

SPATIAL AND TEMPORAL VARIATION IN TUFTED PUFFIN *FRATERCULA CIRRHATA* NESTLING DIET QUALITY AND GROWTH RATES

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SUMMARY

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Seabirds have long been promoted as bio-indicators, because parameters such as reproductive success, nestling growth rates, and diet composition respond markedly to changes in food supply. Although such responses are often associated with broad-scale oceanographic phenomena, they are also influenced by processes that occur on much smaller spatial scales. We quantified Tufted Puffin *Fratercula cirrhata* nestling growth rates, apparent fledging success, and diets at several colonies in Chiniak Bay, Kodiak Island, Alaska from 2003–2005. We also measured the lipid content of forage fish fed to nestlings, because diet selection is expected to be influenced by prey quality. Although apparent fledging success was generally high, complete reproductive failure occurred at one small colony in all years, possibly due to mammalian predators. In 2003, we found a striking difference in diet composition between colonies, with nestlings on Chiniak Island in the outer bay consuming primarily Pacific sand lance *Ammodytes hexapterus* (50%) and capelin *Mallotus villosus* (45%) and nestlings at Cliff Island in the inner bay (22 km away) having a diet dominated (76%) by lower quality Pacific sandfish *Trichodon trichodon*. Our results indicate that Tufted Puffin diets can vary on a relatively small spatial scale and that puffins may settle for lower quality prey when it is readily available in close proximity to the breeding colony.

Key words: prey quality, diet composition, indicator species, breeding performance, Tufted Puffin, *Fratercula cirrhata*, growth, seabird, Alaska

INTRODUCTION

Seabirds have long been recognized as potential indicator species, providing insights into the abundance and distribution of prey populations that are difficult and costly to achieve by other means (Cairns 1987, Montevecchi 1993). In the Gulf of Alaska, declines in seabirds and other apex predators over the past century have been attributed to changes in the distribution and abundance of key forage fishes (Agler *et al.* 1999, Anderson & Piatt 1999). Although climate-driven physical forcing underlies changes in food web structure, measurement of physical parameters alone does not provide definitive information on forage fish dynamics because complex biological interactions, including top-down forces, are important as well (Hunter & Price 1992).

Support for using seabirds as biological indicators comes from numerous studies linking seabird breeding phenology and productivity to prey abundance (e.g. Hamer *et al.* 1993, Reid *et al.* 2005) and indices of ocean climate (e.g. Durant *et al.* 2003, Gjerdrum *et al.* 2003, Buck *et al.* 2007). Few studies have quantified predator-prey response functions (Piatt *et al.* 2007), but there is increasing evidence that foraging strategies and diet selection are influenced by prey quality (Suryan *et al.* 2002). Thus, seabird diets may not always reflect prey availability per se, unless prey quality is factored into measures of availability (e.g. Jodice *et al.* 2008). Breeding failure of seabirds might occur when prey is readily available, but of poor quality, owing to an unfavorable ratio of high and low quality prey species (Piatt & Anderson 1996) or a decrease in the quality of a dominant forage species (Wanless *et al.* 2005).

One important caveat on using seabirds as indicator species is that the scale at which measured parameters fluctuate matters. Seabirds are sensitive to both large-scale and small-scale oceanographic processes. In a revealing example of the latter effect, Hipfner *et al.* (2007) reported that Tufted Puffins *Fratercula cirrhata* successfully reared young in one subcolony on Triangle Island, British Columbia, even as they failed in another subcolony only 1.5 km away. In a multi-year study, the authors found that productivity and diets (inferred from isotope ratios) differed consistently between the subcolonies.

In the present study, we monitored rates of nestling growth and survival at Tufted Puffin colonies in Chiniak Bay, Kodiak Island, Alaska. We sampled nestling diets at one outer-bay colony and one inner-bay colony and measured the lipid content of prey species. Our objective was to assess the degree of congruence between diet composition, diet quality, and reproductive performance at puffin colonies separated by less than 25 km. Our results provide further insight on the importance of small-scale spatial heterogeneity in designing and interpreting seabird monitoring programs.

METHODS

Study area and species

We worked in Chiniak Bay, Alaska (57°40'N, 152°20'W) from 2003–2005. Tufted Puffins are abundant and widely distributed in the region. No recent census data are available, but in 1975 Dick *et al.* (1976) recorded more than 8300 breeding pairs in 21 island

colonies. We monitored fledging success, growth rates, and/or nestling diet at five colonies (Fig. 1): reproductive parameters at two inner-bay colonies (Puffin and Kulichkoff islands), Svitlak Island in Kalsin Bay, and Chiniak Island at the outer edge of Chiniak Bay, and nestling diet at the two largest colonies in the study area—Chiniak Island (>5000 pairs) and Cliff Island in the inner bay (~500 breeding pairs). Due to logistical constraints we were unable to measure reproductive parameters at the inner bay colony (Cliff Island) where dietary information was collected.

Tufted Puffins are monogamous burrow nesters with biparental care. They have been promoted as samplers of forage fish populations (Hatch & Sanger 1992). Their reproductive success and breeding phenology are known to be affected by broad-scale ocean climate conditions (Gjerdrum *et al.* 2003).

Reproductive parameters

We began monitoring Tufted Puffin burrows on 14 July in 2003 and on 22 July in both 2004 and 2005. Nest chambers that were unreachable from their entrances were accessed by digging vertical holes, which we covered between visits with plywood squares or flat stones. We weighed chicks (± 2 g) with Pesola spring scales and measured flattened wingchord (± 1 mm) from wrist to wingtip. We attempted to visit all burrows every 5 d, but inclement weather occasionally prevented access to some colonies. In practice, visits were made every 4–8 d during the linear phase of chick growth and every 4–5 d during the fledging period. When hatch date was unknown, we used a regression (wingchord versus age for known-age nestlings) to estimate age. We calculated growth rate for each chick as the slope of linear regression (mass versus age) between ages 10 and 30 d, the near-linear portion of the growth curve. Nestlings with fewer than three measurements of mass between ages 10 and 30 d were excluded from growth rate analysis.

