APPENDIX N

APEX: 96163N

Exxon Valdez Oil Spill
Restoration Project Annual Report

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

Restoration Project 96163N

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ABSTRACT

Declines in the availability of certain schooling forage fishes (Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea harengus pallasi*, capelin *Mallotus villosus*) 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 forage fishes tend to have high lipid content and, consequently, are assumed to have high nutritional value as food for nestling seabirds. This study tests the hypothesis that 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 or sand lance as representative of high-quality forage fish, or walleye pollock (*Theragra chalcograma*) as representative of low-quality forage fish. Lipid content of capelin diets (31% dry mass) and sand lance diets (22% dry mass) were considerably higher than that of pollock diets (9% dry mass). Experimental diets consisted of iso-biomass and iso-caloric rations of low- and high-lipid fish types.

Seabird nestlings fed rations of either sand lance or capelin had much higher growth rates of body mass and somewhat higher growth rates of wing length than nestlings fed the same biomass of pollock. Puffin chicks fed iso-caloric rations of pollock or capelin showed little difference in rates of mass or wing growth, but the capelin fed chicks deposited larger fat reserves than the chicks fed pollock. In this iso-caloric (ca. 330 kJ/day) comparison, puffin chicks had to be fed 80 g of pollock / day to receive the same calories as 45 g of capelin / day. 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 when provisioning rates of seabirds to their young are constrained, 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.

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 the Exxon Valdez oil spill area in recent years. Total failure of breeding seabirds has been recorded at several sites (Chisik I., Middleton I., etc.), and a lack of high quality, lipid-rich forage species to provision nestlings has been hypothesized as a factor in low productivity.

A major change in the taxonomic composition of diets of several seabird species has been observed in the Northern Gulf of Alaska during the past 20 years. Specifically, some species have switched from diets dominated by oily fishes, like capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterus),* to diets dominated by juvenile walleye pollock (*Theragra chalcograma*) and other gadids (Piatt and Anderson 1996). Due to lower lipid content and energy density (kJ/g), juvenile pollock are lower quality than other prey commonly found in diets of nestling seabirds, such as capelin or sand lance (Baird 1991, Roby et al. 1996, Van Pelt et al. in review). The energy density of capelin or sand lance is almost twice that of juvenile pollock, depending on sex and age class (Roby et al. 1996, Van Pelt et al. in review).

One of the key hypotheses that the APEX project is investigating states that reproductive success in seabirds is directly related to nutritional quality of forage fishes. Adult seabirds that rely on low quality prey to provision their young may experience lower productivity (Nettleship 1990, Martin 1989). As an example, Irons (1996) argues that recent reproductive failures among black-legged kittiwakes in oiled areas of Prince William Sound are linked to food conditions. Reproductive success in seabirds is dependent, in part, on the parents ability to provision the brood with energy (Roby 1991). If an adult were to provide the same amount of energy to its young in the form of juvenile pollock as it could by provisioning with sand lance or capelin, it would have to deliver nearly twice as much food. This may not be possible due to time and energy constraints, unless pollock are readily available close to the colony. Consequently, slower growth and lower fledging weights would be expected in nestlings fed primarily low energy diets. The potential result would be fewer nestlings surviving to fledge and lower post-fledging survival.

This research is designed to provide a better understanding of the relationship between diet quality and seabird productivity. Captive nestlings fed controlled rations of either pollock, sand lance, or capelin are being used to compare the effects of biomass intake, caloric intake, and lipid:protein ratio of the diet on growth and development. By comparing results of captive feeding trials on two different seabird species (a larid vs. an alcid), we are also investigating differences in energy and nutrient management between seabird taxa.

METHODS

The research design utilizes a combination of captive feeding experiments and laboratory analyses. The captive-rearing experiment was conducted at the Kasitsna Bay Laboratory of the Institute of Marine Science, University of Alaska Fairbanks, during the summer of 1996. Chicks used in the study were collected from either East Amatuli Island in the Barren Islands group or colonies in Kachemak Bay. A sample of Black-legged Kittiwake chicks (N = 22) and Tufted Puffin chicks (N = 21) were removed from their nests at 6-10 days post-hatch and 5-18 post-hatch, respectively. Kittiwake thermoregulation is well-developed at 6-8 days post-hatch (Barrett 1978). Puffin chicks are independent of parental brooding at 5 days post-hatch (Wehle 1983) and thereafter can be maintained in captivity at normal ambient temperatures without an artificial heat source. All chicks were placed in individual indoor cages for captive feeding experiments. Cages consisted of covered plastic buckets with the bottom cut out and replaced with a floor of galvanized hardware cloth. This design made cage cleaning easier. By placing a pan underneath each bucket, we were able to conveniently collect excreta. We made one collection of kittiwake excrement and four collections of puffin excrement. Each collection was made for all subjects over a 24-hour period. These samples will be analyzed for energy content during the spring of 1997.

The sample of kittiwake chicks was evenly divided into three diet treatment groups, each receiving a daily ration of one of the following: (1) 100 g of juvenile walleye pollock, (2) 43 g of Pacific sand lance, (3) 100 g of Pacific sand lance. The 43 g sand lance ration was expected to be similar in caloric content to the 100 g pollock diet, based on published values of energy density in the two species of forage fish. Variables that were measured daily in kittiwake chicks included: (1) total body mass (measured with an Ohaus triple beam balance, +/- 0.1 g), (2) wing length (measured flat on a ruler, +/- 1 mm), and (3) head/bill length (measured with calipers, +/- 0.1 mm).

The sample of puffin chicks was also divided into three diet treatment groups, with each receiving a daily ration of one of the following: (1) 80 g of juvenile walleye pollock (2) 45 g of capelin, (3) 80 g of capelin. The 45 g capelin ration was designed to be similar in caloric content to the 80 g pollock diet (approx. 325 kJ/day) based on published values for energy density in the two forage fishes. Variables that were measured daily in puffins 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).

When captive-reared chicks reached early fledging age (31 days post-hatch for kittiwakes and 40 days post-hatch for puffins), they were sacrificed and frozen for later body composition analysis in the lab at Oregon State University. Total body water, lean mass, total body fat, ash-free lean dry mass, ash mass, and fat index were determined for each chick. To calculate a fat index, total body fat was divided by lean dry body mass.

