

Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with pigeon guillemot (*Cephus columba*) diets

Michael A. Litzow, John F. Piatt, Alisa A. Abookire,
Alexander K. Prichard, and Martin D. Robards



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We evaluated pigeon guillemots (*Cephus columba*) as monitors of nearshore fish abundance and community composition during 1995–1999 at Kachemak Bay, Alaska. We studied the composition of chick diets at 10 colonies and simultaneously measured fish abundance around colonies with beach seines and bottom trawls. Sandeels (*Ammodytes hexapterus*) formed the majority of the diet at one group of colonies. Temporal variability in sandeel abundance explained 74% of inter-annual variability in diet composition at these colonies and 93% of seasonal variability. Diets at other colonies were dominated by demersal fish. Among these colonies, 81% of the variability in the proportion of sandeels in diets was explained by spatial differences in sandeel abundance. Pigeon guillemots exhibited a non-linear functional response to sandeel abundance in the area where these fish were most abundant. Temporal and spatial variability in demersal fish abundance was not consistently reflected in diets. Spatial differences in the proportion of different demersal fishes in the diet may have been driven by differences in guillemot prey preference. Prey specialization by individual pigeon guillemots was common, and may operate at the colony level. Inter-annual variability in sandeel abundance may have been tracked more accurately because the magnitude of change (11-fold) was greater than that of demersal fish (three-fold).

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Key words: Alaska, *Ammodytes hexapterus*, biomonitor, *Cephus columba*, diet, forage fish, functional response, pigeon guillemot, sandeel.

Michael A. Litzow, John F. Piatt, Alisa A. Abookire, and Martin D. Robards: Alaska Biological Science Center, U.S. Geological Survey, 1011 E. Tudor Rd, Anchorage, Alaska 99503, USA. Alexander K. Prichard: Institute of Arctic Biology, University of Alaska Fairbanks, P.O. Box 757000, Fairbanks, Alaska 99775, USA. [Correspondence to M. A. Litzow: tel: (907) 786-3429; fax (907) 786-3636; E-mail: mike_litzow@brd.usgs.gov].

Introduction

Populations of ecologically important “forage fish” are notoriously difficult and expensive to monitor. It has often been suggested that seabirds can serve as useful monitors of forage fish stocks, since birds are highly visible predators that sample fish around their colonies during the breeding season (e.g. Cairns, 1987a; Baird, 1990; Montevecchi, 1993). However, seabirds may not sample prey populations randomly and may reflect fluctuations in prey abundance only within certain limits (Hunt *et al.*, 1991). Furthermore, because foraging responses to prey density are non-linear and species-specific (Piatt, 1990; Furness and Camphuysen, 1997),

the usefulness of individual seabird species as indicators of prey status can only be established through concurrent study of seabird biology and local prey stocks. In some cases, aspects of seabird biology have been correlated with independent measures of prey abundance obtained from fisheries data (e.g. Hislop and Harris, 1985; Montevecchi *et al.*, 1987; Monaghan *et al.*, 1989; Velarde *et al.*, 1994; Monaghan, 1996), but there have been few concurrent studies of seabirds and their prey (e.g. Piatt, 1987; Phillips *et al.*, 1996).

Pigeon guillemots (*Cephus columba*) and closely related black guillemots (*C. grylle*) are unique among the Alcidae because they usually forage near the sea floor and within a few kilometres of the nest site (Cairns,