Disturbance of Tufted Puffins during incubation can cause abandonment (Pierce & Simons 1986, Whidden *et al.* 2007); moreover, lower quality individuals tend to lay their eggs later and are thus more likely to be disturbed during incubation. Therefore, we did not include unhatched eggs in our measure of fledging

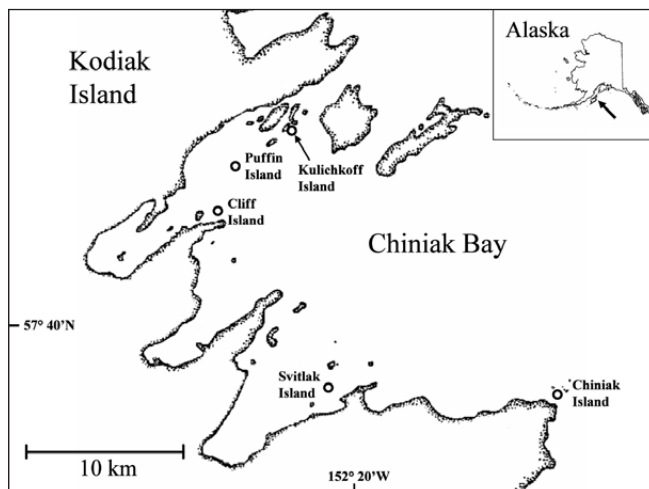


Fig. 1. Distribution of Tufted Puffin colonies in Chiniak Bay, Alaska where nestling diet, growth, and survival were monitored. Diets were sampled at Chiniak and Cliff Island, whereas nestling growth and fledging success were measured at Chiniak, Kulichkoff, Puffin, and Svitlak islands.

success, and because we do not consider failure at the egg stage, our measure of fledging success is an overestimate of true success. Following Gjerdrum *et al.* (2003), we define ‘apparent fledging success’ as the proportion of chicks found on any burrow check that attained a minimum wingchord of 130 mm before disappearing. We do not employ Mayfield estimates or program Mark (Jehle *et al.* 2004), as the fledging success of individual chicks did not appear to be independent of other burrows at the same colony (see Results).

Nestling diet

Samples of food items delivered to nestlings were collected throughout July and August on Cliff and Chiniak Islands. We obtained most samples by screening burrows either individually using small wire screens (15x15 cm) or in groups (20–30 burrows at a time) with a 7x10 m seine. Either method effectively prevented adults from entering with bill loads, and many deposited their loads at burrow entrances. A few samples were collected opportunistically when observers came across fresh prey samples inside the nesting chamber or near burrow entrances where no screens or nets had been placed. A ‘prey sample’ included all prey items collected from one burrow on a given sampling occasion, which is not necessarily equivalent to a bill load—some samples were partial bill loads or comprised multiple bill loads. Prey samples were kept in a cooler with ice packs in the field, transported to cold storage in Kodiak, and kept frozen until they were analyzed. Capelin *Mallotus villosus* were categorized as males (based on secondary sex characters), gravid females (eggs present), or sex unknown.

Lipid extraction

We selected samples of whole fish that appeared to be fresh when they were collected for analysis of lipid concentration. Within a few weeks of collection, we measured mass on a digital scale (± 0.01 g) and took standard lengths (tip of snout to posterior end of last vertebra; ± 1 mm). Prior to lipid extraction, fish were reweighed to quantify water loss during storage. We corrected % lipid per wet mass based on the measured water loss. Mean (\pm SE) water loss was 5.0 ± 0.4 % of body mass. We extracted lipids from a 1.5 g subsample of homogenized whole fish using 2:1 chloroform to methanol according to Folch *et al.* (1957), as modified by Iverson *et al.* (2001). We determined water content of the lipid-free prey by freeze drying a 1.5–3 g homogenized subsample of each fish, and recalculated lipid as a percentage of dry mass. Small fish (<90 mm) were ground whole, and the entire fish was used for lipid extraction; thus, subsamples to determine water content were not available. Although percent lipid per wet mass for whole prey can be overestimated due to the desiccation of fish obtained from burrow screens, we found the same trends for percent lipid per dry mass (see below). We regard lipid content—the most important determinant of energy density (kJ/g) of forage fishes (Van Pelt *et al.* 1997, Anthony *et al.* 2000)—as an appropriate index of prey quality.

Statistical analysis

All analyses were done in SAS 9.2 (SAS Institute), with a criterion of $P < 0.05$ for statistical significance.

Nestling Growth and Survival

We used ANOVA to test for spatial and temporal variation in nestling growth and survival. For each ANOVA, a reproductive

parameter (either growth rate, peak mass, or fledging mass) was the dependent variable, and colony, year, and the interaction between colony and year were independent variables. Because one goal was to link reproductive parameters to diets, and dietary data were only available for the inner bay in 2003, we also tested for differences in reproductive parameters in 2003 between Puffin Island (inner bay) and Chiniak Island (outer bay) using Student's *t*-tests. Unfortunately, we lacked reproductive data from Cliff Island, the inner-bay colony where diet samples were collected. We also used ANOVA to test for annual differences in reproductive parameters at Chiniak Island, where diet samples from all three years were available. ANOVAs indicating significant differences were followed by post-hoc Tukey HSD tests.