Carcasses 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 in order to determine moisture 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 using petroleum ether as the solvent system in order to determine fat content and ash-free lean dry mass by subtraction. Extracted aliquots were ashed in a muffle furnace at 550°C to determine ash content. Body composition of chicks from the captive-feeding experiments were compared to determine the effects of energy intake and diet composition on the allocation of assimilated resources to growth in lean mass and fat reserves. Preliminary results of these analyses are presented here.

Samples of juvenile pollock, sand lance, and capelin 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, forage fish specimens were dried to constant mass in a convection oven at 60° C to determine water content. Lipid content of the dried forage fish was determined by solvent extraction using a soxhlet apparatus and hexane/isopropyl alcohol 7:2 (v:v) as the solvent system. Lean dry fish samples were then ashed in a muffle furnace at 550°C in order to calculate ash-free lean dry mass by subtraction. Energy content of chick diets was calculated from the composition (water, lipid, ash-free lean dry matter [protein], and ash) of forage fish along with published energy equivalents of these fractions (39.4 kJ/g lipid; 17.8 kJ/g protein)(Schmidt-Nielsen 1990:171).

RESULTS

All captive subjects appeared to adjust quickly to captivity, survived for the duration of the experiment and exhibited little variation in growth and development rate within each diet treatment group. All kittiwake and puffin chicks readily consumed whole prey from the first feeding; no force feeding was required. Small aluminum pans were used to weigh out each meal and then the pans were placed in the cages and the chicks generally consumed the meal within 2-3 minutes. On a few occasions, primarily early in the captive feeding trials, individual fish had to be held with tweezers and presented to certain kittiwake chicks to encourage consumption. Puffin chicks did not require this encouragement; most chicks consumed their meals completely within a minute of being fed.

The kittiwakes chicks used as subjects for the experiment were estimated to be from 6-10 days old when first removed from their nests. Each chick was aged using a regression equation derived from data on known-age kittiwake chicks from Prince William Sound, Alaska (D.B. Irons, unpubl. data). Tufted puffin chicks used in the experiment were estimated to be 5-18 days old when they were removed from their nest burrows, with most being less than 12 days old. Puffin chicks were aged using a regression equation derived from data from known-age chicks on Aiktak Island, Alaska (Piatt and Romano, unpubl. data). Because of logistical constraints, we were forced to use puffins from a wider range of ages at the start of the captive feeding trials than we had intended. The primary drawback of including older chicks in the study was they were not allowed to habituate as long to captivity before being placed on their experimental ration as were the younger chicks.

Average energy density of fishes used in the study was 4.07 kJ/g for pollock, 6.85 kJ/g for sand lance, and 7.36 kJ/g for capelin. These values were used to estimate daily energy intake of each experimental group. Estimates of daily energy intake for puffins fed presumed "iso-caloric" diets of capelin or pollock were similar. Puffins fed the pollock ration (80 g/day) received an estimated 326 kJ/day and the "iso-caloric" capelin ration (45 g/day) was an estimated 331 kJ/day. In contrast, puffins fed the iso-biomass capelin ration (80 g/day) received an estimated 589 kJ/day.

Kittiwakes fed the pollock ration (100 g/day) received approximately 407 kJ/day, whereas kittiwakes on the "iso-caloric" sand lance ration (43 g/day) received only about 294 kJ/day. Kittiwakes fed the iso-biomass sand lance ration (100 g/day) received approximately 685 kJ/day. Thus, kittiwake growth could be compared for equal biomass rations of high and low lipid fish, but a comparison of growth on rations of equal caloric content was not possible.

Results of the comparison of growth on iso-biomass rations were similar for both seabird species. Subjects fed the high-lipid diet (capelin for puffins, sand lance for kittiwakes) experienced much higher rates of body mass gain and higher rates of structural development than subjects fed the low-lipid diet (pollock)(Figs. 2-6 for puffins, Figs. 7-10 for kittiwakes). Differences in body mass gain among the three diet groups were much more pronounced than differences in structural development (i.e., wing, culmen, head/bill and tarsus growth).

Tufted puffins fed pollock had slightly but significantly higher average body mass at the end of the feeding trial than those fed an iso-caloric ration diet of capelin. There was no significant difference in wing growth between the two groups (Fig. 6). There were no differences in culmen or tarsus growth between the two diet groups (Figures 4 and 5). However, average fat index for the two groups was very different. Fat index is used to compare body fat reserves among subjects while controlling for differences in body size. The pollock group had an average fat index of 0.0725, whereas the iso-caloric capelin group had an average fat index of 0.1500, more than twice that of the pollock group.

The comparison of kittiwake growth on iso-caloric diets of pollock and sand lance is ambiguous because the diets were not actually similar in energy content. The pollock group (100 g/day) was fed 38% more kJ/day than the sand lance group (43 g/day). Kittiwakes fed the pollock ration experienced significantly higher growth rates of body mass, wing length and head\bill length than kittiwakes fed the 43 g/day sand lance ration.

DISCUSSION

Both kittiwakes and puffins gained mass and grew at a higher rate on a diet of high-lipid fish as opposed to the equivalent biomass of low-lipid fish. This result was predicted because subjects on the high-lipid rations received an estimated 68.3% and 80.7% more kJ/day for kittiwakes and puffins, respectively. These findings support APEX hypothesis #9, that seabird reproductive productivity is determined by forage fish nutritional quality. Several APEX projects have obtained results from field studies that support the hypothesis, but this is the first controlled experimental study that has shown this conclusively.

Differences in mass gain among diet groups were much more pronounced than differences in structural growth. An extreme example of this appears in the kittiwake group receiving the 43 g/day sand lance ration. The average mass gain for chicks in this group was less than 25 g over the course of the 19-day experiment, yet wing growth averaged 75 mm for the same time period (Figs. 7 and 8). This suggests that undernourished seabird chicks preferentially allocate food energy intake to structural development over mass gain. This may be especially significant for kittiwakes, where 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 productivity is closely tied to availability of energy-rich forage fish prey. Nettleship (1984) found that Atlantic Puffins depending primarily on capelin to provision their young experienced high productivity when this forage fish was available. In contrast, during years when capelin was scarce productivity was reduced. Martin (1989) observed a similar pattern in an Atlantic Puffin colony that relied heavily on sand lance. Despite the fact that Martin identified 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 became unavailable.

