Exxon Valdez Oil Spill
Restoration Project Annual Report

EFFECTS OF DIET QUALITY ON POST-NATAL GROWTH OF SEABIRDS: CAPTIVE FEEDING TRIALS

Restoration Project 97163N

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Study History: Captive rearing of seabird nestlings at the Kasitsna Bay Laboratory, Kachemak Bay, Alaska, began during the summer of 1996 (APEX Project 96163N). Experimental feeding trials were continued during the summer of 1997. The field component of this project has been completed and a final report will be submitted in September, 1998.

Abstract: Declines in the availability of certain schooling forage fishes (capelin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea harengus pallasi*) have potentially contributed to the lack of recovery of some fish-eating seabirds (Pigeon Guillemots *Cepphus columba*, Common Murres *Uria aalge*, Marbled Murrelets *Brachyramphus marmoratus*) that were injured by the *Exxon Valdez* oil spill. These fishes tend to have high lipid content and, consequently, are assumed to have high nutritional value as food for nestling seabirds. We tested whether composition of the diet is one factor constraining the growth and development of piscivorous seabirds. We raised seabird nestlings (Black-legged Kittiwakes *Rissa tridactyla* and Tufted Puffins, *Fratercula cirrhata*) in captivity on rations of either capelin, sand lance, or herring, as representative of high-quality forage fish, or walleye pollock (*Theragra chalcograma*) as representative of low-quality forage fish. Experimental diets consisted of iso-biomass and iso-caloric rations of low- and high-lipid fish types. Seabird nestlings fed rations of capelin, sand lance or herring had higher growth rates of body mass and wing length than nestlings fed the same biomass of pollock. Puffin chicks fed iso-caloric rations of pollock, capelin, or herring showed little difference in rates of mass or wing growth, but the capelin and herring fed chicks deposited larger fat reserves than the chicks fed pollock. Differences in mass gain between nestlings fed the different rations were more pronounced than differences in wing growth, suggesting that undernourished nestlings allocate food intake more to structural development than body mass. We conclude that the lipid content and nutritional quality of forage fish fed to nestlings has a marked effect on growth rates and, potentially, on reproductive success. One consequence of subsisting on pollock instead of lipid-rich forage species is that predators must expend more energy and catch more prey to meet the energy requirements of their offspring. In addition, nestlings fed lower lipid diets deposit less fat reserves, potentially reducing post-fledging survival. These conclusions provide more support for the hypothesis that recovery of seabird resources that were injured by the Exxon Valdez oil spill is dependent on recovery of certain key forage fish stocks, especially capelin, sand lance, and herring.

Key Words: black-legged kittiwake, capelin, captive feeding trials, chick growth, herring, lipid:protein ratio, sand lance, pollock, tufted puffin.

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Effect of Prey Type on the Growth of Piscivorous Seabirds: Captive Feeding Trials

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Abstract. - Declines in availability of certain schooling forage fishes (capelin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea harengus pallasi*) potentially contributed to declines in nesting success of some fish-eating seabirds in Alaska. These forage fishes tend to have high lipid content compared with that of other forage fishes, and, consequently, are assumed to have high nutritional value as food for young seabirds. We tested the hypothesis that type of fish consumed constrains the growth and development of piscivorous seabirds. We raised seabird nestlings (Black-legged Kittiwakes, *Rissa tridactyla* and Tufted Puffins, *Fratercula cirrhata*) in captivity on equal biomass rations of either capelin, herring, or sand lance and compared their growth with that of nestlings raised on juvenile walleye pollock (*Theragra chalcograma*), (representative of low-lipid forage fishes). Seabird nestlings fed herring, sand lance, or capelin had higher growth rates (body mass and wing length) than nestlings fed juvenile pollock. Differences in mass gain were more pronounced than differences in wing growth, suggesting that nestlings fed lower-lipid diets allocate assimilated nutrients more toward structural development than to deposition of body mass. Thus, the lipid content of forage fish fed to nestlings has a marked effect on growth rates and, potentially, on pre- and post-fledging survival. This conclusion provides support for the hypothesis that the demography of piscivorous seabirds in Alaska is dependent on certain key forage fish stocks, especially capelin, sand lance, and herring.

Key words. – Black-legged Kittiwake, capelin, captive feeding trials, chick growth, herring, pollock, sand lance, seabirds, Tufted Puffin.

Running head: Diet and Seabird Growth

INTRODUCTION

Recent declines among populations of top trophic level predators in the northern Gulf of Alaska have been linked to decreasing availability of forage fishes (Merrick et al. 1987, Hatch et al. 1993, Piatt and Anderson 1996). Several species of seabirds, including Marbled Murrelets (*Brachyramphus marmoratus*), Common Murres (*Uria aalge*), and Pigeon Guillemots (*Cepphus columba*), have experienced population declines in this area over the last two decades. Recently, total failure of breeding seabirds has been recorded repeatedly at several sites (e.g., Chisik I., Middleton I.). A lack of preferred forage fishes during the nesting season has been hypothesized as one factor leading to low productivity (Hatch et al. 1993).