Nestling Diets

Because neither burrow samples collected on a given day nor fish within a burrow sample were independent, we calculated the daily mean proportion of each prey type for use in statistical analyses. The daily mean proportions calculated for days on which fewer than eight samples were collected proved to be outliers and were therefore excluded from the analyses. We tested for differences in diet between two colonies with sufficient data (Cliff and Chiniak islands in 2003) and among years (Chiniak Island, 2003-2005) in separate multivariate analyses of variance (MANOVAs), followed by univariate tests (ANOVAs). Dependent variables used in both MANOVAs were percentage diet composition (daily means) of the three dominant species in nestling diets — capelin, Pacific sand lance *Ammodytes hexapterus*, and Pacific sandfish *Trichodon trichodon*. The independent variable in the first MANOVA was colony (Cliff or Chiniak island in 2003). The independent variable in the second MANOVA was year (2003, 2004, or 2005 on Chiniak Island). Significant ANOVAs were followed by post-hoc Tukey's HSD tests for multiple comparisons among the 3 years of data from Chiniak Island.

Prey quality

We tested for intraspecific differences in lipid content of prey (dependent variable) using linear regression (least squares method), with year and/or sex as class variables and standard length as a continuous covariate. Significant class effects were examined using post-hoc Tukey's HSD tests. In most cases, the untransformed data failed to meet the assumption of homogeneity of variances required for parametric tests, so a rank transformation was applied. For capelin, we had too few samples within each sex class to test for interannual variability.

RESULTS

Nestling growth and survival

Puffins fledged nestlings at all colonies in all years, with the exception of Kulichkoff Island. On 14 July 2003, the first day nests were checked on Kulichkoff, only 2 of 25 burrows contained eggs, indicating that most birds either failed in early incubation or did not attempt to breed. Both active burrows subsequently failed, one during incubation and one at the chick-rearing stage. Similarly, no eggs or chicks were present at Kulichkoff Island in ~30 burrows checked in 2005. In 2004, all 13 chicks located in burrows on Kulichkoff disappeared prematurely (10) or were found dead and partially eaten in their burrows (3). Partially consumed puffin carcasses were never found at other colonies.

Excluding Kulichkoff Island, apparent fledging success varied from 41% at Svitlak Island in 2003 to 100% at Puffin Island in 2003 (Table 1). The low rate on Svitlak Island reflected the disappearance of 9 nestlings in a 5-day period (21-25 July), the cause of which was unknown. Fledging success for chicks hatched after 26 July on Svitlak Island was relatively high (80%; *n* = 5).

TABLE 1
Parameters measured in Tufted Puffin nestlings at study colonies in Chiniak Bay, Alaska, 2003-2005.
Sample sizes are given in parentheses.

Colony	Year	% Fledging success	Growth Rate (g/day + SD)	Maximum Mass (g ± SD)	Mass at fledging (g ± SD)
Chiniak	2003	77 (34)	15.3 ± 3.5 (29)	544 ± 55 (31)	534 ± 54 (31)
	2004	90 (32)	14.3 ± 2.5 (28)	526 ± 53 (28)	470 ± 63 (28)
	2005	98 (41)	16.2 ± 3.4 (41)	587 ± 51 (38)	564 ± 50 (38)
Puffin	2003	100 (13)	13.8 ± 3.5 (17)	544 ± 44 (18)	529 ± 51 (18)
	2004	84 (19)	16.7 ± 2.2 (20)	582 ± 53 (15)	575 ± 58 (15)
	2005	100 (14)	15.9 ± 2.9 (15)	565 ± 53 (14)	558 ± 53 (14)
Svitlak	2003	41 (17)	13.5 ± 2.5 (7)	586 ± 35 (7)	575 ± 40 (7)
	2004	78 (18)	15.3 ± 3.1 (19)	535 ± 52 (14)	522 ± 54 (14)
	2005	92 (13)	16.5 ± 3.4 (12)	563 ± 32 (11)	561 ± 29 (11)
Kulichkoff	2003	0 (1)	N/A	N/A	N/A
	2004	0 (11)	19.0 ± 2.1 (4)	N/A	N/A
	2005	N/A	N/A	N/A	N/A
All Colonies	2003	71 (65)	14.6 ± 3.4 (53)	550 ± 51 (56)	538 ± 53 (56)
	2004	74 (80)	15.5 ± 3.8 (71)	543 ± 57 (57)	509 ± 74 (57)
	2005	97 (66)	16.2 ± 3.2 (68)	579 ± 49 (64)	565 ± 53 (64)

Growth rates of nestlings did not differ significantly between colonies (Table 1, $F_{2,179} = 0.05$, $P = 0.9$), but the year effect was significant ($F_{2,179} = 4.23$, $P < 0.02$) as was the interaction between year and colony ($F_{4,179} = 2.57$, $P < 0.04$). In 2003, growth rates of nestlings from the outer bay (Chiniak Island, $n = 29$) were similar to nestlings in the inner bay (Puffin Island $n = 17$; $t = 1.38$, $P = 0.17$). No detectable difference emerged among years in growth rates of chicks on Chiniak Island ($F_{2,95} = 2.77$, $P = 0.07$). Peak masses were similar across colonies ($F_{2,168} = 0.07$, $P = 0.8$) and years ($F_{2,168} = 2.88$, $P = 0.06$), but there was a significant interaction between colony and year ($F_{4,168} = 4.77$, $P < 0.002$). In 2003, peak nestling mass in the outer bay (Chiniak Island, $n = 31$) and inner bay (Puffin Island, $n = 18$) were similar ($t = 0.01$, $P = 1.0$), whereas at Chiniak Island, peak mass differed significantly among years ($F_{2,95} = 12.4$, $P < 0.0001$). Post-hoc Tukey tests revealed peak mass was higher in 2005 compared to 2003 and 2004 ($P < 0.05$).