Adult seabirds can increase their short-term foraging effort when prey is scarce in order to provide sufficient food for development of their young. Work with kittiwakes in Prince William Sound has shown that breeding adults have the potential to buffer their chicks against variable prey resources by traveling further and transporting larger food loads to provision young (Irons 1992). If adult seabirds can increase their foraging effort and provide more biomass of low-lipid prey, will the chicks develop at the same rate as chicks whose parents are able to provide the same amount of calories yet less biomass of a lipid-rich prey? This is the question we are addressing with the iso-caloric comparisons.

A large part of the energy content of sand lance and capelin is in the form of lipid, whereas in low-lipid fish, like pollock, most of the energy content is in the form of protein. Protein is much less energy dense than lipid and utilizing it as an energy source requires excretion of the resultant nitrogenous waste products. The growth and development of tufted puffin chicks, however, does not seem to be affected by the source of energy (i.e., lipid vs. protein). In the iso-caloric comparison the growth and development of both groups was similar. The group receiving 80 g/day of pollock had a slight edge in mass gain over the group receiving 45 g/day of capelin, but structural growth (wing, culmen and tarsus) was not significantly different. Fat index was significantly higher (more than double), however, for the capelin group versus the pollock group, indicating that nestlings fed pollock did not store as much body fat. This could have a significant influence on survival of these chicks after they fledge and are foraging for themselves.

Low availability of high-quality forage fishes could have adverse effects on nestling growth and development of piscivorous seabirds. If parental foraging is constrained, the availability of high-quality forage fish is necessary to compensate for reductions in biomass of prey provided to nestlings. If foraging is not constrained, adults should still preferentially choose high-quality prey to provision nestlings, even if this means providing less total biomass. Provisioning young with high-quality prey will generally result in nestlings that gain body mass and develop structurally more rapidly, and that fledge with greater energy reserves.

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Fig. 1. Daily energy consumption of Tufted Puffin and Black-legged Kittiwake nestlings on experimental diets.

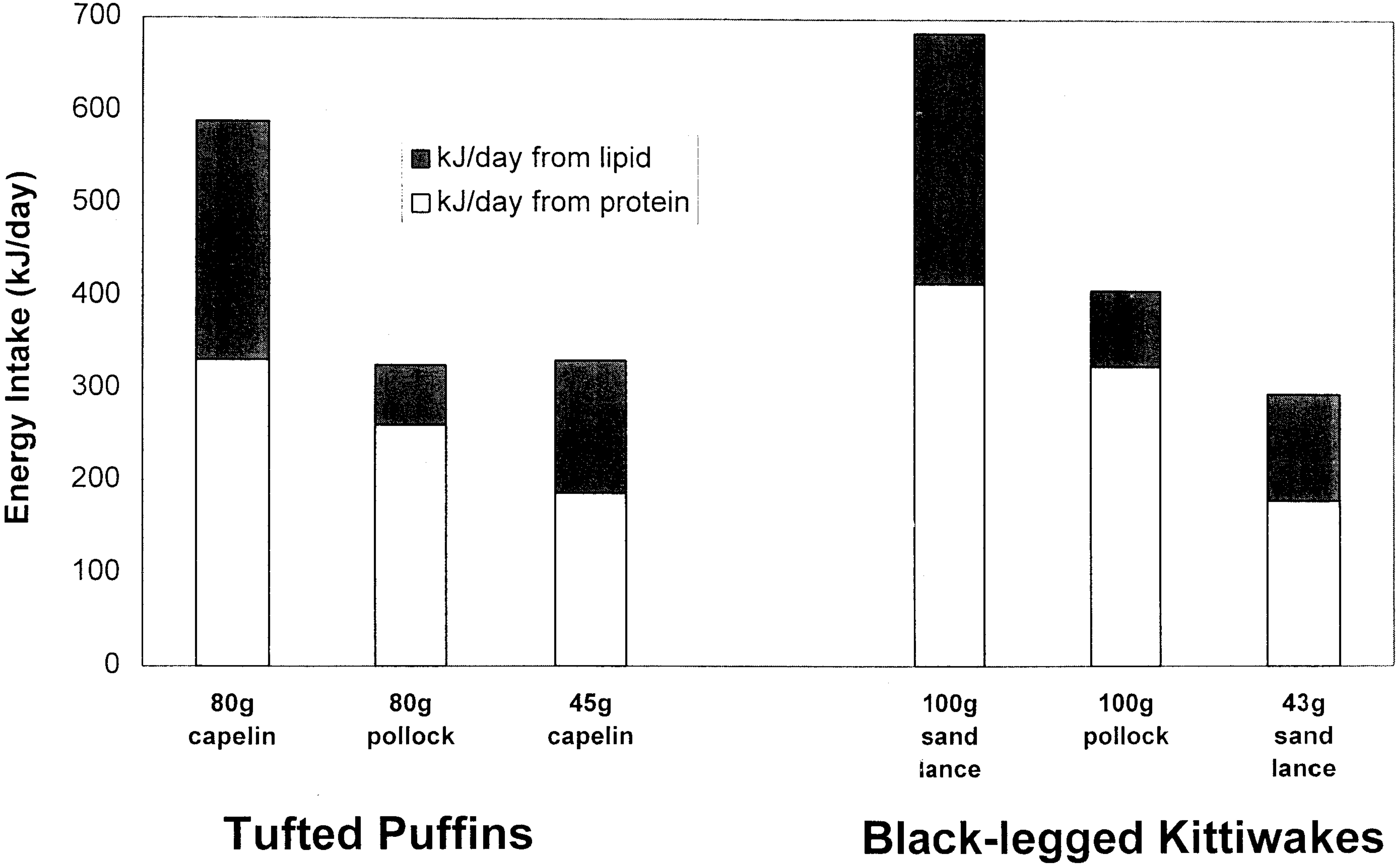


Fig. 2. Growth in body mass of Tufted Puffin nestlings raised on three different experimental diets.