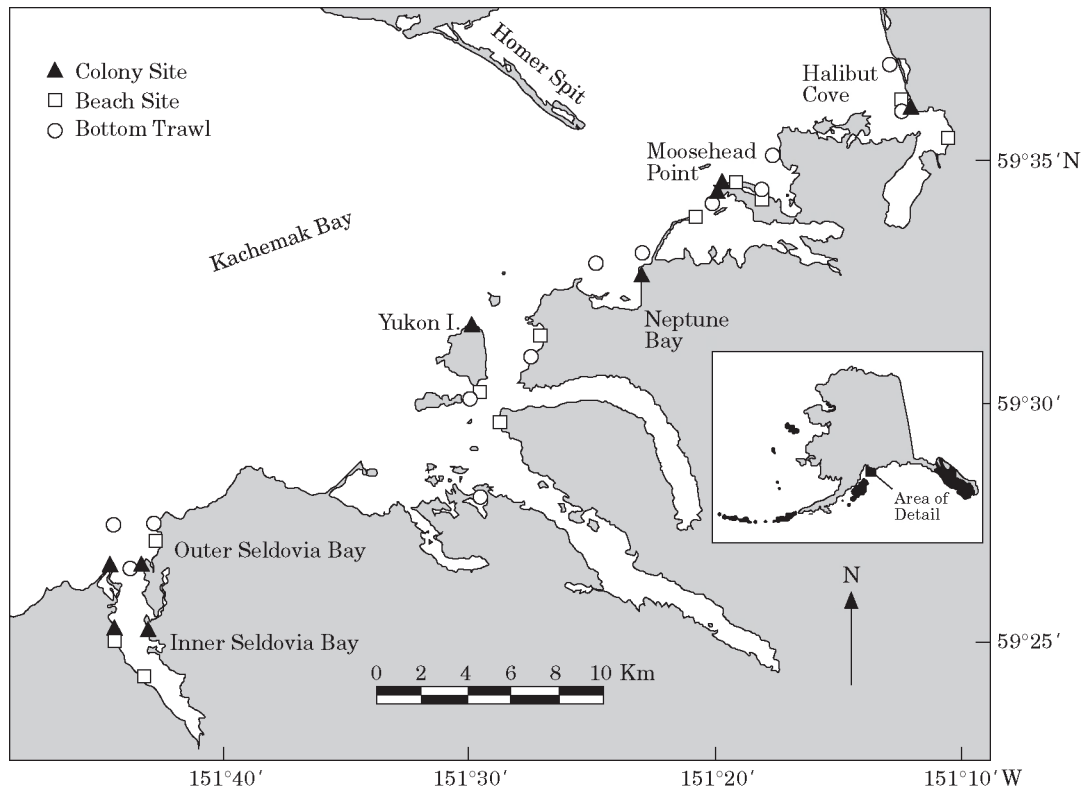


Figure 1. Location of study colonies, and beach seine and bottom trawl stations in Kachemak Bay, Alaska.

1987b; Duffy *et al.*, 1987; Ewins, 1993). *Cephus* guillemots eat a wider variety of prey than other alcids (Bradstreet and Brown, 1985; Ainley *et al.*, 1990) and feed their chicks either demersal or pelagic schooling fish (Oakley and Kuletz, 1996; Prichard, 1997). Diet variability within and between years may be related to changes in the availability of prey species (Ainley *et al.*, 1990; Barrett and Anker-Nilssen, 1997; Hayes and Kuletz, 1997), but this relationship has never been tested through concurrent study of food supply and guillemot diet.

Most seabirds forage offshore over large areas on patchily distributed prey. *Cephus* guillemots have a unique potential as monitors of nearshore ecosystems because they forage coastally on a wide variety of prey. The aims of our study were to: (i) investigate spatial, temporal, and intra-colony variability in nestling diets of pigeon guillemots; and (ii) relate observed diets to independent measures of forage fish abundance around guillemot colonies.

Methods

Study area

Kachemak Bay is located on the east shore of lower Cook Inlet, Alaska (59°35'N, 151°19'W). The bay is

about 60 km long and 38 km wide at its mouth, and is influenced by a flow of cold, nutrient-rich water into the lower inlet (Muench *et al.*, 1978). The Homer Spit bisects the bay into inner and outer sections (Fig. 1). The bay supports a diverse and abundant nearshore fish community, comprising more than 50 species (Robards *et al.*, 1999a). The south shore of the bay includes cliffs and rocky headlands that provide nesting habitat for pigeon guillemots. Pigeon guillemots in Kachemak Bay nest in approximately 30 small colonies (*sensu* Ewins, 1985) of 2–15 nests each, and numerous solitary nests are also scattered along the shore. About 500–600 pigeon guillemots are present along the south shore during the breeding season (Prichard, 1997; M. Litzow *et al.*, unpublished data).