A major change in the taxonomic composition of diets of several seabird species has been observed in the northern Gulf of Alaska, concurrent with population declines over the past 20 years. Some species have switched from diets dominated by capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), and Pacific herring (*Clupea harengus*) to diets dominated by juvenile walleye pollock (*Theragra chalcograma*) and other gadids (Piatt and Anderson 1996). Due to generally lower lipid content and lower energy density (kJ/g live mass), juvenile pollock are considered lower quality prey than other fish commonly found in diets of nestling seabirds (Baird 1991, Van Pelt et al. 1997, Anthony et al. Unpubl. ms.). The lipid content of capelin, sand lance, and herring is generally two to four times that of juvenile pollock, and energy density can be twice that of pollock, depending on sex and age class (Van Pelt et al. 1997, Anthony et al. Unpubl. ms.).

If reproductive success of seabirds is directly related to the nutritional quality of available forage fish, then adult seabirds that rely on low-lipid prey to provision their young may experience lower productivity (Nettleship 1990, Martin 1989). For example, recent reproductive failures among Black-legged Kittiwakes nesting in Prince William Sound, Alaska have been linked to forage fish availability, especially the availability of Pacific herring (Irons 1996). Reproductive success in seabirds is dependent, in part, on the parent's ability to capture and transport food energy from the foraging area to the nest (Ricklefs 1983, Roby 1991). If parent seabirds provide their young with an equivalent amount of food energy in the form of juvenile pollock (or another low-lipid forage fish) as they can provide in sand lance, herring, or capelin, they may have to feed their young twice the biomass of food. This may not be possible due to time and energy constraints, unless pollock are readily available close to the colony. Increased foraging effort by parent seabirds may also expose them to higher risk of predation or other stress – related mortality. Consequently, slower growth and lower fledging mass would be expected in nestlings fed primarily low-lipid forage fishes. The predicted result would be fewer nestlings surviving to fledge and lower post-fledging survival.

This research was designed to provide a better understanding of the relationship between diet quality and seabird productivity. Captive nestlings fed controlled rations of different forage fish species were used to test the hypothesis that differences in prey type result in differences in the growth and development of seabird nestlings. We predicted that seabird nestlings fed diets of capelin, sand lance, or herring would grow and develop more rapidly than nestlings fed the same daily ration of juvenile pollock. We also predicted that these diet-related differences would occur regardless of the taxon of seabird used in captive feeding trials.

METHODS AND MATERIALS

The research design utilized a combination of captive feeding trials and laboratory analyses. Captive feeding trials were conducted at the Kasitsna Bay Laboratory of the Institute of Marine Science, University of Alaska Fairbanks, during the summers of 1996 and 1997. The Laboratory is located on Kachemak Bay near the town of Seldovia in South-central Alaska. Captive feeding trials were conducted following a protocol approved by the Institutional Animal Care and Use Committee at Oregon State University.

Two species of colonial, piscivorous seabirds were chosen for captive feeding trials: Black-legged Kittiwakes (*Rissa tridactyla*) and Tufted Puffins (*Fratercula cirrhata*). The former is a larid that forages at or near the surface by plunge-diving, while the latter is an alcid that forages by pursuit-diving to considerable depth. Both are common breeding species in the northern Gulf of Alaska.

Chicks used in the study were collected from either East Amatuli Island in the Barren Islands, Alaska or from colonies in Kachemak Bay under permits held by the Alaska Biological Science Center. During 1996, 14 Black-legged Kittiwake chicks and 14 Tufted Puffin chicks were removed from their nests at 6-10 days post-hatch (± 3 days) and 5-18 days post-hatch (± 3 days), respectively. In 1997, 12 kittiwake chicks and 12 puffin chicks were removed at 3-9 days post-hatch (± 3 days) and 4-17 days post-hatch (± 3 days), respectively. Kittiwake chicks were aged from a combination of their body mass and wing length, using regression equations for wing length and body mass as a function of age. The equation was derived from known-age chicks in Prince William Sound, Alaska (D.B. Irons, unpubl. data). Tufted Puffin chicks were also aged from a combination of wing length and body mass using regression equations derived from known-age chicks on Aiktak Island, Alaska (Piatt and Romano, unpubl. data).

Young chicks were kept under heat lamps for several days after removal from their nests to preclude any possibility of hypothermia. All chicks were held indoors, in individual cages throughout captive feeding experiments. Cages consisted of covered plastic buckets with the bottom cut out and replaced with a floor of galvanized hardware cloth so that excreta could drain out. Each cage measured approximately 50 cm deep and 40 cm in diameter. We attempted to keep subjects under natural photo-period but the light period was extended during the puffin feeding trials using fluorescent lights during evening feedings. All chicks were kept at ambient temperatures between 16 and 20°C throughout the captive feeding experiments.

During 1996 the sample of kittiwake chicks was evenly divided into two diet groups (N=7 per treatment), each receiving a daily ration of either 100 g of age class 2+ (205-265 mm standard length) juvenile walleye pollock, or 100 g of adult and juvenile (57-148 mm standard length) Pacific sand lance. During 1997 the sample of kittiwake chicks was again divided evenly into two groups (N=6 per treatment). with each nestling receiving a daily ration of either 100 g of age class 2+ (161-264 mm standard length) walleye pollock. or 100 g of age class 1+(129-141 mm standard length) juvenile Pacific herring. All chicks were fed their respective experimental diets beginning at 13 days post-hatch and the experiment was terminated at 31 days post-hatch. The age at the end of the feeding trials was chosen as the earliest possible fledging age. Before beginning the feeding trial at age 13 days, each bird was fed an *ad libidum* diet of equal amounts of the high- and low-lipid forage fishes. Data from the kittiwakes fed 100 g/day pollock were pooled for the two years because no significant between-year differences were found (using a two-sample t-test) in either the energy density of pollock (t=0.216. df=40. P=0.830), or in fledging body mass (t=0.569, df=11, P= 0.581) or fledging wing length (t=1.307, df=11. P= 0.218) of kittiwakes fed pollock.