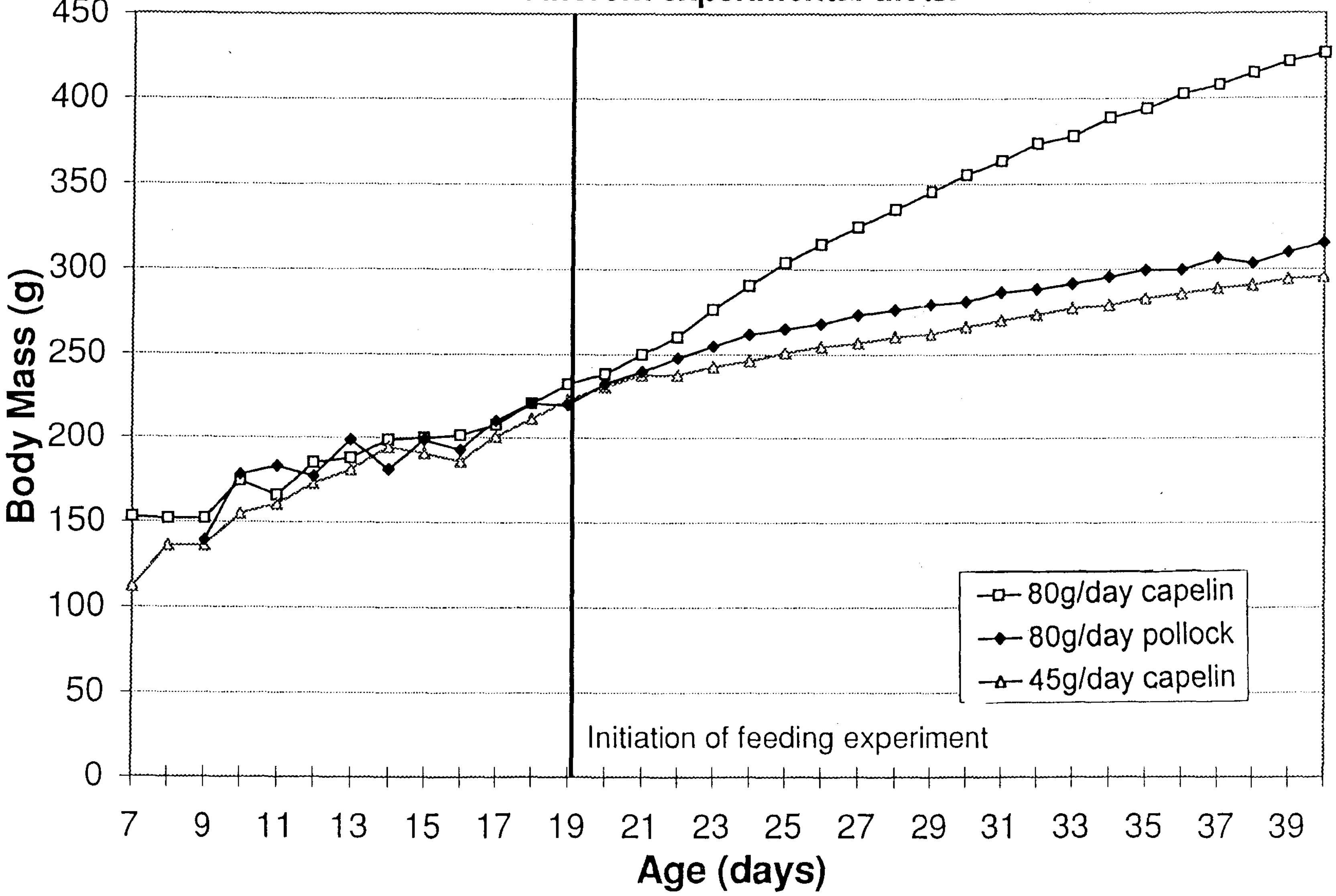


Fig. 3. Growth in wing length of Tufted Puffin nestlings raised on three different experimental diets.