Pigeon guillemot diet

Pigeon guillemots carry single fish in their bills when provisioning chicks and usually rest on the water in front of the colony before delivering food to the nest, making prey identification relatively easy. We studied nestling diets during the years 1995–1999 and collected data for at least one of these years at each of 10 colonies on the south shore of Kachemak Bay; four in the inner bay (Halibut Cove and Moosehead Point colonies no. 1,

2, and 3) and six in the outer bay (Neptune Bay; Yukon Island; Outer Seldovia Bay no. 1 and 2; Inner Seldovia Bay no. 1 and 2; Fig. 1). Mean annual reproductive success during the study was low ($0.15\text{--}0.54$ chicks fledged $\cdot \text{nest}^{-1}$), with many breeding attempts failing during incubation (Prichard, 1997; M. Litzow *et al.*, unpublished data). As a result, no single colony was active for all five years of study. Study colonies were distributed along 35 km of shore (straight line distance), and in five instances were very close to each other: Moosehead Pt no. 1 and Neptune Bay in 1995 (4 km apart); Outer Seldovia no. 1 and Inner Seldovia no. 1 in 1997 (2 km apart); Moosehead Pt no. 2 and 3 in 1998 (1 km apart); Inner Seldovia Bay no. 1 and 2 and Outer Seldovia Bay no. 2 in 1998 (all within 3 km); and Moosehead Pt no. 1 and 2 in 1999 (1 km apart).

We observed chick provisioning at two to five nests during feeding watches. Watches were conducted during 3.5 h shifts distributed evenly across different tide stages and times of day (0600–2000) in 1995 ($n=524$ nest-hours). From 1996 to 1999 we conducted all-day watches (0600–2200 or 0500–2300; $n=21$ nest-days in 1996; $n=39$ in 1997; $n=28$ in 1998; $n=10$ in 1999). Provisioning adults were observed using binoculars (from anchored boats) or telescopes (from hides) and prey items were identified to the lowest possible taxonomic level. Study colonies were all in areas of moderate to high boat traffic, and the presence of an anchored boat had no apparent effect on the behaviour of observed birds. Prey categories included sandeel (Pacific sand lance; *Ammodytes hexapterus*), salmonid (Salmonidae), sculpin (Cottidae), gadoid (Gadidae), flatfish (Pleuronectidae), gunnel (Pholidae), prickleback (*Lumpenus* spp.), ronquil (*Bathymaster signatus*, *Ronquilus jordani*), arctic shanny (*Stichaeus punctatus*), unidentified blenny (Blennioidea), and hermit crab (Anomura). Schooling prey species have a distinctive silver colour, and we placed prey items that we could not positively identify into “unidentified schooling fish” and “unidentified demersal fish” categories. Other items were simply “unidentified”.

Diet variability among nests, colonies, seasons and years was tested with Likelihood Ratio Chi Square tests (G-test). Meals that had not been positively identified were excluded from these tests. Inter-annual comparisons were made for colonies where we had sufficient data for two or more years. We observed the same part of each colony in each year, but Moosehead Pt no. 1 and Inner Seldovia no. 1 were the only colonies where the same nest sites were active each year. We analyzed diet variability within colonies for every case when 30 or more fish had been identified at a minimum of three nests at a colony in a particular year. For comparisons among nests and years we subsumed all categories comprising less than 10% of observations into an “other” category. To examine seasonal effects, diet

observations were divided by data into early (3–19 July), middle (20–29 July), and late (30 July–14 August) subsets. Seasonal effects were tested only in cases with two or more subsets and a contingency table with $\geq 20\%$ of cells having an expected value greater than 5.