The sample of puffin chicks collected in 1996 was evenly divided into two diet groups (N=7 per treatment), with each receiving a daily ration of either 80 g of age class 2+ (205-265 mm standard length) walleye pollock (a low-lipid fish) or 80 g of capelin (71-103 mm standard length)(a high-lipid fish). During 1997. the sample of puffin chicks was again divided into two diet groups (N=6 per treatment) receiving a daily ration of either 100 g of age class 1+ (143-170 mm standard length) walleye pollock or 100 g of age class 1+ (129-141 mm standard length) juvenile Pacific herring (a high-lipid fish). All puffin chicks were fed their respective experimental diets beginning at 19 days post-hatch and the experiment was terminated at 40 days post-hatch. The age at the end of the feeding trials was chosen as the earliest possible fledging age. Before beginning the feeding trial at 19 days. each bird was fed an *ad libidum* diet of equal amounts of the high- and low-lipid forage fishes.

All chicks were fed four times per day. Meals were weighed out in pre-weighed aluminum pans using an Ohaus electronic balance (± 0.1 g). Each chick was fed by placing the aluminum pan in its cage. Lab personnel would then check the cages to make sure each bird had consumed its entire meal.

During 1997 all subjects received a vitamin supplement. Birds received one half of a "Seatabs" vitamin supplement in their final food ration of the day (Pacific Research Labs Inc., El Cajon, CA). The dosage, recommended by aviculturists from the Oregon Coast Aquarium, included 50 mg of thiamine. Piscivorous seabirds kept in captivity often develop a thiamine deficiency due to being fed frozen fish. There was no evidence that the vitamin supplement affected the growth of subjects compared to those raised without the supplement in1996.

Variables that were measured daily for both kittiwakes and puffins in both years of the study included: (1) body mass (measured with an Ohaus triple beam balance, ± 0.1 g), (2) wing length (measured flat on a ruler, ± 1 mm), (3) culmen length (measured with calipers, ± 0.1 mm), and (4) tarsus length (measured with calipers, ± 0.1 mm). The only exception was that tarsus length was not measured for kittiwake nestlings in 1996. All measurements were taken daily between 08:00 and 10:00 ADT, prior to the first feeding of the day.

A variety of methods were used to collect fishes used in the captive feeding experiments. All capelin and sand lance were captured in either beach seines or cast nets in Kachemak Bay, Alaska during late June and early July 1996. Age class 1+ pollock were collected via trawl during a National Oceanographic and Atmospheric Administration research cruise in the Bering Sea during June 1997. Age class 2+ pollock were collected via trawl during two Alaska Department of Fish and Game research cruises in Prince William Sound, Alaska in May 1996 and May 1997. Juvenile herring were purchased during May and June 1997 from a commercial baitfish supplier in Anchorage, Alaska.

Samples of the various fishes that were fed to captive kittiwake and puffin chicks were shipped frozen to the laboratory at Oregon State University, where they were subjected to proximate analysis. In the lab, fish specimens were individually weighed and measured, then dried to constant mass in a convection oven at 60° C to determine water content. The dried fish were then thoroughly ground using a mortar and pestle and lipid content was determined by solvent extraction using a soxhlet apparatus and hexane/isopropyl alcohol 7:2 (v: v) as the solvent system (Radin 1981). Lean dry fish samples were then ashed in a muffle furnace at 600°C for 12 hours in order to determine ash-free lean dry mass (ca. 94% protein: Montevecchi et al. 1984) by subtraction. Energy content of chick diets were calculated from the proximate composition (percent water, lipid, ash-free lean dry matter [protein], and ash) of fish along with published energy equivalents of these fractions (39.4 kJ/g lipid: 17.8 kJ/g protein; Schmidt-Nielsen 1997:171).

Means of final body mass for kittiwakes on different diets were compared using a Kruskal-Wallis ANOVA analysis on ranked data and Dunn's method for multiple comparisons. Dunn's method was chosen over other multiple comparison procedures because it accommodates differences in sample size. Standard ANOVA could not be used because the kittiwake mass data did not meet the assumptions of equal variance, both before and after several transformation attempts. Means of final wing length for kittiwakes were compared among diet groups using one-way ANOVA and a Tukey test for pairwise multiple comparisons. Mean final body mass and mean final wing length for puffins on different diets were compared using t-tests. The lipid content of kittiwake and puffin diets could not be compared using ANOVA because the assumption of equal variance was not met (for both raw and transformed data). A Kruskal-Wallis ANOVA was performed on the ranked data and comparisons were made using Dunn's method for multiple comparisons. Data on energy content of specific forage fish were log transformed to accommodate differences in sample variance. After transformation, mean daily energy intake of the kittiwakes were compared using one-way ANOVA and a Tukey Test for pairwise multiple comparisons. Following log transformation mean daily energy intake for puffins were compared using t-tests.

RESULTS

All subjects adjusted quickly to captivity, survived for the duration of the captive feeding trials, and exhibited little variation in growth and development rate within each species/diet group. All kittiwake and puffin chicks readily consumed whole prey from the first feeding; no force-feeding was required.

