

## AN ABSTRACT OF THE THESIS OF

Marc D. Romano for the degree of Master of Science in Wildlife Science. Presented on  
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*Redacted for Privacy*

Abstract approved: \_\_\_\_\_

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**Abstract.** - Recent declines in nesting success of some fish-eating seabirds in Alaska have been attributed to declines in availability of certain schooling forage fishes (e.g., capelin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, and Pacific herring *Clupea harengus pallasii*). These fishes tend to have high lipid content compared with other species and, consequently, are assumed to have high nutritional value as food for young seabirds. I tested hypotheses that type of fish consumed by the nestling, and lipid:protein ratio of the diet constrain growth and development of piscivorous seabird nestlings. I raised seabird nestlings (Black-legged Kittiwakes, *Rissa tridactyla* and Tufted Puffins, *Fratercula cirrhata*) on controlled diets of either capelin, herring, or sand lance (high-lipid fish), or juvenile walleye pollock (*Theragra chalcogramma*; a low-lipid fish). Seabird nestlings fed herring, sand lance, or capelin had higher growth rates (body mass and wing length) than nestlings fed equal biomass rations of pollock. Growth in body mass and wing length of kittiwake nestlings was not affected by lipid:protein ratio of the diet when on a high nutritional plane (i.e., high caloric intake), but growth was

significantly affected by dietary lipid:protein ratio when on a low plane of nutrition.

Growth in body mass and wing length of puffins was not significantly affected by the lipid:protein ratio of the diet. Diets with a higher lipid:protein ratio resulted in greater fat reserves in both seabird species, regardless of nutritional plane. Additionally, diets with a higher lipid:protein ratio resulted in higher apparent metabolizable energy coefficients.

The increased growth rates, fat reserves, and energy utilization efficiencies of chicks fed high-lipid diets suggest that pre- and post-fledging survival are enhanced when parent seabirds have access to high-lipid forage fish.

Effects of Diet on Growth and Development of Nestling Seabirds

by

Marc D. Romano

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Marc D. Romano, Author

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## CONTRIBUTION OF AUTHORS

Daniel D. Roby:

- helped secure funding for research
- edited research proposal and drafts of the thesis chapters
- assisted in developing both field and laboratory research methods

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# Effects of Diet on Growth and Development of Nestling Seabirds

## 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). Seabird species such as Marbled Murrelets (*Brachyramphus marmoratus*), Common Murres (*Uria aalge*), Pigeon Guillemots (*Cepphus columba*), and Black-legged Kittiwakes (*Rissa tridactyla*) have been particularly affected. Changes in diet composition of several seabird species were observed in the northern Gulf of Alaska concurrent with population declines. Some species switched from diets dominated by high-lipid fishes, such as capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), or Pacific herring (*Clupea harengus pallasii*), to diets dominated by juvenile walleye pollock (*Theragra chalcogramma*) and other low-lipid fishes (Piatt and Anderson 1996). Because of lower lipid content and lower energy density (kJ/g live mass), juvenile pollock are generally considered lower quality prey than other fish commonly found in diets of nestling seabirds (Baird 1991, Van Pelt et al. 1997, Anthony et al. in press). If reproductive success of seabirds is related directly to the nutritional quality of available forage fish, then adult seabirds that rely on low-quality prey to provision their young may experience lower productivity (Martin 1989, Nettleship 1990).

I fed captive Tufted Puffin (*Fratercula cirrhata*) and Black-legged Kittiwake nestlings controlled rations of different forage fish species to test the hypothesis that

differences in prey type and lipid:protein ratio of the diet result in differences in growth and development of seabird nestlings. The use of captive seabird nestlings provided a unique opportunity to test these predictions because it allowed elimination of many confounding variables that would occur if nestlings were studied in the wild, such as predation, variability in provisioning rates, and extremes in ambient temperature.

This thesis was organized in two separate chapters, with each chapter intended as a manuscript for publication in a peer-reviewed journal. Chapter one focused on the effect of prey type on growth and development of puffin and kittiwake nestlings. Puffin and kittiwake nestlings were divided into several diet treatment groups and each group received equal biomass rations of one of four different fish species. Nestling growth was compared to determine whether a ration of high-lipid fish resulted in greater growth rates than an equal biomass ration of a low-lipid fish. Chapter two focused on the effect of lipid:protein ratio of the diet on growth and development of seabird nestlings. Again, puffin and kittiwake nestlings were divided into diet treatment groups, but this time the groups received equal caloric rations of either a high-lipid or a low-lipid forage fish. The body condition of seabird nestlings used in this part of the study was determined using proximate composition analysis. Apparent metabolizable energy coefficients were measured for these same nestlings to determine how efficiently they utilized energy from ingested fish.

## **Chapter 1**

### **Effects of Prey Type on Growth of Piscivorous Seabirds in Captivity**

Marc D. Romano, John F. Piatt, and Daniel D. Roby

This manuscript has not yet been submitted.

## Chapter 1: Effects of Prey Type on Growth of Piscivorous Seabirds in Captivity

### ABSTRACT

Recent declines in nesting success of some fish-eating seabirds in Alaska have been attributed to declines in availability of certain schooling forage fishes (e.g., capelin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea harengus pallasii*). These fishes tend to have high lipid content compared with other forage fishes and, consequently, are assumed to have higher nutritional value as food for young seabirds. I tested the hypothesis that type of fish consumed constrains growth and development of piscivorous seabird nestlings. I 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 chalcogramma*), a low-lipid fish. Seabird nestlings fed herring, sand lance, or capelin had higher growth rates (body mass and wing length) than nestlings fed pollock. Diet-related differences in body mass growth were more pronounced than differences in wing growth, suggesting that undernourished nestlings allocate assimilated nutrients more toward structural development than to deposition of body mass. Lipid content of forage fish fed to nestlings had a marked effect on growth rates and, potentially, on pre- and post-fledging survival. These results support the hypothesis that energy is the limiting nutrient for young piscivorous seabirds, rather than protein.

## 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). Marbled Murrelets (*Brachyramphus marmoratus*), Common Murres (*Uria aalge*), and Pigeon Guillemots (*Cepphus columba*) all underwent population declines in this region during the last 2 decades. Recent reproductive failure among Black-legged Kittiwake colonies in Prince William Sound, Alaska was attributed to availability of forage fish, especially Pacific herring (*Clupea harengus pallasii*; Irons 1996). Total reproductive failure has been recorded repeatedly at several other colonies (e.g., Chisik I., Middleton I.). A paucity of forage fish during the breeding season was hypothesized as the leading cause of low productivity (Hatch et al. 1993).

A major change in diet composition of several seabird species was observed in the northern Gulf of Alaska concurrent with population declines. Some species switched from diets dominated by capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), or Pacific herring, to diets dominated by juvenile walleye pollock (*Theragra chalcogramma*) and other gadids (Piatt and Anderson 1996). Because of lower lipid content and lower energy density (kJ/g live mass), juvenile pollock are generally considered lower quality prey than other fish commonly found in diets of nestling seabirds (Baird 1991, Van Pelt et al. 1997, Anthony et al. in press). During the seabird nesting season, lipid content of capelin, sand lance, and herring are generally 2 - 4 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. in press).

If reproductive success of seabirds is related directly to the nutritional quality of available forage fish, then adult seabirds that rely on low-quality prey to provision their young may experience lower productivity (Martin 1989, Nettleship 1990). Reproductive success in seabirds is dependent, in part, on the parent's ability to capture and transport food energy from the foraging area to nestlings (Ricklefs 1983, Roby 1991). In order to provide their young with an equivalent amount of food energy in the form of low-lipid fish as they can provide in high-lipid fish, parent seabirds may have to feed their young twice the biomass of food.

Unless low-lipid fish are readily available close to the colony, time and energy constraints may preclude such a foraging strategy. Also, increased foraging effort by parent seabirds may expose them to greater risk of predation or other stress-related mortality. Slower growth and lower fledging mass would be expected in nestlings fed primarily low-lipid fishes. Fewer nestlings surviving to fledge and lower post-fledging survival would also be predicted (Perrins et al. 1973, Jarvis 1974, Coulson and Porter 1985, Magrath 1991; however, see Hedgren 1981, Harris and Rothery 1985).

I fed captive nestlings controlled rations of different forage fish species to test the hypothesis that differences in prey type result in differences in growth and development of seabird nestlings. I predicted that seabird nestlings fed diets of high-lipid fish would grow and develop more rapidly than nestlings fed the same biomass ration of low-lipid fish. I also predicted that these diet-related differences would occur regardless of seabird taxon. The use of captive seabird nestlings provides a unique opportunity to test these predictions because it allows elimination of many confounding variables that would

occur studying wild birds, such as predation, variability in provisioning rates, and extremes in ambient temperature.

## METHODS AND MATERIALS

I used a combination of captive feeding trials and laboratory analyses in this study. Captive feeding trials were conducted at the Kasitsna Bay Laboratory, Institute of Marine Science, University of Alaska Fairbanks, during the 1996 and 1997 breeding seasons. The Laboratory is located on Kachemak Bay near the town of Homer 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, whereas the latter is an alcid that forages by pursuit-diving to considerable depth. Kittiwakes transport meals to chicks in the esophagus and stomach, while puffins transport one or more whole prey in their bill. Both are common breeding species in the northern Gulf of Alaska.

Tufted Puffin nestlings used in the study were collected from East Amatuli Island in the Barren Islands, Alaska, while Black-legged Kittiwake nestlings were collected from colonies in Kachemak Bay, Alaska under permits held by the Alaska Biological Science Center of the U.S. Geological Survey. Age of kittiwake chicks when removed from their nests was estimated from a combination of their head/bill length and wing length, using regression equations for head/bill length and wing length vs. age derived from known-age chicks in Prince William Sound, Alaska (D.B. Irons, unpubl. data):



$$\text{age} = (39.632 - [\text{head/bill length}]) / -1.81$$

$$\text{age} = (4.943 - [\text{wing length}]) / -4.823$$

where age is in days and head/bill and wing length are in mm.

When age estimates from the regression of head/bill length vs. age and the regression of wing length vs. age did not agree for an individual chick, I used the average of the two predicted ages.

I estimated age of puffin chicks from a combination of culmen length and body mass by use of regression equations for culmen length and body mass vs. age. These equations were derived from known-age chicks measured on Aiktak Island, Alaska (Piatt and Romano, unpubl. data):

$$\text{age} = -36.772 + (1.802 * [\text{culmen length}])$$

$$\text{age} = 2.445 + (0.614 * [\text{body mass}])$$

where age is in days, culmen length is in mm, and body mass is in grams.

When age estimates from the regression of culmen length vs. age and the regression of body mass vs. age did not agree for an individual chick, I used the average of the two predicted ages.

During 1996, 14 kittiwake chicks and 14 puffin chicks were removed from their nests at estimated ages of 6-10 days post-hatch and 5-18 days post-hatch, respectively. In 1997, 12 kittiwake chicks and 12 puffin chicks were removed at estimated ages of 3-9 days post-hatch and 4-17 days post-hatch, respectively. The sample sizes were based on the number of chicks that could be raised at one time in the facility. Unfortunately space was limited within the lab but all attempts were made to raise as many birds as possible.

Chicks were kept under a heat lamp for several days after removal from nests to insure proper thermoregulation; afterward they were held indoors at 16-20°C in individual cages throughout feeding trials. Cages consisted of covered plastic buckets (50 cm deep, 40 cm diameter) with bottoms removed and replaced with a floor of galvanized hardware cloth so that excreta could drain. I attempted to keep subjects under natural photo-period, but the light period had to be extended during puffin feeding trials (approx. 1-2 hours) with fluorescent lights.