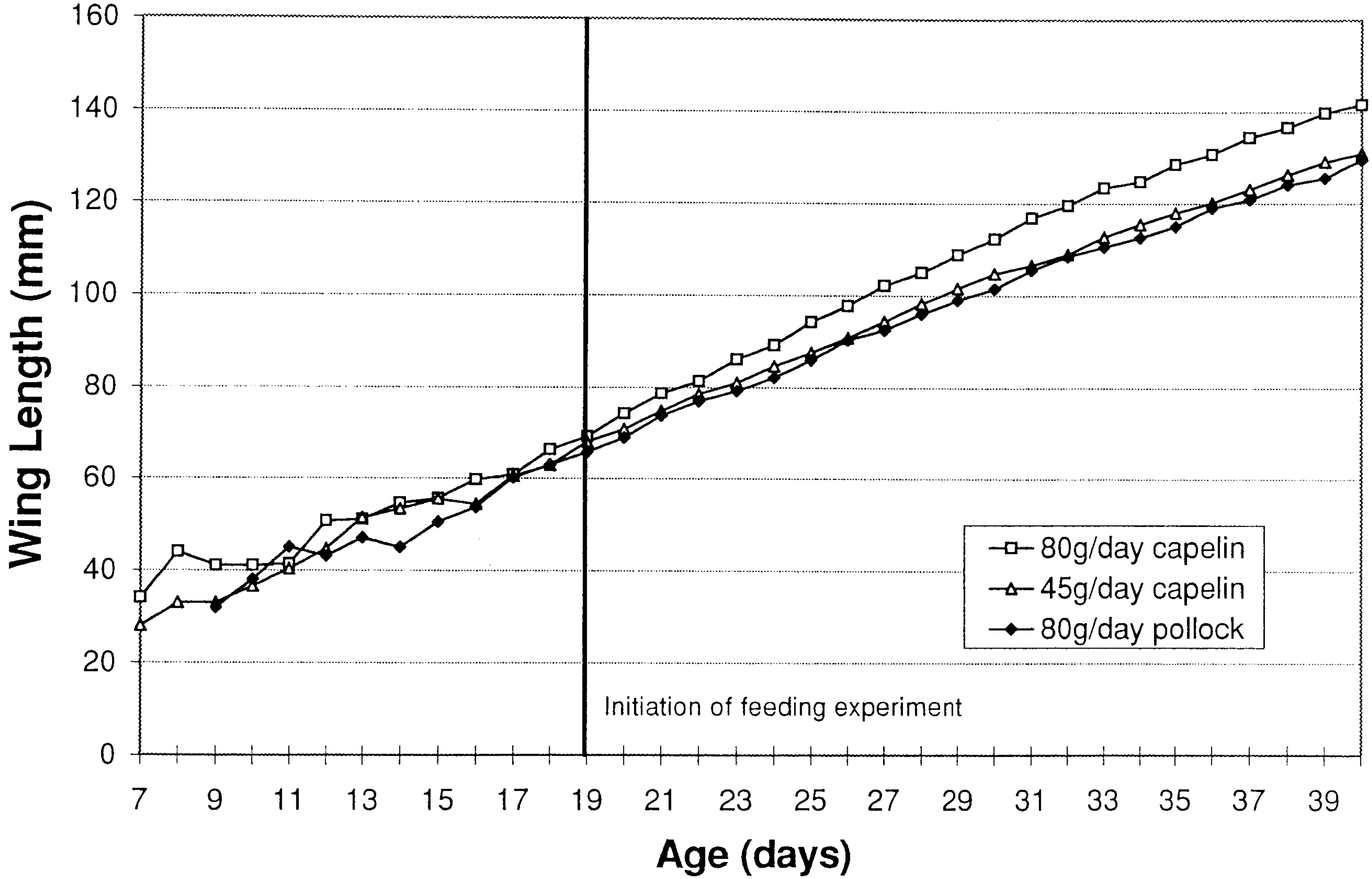


Fig. 4. Growth in culmen length of Tufted Puffin nestlings raised on three different diet treatments.

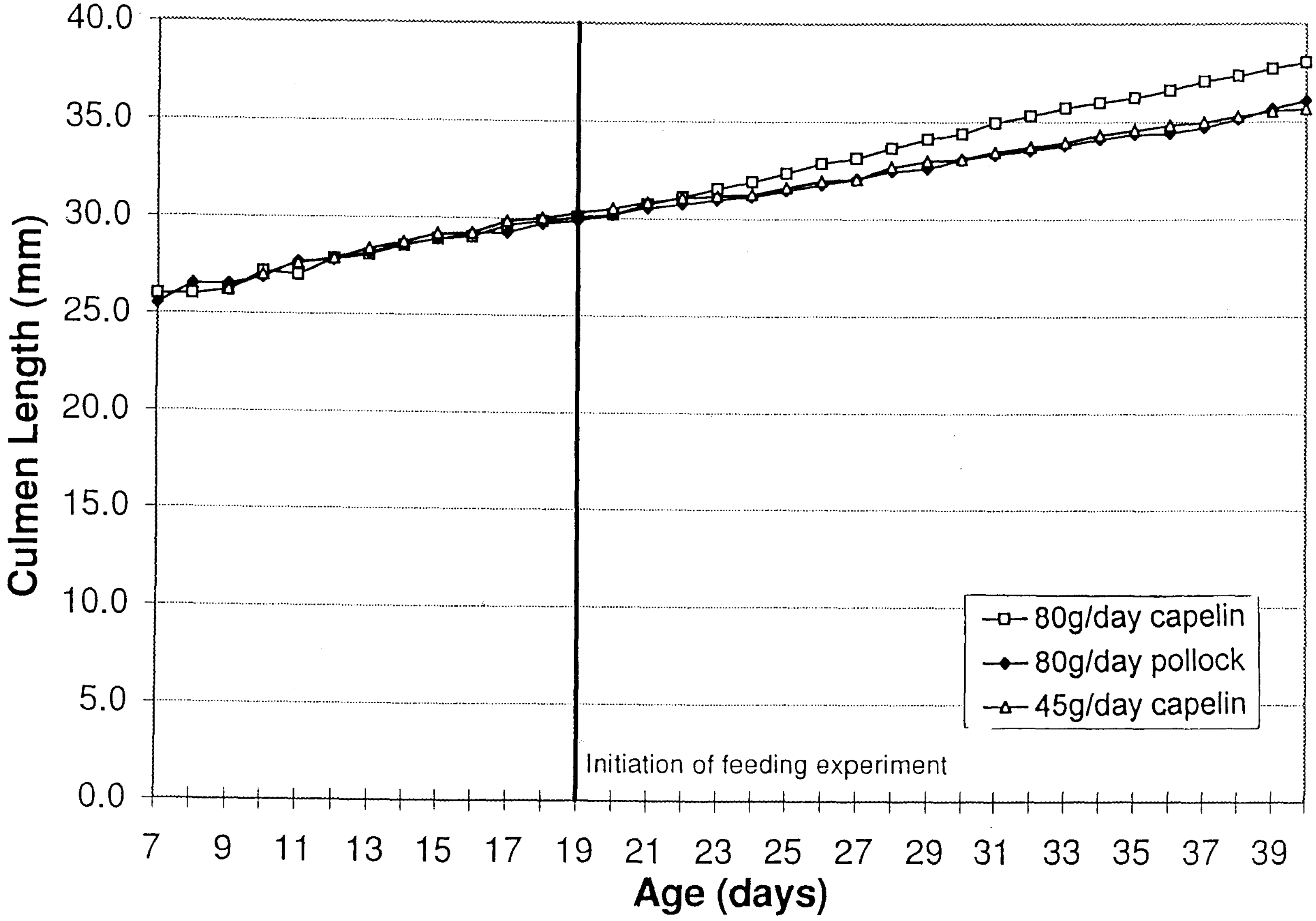


Fig. 5. Growth in tarsus length of Tufted Puffin nestlings raised on three different experimental diets.