There was a significant difference among the 3 diet groups in average body mass of kittiwakes at the end of the feeding trials (Kruskal-Wallis analysis on ranks, df = 2, $P < 0.001$; Fig. 1 a). Kittiwake nestlings on the pollock diet were significantly lighter by the end of the feeding trials than kittiwakes on either the sand lance (Dunn's method of multiple comparisons, $P < 0.05$) or herring (Dunn's method of multiple comparisons, $P < 0.05$) diets (Table 1). Kittiwake fledglings that had been raised on the herring diet had a significantly higher average body mass than fledglings raised on the sand lance diet.

Puffin fledglings raised on the herring diet (100 g/day) were significantly heavier at the end of the feeding trials than puffins raised on the pollock diet (100 g/day)($t = 8.096$, df = 10, $P < 0.001$)(Table 1). Puffin fledglings raised on the capelin diet (80 g/day) had a significantly higher average body mass than puffins raised on the pollock diet (80 g/day) ($t = 12.739$, df = 12, $P < 0.001$) (Table 1 b,c).

There was a significant difference among the 3 diet groups in average wing length of kittiwakes at the end of the feeding trials(ANOVA, $F_{2,24} = 54.408$, $P < 0.001$; Fig. 2a). Pre-fledging wing length for kittiwakes fed the pollock diet was significantly less than that of kittiwakes fed either sand lance (Tukey test, $P < 0.05$) or herring (Tukey test, $P < 0.05$). There was no significant difference between the pre-fledging wing length of kittiwakes fed either sand lance or herring diets (Tukey test, $P > 0.05$) (Table 1).

The pre-fledging wing length of puffins fed the herring diet (100 g/day) was not significantly different from that of puffins fed the pollock diet (100 g/day)($t = 0.792$, df =

10, $P = 0.447$)(table 1). Puffins fed the capelin diet (80 g/day) had significantly greater pre-fledging wing length than puffins fed the pollock diet ($t = 4.494$, $df = 12$, $P < 0.001$)(Table 1, Fig. 2 b,c).

Differences in body mass gain between chicks fed high-lipid fishes vs. chicks fed pollock were much more pronounced than differences in structural growth (i.e., wing length)(Figs. 1 & 2).

Lipid content of age class 2+ pollock (2.2% wet mass) was significantly less than the herring (10.9% wet mass)(Dunn's method of multiple comparisons, $P < 0.05$), capelin (8.7%)($P < 0.05$), or sand lance (6.0%)($P < 0.05$) (table 2). Age class 1+ pollock had a significantly lower lipid content (6.4%) than herring (Dunn's method of multiple comparisons, $P < 0.05$) or capelin ($P < 0.05$), yet there was no significant difference in lipid content between age class 1+ pollock and sand lance ($P > 0.05$) (Table 2).

There was a significant difference in the energy density of the 3 diets fed to kittiwake nestlings (ANOVA, $F_{2,97} = 155.0$, $P < 0.001$). The average energy density of diets fed to kittiwakes were highest for herring, lowest for pollock, and intermediate for sand lance (Tukey test, $P < 0.05$). Average energy density of diets fed to puffins were higher for herring than for age class 1+ pollock ($t = 10.249$, $df = 42$, $P < 0.001$) and higher for capelin than for age class 2+ pollock ($t = 10.822$, $df = 33$, $P < 0.001$)(Table 2).

Kittiwakes fed the pollock diet consumed approximately 373 kJ/day (SE = 10.4), whereas kittiwakes fed the sand lance diet consumed approximately 527 kJ/day (SE =

8.2) and kittiwakes fed the herring diet consumed approximately 717 kJ/day (SE =16.4) (Fig. 3). Puffins fed the pollock diet (100 g/day) received approximately 528 kJ/day (SE = 16.9) and puffins fed the herring diet (100 g/day) consumed approximately 717 kJ/day (SE = 16.4)(Fig. 3). Puffins fed the pollock diet (80 g/day) consumed an estimated 296 kJ/day (SE = 8.0) while puffins fed the capelin diet (80 g/day) consumed approximately 492 kJ/day (SE = 17.7)(Fig. 3).

DISCUSSION

Both kittiwake and puffin nestlings raised on diets of high-lipid fish (capelin, herring, or sand lance) grew faster and were heavier at fledging age than nestlings fed the same biomass of low-lipid fish (juvenile walleye pollock). This result was predicted *a priori* because subjects fed high-lipid fish should consume considerably more energy (kJ/day) than subjects fed low-lipid fish. The metabolizable energy content of lipid is more than twice that of protein for uricotelic vertebrates like birds (39.4 kJ/g lipid vs. 17.8 kJ/g protein)(Schmidt-Nielsen 1997:171). The protein content of the forage fishes used in these feeding trials was similar and interspecific differences in lipid content of fishes explained nearly all of the variation in energy density of the diets. Because protein content of diets were similar, differences in lipid content of the diet were responsible for most of the differences in body mass growth between diet groups.

The age class 1+ juvenile walleye pollock that were fed to the puffins had an uncharacteristically high lipid content (6.4%, wet mass), and average energy density (5.3 kJ/g) for juvenile walleye pollock. Their lipid content and energy density were considerably higher than previously analyzed pollock from the northern Gulf of Alaska (Van Pelt et al. 1997, Anthony et al. Unpubl. ms.). There was also a large difference in lipid content and energy density between the two age classes of pollock that were used in the puffin feeding trials. This may explain the growth performance of puffins on the diet of age class 1+ pollock (i.e.. no significant difference in pre-fledging wing length as compared to chicks on the herring diet.). These data suggest that juvenile walleye pollock are not necessarily a low-lipid diet for nestling seabirds. Juvenile walleye pollock that are as high in lipids as the 1+ pollock used in this study are apparently uncommon (Van Pelt et al. 1997, Anthony et al. Unpubl. ms.).