During 1996 the sample of kittiwake chicks was divided evenly into two diet groups (N = 7 per treatment), each receiving a daily ration of either 100 g of age class 2+ walleye pollock (205-265 mm standard length), or 100 g of juvenile and adult Pacific sand lance (56-148 mm standard length). During 1997 the sample of kittiwake chicks again was divided evenly into two diet groups (N = 6 per treatment), with each nestling receiving a daily ration of either 100 g of age class 2+ walleye pollock (161-264 mm standard length), or 100 g of age class 1+ juvenile Pacific herring (129-141 mm standard length). Some of the smaller pollock may have been age class 1+, but very few were less than 200 mm standard length. All chicks were fed their respective experimental diets beginning at 13 days post-hatch until the experiment was terminated at 31 days post-hatch, the earliest possible fledging age. Before beginning feeding trials at age 13 days, each bird was fed an *ad libitum* diet of approximately equal amounts of the high- and low-lipid fishes.

The sample of puffin chicks collected in 1996 was divided evenly into two diet groups (N = 7 per treatment), with each receiving a daily ration of either 80 g of age class 2+ walleye pollock (205-265 mm standard length), or 80 g of juvenile and adult capelin

(68-103 mm standard length). During 1997, the sample of puffin chicks was divided into two groups ( $N = 6$  per treatment), each receiving a daily ration of either 100 g of age class 1+ walleye pollock (143-170 mm standard length) or 100 g of age class 1+ juvenile Pacific herring (129-141 mm standard length). All puffin chicks were fed their respective experimental diet beginning at 19 days post-hatch until the experiment was terminated at 40 days post-hatch, the earliest possible fledging age. Before beginning the feeding trial at 19 days, each bird was fed an *ad libitum* diet of approximately equal amounts of the high- and low-lipid fishes.

Each diet ration was fed to the birds as four, equal-sized meals daily (25 g four times/day for all kittiwakes and for puffins in 1997, 20 g four times/day for puffins in 1996). Feeding commenced at roughly 10:00 ADT and the remaining three meals were spaced evenly throughout the remainder of the day (typically at 14:00, 18:00, and 22:00 ADT,  $\pm$  one hour). The final meal of the day was always completed by 23:00 ADT. All meals were weighed on an Ohaus electronic balance ( $\pm 0.1$  g). The feedings were spaced evenly throughout the day in an attempt to reduce any possible effect that time of feeding could have on growth and development. The mass of daily ration was determined with advice from Black-legged kittiwake biologists (David Irons and Robert Suryan), and aviculturists from the Oregon Coast Aquarium.

During 1997 subjects were fed one half of a Seatabs vitamin supplement (Pacific Research Labs Inc.) in their daily ration. The dosage, recommended by aviculturists from the Oregon Coast Aquarium, included 50 mg of thiamine. Piscivorous animals in captivity that are fed frozen fish often develop a thiamine deficiency (White 1970, Geraci

1972). There was no evidence that the vitamin supplement in 1997 affected growth of subjects compared with 1996, when no vitamin supplement was fed.

Variables measured for both kittiwake and puffin chicks in both years of the study included: (1) body mass (measured to  $\pm 0.1$  g), (2) flattened wing length (measured to  $\pm 1$  mm), and (3) culmen length (measured to  $\pm 0.1$  mm using calipers). All variables were measured daily between 08:00 and 10:00 ADT, before the first feeding of the day.

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 by trawl during a National Oceanographic and Atmospheric Administration research cruise in the Bering Sea in June 1997, and age class 2+ pollock were collected by 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 bait-fish supplier in Anchorage, Alaska. The supplier reported that the herring were caught off the coast of British Columbia in early spring, 1997. All fish were stored frozen ( $-20^{\circ}\text{C}$ ) until they were used to feed the birds.

Samples of fish fed to chicks were shipped frozen to the laboratory at Oregon State University, where they were subjected to proximate composition analysis. Specimens were weighed and measured individually, then dried to constant mass in a convection oven at  $60^{\circ}\text{C}$  to determine water content. Dried fish were ground using a mortar and pestle, and lipid content was determined by solvent extraction in a soxhlet apparatus with hexane/isopropyl alcohol 7:2 (v:v) as the solvent system (Radin 1981). Lean dry fish samples were ashed in a muffle furnace at  $600^{\circ}\text{C}$  for 12 hours to calculate ash-free lean dry mass (ca. 94% protein; Montevecchi et al. 1984) by subtraction. Energy content of

diets was calculated from the proximate composition (percent water, lipid, ash-free lean dry matter [AFLDM], and ash) of fish along with published energy equivalents of these fractions (39.3 kJ/g lipid; 17.8 kJ/g protein for uricotelic vertebrates; Schmidt-Nielsen 1997:171).

The mean growth increment in body mass and wing length of kittiwake chicks was compared among diet treatments using one-way ANOVA and the Bonferroni test for multiple comparisons. Growth increment was defined as the final body mass, or wing length, of each chick minus the body mass, or wing length, for that chick at the start of the feeding trials. The mean final body mass and mean final wing length of kittiwake chicks fed different diets were also compared using one-way ANOVA and the Bonferroni test for multiple comparisons. Significance for the kittiwake comparisons was set at 0.05. Means for growth increment of body mass and wing length, final body mass, and final wing length of puffin chicks were compared between diet groups using t-tests. A Bonferroni Adjustment to the level of significance was required because of the large number of t-tests performed. Significance for the puffin comparisons was set at 0.0125. Data for energy content of kittiwake diets were compared by a Kruskal-Wallis one-way ANOVA on ranks. This test was used because the data failed a Modified-Levene Equal-variance test ( $P < 0.001$ ). Following log transformation, energy content of puffin diets were compared using t-tests. The lipid content of fish fed to the birds was compared using a Kruskal-Wallis one-way ANOVA on ranked data. Again, this test was used because the data failed a Modified-Levene Equal-variance test ( $P < 0.001$ ).

## RESULTS

There was a difference in lipid content (% wet mass) among fishes used in these feeding experiments (Kruskal-Wallis one-way ANOVA on ranks, d.f. = 4,  $P < 0.001$ ; Table 1.1). Lipid content of age class 2+ pollock was significantly less than that of age class 1+ herring (Bonferroni Multiple Comparison,  $P < 0.001$ ), capelin (Bonferroni Multiple Comparison,  $P < 0.001$ ) or sand lance (Bonferroni Multiple Comparison,  $P < 0.001$ ). Age class 1+ pollock had a lower lipid content than age class 1+ herring (Bonferroni Multiple Comparison,  $P < 0.001$ ; Table 1.1), but a higher lipid content than age class 2+ pollock (Bonferroni Multiple Comparison,  $P < 0.001$ ; Table 1.1).

Diets fed to kittiwake nestlings differed significantly in energy density (kJ/g wet mass; Kruskal-Wallis One-ANOVA on ranks, d.f. = 2,  $P < 0.001$ ; Fig 1.1A). The energy density of diets fed to kittiwakes was higher for the herring diet than for the pollock diet, (Bonferroni Multiple Comparison,  $P < 0.001$ ) and higher for the sand lance diet than for the pollock diet (Bonferroni Multiple Comparison,  $P < 0.001$ ). Average energy density of diets fed to puffins was higher for the herring diet than for the age class 1+ pollock diet ( $t = 10.429$ , d.f. = 42,  $P < 0.001$ ) and higher for the capelin diet than for the age class 2+ pollock diet (two-sample t-test,  $t = 10.822$ , d.f. = 33,  $P < 0.001$ ; Fig. 1.1B). Growth data from kittiwakes fed 100 g/day of pollock in the two years of the study were pooled because no significant between-year differences were found in either the energy density of age class 2+ pollock (two –sample t-test,  $t = 0.216$ , d.f. = 40,  $P = 0.830$ ), or in final body mass (two –sample t-test,  $t = 0.569$ , d.f. = 11,  $P = 0.581$ ) or final wing length (two –sample t-test,  $t = 1.307$ , d.f. = 11,  $P = 0.218$ ) of the chicks.

Table 1.1. Results of proximate composition 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 exactly 100%.

<b>Fish type</b>	<b>N</b>	<b>% Water <math>\pm</math> SE</b>	<b>% Lipid <math>\pm</math> SE</b>	<b>% AFLDM* <math>\pm</math> SE</b>	<b>% Ash <math>\pm</math> SE</b>
Pollock 2+	27	78.1 $\pm$ 0.38	2.2 $\pm$ 0.17	16.2 $\pm$ 0.33	3.9 $\pm$ 0.31
Pollock 1+	20	75.7 $\pm$ 0.25	6.4 $\pm$ 0.21	15.5 $\pm$ 0.16	3.3 $\pm$ 0.04
Sand lance	34	73.8 $\pm$ 0.49	6.0 $\pm$ 0.43	16.4 $\pm$ 0.47	3.8 $\pm$ 0.13
Capelin	19	73.1 $\pm$ 0.54	8.7 $\pm$ 0.65	15.3 $\pm$ 0.29	2.9 $\pm$ 0.14
Herring	24	70.1 $\pm$ 0.39	10.9 $\pm$ 0.44	16.3 $\pm$ 0.13	4.4 $\pm$ 0.06

\* AFLDM = ash-free lean dry matter

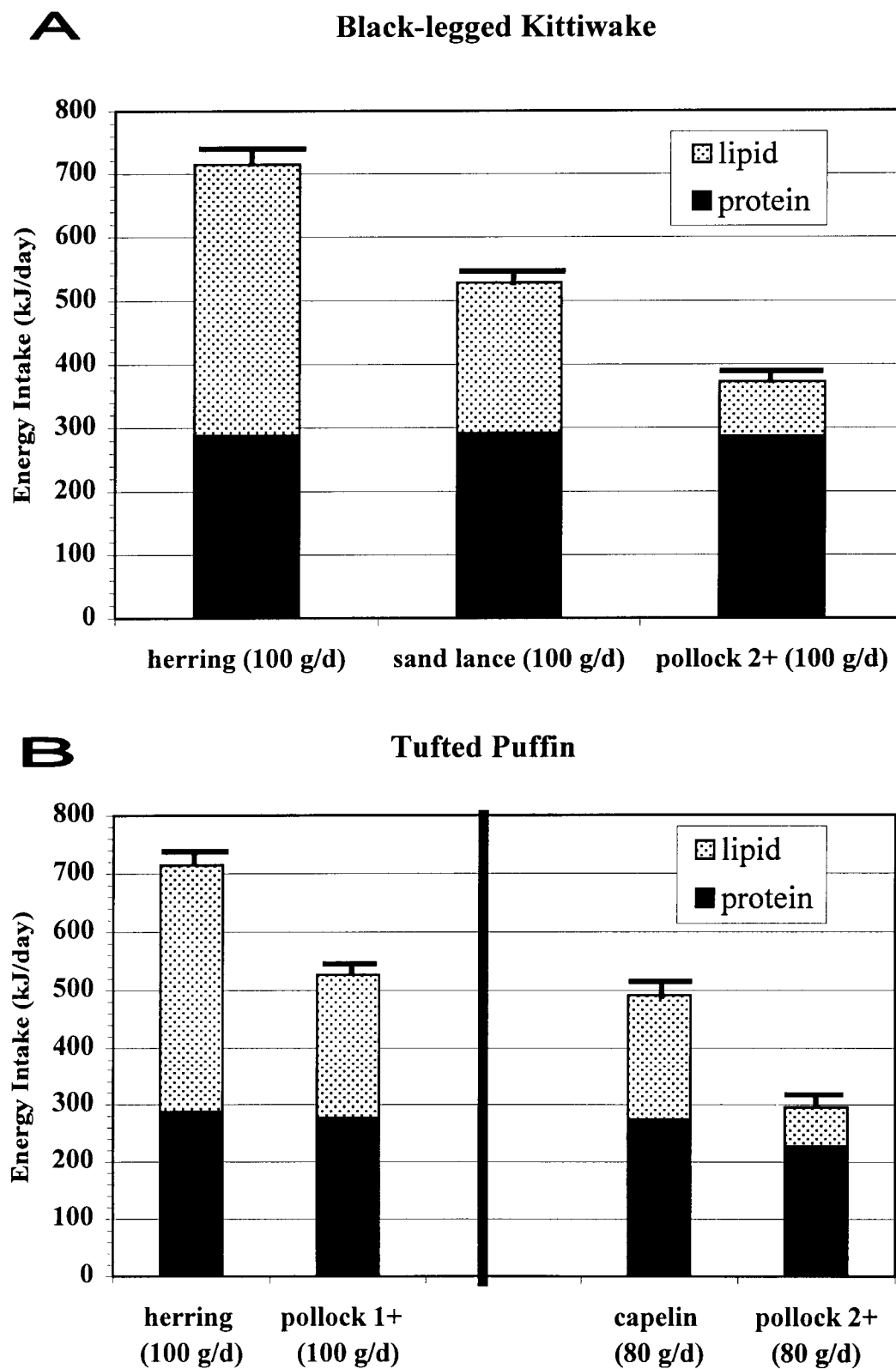


Figure 1.1. Average (+ 1 SE) daily energy intake of captive Black-legged Kittiwake (A) and Tufted Puffin (B) chicks fed rations of different forage fishes.