Nearshore fish abundance

We measured sandeel abundance with beach seines set about every two weeks at ten sites between 100 m and 3 km from study colonies in June and July 1995 and June, July, and August 1996–1999 (Fig. 1). The exact location of seine sites was restricted by the availability of beaches (sand, gravel or cobble) suitable for seining. We used a 44 m net, 4 m deep with a 3 mm mesh set 25 m from shore (Robards *et al.*, 1999a). We seined within 1 h of low tide, although some extra high-tide sets were made in 1995 and at Moosehead Pt in 1996. Sandeel were classified as age 0 or age 1+ based on length (M. Robards *et al.*, unpublished data). Age 0 sandeels were excluded from analyses of seine data because they were rarely observed in pigeon guillemot diets. Other species of fish were counted and identified, and in 1997–1999 were measured and classified as “forage” size (8–15 cm forklength, but 8–20 cm for *Lumpenus* pricklebaks) or “non-forage” size. We used catch per unit effort (c.p.u.e.; number of age 1+ sandeels caught per seine) and catch composition (proportion of total catch) to quantify sandeel abundance.

We measured demersal fish abundance with bottom trawls. Bottom trawls were conducted at 13 sites within a few 100 m to 6 km of study colonies (Fig. 1) once in 1996 and 1999 (early August) and three times in 1997 and 1998 (early July, late July, early August). Trawl stations were restricted to sites with relatively smooth bottoms and few obstructions (e.g. boulders), although we were able to trawl in sites with fairly high kelp density. We used a 3.05 m plumbstaff beam trawl with a 7 mm mesh and a 4 mm codend liner (Gunderson and Ellis, 1986) towed by a 9.3 m boat. Standard tow duration was 5 min. Station depth did not exceed 25 m, and at least one station in the 5–10 m range and another in the 10–20 m range were sampled at each colony. Fish with fork length 8–15 cm and fish of the genus *Lumpenus* with fork length 8–20 cm were considered in analyses of forage fish abundance. We divided fish into four groups for analysis: blennies, flatfish, sculpins, and other. The c.p.u.e. data were standardized as number of fish caught per 1000 m² trawled.

Salmonids, age 0 sandeels, and larval sculpins were excluded from analysis of 1995 and 1996 catch composition data because these groups were predominantly outside the “forage” size range. Because we were interested in the relationship between nestling diet and local fish abundance, we only included data from colonies

where we gathered diet data in analyses of spatial variability in prey abundance. We analyzed spatial differences in sandeel abundance at the level of areas (e.g. Moosehead Pt, Yukon I., Seldovia Bay) instead of colonies (e.g. Inner Seldovia no. 1, Inner Seldovia no. 2) in order to increase statistical power. For spatial analysis we only included areas with at least ten seines, or colonies with at least three trawls, in a given year. Sampling effort in 1995 was not great enough to allow spatial analysis of seine data. All c.p.u.e. data were $\ln(x+1)$ transformed to correct for heterogeneity of variance, and all means are presented ± 1 s.e. Comparisons were made with two-tailed t-tests and one-way ANOVAs followed by Student-Newman-Keuls pairwise comparisons when assumptions of normality were met. Data that violated assumptions of normality were assessed with two-tailed Mann-Whitney U tests and Kruskal-Wallis ANOVAs on ranked data followed by Dunn's pairwise comparisons.