Mean mass of fledglings differed between colonies ($F_{2,168} = 6.5$, $P < 0.002$) and years ($F_{2,168} = 6.97$, $P < 0.002$). The interaction of colony and year was also significant ($F_{4,168} = 8.21$, $P < 0.0001$). In 2003, the fledging mass of nestlings in the outer bay (Chiniak Island, $n = 31$) did not differ significantly from chicks in the inner bay (Puffin Island, $n = 18$; $t = 0.28$, $P = 0.178$). At Chiniak Island, fledging mass differed among years ($F_{2,95} = 24.68$, $P < 0.0001$). Post-hoc Tukey tests revealed all pairwise comparisons of years were significant, with the highest fledging masses occurring in 2005 and the lowest in 2004 ($P < 0.05$).

Nestling diets

During all years, nestling diets at Chiniak and Cliff islands were dominated by capelin, Pacific sand lance, and Pacific sandfish (Table 2). In 2003, diet composition differed between Chiniak Island (outer bay) and Cliff Island (inner bay) ($F_{3,8} = 42.8$, $P < 0.0001$). Nestlings on Cliff Island were fed mostly sandfish, whereas chicks at Chiniak Island consumed significantly more capelin and sand lance (Table 2). Pacific sandfish collected at all colonies were judged to be juveniles (i.e. < 13 cm; Thedinga *et al.* 2006). Four of five diet samples collected opportunistically on Puffin Island were composed of Pacific sandfish.

TABLE 2
Species composition (% mass) of Tufted Puffin nestling diets at Chiniak and Cliff islands, Chiniak Bay, Alaska, 2003-2005^{a,b}

Prey	Chiniak Island			Cliff Island		
	2003	2004	2005	2003	2004	2005
Pacific sand lance	50	66	22	6	77	67
Capelin	45	21	69	16	12	33
Pacific sandfish	6	5	5	76	8	0
Salmonids	0	3	4	2	4	0
Pacific cod	0	4	0	<1	0	0
No. of samples ^c	190	156	146	75	26	9

^a Samples weighted equally in calculating percent contribution of each prey type.

^b Species unlisted accounted for $< 1\%$ in all years.

^c Each sample included one to many fish (see Methods).

Nestling diets on Chiniak Island were dominated by capelin and/or Pacific sand lance in all 3 years (Table 2), although we found annual variation in diet composition ($F_{6,38} = 6.88$, $P = 0.0003$). ANOVA tests revealed annual differences in the percentage contributions of capelin and sand lance, but not of sandfish. Post-hoc Tukey tests indicated nestling diets in 2004 contained significantly more sand lance and less capelin compared to 2003 and 2005 ($P < 0.05$). We also found substantial differences in the size classes of sand lance in nestling diets (Fig. 2). Unlike 2005, diets in 2003 and 2004 were dominated by smaller sand lance (< 90 mm).

For unknown reasons, we obtained far fewer samples at Cliff Island in 2004 and 2005 than in 2003, despite increased effort in the later field seasons. While the later collections were insufficient for statistical comparisons, nestling diets at Cliff Island in 2004 and 2005 were qualitatively similar to Chiniak Island—i.e. dominated by capelin and sand lance, rather than sandfish (Table 2).

Prey quality

Forage fish in the bill loads of Tufted Puffins exhibited intraspecific variation in lipid content. Sand lance ranged from 0.7 to 12.6% lipid relative to wet mass (6.2 to 43.0% of dry mass), with a significant effect of year on percent lipid per wet mass ($F_{2,49} = 43.2$, $P < 0.0001$; Fig. 3a). Lipid content was positively correlated with standard length ($F_{1,49} = 46.2$, $P < 0.0001$), and the interaction of year and standard length was significant ($F_{2,49} = 2.60$, $P = 0.01$). The percentage of lipid on a dry mass basis was significantly related to year ($F_{2,31} = 6.83$, $P = 0.004$; Fig. 3b) and standard length ($F_{1,31} = 7.77$, $P = 0.009$), with no significant interaction of year and standard length ($P = 0.15$). Tukey HSD tests revealed lipid content of sand lance was higher in 2005 than in 2004 (measured as either % wet mass or % dry mass) or 2003 (% wet mass only).

Lipid content of capelin was also highly variable, ranging from 0.6 to 10.9 % of wet mass (5.0 to 48.9 % dry mass). Male and female capelin differed in percentage of lipid per wet mass ($F_{2,36} = 9.43$, $P < 0.0005$; Fig. 4a). A post-hoc Tukey-HSD test revealed that male capelin had lower lipid content per gram wet mass than either gravid females or individuals of unknown sex ($P < 0.05$). A similar,

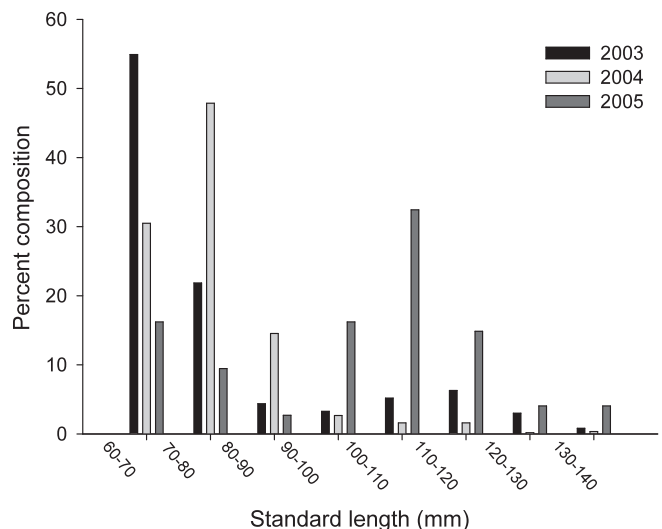


Fig. 2. Size classes of Pacific sand lance in the diets of Tufted Puffin nestlings on Chiniak Island, 2003-2005.

though nonsignificant, difference applied also to dry mass ($F_{2,27} = 3.00$, $P = 0.066$; Fig. 4b). In capelin, neither standard length nor the interaction between standard length and sex affected percent lipid per wet or dry mass (all $P > 0.1$).