There was a significant difference in the mean body mass of kittiwakes at the end of the feeding trials among diet treatment groups (ANOVA,  $F_{2,24} = 89.18$ ,  $P < 0.001$ ; Fig. 1.2A). Kittiwakes receiving 100 g/day of pollock had a lower mean final body mass than those receiving 100 g/day of herring (Bonferroni Multiple Comparison,  $P < 0.001$ ) or 100 g/day of sand lance (Bonferroni Multiple Comparison,  $P < 0.001$ ; Table 1.2). Kittiwakes receiving 100 g/day of herring had a greater mean final body mass than those receiving 100 g/day of sand lance (Bonferroni Multiple Comparison,  $P = 0.002$ ; Table 1.2).

Growth increment of body mass in kittiwake nestlings was not equal among diet treatments (ANOVA,  $F_{2,24} = 118.44$ ,  $P < 0.001$ ; Fig. 1.2A). Kittiwake nestlings on the pollock diet averaged less than half the body mass growth than nestlings on either the sand lance (Bonferroni Multiple Comparison,  $P < 0.001$ ) or herring (Bonferroni Multiple Comparison,  $P < 0.001$ ) diets (Table 1.2). Kittiwakes raised on the herring diet had greater body mass growth than those raised on the sand lance diet (Bonferroni Multiple Comparison,  $P < 0.001$ ; Table 1.2).

There was a significant difference in the mean wing length of kittiwakes among diet treatment groups at the termination of the feeding trials (ANOVA,  $F_{2,24} = 28.79$ ,  $P < 0.001$ ; Fig. 1.3A). Kittiwakes receiving pollock had a smaller mean final wing length than kittiwakes receiving either 100 g/day of herring (Bonferroni Multiple Comparison,  $P < 0.001$ ) or 100 g/day of sand lance (Bonferroni Multiple Comparison,  $P < 0.001$ ; Table 1.2). There was, however, no significant difference in mean final wing length between kittiwakes fed 100 g/day of herring and those fed 100 g/day of sand lance (Bonferroni Multiple Comparison,  $P = 0.95$ ; Table 1.2).

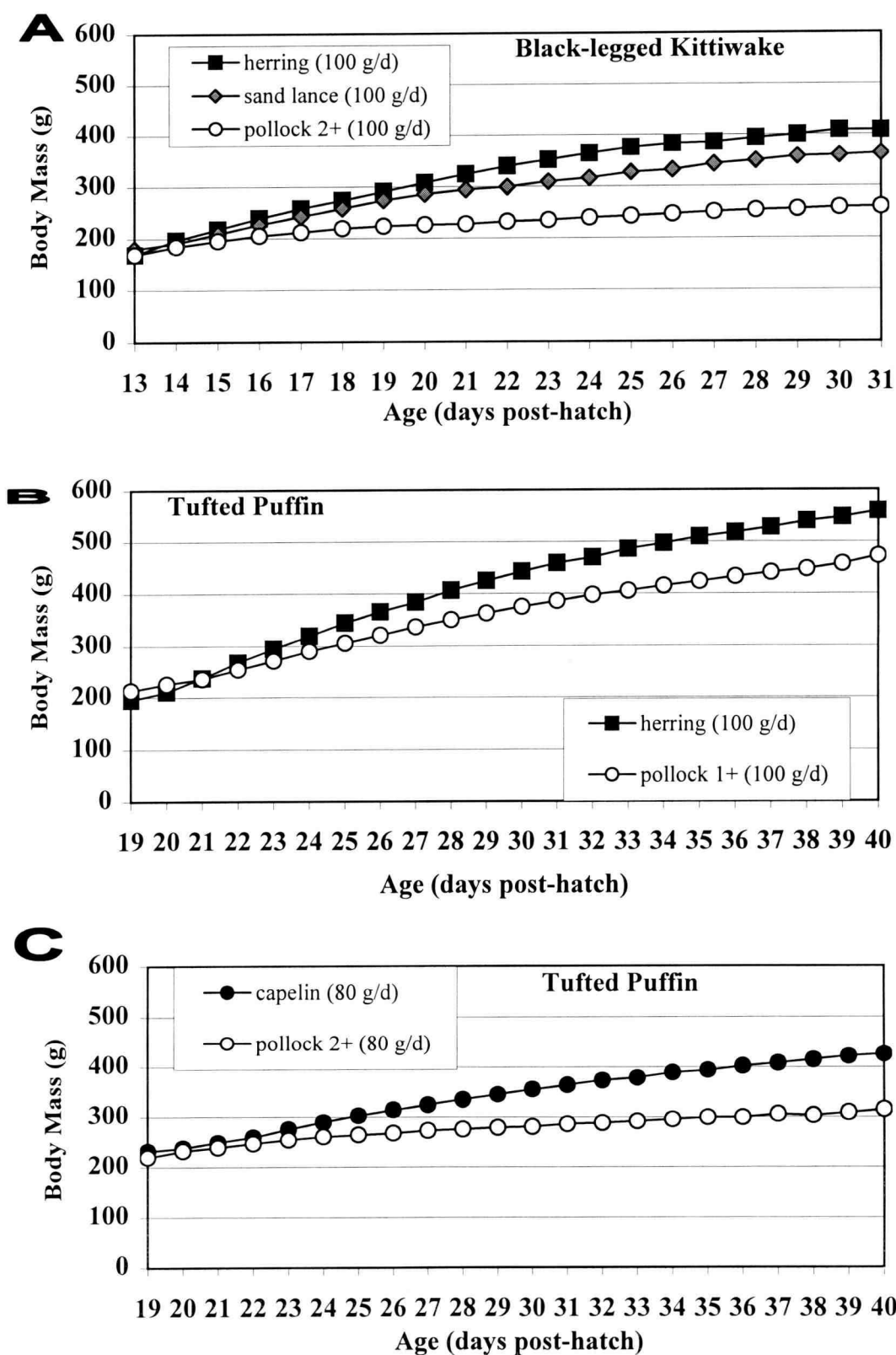


Figure 1.2. Average growth in body mass of Black-legged Kittiwakes (A) and Tufted Puffins (B & C) raised on diets of high-lipid fishes (herring, sand lance, and capelin) and low-lipid fish (juvenile walleye pollock).

Table 1.2. Growth increment in body mass and wing length (during feeding trials) and mean final body mass and wing length of Black-legged Kittiwakes and Tufted Puffins raised on diets of different forage fishes.

Diet Treatment	N	Body Mass Growth (g) $\pm$ SE	Wing Growth (mm) $\pm$ SE	Final Body Mass (g) $\pm$ SE	Final Wing Length (mm) $\pm$ SE
<b><u>Black-legged Kittiwakes</u></b>					
Herring (100 g/day)	6	239.7 $\pm$ 14.25	148 $\pm$ 2.23	408.2 $\pm$ 13.31	214 $\pm$ 2.34
		**	ns	**	ns
Sand lance (100 g/day)	7	183.8 $\pm$ 3.74	145 $\pm$ 2.81	362.0 $\pm$ 4.63	214 $\pm$ 1.63
		**	**	**	**
Pollock 2+ (100 g/day)	13	91.5 $\pm$ 4.70	128 $\pm$ 1.65	260.0 $\pm$ 2.11	193 $\pm$ 1.53
		**	**	**	**
<b><u>Tufted Puffins</u></b>					
Herring (100 g/day)	6	368.0 $\pm$ 15.63	85 $\pm$ 1.79	559.3 $\pm$ 9.11	141 $\pm$ 1.48
		**	**	**	ns
Pollock 1+ (100 g/day)	6	260.2 $\pm$ 7.38	76 $\pm$ 1.70	472.3 $\pm$ 5.71	138 $\pm$ 2.55
		**	**	**	**
Capelin (80 g/day)	7	194.1 $\pm$ 8.42	72 $\pm$ 1.54	426.3 $\pm$ 5.44	142 $\pm$ 1.39
		**	**	**	**
Pollock 2+ (80 g/day)	7	95.3 $\pm$ 9.15	64 $\pm$ 1.60	315.0 $\pm$ 6.83	130 $\pm$ 2.28
		**	**	**	**

\* =  $P \leq 0.05$ , \*\* =  $P < 0.01$ , ns =  $P > 0.05$  (Bonferroni Test of Multiple Comparisons for kittiwakes)

\* =  $P \leq 0.0125$ , \*\* =  $P < 0.001$ , ns =  $P > 0.0125$  (Student's t-test with a Bonferroni Adjustment for puffins)

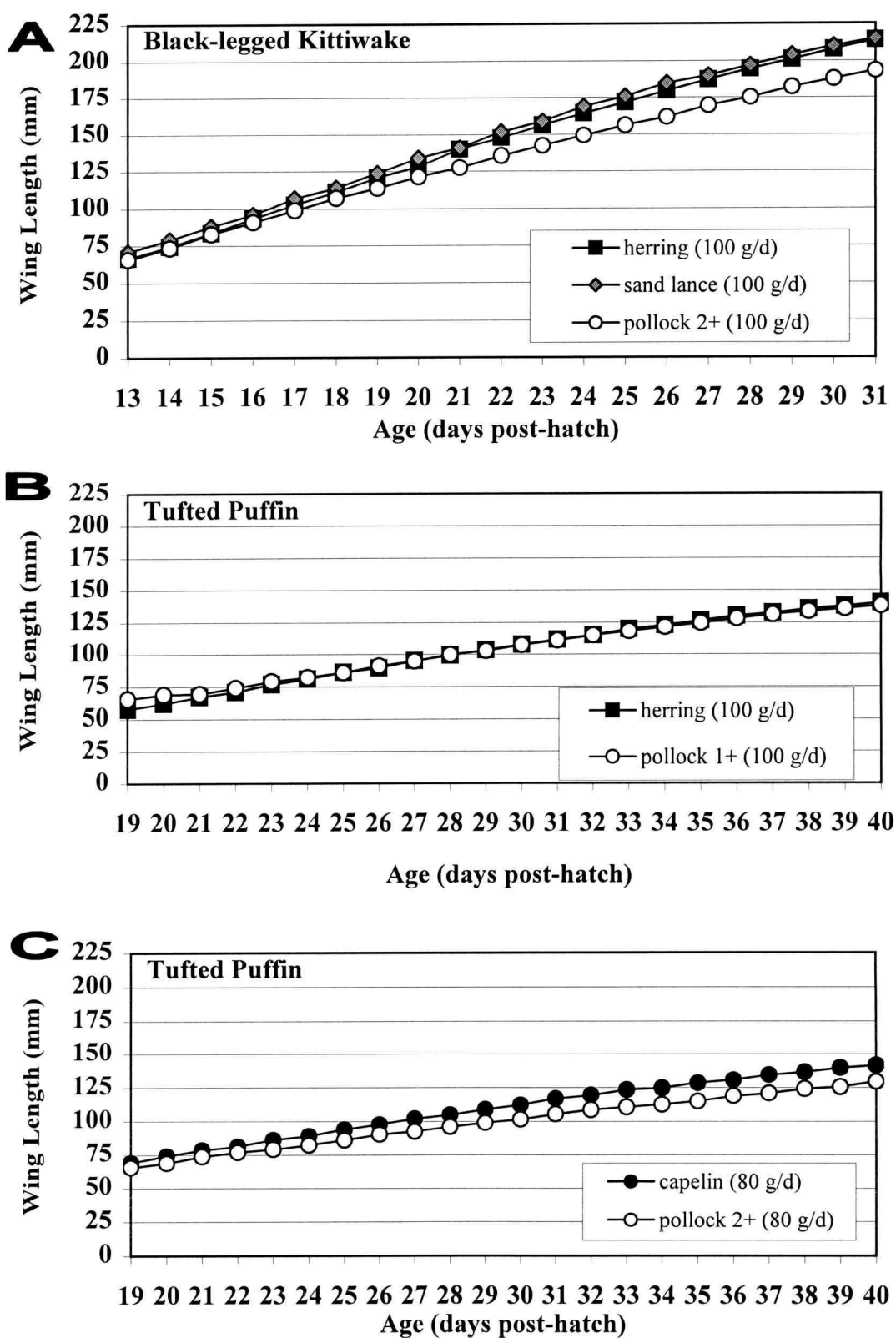


Figure 1.3. Average growth in wing length of Black-legged Kittiwakes (A) and Tufted Puffins (B & C) raised on diets of high-lipid fishes (herring, sand lance, and capelin) and low-lipid fish (juvenile walleye pollock).