Differences in mass gain among diet groups were much more pronounced than differences in structural growth. In all four comparisons. chicks on the low-lipid diet (pollock) lagged behind in body mass growth by at least a week (i.e.. at their rate of gain it would take a minimum of a week of additional growth for the chicks on the low-lipid diet to reach the final body mass of the chicks on the high-lipid diet). In contrast. wing length growth tended to be similar among diet groups. The chicks on the low-lipid diet lagged only a few days behind those on the high-lipid diet. Puffins fed 100 g of either pollock or herring showed this clearly; the difference in fledging body mass between chicks on the two diets was significant, yet there was no difference in the pre-fledging wing length for chicks on the two diets. Likewise there was a significant difference in fledging body mass between the kittiwakes fed herring and those fed sand lance. yet there was no difference between the two groups in pre-fledging wing length. This suggests that undernourished seabird chicks preferentially allocate assimilated nutrients to structural development over mass gain. This may be especially significant for kittiwakes.

which can raise two or even three young per nesting attempt (puffins raise only a single chick at a time). Sibling competition may exact a heavy toll on young that fail to grow on limited resources.

Work on Atlantic Puffins (*Fratercula arctica*) has shown that their productivity is closely tied to the availability of energy-rich forage fish prey. Atlantic Puffins at colonies that provision their young with capelin experienced high productivity when this forage fish was available. In contrast, during years when capelin were scarce productivity was reduced (Nettleship 1984). Martin (1989) observed a similar pattern in an Atlantic Puffin colony that relied heavily on sand lance. Despite 13 different prey species in the diet, breeding puffins were not able to obtain sufficient alternative food when sand lance stocks declined. The result was a severe breeding failure when sand lance were scarce.

CONCLUSIONS

Low availability of high-lipid forage fishes could have adverse effects on nestling growth and development in piscivorous seabirds. If parental foraging is constrained, or the ability of the parent seabirds to transport food back to the nest is limited, consumption of high-lipid forage fish may be necessary to compensate for constraints on biomass of prey provided to nestlings. Provisioning young with high-lipid prey will generally result in nestlings that gain body mass and develop structurally more rapidly. This allows nestlings to fledge at a younger age and at higher body mass, traits that should enhance fitness.

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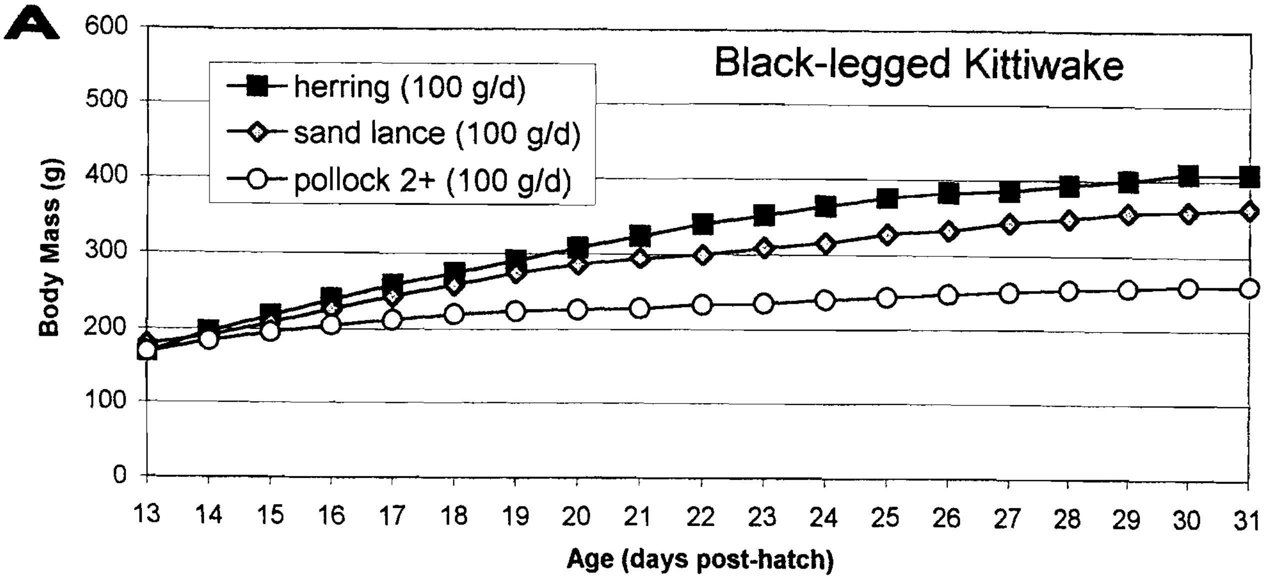
FIGURE CAPTIONS

Figure 1: Body mass growth of Black-legged Kittiwakes (A) and Tufted Puffins (B & C) raised on diets of high-lipid (herring, sand lance, capelin) or low-lipid (juvenile walleye pollock) fishes.