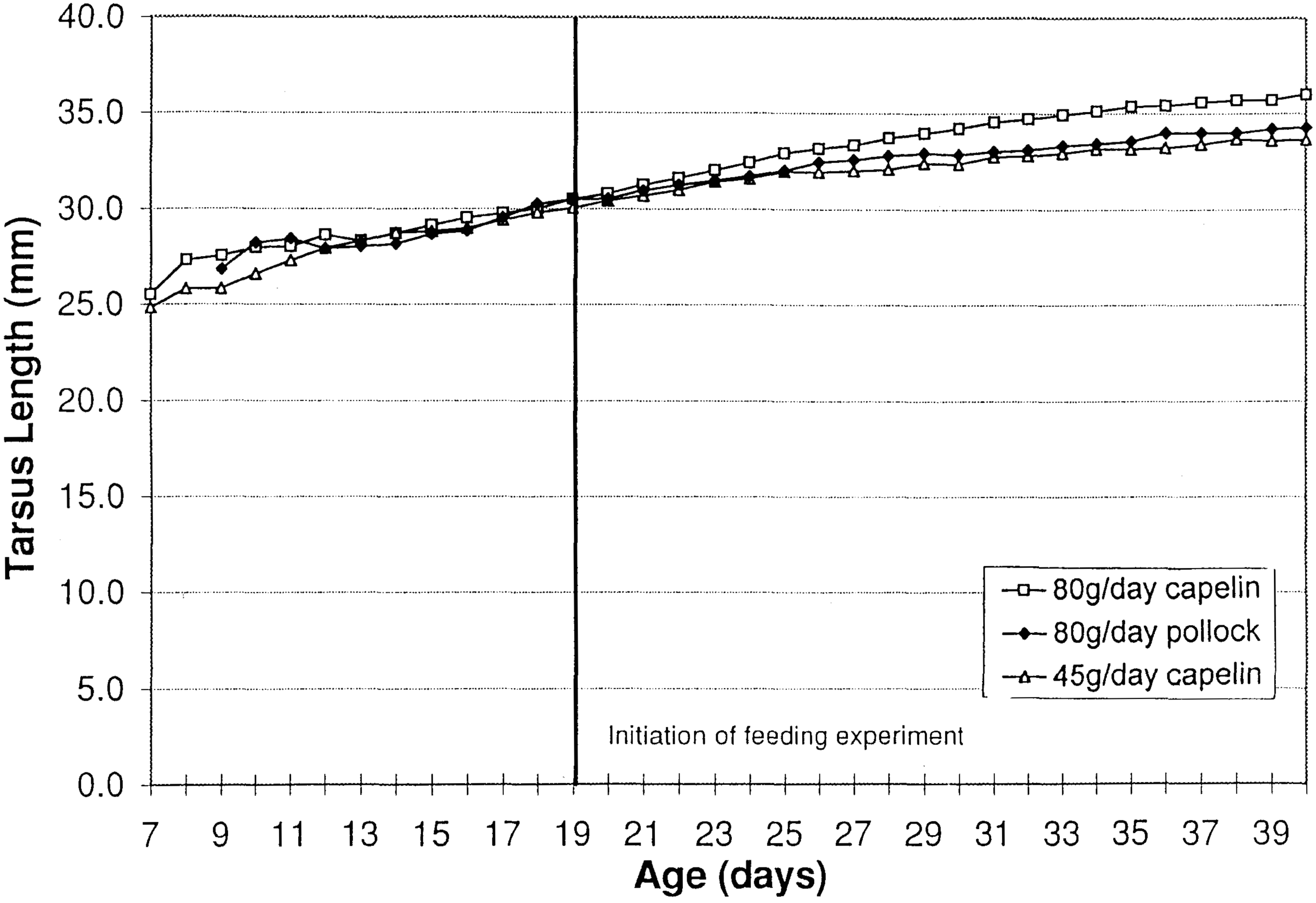
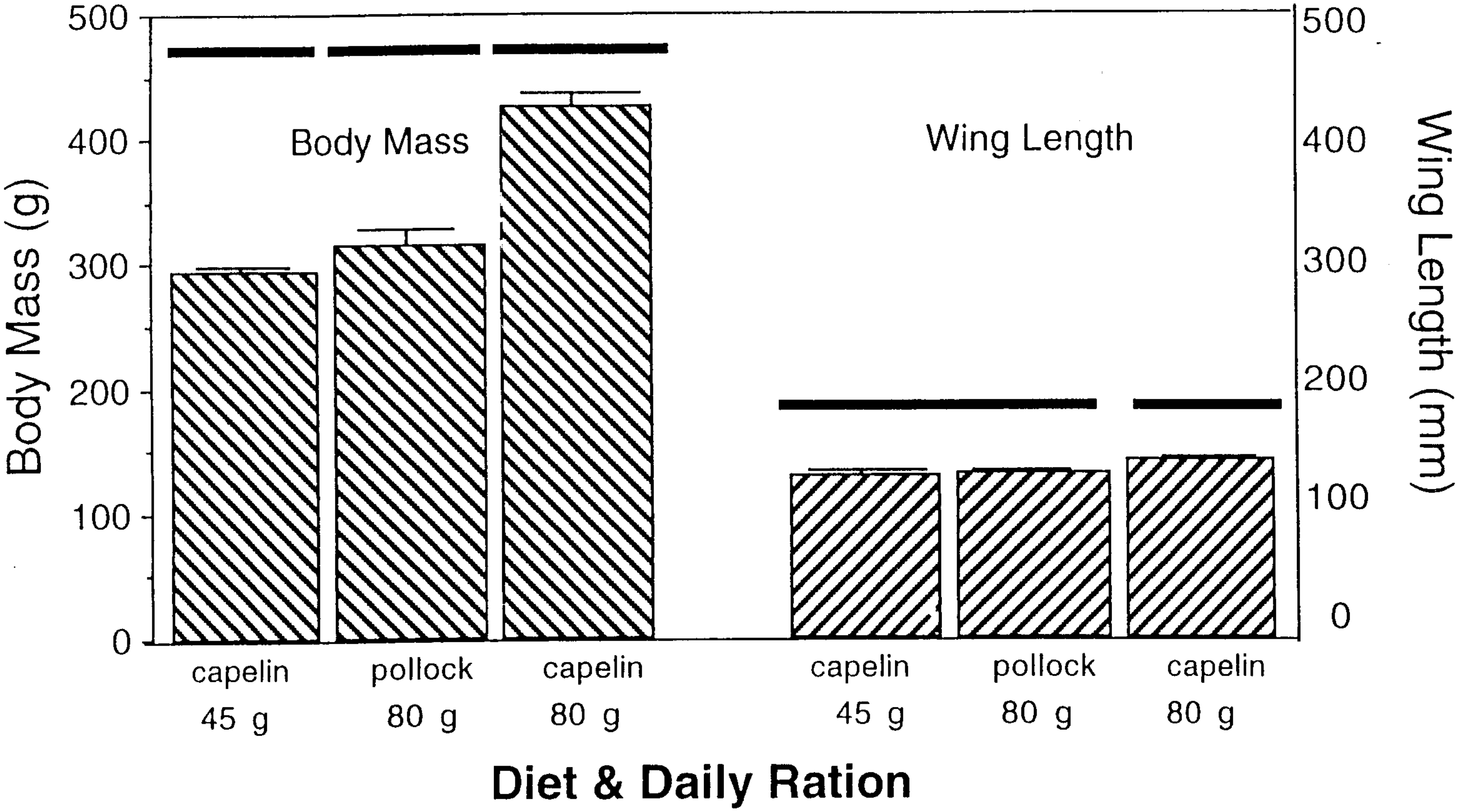


Fig. 6. Average body mass and wing length of Tufted Puffin fledglings (40 days post-hatch) raised on three different experimental diets.