Wing growth increment was also significantly different among kittiwake diet groups (ANOVA,  $F_{2,24} = 26.85$ ,  $P < 0.001$ ; Fig. 1.3a). Wing growth increment for kittiwakes fed the pollock diet was more than 10% less than that of kittiwakes fed either sand lance (Bonferroni Multiple Comparison,  $P < 0.001$ ) or herring (Bonferroni Multiple Comparison,  $P < 0.001$ ). There was no significant difference in wing growth increment between kittiwakes fed the sand lance or herring diets (Bonferroni Multiple Comparison,  $P = 0.85$ ; Table 1.2).

Mean final body mass at the termination of the experiment was greater for puffins reared on 100 g/day herring than for those raised on 100 g/day age class 1+ pollock (two –sample t-test,  $t = 8.096$ , d.f. = 10,  $P < 0.001$ ; Table 1.2). Puffins raised on 80 g/day of capelin also had a greater mean body mass at the termination of the experiment than puffins raised on 80 g/day age class 2+ pollock (two –sample t-test,  $t = 12.739$ , d.f. = 12,  $P < 0.001$ ; Table 1.2).

Tufted Puffins raised on a diet of herring had greater body mass growth than puffins raised on age class 1+ pollock (two –sample t-test,  $t = 6.238$ , d.f. = 10,  $P < 0.001$ ; Table 1.2, Fig. 1.2B). Puffins raised on the capelin diet had twice the body mass growth increment of puffins raised on age class 2+ pollock (two –sample t-test,  $t = 7.952$ , d.f. = 12,  $P < 0.001$ ; Table 1.2, Fig. 1.2C).

There was no significant difference in the mean final wing length of puffins raised on 100 g/day of herring and that of those raised on 100 g/day of age class 1+ pollock (two –sample t-test,  $t = 0.792$ , d.f. = 10,  $P = 0.447$ ; Table 1.2). Puffins fed 80 g/day of capelin, however, had greater final wing length than puffins fed 80 g/day of age class 2+ pollock (two –sample t-test,  $t = 4.494$ , d.f. = 12,  $P < 0.001$ ; Table 1.2).

Puffins fed herring had greater increment of wing growth than puffins fed age class 1+ pollock (two –sample t-test,  $t = 3.578$ , d.f. = 10,  $P = 0.005$ ; Table 1.2, Fig. 1.3B).

Puffins fed the capelin diet also had greater increment of wing growth than puffins fed the age class 2+ pollock diet (two –sample t-test,  $t = 3.865$ , d.f. = 12,  $P = 0.002$ ; Table 1.2, Fig. 1.3C).

## DISCUSSION

Both kittiwake and puffin nestlings raised on diets of juvenile herring, sand lance, or capelin had a greater growth increment of body mass than nestlings fed the same biomass of juvenile pollock. This result was predicted *a priori* because juvenile pollock are generally low in lipid and subjects fed a given mass of high-lipid fish should consume considerably more energy (kJ/day) than subjects fed the same mass of low-lipid fish. The metabolizable energy content of lipid is more than twice that of protein for uricotelic vertebrates such as birds (39.3 kJ/g lipid vs. 17.8 kJ/g protein; Schmidt-Nielsen 1997:171). The protein content of forage fish types used in these feeding trials was similar. Intraspecific differences in lipid content of fishes explained nearly all the variation in energy density among diets (Fig. 1.3). Because protein content of diets were similar, it is reasonable to conclude that differences in lipid content of diets were responsible for differences in body mass growth among diet treatment groups.

The possibility does exist that pollock may lack certain fat-soluble vitamins critical to seabird nestling growth and development. This could explain why birds receiving herring, capelin, or sandlance were able to grow and develop at a more rapid pace than birds receiving pollock. My data, however, do not support this hypothesis. In 1996

kittiwakes receiving 100 g/day of pollock did not receive a vitamin supplement. However, during 1997, kittiwakes receiving 100 g/day of pollock did receive a multi-vitamin. Despite this difference there was no significant difference in growth between birds that received the vitamin supplement and those that did not. Additionally, none of the birds in the study exhibited any of the overt signs of a vitamin deficiency.

The age class 1+ juvenile walleye pollock fed to puffins had an uncharacteristically high lipid content (6.4% wet mass) and average energy density (5.3 kJ/g) for juvenile walleye pollock captured during the seabird nestling season (Van Pelt et al. 1997, Anthony et al. in press). There was a large difference in energy intake rates between puffins fed the two age classes of pollock. The better growth performance of puffins on the 1+ pollock diet was apparently due to the higher lipid content of the fish. This result indicates that juvenile walleye pollock is not necessarily a low-quality food for nestling seabirds, although juvenile pollock collected during the seabird nesting season (June – August) are generally low in lipid (Van Pelt et al. 1997, Anthony et al. in press). These results are consistent with the hypothesis that lipid content is the primary determinant of nutritional quality among forage fishes.

Differences in mass gain between diet treatments were much more pronounced than differences in structural growth (Figs. 1.2 & 1.3). In all four comparisons, body mass of chicks on the low-lipid (pollock) diets lagged considerably behind those on the high-lipid diets (herring, sand lance, capelin). In contrast age-specific wing length tended to be similar among diet groups. Wing length of chicks on the low-lipid diets lagged behind those on the high-lipid diets by only a few days. In the kittiwake feeding trials, a significant difference in body mass growth was evident between nestlings fed the herring

and sand lance diets, but no difference in wing growth was detected. Similarly, in the puffin feeding trials, a significant difference in body mass growth was evident between birds receiving 100 g/day of herring and 100 g/day of pollock, yet no difference was found in their wing growth. This suggests that undernourished seabird chicks preferentially allocate assimilated nutrients to wing growth over mass gain. The tendency for mass gain to be more susceptible than wing growth to differences in energy intake has been observed previously (Prince and Ricketts 1981). This strategy may allow even underweight young to fledge and could increase their chances for survival (Harris 1969).

Studies that have investigated the role that diet quality plays in the growth and development of seabird chicks have reported mixed results. Prince and Ricketts (1981) observed no difference in the size of meals, nor the frequency of meal delivery, between Black-browed and Grey-headed albatrosses (*Diomedea melanophris* and *D. chrystoma*) nesting on Bird Island, South Georgia despite higher nestling growth rates in the former. Black-browed Albatrosses delivered more energy-dense prey (krill and fish) to their young than did Grey-headed Albatrosses (squid). Thus, Black-browed adults provisioned their young with energy at a higher rate than did Grey-headed adults. When chicks of the two species were cross-fostered, growth of Grey-headed chicks increased on the energy-rich diet provided by Black-browed parents. Conversely, Black-browed chicks experienced suppressed growth when raised on the lower energy diet provided by Grey-headed parents (Prince and Ricketts 1981). Therefore, diet quality was the primary cause of interspecific differences in growth rate.



Atlantic Puffins (*Fratercula arctica*) exhibited differences in breeding success when they were forced to switch to prey of lower caloric content to provision their young. During the 1974 season, the Atlantic Puffin colony on Dun Island in the St. Kilda group experienced low production of young, low chick masses, and slow chick growth as compared to the 1975-78 seasons (Harris 1980). In 1974 fish loads brought to the young had lower average caloric value compared to all of the other years of the study. Additionally, in years when whiting (a low energy density prey) made up over 50% of the nestling diet, age-specific body mass of nestlings was significantly less than when sprats (a high energy density prey) were the most important item in the diet (Harris 1980).

Ricklefs et al. (1987) supplemented the natural diet of Leach's Storm-petrel (*Oceanodroma leucorhoa*) chicks with either lipid or protein in a study designed to investigate the influence of diet quality on chick growth. Neither the lipid nor the protein supplements resulted in greater growth in body mass or size in chicks. The authors concluded that parent storm-petrels were providing nutrients in excess of that required for growth and thus when the chick consumed greater amounts of food no growth response occurred. They also concluded that the chick regulates its own energy intake and thus partly compensated for the diet supplements by consuming less of the food provided by its parents (Ricklefs et al. 1987). In contrast, the chicks in my study rarely refused food, and it appears that their energy requirements were not met as completely as those of the storm-petrel chicks in the Ricklefs et al. (1987) study. Nestlings whose energy requirements are not fully met would be expected to grow at different rates depending on the energy content of their diet.

The results of this experiment agree with the findings of Prince and Ricketts (1981), that chick growth is limited by the quality and energy density of the diet. It is important to consider whether shorter development times and greater mass at fledging (both benefits of a high-lipid diet) increase post-fledging survival. Some studies report a positive relationship between nestling/fledging weight and juvenile survival (Perrins et al. 1973, Jarvis 1974, Coulson and Porter 1985, Magrath 1991), yet others failed to detect a significant relationship between the two (Hedgren 1981, Harris and Rothery 1985, Sullivan 1989). Manx Shearwaters (*Puffinus puffinus*) were found to have greater juvenile survival when they fledged earlier in the season and also when they fledged with a greater body mass (Perrins et al. 1973). Jarvis (1974) obtained a similar result for the South African Gannet (*Sula capensis*). Coulson and Porter (1985) reported a positive relationship between nestling body mass and juvenile survival for Black-legged Kittiwakes. However, Harris and Rothery (1985) observed that neither fledging date nor fledging weight influenced post-fledging survival in Atlantic Puffins. Finally, Hedgren (1981) found no association between nestling weight and juvenile survival in a population of Common Murres. However, murres receive post-fledging parental care and feeding, thus they do not rely solely on their fat reserves for energy while learning to forage efficiently. It is interesting to note that the three species that exhibit a relationship between fledging weight and post-fledging survival are plunge-diving foragers whereas the two species that do not are pursuit-divers.

Presently there are no data available to test the hypothesis that foraging mode of fledglings influences the relationship between body mass at fledging and survival. It is possible that developing proficiency at plunge-diving requires a longer time period than

for pursuit-diving. If true, then plunge-diving seabirds may have to subsist on their fat stores for longer periods after fledging than pursuit-diving seabirds. Jarvis (1974) observed significant weight loss in recently fledged South African Gannets, suggesting that these birds were relying, at least in part, on fat reserves to meet their daily energy requirements. Orians (1969) found that juvenile Brown Pelicans (*Pelicanus occidentalis*), which also forage by plunge-diving, are less successful hunters than adults. If plunge-diving is a highly specialized skill that takes time to perfect, fledglings employing this foraging strategy may experience greater survival if they fledge at a greater body mass (with presumably larger fat stores).