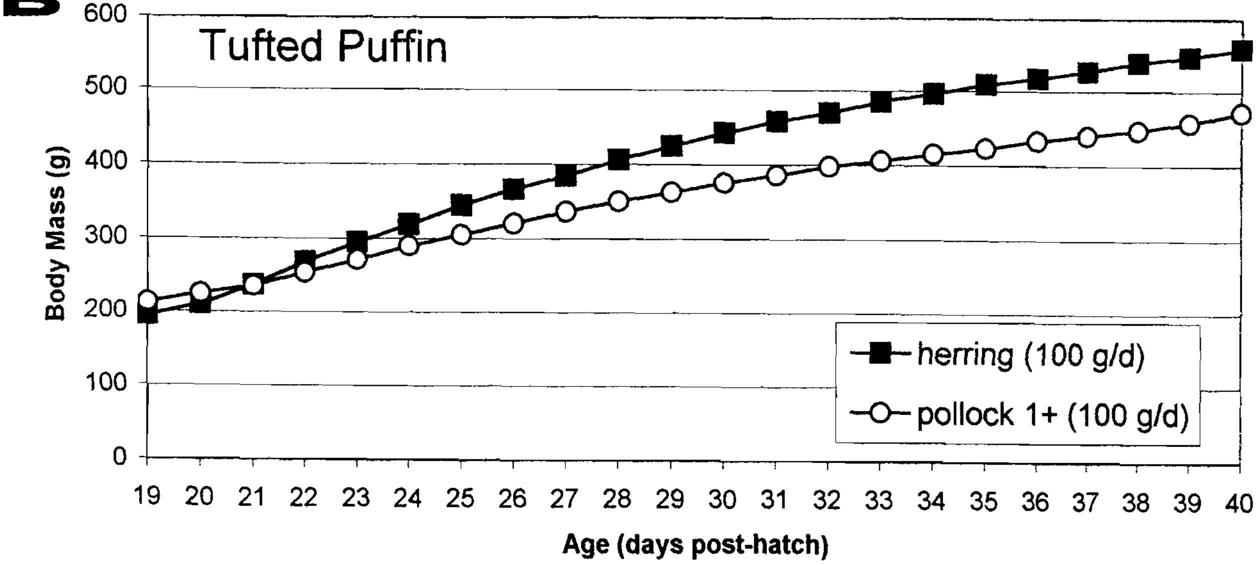
Figure 2: Wing growth of Black-legged Kittiwakes (A) and Tufted Puffins (B & C) raised on diets of high-lipid (herring, sand lance, capelin) or low-lipid (juvenile walleye pollock) fishes.

Figure 3: Estimated daily energy intake of Black-legged Kittiwakes (A) and Tufted Puffins (B) fed rations of different forage fishes. Error bars represent one standard error of the mean.

