ± 1.30 | 78.5 ± 1.00 | 15.8 ± 0.51 | 3.84 ± 0.12 |
| Walleye pollock | < 100 | 17 | 7.93 ± 1.98 | 80.3 ± 0.30 | 7.10 ± 0.30 | 85.9 ± 0.50 | 17.0 ± 0.14 | 3.47 ± 0.06 |
| Walleye pollock | ≥ 100 | 27 | 29.0 ± 1.68 | 80.2 ± 0.20 | 6.70 ± 0.40 | 85.2 ± 0.30 | 16.5 ± 0.13 | 3.24 ± 0.06 |