In some species nestling body mass and time of fledging apparently influences post-fledging survival, whereas in other species it does not. We are not aware of any study that found a negative correlation between nestling body mass and juvenile survival. Our experiment demonstrated significant differences in growth rate in relation to differences in diet quality. Nestlings raised in the wild on high-lipid forage fish may have faster growth rates and fledge at greater body mass than those raised on low-lipid fish. In some species this may increase post-fledging survival, and ultimately increase population productivity. Thus the availability and abundance of high-lipid forage fish may constrain the growth of certain seabird populations.

## CONCLUSIONS

The results of this experiment are consistent with the hypothesis that lipid content of the diet, rather than protein, limits postnatal growth in piscivorous seabirds. 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

parent seabirds to transport food back to the nest is limited, selection of high-lipid fish may be necessary to compensate for constraints on biomass of prey provided to nestlings. Provisioning young with high-lipid prey generally results in higher rates of body mass gain and more rapid structural development in nestlings. This allows nestlings to fledge at a younger age and at higher body mass, traits associated with higher post-fledging survival in some seabird species.

## **Chapter 2**

### **Effects of Diet on Growth and Body Composition of Nestling Seabirds**

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This manuscript has not yet been submitted.

## Chapter 2: Effects of Diet on Growth and Body Composition of Nestling Seabirds

### ABSTRACT

Declines in availability of certain schooling fishes (capelin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea harengus pallasii*) potentially contributed to recent declines in productivity of several piscivorous seabird species in Alaska. These fishes tend to have higher lipid content compared with other forage fishes, and thus a higher proportion of their energy content is in the form of lipid as opposed to protein. I tested the hypothesis that the growth and development of nestling seabirds is affected by the lipid:protein ratio of their diet. I fed nestlings daily rations of fish that differed in lipid content, but not in total energy content. Tufted Puffins (*Fratercula cirrhata*) and Black-legged Kittiwakes (*Rissa tridactyla*) were raised in captivity on equal caloric diets of capelin or herring (fishes with a high lipid:protein ratio) or juvenile walleye pollock (*Theragra chalcogramma*) (fish with a low lipid:protein ratio). Growth in body mass and wing length of puffin nestlings was not affected by the lipid:protein ratio of the diet. Growth in body mass and wing length of kittiwake nestlings was also not affected by lipid:protein ratio when on a high nutritional plane (i.e., high daily caloric intake), but growth was significantly affected by dietary lipid:protein ratio when on a low nutritional plane. Regardless of daily caloric intake, diets with a higher lipid:protein ratio resulted in greater fat reserves at fledging in both seabird species. Additionally, diets with a higher lipid:protein ratio resulted in greater apparent metabolizable energy coefficients. I conclude that the lipid:protein ratio of fish fed to nestling seabirds constrains growth in some species when food availability is limiting, but may affect

nestling fitness and overall productivity most by constraining the deposition of fat reserves in nestlings.

## INTRODUCTION

Recent breeding failures among several piscivorous seabird species in Alaska have raised questions about the role of prey quality in chick growth and, ultimately, breeding success (Hatch et al. 1993, Irons 1996). Low availability of lipid-rich forage fishes has been implicated as a factor contributing to low productivity. Over the past 20 years there has been a major shift in the taxonomic composition of prey items in diets of seabirds from the northern Gulf of Alaska (Piatt and Anderson 1996). Some seabird species have switched from a diet consisting of lipid-rich fish, such as juvenile Pacific herring (*Clupea harengus pallasii*), Pacific sand lance (*Ammodytes hexapterus*), and capelin (*Mallotus villosus*), to a diet composed largely of juvenile walleye pollock (*Theragra chalcogramma*) and other gadids (Piatt and Anderson 1996). Juvenile gadids, because of their generally low lipid content, have a lower proportion of calories as lipid than fishes like capelin, herring, and sand lance. The lipid content of capelin, herring, and sand lance is generally two to four times that of juvenile pollock and, consequently, their energy density can be twice that of juvenile pollock (Van Pelt et al. 1997, Anthony et al. in press). Diets consisting mostly of pollock or other low-lipid fishes may not pose a problem for young growing seabirds if dietary protein is nutritionally limiting more than energy, or if parents can double the rate of food delivery, thus compensating for low energy density of prey. If, however, energy is the limiting nutrient for young seabirds and parents can not increase delivery rate the lower lipid:protein ratio of low-lipid fishes may necessitate the

use of protein as an energy source to meet maintenance requirements, thus reducing metabolizable energy coefficients and energy utilization efficiency.

In a previous study (see Chapter 1), I investigated the growth response of captive seabird nestlings to diets consisting of equal biomass rations of either a high-lipid fish (i.e., capelin, herring, or sand lance) or a low-lipid fish (i.e., juvenile walleye pollock). My results demonstrated that seabird nestlings deposit body mass and develop at a higher rate on diets of high-lipid fish compared with equal biomass diets of low-lipid fish. The higher energy density of high-lipid fishes appeared to be the primary factor responsible for these differences in growth rate, as protein content was similar in the diets. Thus, if both high- and low-lipid fishes are equally available, it may be advantageous for parent seabirds to provision their young with high-lipid fish.

With the changing distribution and abundance of forage fish in the northern Gulf of Alaska, however, high- and low-lipid forage fishes may not be equally available. Often, as in the case of some seabird colonies in the Aleutian Islands and Bering Sea, juvenile pollock and other gadids are more prevalent in seabird diets than prey with a higher lipid content (Piatt et al. unpubl. data, Hatch and Sanger 1992, Hatch et al. 1993). Parent seabirds may be able to provision their young with greater amounts of low-lipid fishes than high-lipid fishes, and potentially compensate for the lower energy density of low-lipid fishes. If parent seabirds can provide sufficient low-lipid forage fish to their young to exceed the total caloric intake possible on a diet of high-lipid fish, then provisioning young with low-lipid fish may be an adaptive strategy for seabird parents. But if high-lipid fish are nutritionally superior above and beyond their higher energy density, then



nestlings fed low-lipid fish may be at a nutritional disadvantage, regardless of similar energy intake rates.

In this study I compared the growth and development of captive seabird nestlings fed controlled, equal caloric diets of either high-lipid or low-lipid fish. I hypothesized that, despite equal daily caloric intake, nestlings fed diets with a higher lipid content (higher lipid:protein ratio) would grow and develop faster. I reasoned that nestlings fed a diet with a low lipid content (low lipid:protein ratio) would be forced to meet much of their maintenance energy requirements by metabolizing protein, whereas nestlings fed a diet with a high lipid content could meet most of their maintenance energy requirements by metabolizing lipid (Roby 1991). Utilizing protein as an energy source requires synthesis and excretion of the resultant nitrogenous waste products (uric acid) and competes with deposition of protein in growing tissues (Robbins 1993).

## METHODS AND MATERIALS

A combination of captive feeding trials and laboratory analyses were used in this study. I conducted captive feeding trials at the Kasitsna Bay Laboratory, Institute of Marine Science, University of Alaska Fairbanks, during the 1996 and 1997 breeding seasons. The Laboratory is located on Kachemak Bay near Homer, in south-central Alaska. All laboratory analyses were carried out in laboratories at the Department of Fisheries and Wildlife, and the Department of Animal Science at Oregon State University. 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: Tufted Puffins (*Fratercula cirrhata*) and Black-legged Kittiwakes (*Rissa tridactyla*). Both species utilize varied diets during the breeding season, but generally consume fish. The foraging mode of the two species differs considerably, with puffins feeding in the water column by pursuit-diving and kittiwakes feeding near the surface by plunge-diving. Puffin chicks used in the study were collected from East Amatuli Island in the Barren Islands, Alaska, and kittiwake chicks were collected from colonies in Kachemak Bay, both under permits held by the Alaska Biological Science Center. During 1996, 14 puffin chicks were removed from their nests at an estimated age of 6-18 days post-hatch. In 1997, 23 kittiwake chicks were removed from their nests at an estimated age of 5-10 days post-hatch. Age of chicks was estimated using methods described in Chapter 1. Procedures used to acclimate and hold chicks in captivity are also described in Chapter 1.

The sample of puffin chicks was divided evenly into two diet groups (N = 7 per treatment), with each receiving a daily ration of either 80 g of age class 2+ walleye pollock or 45 g of capelin. These daily rations were designed to have similar total energy content but different lipid:protein ratios. All puffin chicks were fed their respective experimental diet from 19 days post-hatch until the experiment was terminated at 40 days post-hatch, the earliest possible fledging age for the species (Wehle 1980). Before beginning the feeding trial at 19 days, each bird was fed an *ad libitum* diet of approximately equal amounts of juvenile pollock and capelin.

The sample of kittiwake chicks was divided into four groups, with each nestling receiving a daily ration of either 100 g of juvenile Pacific herring (N = 6 chicks), 192 g of age class 2+ pollock (N = 6 chicks), 100 g of age class 2+ pollock (N = 6 chicks), or 52 g

of juvenile herring ( $N = 5$  chicks). The 100 g/day herring ration and the 192 g/day pollock ration were designed to have similar energy content, as were the 52 g/day herring ration and the 100 g/day pollock ration. The first two diets were considered the high-calorie diets (approx. 717 kJ/day), while the latter two diets were considered the low-calorie diets (approx. 372 kJ/day). All kittiwake chicks were fed experimental diets beginning at 13 days post-hatch until the experiment was terminated at 31 days post-hatch, the earliest possible fledging age. Before beginning feeding trials, each chick was fed an *ad libitum* diet of approximately equal amounts of juvenile pollock and juvenile herring.

The following variables were measured daily for both puffin and kittiwake chicks: (1) body mass ( $\pm 0.1$  g), (2) flattened wing length ( $\pm 1$  mm), and (3) culmen length (measured with calipers,  $\pm 0.1$  mm). All measurements were taken between 08:00 and 10:00 ADT, before the first feeding of the day.

Aluminum trays were placed beneath the galvanized hardware cloth floor of each cage to collect excreta samples. Samples were collected from puffins at 39 days post-hatch and from kittiwakes at 30 days post-hatch. Collection commenced after each bird had been weighed and measured, and continued for exactly 24 hours. Samples were weighed immediately after collection (to determine wet mass) and dried in a convection drying oven at 60°C (to determine dry mass). The samples were then shipped to Oregon State University. In the laboratory, the samples were homogenized using a mortar and pestle and then the total chemical energy of a one gram subsample from each bird was determined using a Parr adiabatic bomb calorimeter.

Capelin for feeding puffin chicks were captured using a cast net in Kachemak Bay, Alaska during late July 1996. Age class 2+ pollock were collected by 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 bait-fish supplier in Anchorage, Alaska. The supplier reported that the herring were caught off the coast of British Columbia in early spring of 1997.

I estimated the absolute energy content of specific diet treatments using proximate composition analysis of fish subsampled from the diet. All fish were shipped frozen to the laboratory at Oregon State University to undergo analysis. Specimens were weighed and measured individually, then dried to constant mass in a convection oven at 60° C to determine water content. Dried fish were ground using a mortar and pestle, and lipid content was determined by solvent extraction in a soxhlet apparatus, using hexane/isopropyl alcohol 7:2 (v: v) as the solvent system (Radin 1981). Lean dry fish samples were ashed in a muffle furnace at 600°C for 12 hours to calculate ash-free lean dry mass (ca. 94% protein; Montevecchi et al. 1984) by subtraction. Energy content of diets were calculated from proximate composition (percent water, lipid, ash-free lean dry matter [protein], and ash) of forage fish along with published energy equivalents of these fractions (39.3 kJ/g lipid; 17.8 kJ/g protein; Schmidt-Nielsen 1997:171).