Compared to sand lance and capelin, lipid content of Pacific sandfish, Pacific cod *Gadus macrocephalus*, and salmonids was generally lower and much less variable (Table 3). In sandfish, lipid content was 1.2–2.6 % wet mass (5.9–14.3 % dry mass). The wet mass measurement was affected by year ($F_{2,29} = 2.47$, $P = 0.02$) but not by standard length ($F_{1,29} = 1.87$, $P = 0.18$). Percent lipid content of dry mass was significantly affected by year ($F_{2,19} = 5.84$, $P = 0.01$) and was negatively correlated with standard length ($F_{1,19} = 5.84$, $P = 0.03$). Percent lipid content (dry mass and wet mass) of sandfish was lower in 2004 than in 2003 or 2005 (Tukey HSD, $P \leq 0.05$).

Pacific cod were fed to puffin nestlings in 2004 only. Lipid content was 1.3 – 1.9% of wet mass and 6.5 – 13.8% of dry mass, but was not correlated with standard length ($P > 0.2$). Percent lipid content of salmonids was 1.5 – 1.8% of wet mass, 5.7 – 8.3% of dry mass, and was uncorrelated with standard length ($P > 0.5$).

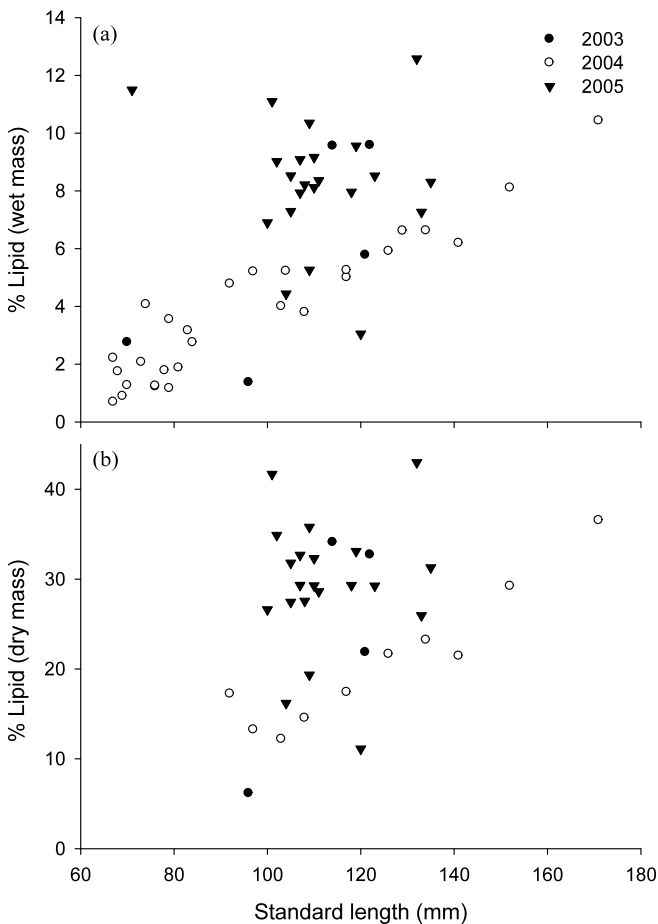


Fig. 3. Relationship between fish length and lipid content of Pacific sand lance expressed as a percentage of: (a) wet mass, and (b) dry mass. Fish samples collected by screening Tufted Puffin burrows in Chiniak Bay colonies, 2003–2005. Lipid content on a dry mass basis was not determined for fish <90mm as lipids were extracted from the whole fish.

DISCUSSION

Variation in seabird breeding success and diets could result from heterogeneity in foraging conditions, terrestrial habitat quality, or intrinsic characteristics of the birds themselves (i.e. population structural differences in age, experience, and/or individual quality). Thus, the degree to which seabird diets reflect broad-scale changes in ecosystem structure may be compromised in part by local oceanography and its effects on the abundance and distribution of prey populations. We found that the composition and quality of Tufted Puffin diets can vary on a spatial scale of <22km, which is smaller than the birds' presumed foraging range (up to 100 km; Piatt & Kitaysky 2002). Although our study was not designed to evaluate underlying mechanisms, we suggest the large dietary differences observed within Chiniak Bay in 2003 reflected small-scale heterogeneity in prey populations. We also found small-scale spatial heterogeneity in rates of nestling growth and survival, although variation in nestling growth was small relative to other studies of Tufted Puffins (Piatt & Kitaysky 2002).

Hipfner *et al.* (2007) reported differences in both reproductive success and diets (inferred from stable isotopes) at a spatial scale