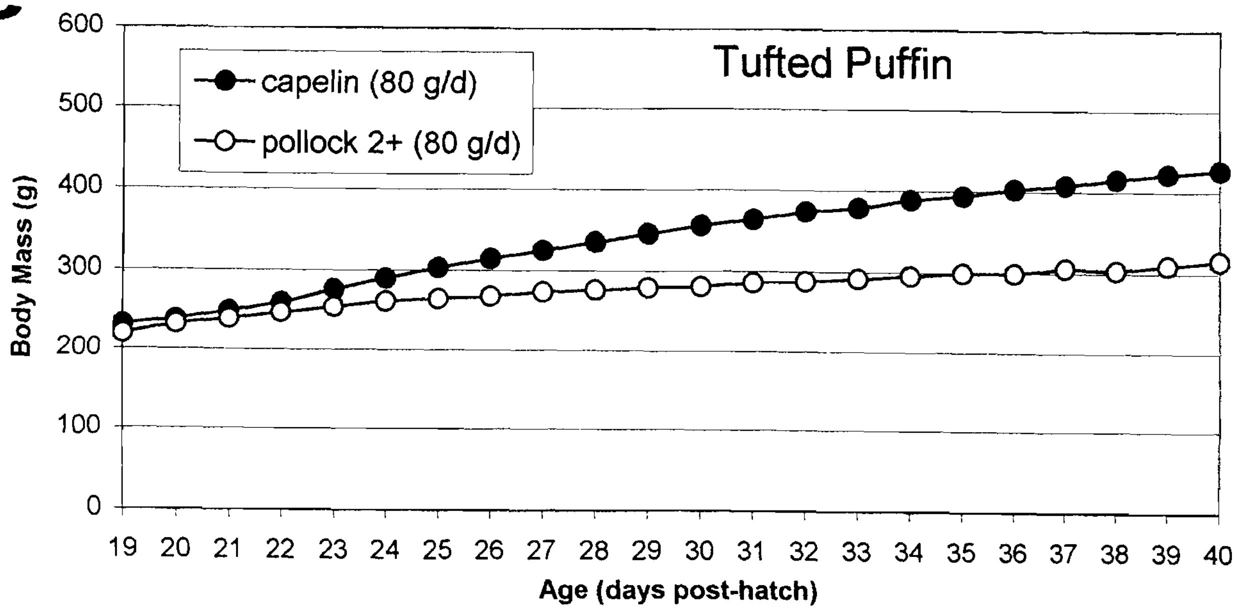
A

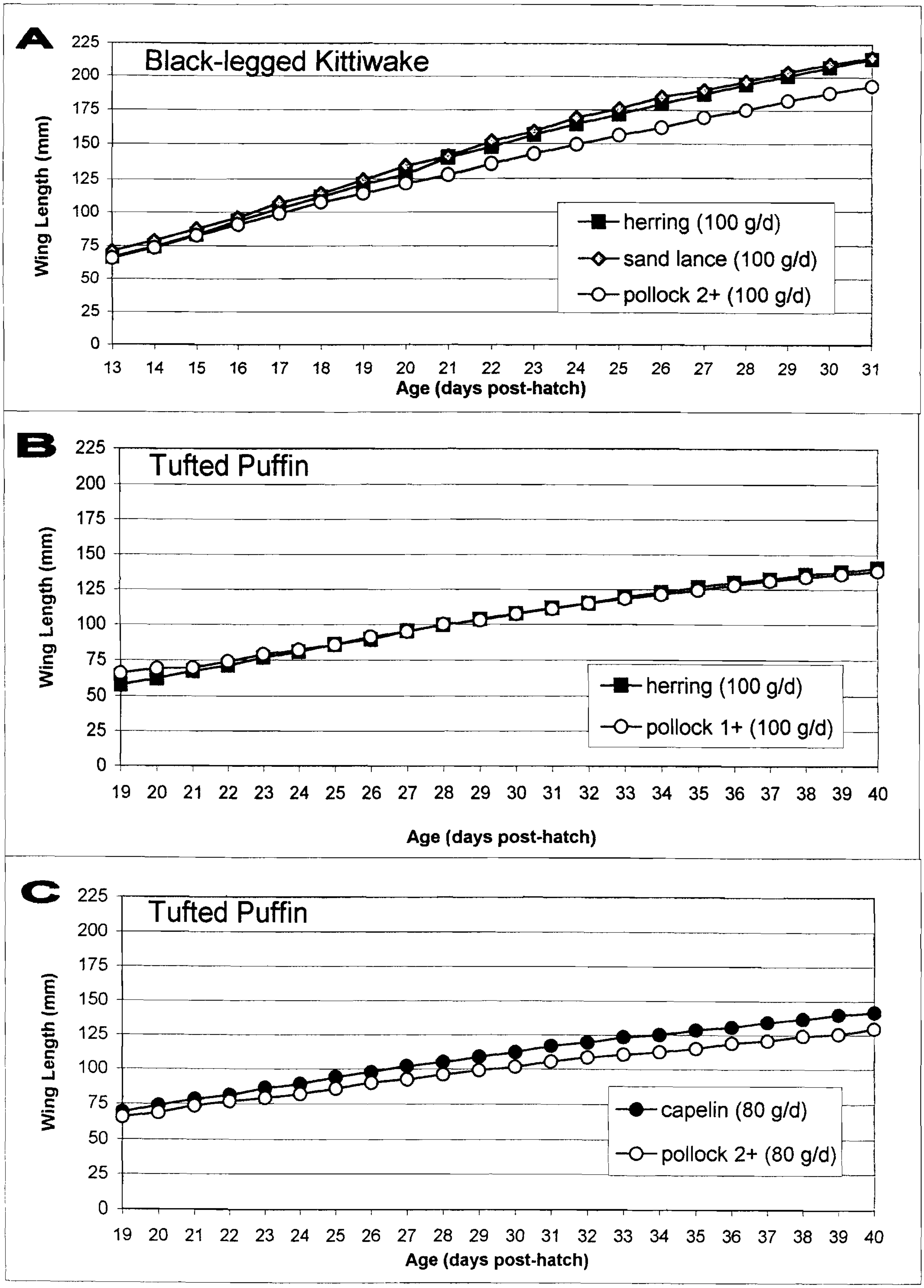

Black-legged Kittiwake
herring (100 g/d)
sand lance (100 g/d)
pollock 2+ (100 g/d)
Body Mass (g)
0
100
200
300
400
500
600
Age (days post-hatch)
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

B


Tufted Puffin
herring (100 g/d)
pollock 1+ (100 g/d)
Body Mass (g)
0
100
200
300
400
500
600
Age (days post-hatch)
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40

C


Tufted Puffin
capelin (80 g/d)
pollock 2+ (80 g/d)
Body Mass (g)
0
100
200
300
400
500
600
Age (days post-hatch)
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40


A
Black-legged Kittiwake
Wing Length (mm)
225
200
175
150
125
100
75
50
25
0
13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
Age (days post-hatch)
herring (100 g/d)
sand lance (100 g/d)
pollock 2+ (100 g/d)
B
Tufted Puffin
Wing Length (mm)
225
200
175
150
125
100
75
50
25
0
19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40
Age (days post-hatch)
herring (100 g/d)
pollock 1+ (100 g/d)
C
Tufted Puffin
Wing Length (mm)
225
200
175
150
125
100
75
50
25
0
19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40
Age (days post-hatch)
capelin (80 g/d)
pollock 2+ (80 g/d)