At the termination of the feeding trials all fledglings were euthanized via cervical dislocation and frozen immediately. Subjects were anaesthetized with di-ethyl ether prior to euthanasia. Carcasses were shipped frozen to the lab at Oregon State University where they were weighed, partially thawed, plucked, and reweighed to determine plumage mass. Plucked carcasses were air-dried to constant mass at 60° C in a forced convection

oven to determine water content. Dried carcasses were ground and homogenized by passing repeatedly through a meat grinder. Aliquots of the dried homogenate were extracted in a soxhlet apparatus with petroleum ether as the solvent system to determine total carcass fat (Dobush et al. 1985). Lean dry samples were ashed in a muffle furnace at 600°C for 12 hours to calculate ash-free lean dry mass and ash mass.

Body mass, wing length, and culmen length of puffins in the two diet treatment groups were compared at the beginning of feeding trials using standard t-tests. A Bonferroni Adjustment was used for all t-tests because of the large number of t-tests employed. Body mass, wing length, and culmen length of kittiwakes in all four diet groups were compared at the beginning of feeding trials using one-way ANOVA. The data were examined and the assumptions of ANOVA were met. Total growth increment in body mass, wing length, and culmen length was calculated for each subject. Growth increment was defined as the final body mass, wing length, or culmen length of each chick minus the body mass, wing length, or culmen length, respectively for that chick at the start of the feeding trials. Means for the growth increments of each diet group were compared using t-tests, with the exception of the comparison of wing length increment for the low nutritional plane kittiwake diet groups, where the Mann-Whitney Rank Sum Test was used because the data did not pass a Modified-Levene equal-variance test. The level of significance of these tests was set at 0.0167. The energy content of diet rations was compared using t-tests. The level of significance of these tests was set at 0.0167. Total body fat for puffin chicks and for kittiwake chicks in the high-calorie diet groups were compared using t-tests. The level of significance of these tests was set at 0.01. A fat index was calculated for each bird as the ratio of total body fat to lean dry body mass.

The fat index allows comparison of body fat while accounting for variation in individual body size. All fat index data were compared between diet groups using the Mann-Whitney Rank Sum Test. The remainder of the body composition data, including all data from kittiwakes on low-calorie diets, were compared using the Mann-Whitney Rank Sum Test because the data failed a Modified-Levene equal-variance test.

Apparent metabolizable energy coefficients were estimated by subtracting total excreta energy from total ingested energy over a 24 hour period (Harris 1966). The apparent metabolizable energy coefficient was calculated for a sample of the chicks in each diet group using the formula:

$$\text{AMEC} = [(\text{EE}_{\text{in}} - \text{GE}_{\text{out}}) / \text{EE}_{\text{in}}] \times 100$$

where AMEC is apparent metabolizable energy coefficient,  $\text{EE}_{\text{in}}$  is estimated energy intake (kJ) in 24 hours (taken from proximate composition of diet and energy equivalents) and  $\text{GE}_{\text{out}}$  is gross energy excreted (kJ) in 24 hours. A multiple linear regression model was used to determine which explanatory variables (biomass intake, energy intake, lipid intake, protein intake, and dietary lipid:protein ratio) best explained variation in AMEC. Forward selection technique and Mallows'  $\text{cp}$  statistic were used to choose the best-fit model for the multiple linear regression.

## RESULTS

### Chick Growth

Estimated energy content of the 45 g/day capelin diet was not different from that of the 80 g/day age class 2+ walleye pollock diet ( $t = 1.485$ , d.f. = 33,  $P = 0.147$ ; Table 2.1). The 45 g/day capelin diet contained somewhat more energy in the form of lipid than in

Table 2.1. Energy content of experimental diets fed to captive-reared Tufted Puffins and Black-legged Kittiwakes. Total energy content of each diet is presented, and the amount of energy in lipid vs. protein. Iso-caloric diets are presented together for comparison.

Diet Treatment	Daily Energy Intake $\pm$ SE (kJ)	Daily Energy Intake in Lipid $\pm$ SE (kJ)	Daily Energy Intake in Protein $\pm$ SE (kJ)	Ratio of lipid calories to protein calories
<b><u>Tufted Puffins</u></b>				
45 g/day capelin	276.5 $\pm$ 9.93	154.1 $\pm$ 11.47	122.5 $\pm$ 2.29	1.26
80 g/day pollock	296.0 $\pm$ 7.96	68.8 $\pm$ 6.10	227.2 $\pm$ 3.40	0.30
	<b>ns</b>	<b>**</b>	<b>**</b>	<b>**</b>
<b><u>Black-legged Kittiwakes</u></b>				
100 g/day herring	716.6 $\pm$ 16.40	426.5 $\pm$ 17.38	290.2 $\pm$ 2.33	1.47
192 g/day pollock	716.7 $\pm$ 20.35	163.8 $\pm$ 13.27	552.9 $\pm$ 11.38	0.30
	<b>ns</b>	<b>**</b>	<b>**</b>	<b>**</b>
52 g/day herring	372.7 $\pm$ 8.53	221.8 $\pm$ 9.04	150.9 $\pm$ 1.21	1.47
100 g/day pollock	372.0 $\pm$ 7.50	85.6 $\pm$ 5.11	286.4 $\pm$ 3.95	0.30
	<b>ns</b>	<b>**</b>	<b>**</b>	<b>**</b>

ns =  $P > 0.0167$ , \* =  $P \leq 0.0167$ , \*\* =  $P \leq 0.001$  (Student's t-test)

the form of protein (Table 2.1). The 80 g/day pollock diet contained less than one-third the energy in the form of lipid as in the form of protein (Table 2.1).

The estimated energy content of the 100 g/day herring diet was not different from the 192 g/day pollock diet ( $t = 0.0043$ , d.f. = 48,  $P = 0.997$ ; Table 2.1). Kittiwakes on the 100 g/day herring diet, however, ingested nearly 50% more energy in the form of lipid than in the form of protein (Table 2.1). Kittiwakes on the 192 g/day pollock diet were fed less than one-third the calories in the form of lipid as in the form of protein (Table 2.1).

Kittiwakes on the low-calorie rations were fed diets of either 52 g/day of juvenile Pacific herring or 100 g/day of juvenile walleye pollock; these diets were not different in energy content ( $t = 0.0477$ , d.f. = 48,  $P = 0.962$ ; Table 2.1). The ratios of lipid calories to protein calories were the same as the ratios in the high-calorie rations for the respective fish species (Table 2.1).

There was no difference in mean body mass ( $t = 0.176$ , d.f. = 12,  $P = 0.864$ ), mean wing length ( $t = 0.756$ , d.f. = 12,  $P = 0.464$ ), and mean culmen length ( $t = 1.041$ , d.f. = 12,  $P = 0.318$ ) between puffin chicks in the two diet groups at the start of the feeding trials (Fig. 2.1). There was no significant difference in body mass increment by the end of the feeding trials between puffins raised on the 45 g/day capelin ration and puffins raised on the 80 g/day pollock ration ( $t = 2.070$ , d.f. = 12,  $P = 0.061$ ; Table 2.2). There was no difference in wing length increment between puffins raised on the 45 g/day capelin ration and puffins raised on the 80 g/day pollock ration ( $t = 0.404$ , d.f. = 12,  $P = 0.693$ ; Table 2.2). There was also no significant difference in culmen length increment



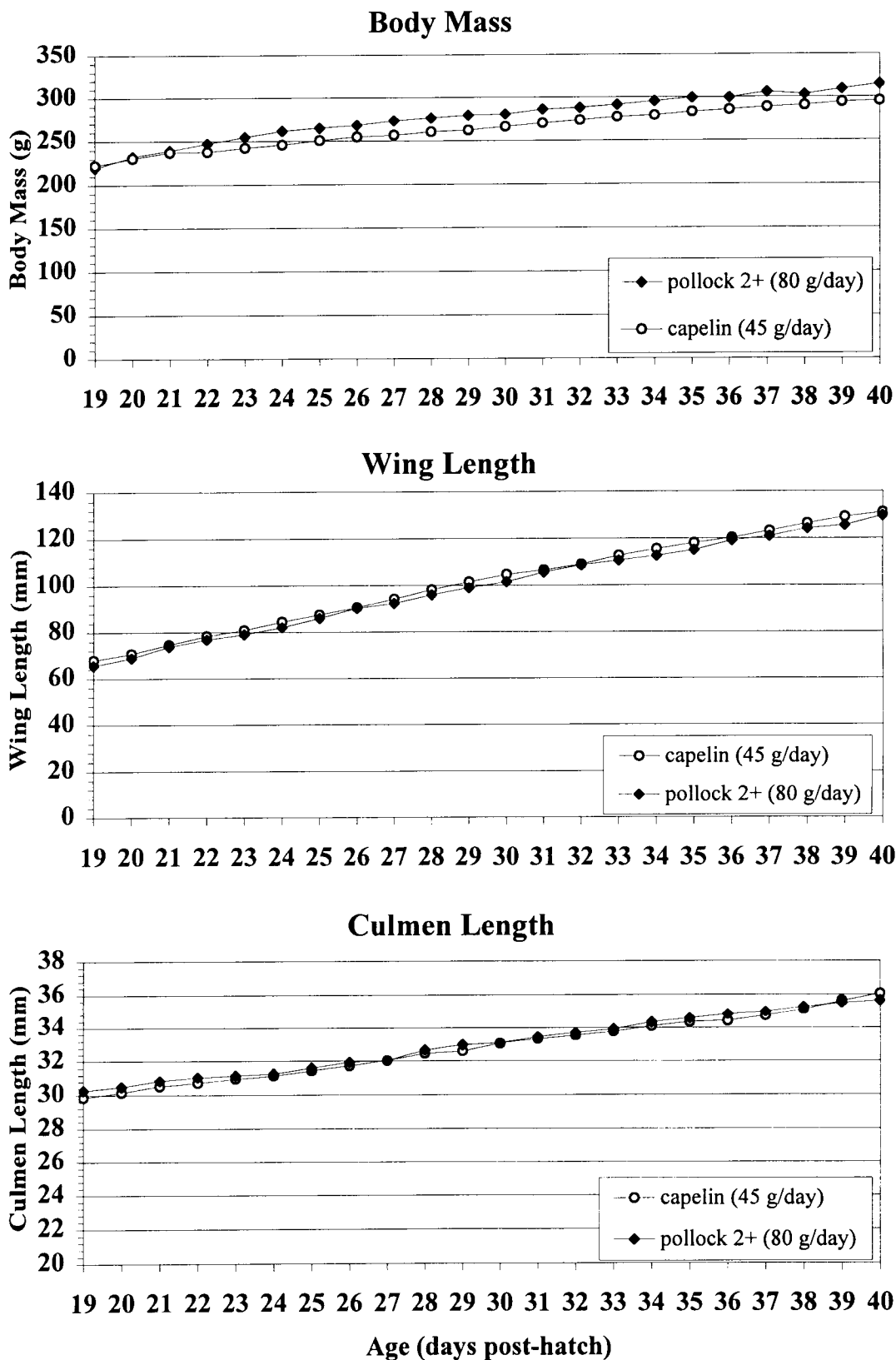


Figure 2.1. Body mass, wing length, and culmen length of Tufted Puffin nestlings fed controlled diets of either juvenile walleye pollock or capelin, as a function of age.

Table 2.2. Growth increment in body mass, wing length, and culmen length of Tufted Puffin and Black-legged Kittiwake fledglings during the experimental period (19 days to 40 days post-hatch for puffins and 13 days to 31 days post-hatch for kittiwakes). Measurements of fledglings on diets of similar caloric content are grouped together for comparison.