(error bars indicate 95% confidence interval;
breaks in horizontal bars indicate significant differences between means)

Fig. 7. Growth in body mass of Black-legged Kittiwake nestlings raised on three different experimental diets.

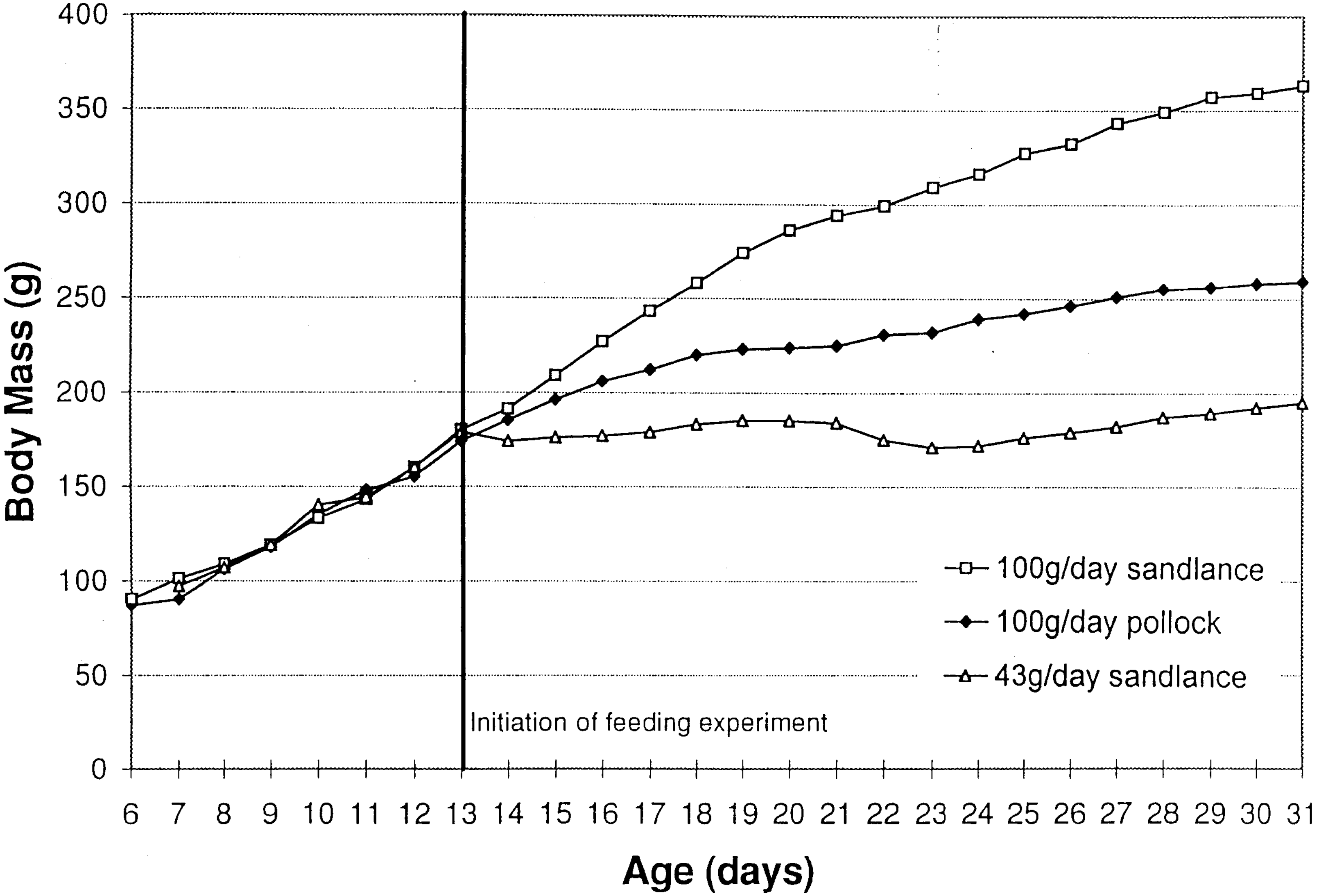


Fig. 8. Growth in wing length of Black-legged Kittiwake nestlings raised on three different experimental diets.