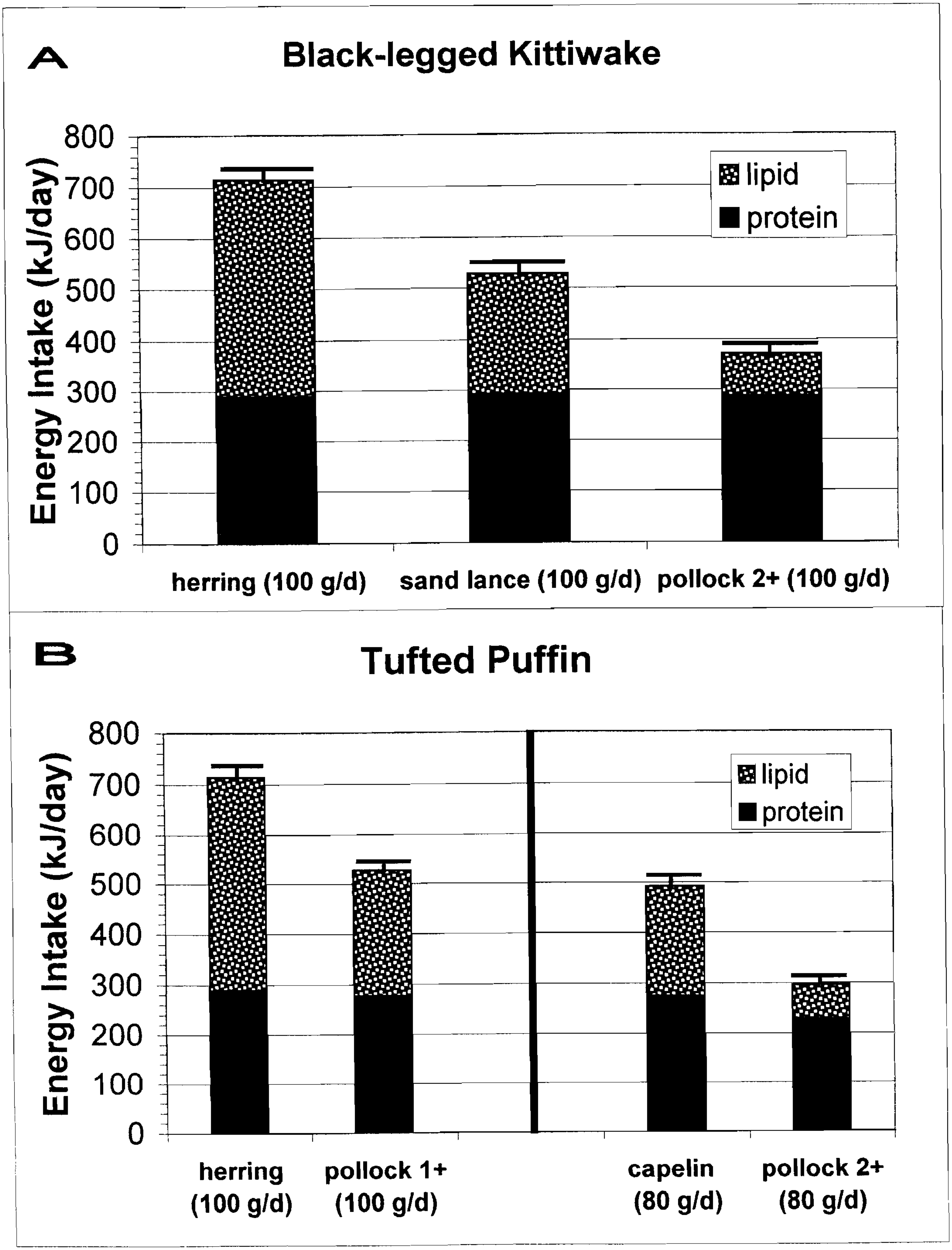
A
Black-legged Kittiwake
Energy Intake (kJ/day)
0
100
200
300
400
500
600
700
800
▨ lipid
■ protein
herring (100 g/d)
sand lance (100 g/d)
pollock 2+ (100 g/d)
B
Tufted Puffin
Energy Intake (kJ/day)
0
100
200
300
400
500
600
700
800
▨ lipid
■ protein
herring (100 g/d)
pollock 1+ (100 g/d)
capelin (80 g/d)
pollock 2+ (80 g/d)

Table 1. Pre-fledging body mass and wing length for black-legged kittiwakes (BLKI, age 31 days) and tufted puffins (TUPU, age 40 days) raised on diets of different forage fishes.

Bird Species	**Diet Treatment**	**Mean Body Mass (g) ± S.E.**	**Mean Wing Length (mm) ± S.E.**
BLKI (N=6)	Herring (100 g/day)	408.2 ± 13.31	214 ± 2.34
BLKI (N=7)	Sand lance (100 g/day)	362.0 ± 4.63	214 ± 1.63
BLKI (N=13)	Pollock 2+ (100 g/day)	260.0 ± 2.11	193 ± 1.53
TUPU (N=7)	Capelin (80 g/day)	426.3 ± 5.44	142 ± 1.39
TUPU (N=7)	Pollock 2+ (80 g/day)	315.0 ± 6.83	130 ± 2.28
TUPU (N=6)	Herring (100 g/day)	559.3 ± 9.11	141 ± 1.48
TUPU (N=6)	Pollock 1+ (100 g/day)	472.3 ± 5.71	138 ± 2.55

Table 2: Results of proximate analysis of fishes used to feed young seabirds during captive feeding trials. Values listed are averages for all fish of a single type, hence values in rows may not sum to 100%.

Fish type	**% Water ± S.E.**	**% Lipid ± S.E.**	**% AFLDM ± S.E.**	**% Ash ± S.E.**
Pollock 2+ (N=27)	78.12 ± 0.38	2.17 ± 0.17	16.18 ± 0.33	3.92 ± 0.31
Pollock 1+ (N=20)	75.68 ± 0.25	6.38 ± 0.21	15.53 ± 0.16	3.27 ± 0.04
Sand lance (N=34)	73.78 ± 0.49	6.02 ± 0.43	16.36 ± 0.47	3.84 ± 0.13
Capelin (N=19)	73.14 ± 0.54	8.71 ± 0.65	15.29 ± 0.29	2.86 ± 0.14
Herring (N=24)	70.06 ± 0.39	10.85 ± 0.44	16.30 ± 0.13	4.36 ± 0.06