Diet Treatment	Increment in Body Mass Growth ± SE (g)		Increment in Wing Growth ± SE (mm)		Increment in Culmen Growth ± SE (mm)	
<b><u>Tufted Puffins</u></b>						
45 g/day capelin	72.7 ± 5.9	<b>ns</b>	63.0 ± 1.4	<b>ns</b>	6.2 ± 0.2	<b>ns</b>
80 g/day pollock	95.3 ± 9.2		63.9 ± 1.6		5.4 ± 0.2	
<b><u>Black-legged Kittiwakes</u></b>						
100 g/day herring	239.7 ± 34.9	<b>ns</b>	147.5 ± 2.2	<b>ns</b>	10.6 ± 0.4	<b>ns</b>
192 g/day pollock	231.2 ± 9.2		148.7 ± 2.3		11.3 ± 0.7	
52 g/day herring	128.2 ± 10.4	<b>**</b>	139.8 ± 1.3	<b>**</b>	8.0 ± 0.5	<b>ns</b>
100 g/day pollock	99.5 ± 12.4		130.0 ± 4.9		8.2 ± 1.1	

\* =  $P \leq 0.0167$ , \*\* =  $P \leq 0.001$ , ns =  $P > 0.0167$  (Student's t-test)

between puffins fed the 45 g/day capelin ration and those fed the 80 g/day pollock ration ( $t = 2.642$ , d.f. = 12,  $P = 0.021$ ; Table 2.2).

At the start of the feeding trials, there was no difference in mean body mass (ANOVA,  $F_{3,19} = 0.424$ ,  $P = 0.738$ ), mean wing length (ANOVA,  $F_{3,19} = 0.242$ ,  $P = 0.866$ ), and mean culmen length (ANOVA,  $F_{3,19} = 0.412$ ,  $P = 0.746$ ) of kittiwake chicks in the four diet groups (Fig. 2.2). By the end of the feeding trials there was no significant difference in the body mass increment ( $t = 0.502$ , d.f. = 10,  $P = 0.627$ ), wing length increment ( $t = 0.367$ , d.f. = 10,  $P = 0.721$ ), or culmen length increment ( $t = 1.453$ , d.f. = 10,  $P = 0.177$ ) between kittiwakes fed the 100 g/day herring diet and those fed the 192 g/day pollock diet (the high-calorie diets; Table 2.2). There were, however, significant differences in body mass and wing length increments between kittiwakes fed the two low-calorie rations. Kittiwakes on the 52 g/day herring ration had greater average body mass increment ( $t = 4.101$ , d.f. = 9,  $P = 0.003$ ) and greater average wing length increment (Mann-Whitney Rank Sum Test,  $P = 0.004$ ) than kittiwakes on the 100 g/day pollock ration (Table 2.2). Kittiwakes in these two diet groups did not, however, have significant differences in culmen growth increment ( $t = 0.349$ , d.f. = 9,  $P = 0.735$ ; Table 2.2).

### Chick Body Composition

Puffins fed the 45 g/day capelin diet had greater mean body fat than puffins on the 80 g/day pollock diet by the end of the feeding trials ( $t = 5.891$ , d.f. = 39,  $P < 0.001$ ; Table 2.3). Additionally, puffins fed 45 g/day of capelin had a greater fat index (total body fat/lean dry body mass) than puffins fed 80 g/day of pollock (Mann-Whitney Rank Sum Test,  $P < 0.001$ ; Table 2.3). In contrast, puffins fed the pollock diet had a greater mean

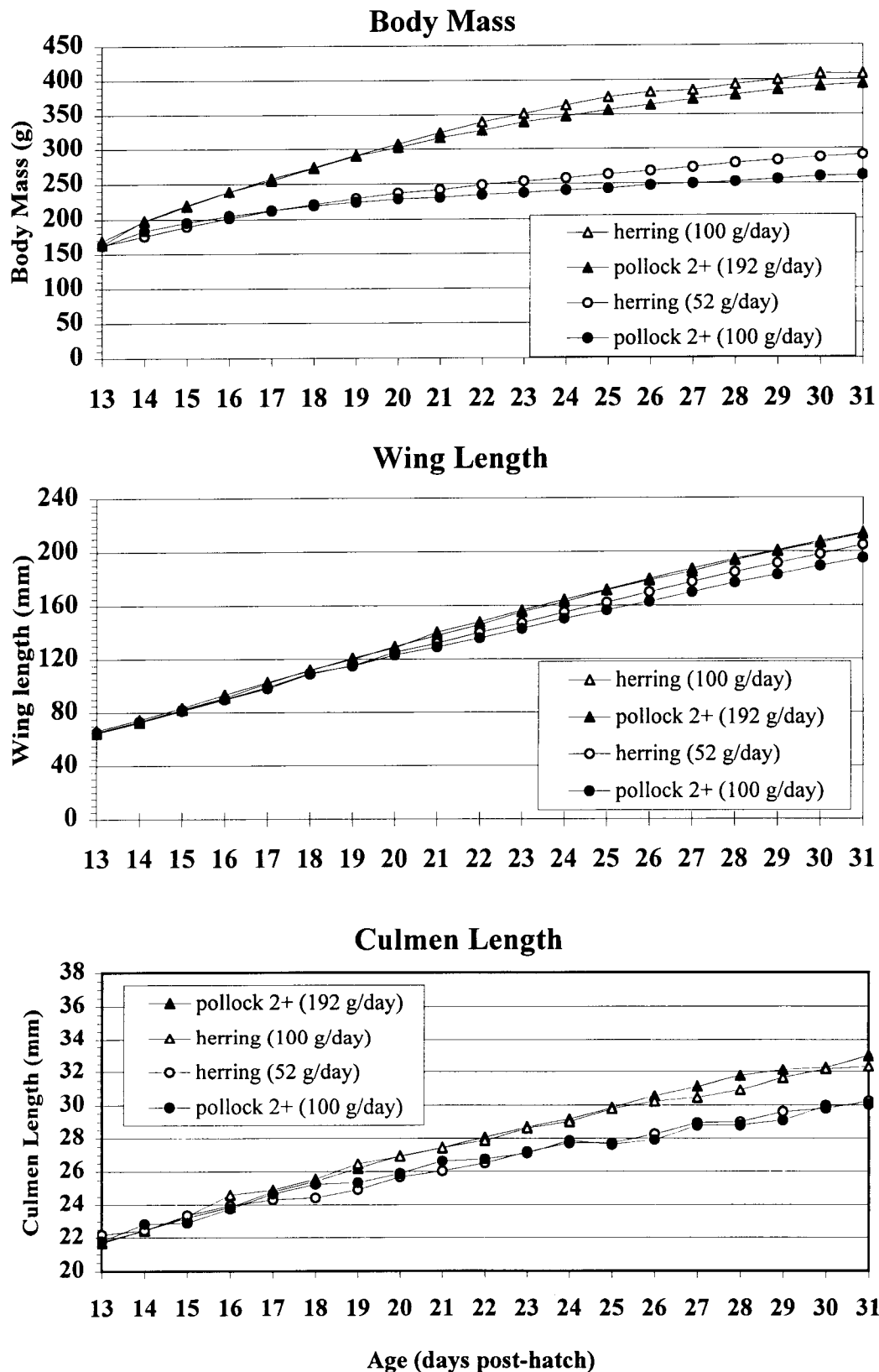


Figure 2.2. Body mass, wing length, and culmen length of Black-legged Kittiwake nestlings fed controlled diets of either Pacific herring or juvenile walleye pollock, as a function of age.

Table 2.3. Body composition of Tufted Puffin and Black-legged Kittiwake chicks raised on controlled diets. Values are mean content of carcass with feathers removed. Fat Index = Total Body Fat (g) / Lean Dry Body Mass (g).

Diet Treatment	Total Fat Content (g) ± SE		Total AFLDM (Protein) Content (g) ± SE		Total Water Content (g) ± SE		Total Ash Content (g) ± SE		Fat Index ± SE
<b><u>Tufted Puffin</u></b>									
45 g/day capelin	13.8 ± 0.89		48.1 ± 0.48		176.7 ± 1.42		10.3 ± 0.47		0.18 ± 0.02
		<b>**</b>		<b>**</b>		<b>**</b>		<b>ns</b>	
80 g/day pollock	8.1 ± 0.40		53.0 ± 0.74		190.9 ± 2.56		11.9 ± 0.26		0.10 ± 0.01
<b><u>Black-legged Kittiwake</u></b>									
100 g/day herring	54.9 ± 3.57		58.5 ± 0.82		197.7 ± 3.57		11.5 ± 0.32		0.76 ± 0.05
		<b>**</b>		<b>ns</b>		<b>ns</b>		<b>ns</b>	
192 g/day pollock	23.9 ± 1.11		58.9 ± 0.62		204.1 ± 2.89		12.1 ± 0.20		0.31 ± 0.02
52 g/day herring	8.8 ± 0.40		43.5 ± 0.77		158.8 ± 0.75		9.7 ± 0.85		0.15 ± 0.01
		<b>**</b>		<b>ns</b>		<b>ns</b>		<b>ns</b>	
100 g/day pollock	3.5 ± 0.16		39.7 ± 0.37		142.0 ± 1.62		8.5 ± 0.13		0.06 ± 0.01

ns = P > 0.01, \*\* = P ≤ 0.01 (Student's t-test with a Bonferroni adjustment).

body AFLDM (protein) content than puffins on the capelin diet (Mann-Whitney Rank Sum Test,  $P < 0.001$ ; Table 2.3).

For kittiwakes on the high-calorie diets, those on the 100 g/day herring ration had fat reserves greater than twice those on the 192 g/day pollock diet ( $t = 15.799$ , d.f. = 31,  $P < 0.001$ ; Table 2.3). The fat index of kittiwakes fed 100 g/day of herring was twice that of kittiwakes fed 192 g/day of pollock (Mann-Whitney Rank Sum Test,  $P < 0.001$ ; Table 2.3). The mean AFLDM content of kittiwakes on the 100 g/day herring ration was not significantly different from that of kittiwakes on the 192 g/day pollock diet (Mann-Whitney Rank Sum Test,  $P = 0.987$ ; Table 2.3).

The fat index for kittiwakes fed 52 g/day of herring was greater than for kittiwakes fed 100 g/day of pollock (Mann-Whitney Rank Sum Test,  $P < 0.001$ ). Because the body mass increment of kittiwakes on the two low-calorie diets was different, I also compared body composition of fledglings in these two diet groups using AFLDM as a percentage of total body mass. The %AFLDM content of kittiwakes fed 100 g/day of pollock was greater than that of kittiwakes fed 52 g/day of herring (Mann-Whitney Rank Sum Test,  $P < 0.001$ ).

#### Apparent Metabolizable Energy

The apparent metabolizable energy coefficients (AMEC) of puffins fed 80 g/day pollock was significantly less than those fed 45 g/day capelin ( $t = 6.174$ , d.f. = 11,  $P < 0.001$ ; Table 2.4). The AMEC of kittiwakes fed 192 g/day of pollock was also less than those fed 100 g/day of herring ( $P < 0.001$ ; Table 2.4). I also found a similar significant difference in the AMEC of kittiwakes fed 100 g/day of pollock and those fed 52 g/day of

Table 2.4. Apparent metabolizable energy coefficients of captive-reared Tufted Puffins and Black-legged Kittiwakes, raised on diets of either capelin, Pacific herring, or juvenile walleye pollock.