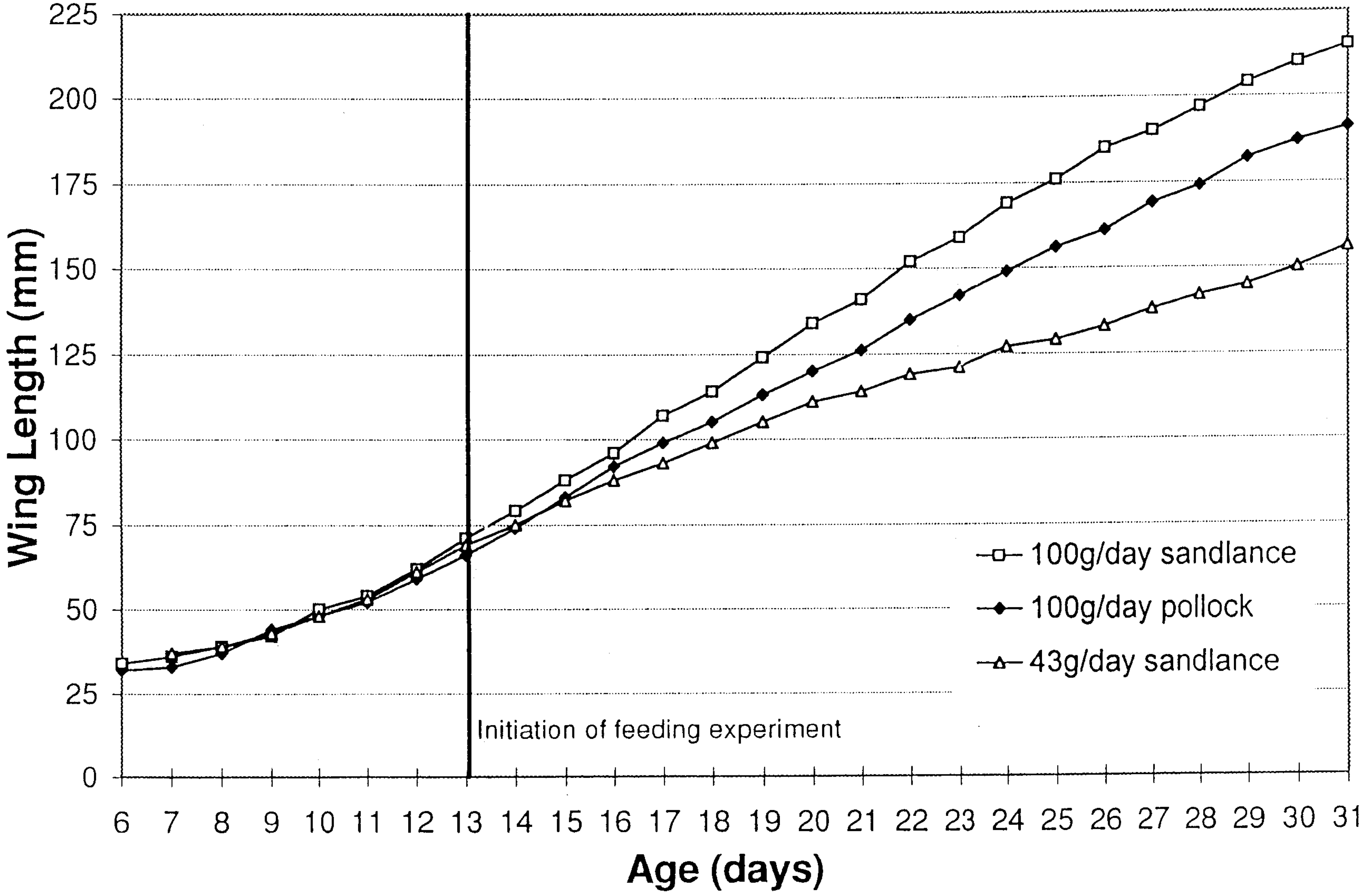


Fig. 9. Growth in head-bill length of Black-legged Kittiwake nestlings raised on three different experimental diets.

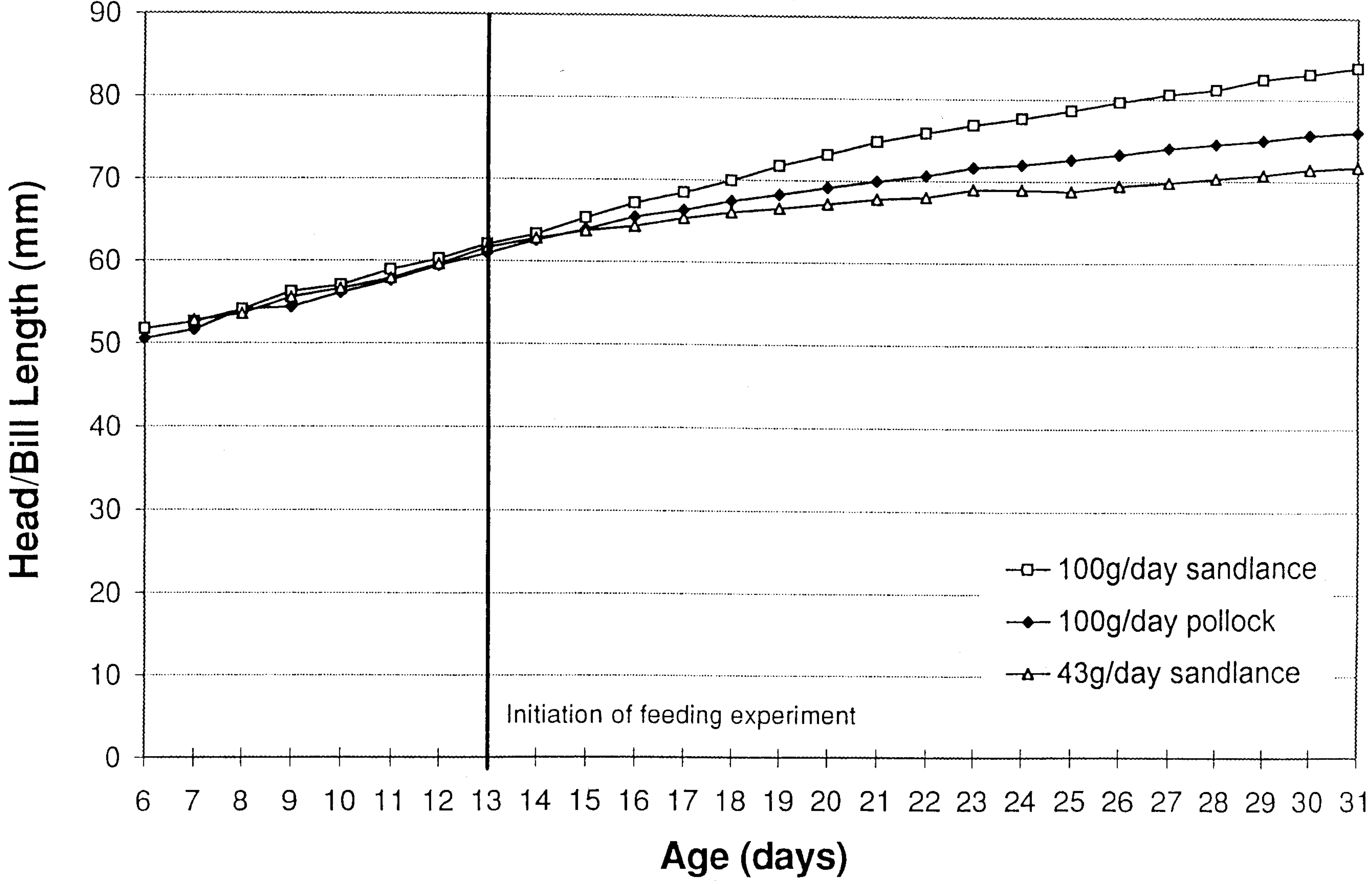


Fig. 10. Average body mass and wing length of Black-legged Kittiwake fledglings (31 days post-hatch) raised on three different experimental diets.

(error bars indicate 95% confidence interval;
breaks in horizontal bars indicate significant differences between means)

Fig. 11. Fat Index of Tufted Puffin and Black-legged Kittiwake nestlings raised on different experimental diets.