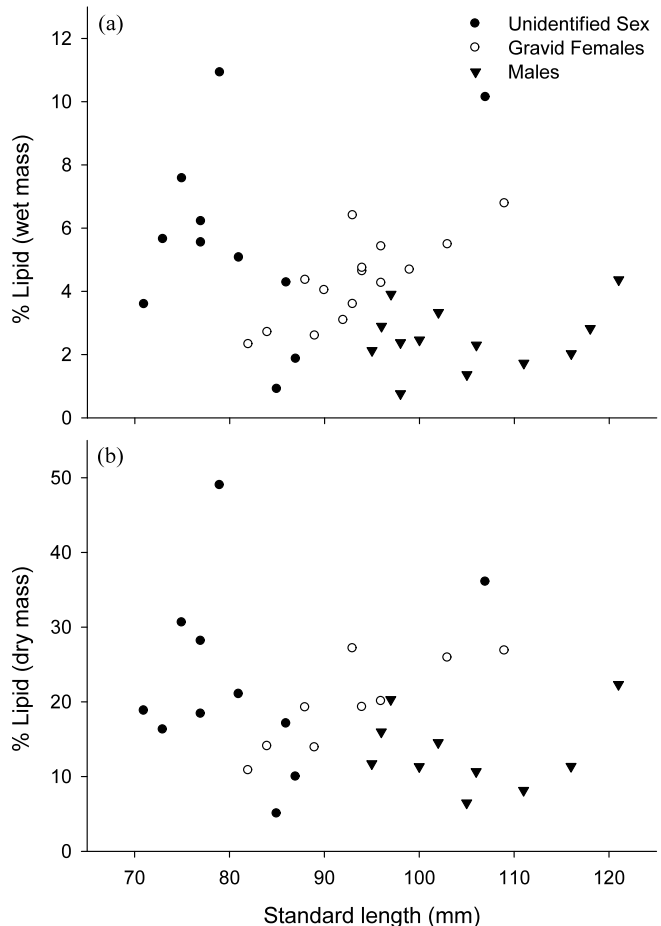


Fig. 4. Relationship between fish length and lipid content of capelin expressed as a percentage of: (a) wet mass, and (b) dry mass. Fish samples collected by screening Tufted Puffin burrows in Chiniak Bay colonies, 2003–2005.

of ~1.5 km, for which the underlying mechanisms remain obscure. Litzow *et al.* (2002) found congruent differences in prey quality and reproductive success of Pigeon Guillemots *Cephus columba* at a scale similar to our study (tens of kilometres) and suggested such differences reflected differences in prey availability shaped by local oceanographic conditions. Notably, Pigeon Guillemots are nearshore feeders, whereas Tufted Puffins are thought to range farther from the colony during breeding (Piatt & Kitaysky 2002). As juvenile Pacific sandfish and sand lance typically occur in shallow, nearshore waters (Thedinga *et al.* 2006, Robards *et al.* 1999a), Tufted Puffins from Chiniak Bay may not rely on pelagic habitat when foraging for their offspring. The mean trophic level at which Tufted Puffins feed increases from early to late in the breeding season (Williams *et al.* 2008a, Davies *et al.* 2009), consistent with the observed switch to local resources during the chick-rearing period. In British Columbia, the dietary shift did not occur in sympatrically breeding alcids, suggesting it is was not a simple outcome of seasonal changes in prey availability (Davies *et al.* 2009).

Factors other than prey availability, notably predation (Kildaw *et al.* 2008), can produce small-scale heterogeneity in reproductive success. In our study, complete colony failure occurred at Kulichkoff Island, possibly due to predation by mammals (Kulichkoff being in close proximity to larger islands and the town of Kodiak). Differences in habitat quality could also produce heterogeneity through differential recruitment and resulting dissimilar age structures at the level of colonies or subcolonies (Kildaw *et al.* 2005, 2008). Breeding performance will reflect age structure through the positive effect of breeding experience and/or the negative effect of senescence (Berman *et al.* 2009, Vieyra *et al.* 2009). Given our findings and other studies (e.g. Kildaw *et al.* 2005, Hipfner *et al.* 2007) showing that diets and reproductive success can vary on small spatial scales, programs intending to use seabirds as indicators should beware. Multiple colonies should be sampled to ensure diets and reproductive parameters reflect large-scale patterns in prey availability, as opposed to small-scale spatial heterogeneity in oceanography, terrestrial habitat quality, and/or seabird population structure.

From 2003–2005, Tufted Puffin nestlings were fed a diet composed almost entirely of forage fish, but the quality of the diet varied due to intraspecific (sex, size-class, and year) and interspecific differences in the lipid content of prey. Although the lipid content of puffin prey in Chiniak Bay seemed consistent with previous studies (see below), the high intraspecific variability in lipid content suggests that classifying species categorically as ‘high quality’ or ‘low quality’ could be misleading. For example, we found that male capelin were lower quality prey than gravid females, consistent with two previous studies (Montevicchi & Piatt 1984, Van Pelt *et al.* 1997). Another investigation of capelin found no sex difference (Anthony *et al.* 2000). The inconsistency may reflect the timing of collection relative to spawning, as spawned-out males are likely of lower quality. Payne *et al.* (1999) noted interannual variability in the lipid content of capelin from the Barents Sea, but sex composition was not reported, thus the source of interannual variation is unclear. Our positive relationship between lipid content and size in sand lance is consistent with previous studies (Van Pelt *et al.* 1997, Robards *et al.* 1999b, Anthony *et al.* 2000).

While seasonal differences in prey quality are well documented (e.g. Robards *et al.* 1999b), few longitudinal studies have assessed interannual variation or determined the factors underlying such variability. In the North Sea, Wanless *et al.* (2005) found that sprat

Sprattus sprattus and lesser sandeels *Ammodytes marinus* in the diets of Common Murres *Uria aalge* were of lower quality in 2004 than in 1976 or 1986–88. They concluded the drop in prey quality was likely responsible for a collapse in murre breeding success. Low-quality food will affect seabird reproduction if parents are unable to provide a larger quantity of prey to offset the lower energy density of low-lipid food (Wanless *et al.* 2005, Romano *et al.* 2006).

Low-lipid diets may reduce digestive efficiency (Romano 2000) and can trigger an increase in the mass of digestive organs (Dahdul and Horn 2003). In Red-legged Kittiwakes *Rissa brevirostris*, nutritional stress caused elevated glucocorticoids during development, leading ultimately to impaired cognitive ability later in life (Kitaysky *et al.* 2006). In related experimental studies, Tufted Puffin nestlings exhibited no measurable stress response to low-calorie or low-quality diets (Kitaysky *et al.* 2005, Williams *et al.* 2008b), and they grew rapidly on a high-calorie, low-lipid diet (Romano 2000). Nevertheless, fat stores at fledging were smaller in chicks reared on the low-lipid diet (Romano 2000), which may have negative consequences for survival.