Diet Treatment	Apparent Metabolizable Energy Coefficient % $\pm$ SE		Daily Energy Intake $\pm$ SE (kJ)		Daily Energy Excreted $\pm$ SE (kJ)	
<u>Tufted Puffins</u>						
45 g/day capelin	88.1 $\pm$ 1.06	**	276.5 $\pm$ 9.93	ns	32.9 $\pm$ 2.94	**
80 g/day pollock	72.0 $\pm$ 2.23		296.0 $\pm$ 7.96		82.9 $\pm$ 6.59	
<u>Black-legged Kittiwakes</u>						
100 g/day herring	87.7 $\pm$ 0.89	**	716.6 $\pm$ 16.40	ns	88.4 $\pm$ 6.40	**
192 g/day pollock	75.0 $\pm$ 0.60		716.7 $\pm$ 20.35		179.0 $\pm$ 4.30	
52 g/day herring	86.6 $\pm$ 0.72	**	372.7 $\pm$ 8.53	ns	49.9 $\pm$ 2.70	**
100 g/day pollock	73.2 $\pm$ 2.02		372.0 $\pm$ 7.50		99.6 $\pm$ 7.53	

ns =  $P > 0.0167$ , \* =  $P \leq 0.0167$ , \*\* =  $P < 0.001$  (Student's t-test)

herring ( $P < 0.001$ ; Table 2.4). These differences in AMEC between kittiwakes on the high-lipid and low-lipid diets represent about 13% of metabolizable energy intake. There was no difference in the AMEC of puffins fed 45 g/day capelin, kittiwakes fed 100 g/day of herring, and kittiwakes fed 52 g/day of herring (ANOVA,  $F_{2,12} = 0.58$ ,  $P = 0.573$ ; Table 2.4). Additionally, I found no difference in the AMEC of puffins fed 80 g/day of pollock, kittiwakes fed 100 g/day pollock, and kittiwakes fed 192 g/day pollock (ANOVA,  $F_{2,14} = 0.64$ ,  $P = 0.543$ ; Table 2.4). Lipid:protein ratio of the diet explained 61.1% ( $P < 0.001$ ) of the variation in AMEC for the combined sample of puffins and kittiwakes, whereas daily AFLDM intake explained 17.8% ( $P = 0.034$ ) of the variation in AMEC. The regression coefficient for AMEC as a function of AFLDM was negative, indicating that an increase in dietary AFLDM resulted in a decrease in AMEC.

## DISCUSSION

The different diet treatments resulted in large differences in total fat stores of fledglings despite equal caloric intake rates for chicks in the respective diet comparisons. Subjects fed diets with a higher proportion of energy in the form of lipid had greater fat reserves by the end of feeding trials, despite no differences in body mass growth for two out of the three comparisons. The deposition of fat comprises a significant component of the energy budget for developing chicks of many avian species, especially seabirds (Ricklefs 1983). Larger fat depots translate into larger energy reserves, and fledglings with large fat reserves presumably have a survival advantage over fledglings with scant fat reserves.

Several hypotheses for explaining the adaptive significance of fat deposition in nestling birds have been proposed. Lack (1968) argued that fat deposits in chicks serve



as insurance against poor feeding conditions experienced by parent birds. Pelagic seabirds exploit food supplies that can be patchy and unpredictable (Ashmole 1971); thus, fat reserves may allow nestlings to survive prolonged fasting. According to this hypothesis, nestlings fed a higher proportion of energy in the form of lipid (i.e., high-lipid food sources like herring and capelin) would have a survival advantage due to their larger fat reserves. Previous studies on seabirds, however, have noted that nestling fat reserves are often in excess of those required for chicks to survive even the longest observed intervals between feeding (Ricklefs et al. 1980, Taylor and Konarzewski 1989). Thus a diet with higher lipid:protein ratio would only benefit chicks when foraging conditions are extremely poor for an extended period of time.

An alternative hypothesis is that fat reserves may serve as an energy sink, allowing nestlings to consume large amounts of lipid-rich but nutrient-poor food, while still accumulating limiting nutrients, such as certain amino acids (Ricklefs 1976, Ricklefs et al. 1980). This hypothesis is not supported by the results of our study. Nutrients that are potentially limiting in the diet of chicks include calcium for bone development and sulfur amino acids for feather growth (Ricklefs 1983). However, seabird species that feed on bony prey typically are not limited by calcium (Ricklefs 1983). The lack of a significant difference in wing length increment of puffin fledglings raised on the two diets suggests that intake of sulfur amino acids was not limiting feather growth in our experiments (Table 2.2). In addition, kittiwakes fed the low-calorie pollock ration actually had lower wing length increment (despite consuming more dietary protein) than those fed the low-calorie herring ration. Thus protein intake did not appear to limit kittiwake feather growth, even when nestlings were undernourished.

Another alternative hypothesis is that fat depots provide energy reserves needed once the chick becomes independent of parental feeding (Perrins et al. 1973, Jarvis 1974, Burger 1980, Ricklefs 1983, Taylor and Konarzewski 1989). While no data are yet available to unequivocally test this hypothesis, Bradstreet (1982) did observe a decline in the fat levels of Dovekie (*Alle alle*) fledglings at sea, suggesting they were utilizing fat reserves to meet their maintenance energy requirements. Jarvis (1974) suggested that newly fledged South African Gannets (*Sula capensis*) must live initially on their fat reserves while learning the specialized task of foraging by plunge-diving, the same mode of foraging employed by kittiwakes. Fledglings raised on diets with high lipid:protein ratios, and thus depositing larger fat reserves, may have an advantage over fledglings raised on diets with low lipid:protein ratios, once they are independent of parental provisioning. In migratory seabirds such as the Manx Shearwater (*Puffinus puffinus*) the fledglings ability to complete the fall migration without stopping to forage along the way may depend on fat reserves. The chances of surviving the fall migration appear to be inversely related to the amount of time the fledgling must spend foraging during migration (Perrins et al. 1973).

The comparisons of kittiwakes on high-calorie and low-calorie diets revealed an interaction between the effects of nutritional plane on growth and effects of diet composition. In the high-calorie comparison there was no difference in growth between chicks on the high-lipid vs. low-lipid diets, yet in the low-calorie comparison there were marked differences in growth between chicks on the two diets. Maintenance energy costs of kittiwakes on the low-calorie diets were apparently barely met by ingested energy, leaving little surplus energy to invest in growth. The growth performance of kittiwake

chicks on the low-calorie diets was well below that of most kittiwake chicks in the wild (Barret and Runde 1980, Irons and Suryan 1996). Thus the subjects fed these two low-calorie diets may have been undernourished, and utilizing lipid as an energy source for meeting maintenance requirements would be more efficient than utilizing protein as an energy source. Protein metabolism requires excretion of the resultant nitrogenous waste products, so metabolizable energy coefficients should be lower. This is supported by the low AMEC of puffin and kittiwake chicks fed pollock.

Energy assimilation efficiency in adult Black-legged Kittiwakes and Thick-billed Murres (*Uria lomvia*) was higher when the birds were fed high-lipid prey (Brekke and Gabrielsen 1994). My results for both puffins and kittiwakes indicated that chicks fed high-lipid herring or capelin had greater apparent metabolizable energy coefficients than chicks fed low-lipid pollock. Several other studies have found that metabolizable energy coefficients increase with dietary fat content and decrease with increased dietary protein (Blem 1976, Buchsbaum et al. 1986, Castro et al. 1989). Thus, undernourished kittiwake chicks on a diet with high lipid:protein ratio would metabolize less protein to meet energy requirements, and have more protein available to support growth. For kittiwakes, this greater efficiency resulted in higher growth rates and greater lean body mass. Both kittiwake groups in the high-calorie comparison, conversely, were apparently receiving adequate calories to meet maintenance energy costs and to grow normally. The better match between nutritional requirements and diet composition for kittiwakes fed herring supported deposition of greater fat reserves, regardless of whether nestlings were on the high- or low-calorie diet.

The growth performance of puffin chicks fed the experimental diets was well below that of most puffin chicks in the wild (Wehle 1980, Wehle 1983, Byrd et al. 1992, Roseneau et al. 1996, although see Roseneau et al. 1997), indicating subjects were undernourished. This result was not intentional. Data on average daily ration of puffin nestlings is limited, yet it appears that the data that do exist (Wehle 1980) may have underestimated daily provisioning rates. Differences in growth increment between puffins receiving the high- and low-lipid diets were not significant at the 0.05 level ( $P = 0.061$ ), but due to small sample size the power to detect a difference was low (Table 2.2). It appears that puffins on the low-lipid diet grew slightly better than those on the high-lipid diet. The higher growth increment in body mass of puffins fed pollock was due to higher accumulation rates of lean mass and body water, as fat reserves were lower than for puffins fed capelin. This is in marked contrast to the results from kittiwakes fed low-calorie diets. In general, Tufted Puffins are known to deliver a large proportion of low-lipid fish to their young, more so than Black-legged Kittiwakes (Byrd et al. 1992, Hatch and Sanger 1992, Irons and Suryan 1996, Roseneau et al. 1996, Roseneau et al. 1997, Piatt et al. 1997), suggesting puffins may be able to utilize low-lipid prey more efficiently than other seabirds. But contrary to expectations, puffins did not exhibit higher AMEC on low-lipid diets compared with kittiwakes.

## CONCLUSIONS

Diets higher in lipid content had a pronounced positive effect on fat reserves of both puffin and kittiwake nestlings. The effect of dietary lipid content on growth in nestling body mass differed between Tufted Puffins and Black-legged Kittiwakes. The body mass

and wing growth of undernourished puffin nestlings was not enhanced by higher lipid content of the diet. In kittiwakes, however, when daily energy intake was low and nestlings were undernourished, diets with higher lipid:protein ratios enhanced growth in total body mass, wing length, and deposition of lean body mass. For both species, the apparent metabolizable energy coefficient (AMEC) was greater for nestlings raised on high-lipid fish (capelin and herring), compared with diets of low-lipid fish (pollock). The lipid:protein ratio of the diet explained the majority of variation in AMEC for puffin and kittiwake nestlings combined. The energy utilization efficiency of puffin or kittiwake nestlings on diets of high-lipid forage fish was at least 18% greater than those on diets of low-lipid forage fish. This may constitute a significant benefit for seabirds breeding under conditions of low food availability.

## Synopsis and Conclusions

In this study I demonstrated effects of diet on the growth and development of piscivorous seabird nestlings. Forage fish species commonly used by parent seabirds to provision their young during the nestling period can vary significantly in lipid content and energy density. Provisioning young with high-lipid prey generally results in higher rates of body mass gain and more rapid structural development in nestlings, when both high-lipid and low-lipid prey are equally available. This allows nestlings to fledge at a younger age and at higher body mass, traits that have been shown to be associated with higher post-fledging survival in some species. Given the variability of forage fish populations, however, high-lipid and low-lipid fish are not always equally available to foraging parent seabirds.

Even when low-lipid forage fish are abundant, adults provisioning young with high-lipid prey may enhance the fitness of their nestlings. Lipid content of the diet was positively correlated with fat reserves of seabird nestlings, and this may increase post-fledging survival in some species. The effect of dietary lipid content on nestling growth appears to differ between seabird species. Growth in body mass and wing length of undernourished puffin nestlings was not enhanced by higher lipid content of the diet. In kittiwakes, however, when daily energy intake was low and nestlings were undernourished, diets with higher lipid:protein ratios enhanced growth in total body mass, wing length, and deposition of lean body mass. It appears that the growth of some seabird species may be more sensitive to the lipid content of their diet when total caloric intake is limited. Variation in apparent metabolizable energy coefficient (AMEC) among seabird nestlings appeared to be largely dictated by differences in the lipid content of fish

consumed. The higher AMEC of nestlings fed high-lipid forage fish is another benefit from selection of high-lipid prey by parent seabirds feeding young.

The results of my study suggest that high-lipid forage fish are an important resource for young developing seabirds. The availability of high-lipid forage fish may be one of the factors constraining the recovery of seabird populations damaged by the *Exxon Valdez* Oil Spill. In the future, researchers may have a better understanding of the potential for recovery of a piscivorous seabird species damaged by a large-scale environmental perturbation (such as an oil spill), if they can determine the health of high-lipid forage fish populations. Additionally, proactive management decisions that increase high-lipid forage fish stocks and their availability to seabirds and other marine predators may serve to lessen the impact of such perturbations.

Traditionally, fledgling body mass and wing length have been the two parameters employed by researchers as an index to fitness and post-fledging survival in nestling seabirds. My results, however, indicate that fat depots can vary considerably between nestlings without a significant difference in body mass or wing length. In some species these fat depots may have a pronounced effect on post-fledging survival. Unfortunately non-lethal techniques for determining fat depots of nestling seabirds in the field have proven to be too inaccurate, too inconvenient, and too expensive. Potential future research should focus on developing non-lethal techniques for determining body fat of nestlings in the field. Additionally, more research is needed to determine the relationship between nestling fat depots and post-fledging survival.

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