At the largest colony in outer Chiniak Bay (Chiniak Island), nestling growth rates were high in all years, regardless of diet or prey quality. However, peak mass was lower and nestlings fledged lighter in 2004, when the diet was dominated by smaller, lower

TABLE 3
Lipid content (% wet mass) of prey in Tufted Puffin nestling diets at study colonies in Chiniak Bay, Alaska, 2003–2005

Prey	Year	n (individuals)	Range	Mean ± SD
Pacific sand lance (>90mm ^a)	2003	4	1.4 – 9.9	6.8 ± 4.0
Pacific sand lance (<90mm ^a)	2004	15	0.7 – 4.1	2.0 ± 1.0
Pacific sand lance (>90mm ^a)	2004	13	3.8 – 10.4	5.9 ± 1.8
Pacific sand lance (>90mm ^a)	2005	21	3.1 – 12.6	8.1 ± 2.1
Capelin (Males)	2003-05	13	0.8 – 4.4	2.5 ± 1.0
Capelin (Females)	2003-05	15	2.3 – 6.8	4.3 ± 1.3
Capelin (Sex Unknown)	2003-05	11	0.9 – 10.9	5.6 ± 3.0
Pacific sandfish	2003-05	16	1.3 – 3.1	2.0 ± 0.5
Pacific sandfish	2004	18	1.2 – 2.3	1.5 ± 0.4
Salmonids	2004-05	10	1.2 – 2.1	1.4 ± 0.3
Pacific cod	2004	10	1.2 – 3.1	1.8 ± 0.5

^a Standard length.

quality Pacific sand lance. Nestlings reared at colonies in the inner bay, by contrast, consumed mostly low quality Pacific sandfish in 2003, yet their growth, peak mass, and fledgling mass remained high. Adult puffins in the inner bay may have maintained their rate of energy delivery by targeting lower quality, but locally abundant prey. Lacking data on bill-load size and delivery rates, however, we cannot gauge whether or how adults compensated for the lower quality prey consumed by nestlings in the inner bay.

Whereas Durant *et al.* (2003) found the productivity of multi-prey loading Atlantic Puffins *Fratercula arctica* was related to prey quality, low quality prey may be especially taxing for single-prey loaders such as Common Murres and Pigeon Guillemots. Correlations between prey quality and breeding success are reported in both of the latter species (Litzow *et al.* 2002, Wanless *et al.* 2005). Frederiksen *et al.* (2006) found the productivity of multi-prey loaders was correlated with available prey biomass, whereas productivity in single-prey loading Common Murres was linked to the energy density of individual fish. Clearly, routine assessment of prey quality in monitoring programs would help clarify the effects of prey abundance and prey quality on seabird breeding performance.

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REFERENCES

- AGLER, B.A., KENDALL, S.J., IRONS, D.B. & KLOSIEWSKI, S.P. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. *Waterbirds* 22: 98-103.
- ANDERSON, P.J. & PIATT, J.F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189: 117-123.
- ANTHONY, J.A., ROBY, D.D. & TURCO, K.R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* 248: 53-78.
- BERMAN, M. GAILLARD, J.M. & WEIMERSKIRCH, H. 2009. Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B* 276: 375-382.
- BUCK, C.L., O'REILLY, K.M. & KILDRAW, S.D. 2007. Interannual variability of Black-legged Kittiwake productivity is reflected in baseline plasma corticosterone. *General and Comparative Endocrinology* 150: 430-436.
- CAIRNS, D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261-271.
- DAHDUL, W.M. & HORN, M.H. 2003. Energy allocation and postnatal growth in captive Elegant Tern (*Sterna Elegans*) chicks: responses to high- versus low-energy diets. *Auk* 120: 1069-1081.
- DAVIES, W.E., HIPFNER, J.M., HOBSON, K.A. & YDENBERG, R.C. 2009. Seabird seasonal trophodynamics: isotopic patterns in a community of Pacific alcids. *Marine Ecology Progress Series* 382: 211-219.
- DICK, M.H., WARNER, I.M. & MACINTOSH, R. 1976. Distribution and abundance of breeding and other seabirds in Chinak and southern Marmot Bays, Kodiak Island, Alaska 1975 [unpublished report]. Anchorage, AK: U.S. Department of the Interior, Fish and Wildlife Service.
- DURANT, J.M., ANKER-NILSSEN, T. & STENSETH, N.C. 2003. Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proceedings of the Royal Society of London B* 270: 1461-1466.
- FOLCH, J., LEES, M. & SLOANE-STANLY, G.H. 1957. A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry* 226:497-509
- FREDERIKSEN, M., EDWARDS, M., RICHARDSON, NICHOLAS C. HALLIDAY, A.J. & WANLESS, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* 75: 1259-1268.
- GJERDRUM, C., VALLEE, A.M.J., ST CLAIR, C.C., BERTRAM, D.F., RYDER, J.L. & BLACKBURN, G.S. 2003. Tufted Puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Science* 100: 9377-9382.
- HAMER, K.C., MONAGHAN, P., UTTLEY, J.D., WALTON, P. & BURNS, M.D. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. *Ibis* 135: 255-263.
- HATCH, S.A. & SANGER, G.A. 1992. Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. *Marine Ecology Progress Series* 80: 1-14.
- HIPFNER, J.M., CHARENTE, M.R. & BLACKBURN, J.S. 2007. Subcolony variation in breeding success in the Tufted Puffin (*Fratercula cirrhata*): association with foraging ecology and implications. *Auk* 124: 1149-1157.
- HUNTER, M.D. & PRICE, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.
- IVERSON, S.J., LANG, S.L.C. & COOPER, M.C. 2001. Comparison of the Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. *Lipids* 36: 1283-1287.
- JEHLE, G., YACKEL, A.A., ADAMS, J.A. & SKAGEN, S.K. 2004. Nest survival estimation: a review of alternatives to the Mayfield estimator. *Condor* 106:472-484
- JODICE, P.G.R., ROBY, D.D., TURCO, K.R., SURYAN, R.M., IRONS, D.B., PIATT, J.F., SHULTZ, M.T., ROSENEAU, D.G. & KETTLE, A.B. 2008. Growth rates of Black-legged Kittiwake *Rissa tridactyla* chicks in relation to delivery rate, size, and energy density of meals. *Marine Ornithology* 36: 107-114.
- KILDRAW, S.D., IRONS, D.B., NYSEWANDER, D.R. & BUCK, C.L. 2005. Formation and growth of new seabird colonies: the significance of habitat quality. *Marine Ornithology* 33: 49-58.
- KILDRAW, S.D., IRONS, D.B. & BUCK, C.L. 2008. Habitat quality and metapopulation dynamics of Black-legged Kittiwakes *Rissa tridactyla*. *Marine Ornithology* 36: 35-45.
- KITAYSKY, A.S., ROMANO, M.D., PIATT, J.F., WINGFIELD, J.C. & KIKUCHI, M. 2005. The adrenocortical response of Tufted Puffin chicks to nutritional deficits. *Hormones and Behavior* 47: 606-619.
- KITAYSKY, A.S., KITAISKAIA, E.V., PIATT, J.F. & WINGFIELD, J.C. 2006. A mechanistic link between chick diet and decline in seabirds? *Proceedings of the Royal Society B* 273: 445-450.

- LITZOW, M.A., PIATT, J.F., PRICHARD, A.K. & ROBY, D.D. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* 132: 286-295.
- MONTEVECCHI, W.A. & PIATT, J.F. 1984. Composition and energy density of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. *Comparative Biochemistry and Physiology* 78: 15-20.
- MONTEVECCHI, W.A. 1993. Birds as indicators of change in marine prey stocks. In: Furness, R.W. & Greenwood, J.J.D. (Eds). *Birds as monitors of environmental change*. London: Chapman & Hall. pp. 217-266.
- PAYNE, S.A., JOHNSON, B.A. & OTTO, R.S. 1999. Proximate composition of some north-eastern Pacific forage fish species. *Fisheries Oceanography* 8: 159-177.
- PIATT, J.F. & ANDERSON, P.J. 1996. Response of common murrelets to the Exxon Valdez oil Spill and long-term changes in the Gulf of Alaska marine ecosystem. In: Rice, S.D., Spies, R.B., Wolf, D.A. & Wright, B.A. (Eds). *Exxon Valdez oil spill symposium proceedings*. Symposium 18. Bethesda, MD: American Fisheries Society. pp. 720-727.
- PIATT, J.F. & KITAYSKY, A.S. 2002. Tufted Puffin (*Fratercula cirrhata*). In: Poole A. & Gill, F. (Eds). *The birds of North America*, No. 708. Philadelphia & Washington, DC: Academy of Natural Sciences & American Ornithologists' Union. 32 pp.
- PIATT, J.F., HARDING, A.M.A., SHULTZ, M., SPECKMAN, S.G., VAN PELT, T.I., DREW, G.S. & KETTLE, A.B. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352: 221-234.
- PIERCE, D. J. & SIMONS, T.R. 1986. The influence of human disturbance on Tufted Puffin breeding success. *Auk* 103: 214-216.
- REID, K., CROXALL, J.P., BRIGGS, D.R., & MURPHY, E.J. 2005. Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES Journal of Marine Science* 62: 366-373.
- ROBARDS, M.D., WILSON, M.F., ARMSTRONG, R.H. & PIATT, J.F. 1999a. Sand lance: review of biology and predator relations and annotated bibliography. Research Paper 521. Portland, OR: U.S. Forest Service, Pacific Northwest Research Station. 327 pp.
- ROBARDS, M.D., ANTHONY, J.A., ROSE, G.A. & PIATT, J.F. 1999b. Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. *Journal of Experimental Marine Biology and Ecology* 242: 245-258.
- ROMANO, M.D., 2000. Effects of diet on growth and development of nestling seabirds. MS Thesis, Oregon State University, Corvallis.
- ROMANO, M.D., PIATT, J.F. & ROBY, D.D. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. *Waterbirds* 29: 407-414.
- SURYAN, R.M., IRONS, D.B., KAUFMAN, M., BENSON, J., JODICE, P.G.R., ROBY, D.D. & BROWN, E.D. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 236: 273-286.
- THEDINGA, J.F., JOHNSON, S.W. & MORTENSEN, D.G. 2006. Habitat, age, and diet of a forage fish in southeastern Alaska: Pacific sandfish (*Trichodon trichodon*). *Fishery Bulletin* 104: 631-637.
- VAN PELT, T.I., PIATT, J.F., LANCE, B.K. & ROBY, D.D. 1997. Proximate composition and energy density of some North Pacific forage fishes. *Comparative Biochemistry and Physiology A* 118: 1393-1398.
- VIEYRA, L., VELARDE, E. & EZCURRA, E. 2009. Effects of parental age and food availability on the reproductive success of Heermann's Gulls in the Gulf of California. *Ecology* 90: 1084-1094.
- WANLESS, S., HARRIS, M.P., REDMAN, J.R. & SPEAKMAN, J.R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1-8.
- WHIDDEN, S.E., WILLIAMS, C.T., BRETON, A.R. & BUCK, C.L. 2007. Effects of transmitters on the reproductive success of Tufted Puffins. *Journal of Field Ornithology* 78: 206-212.
- WILLIAMS, C.T., IVERSON, S.J. & BUCK, C.L. 2008a. Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in Tufted Puffins. *Marine Ecology Progress Series* 363: 287-298.
- WILLIAMS, C.T., KITAYSKY, A.S. & BUCK, C.L. 2008b. Food restricted Tufted Puffin (*Fratercula cirrhata*) nestlings increase vocal activity during handling without modulating total or free corticosterone. *Journal of Ornithology* 149: 277-283.