Comparisons of chick diet and fish abundance

We assessed the relationship between diet composition and sandeel abundance at the spatial-temporal scale of the colony-year. We compared the proportion of sandeels in the chick diets at a colony with the c.p.u.e. of seines set around that colony during the peak of the chick rearing period (July and the first week of August). Colonies were included in this analysis if we had conducted at least four nest-days of diet observation and had made at least five seines near the colony. In the outer bay our replication was primarily spatial; three colonies were sampled for one year each and two were sampled for two years each. At Moosehead Pt replication was primarily temporal; three colonies were sampled for four years, two years, and one year, respectively. Seasonal correlations were assessed by comparing individual all-day diet watches with the c.p.u.e. and catch composition of local seines set within four days of a watch.

The proportion of demersal fish in colony diets was compared with the mean total c.p.u.e. of local trawls on an annual scale. We also compared c.p.u.e. for blennies, flatfish, and sculpins with the proportion of each group in the demersal diet (proportion of total identified demersal fish meals) at each colony on an annual scale.

These relationships were tested with linear regressions on both non-transformed and \ln -transformed data, and the regression with the better fit (highest r^2 value) was retained. We conducted power analysis in order to assess the confidence that we could ascribe to regressions of diet composition on fish data that returned negative results. We calculated the power of regressions with correlation coefficients that were obtained with Pearson correlations on the same data that had been used in

regression analysis (Zar, 1996). An alternative hypothesis of $r=0.86$ (the lowest correlation coefficient that we obtained from a significant regression) was used in power analysis. We used a one-tailed power analysis because we were only interested in detecting positive correlations. The probability of type-I and type-II errors was set at 0.05 for all tests of significance.

Results

Pigeon guillemot diet

We observed 2653 prey items (Table 1). Most items identified (98.9%) were fish. The most common taxa observed were sandeels (35.9%), gunnells (17.3%), pricklebacks (12.0%), sculpins (8.3%) and flatfish (6.4%). Unidentified blennies and unidentified demersal fish together comprised 8.1% of the total, and 6.4% of prey items were not identified. Identified schooling fish were mostly (98.1%) sandeels.

Pigeon guillemot diet varied both temporally and spatially (Fig. 2). Nestling diet was significantly different among colonies in every year (Table 2). Sandeels dominated the diet at Moosehead Pt, while demersal fish formed the majority of diets in other areas. Differences among years at individual colonies were significant in three cases (Table 3). Seasonal variability was apparent twice at Moosehead Pt colonies (Table 4).

Diet differences among individual nests were common. Over all years of study, we identified 30 or more chick meals at 27 individual nests. Blennies comprised at least 49% of the diet at eight of these nests. Sandeels comprised the majority of the diet at 10 nests and flatfish comprised the majority at one nest. No single taxon formed the majority of the diet at the remaining eight nests. Variation in diet composition between nests within a given colony was significant in five of the six cases we tested (Table 5).

Nearshore fish abundance

We caught a total of 65 158 age 1+ sandeels in seines from June 1995 to August 1999. Sandeel abundance varied 11-fold among years (Fig. 3) and inter-annual differences in mean c.p.u.e. were significant (1995: 363 ± 226 ; 1996: 33 ± 13 ; 1997: 93 ± 34 ; 1998: 343 ± 138 ; 1999: 123 ± 45 ; $F=3.34$, 4 d.f., $p=0.01$). Pairwise comparisons showed that c.p.u.e. was greater in 1995 than in 1996, 1997, and 1999 ($p<0.05$). Sandeel c.p.u.e. in 1996 did not differ among Moosehead Pt and Yukon I. ($U=181$, 33 d.f., $p=0.08$), but differed significantly among months ($F=4.8$, 2 d.f., $p=0.01$); catches were greater in June and July than in August. In 1997 there were no seasonal differences ($F=0.9$, 4 d.f., $p=0.45$), but abundance varied among colonies ($H=6.2$, 2 d.f., $p=0.04$); catches were greater at Seldovia Bay than at

Table 1. Percent composition (by number) of prey items in pigeon guillemot nestling diets at Kachemak Bay, Alaska, 1995–1998.

| Taxon | Halibut Cove 1995 | Moosehead Point 1 | | | Moosehead 2 | | Moosehead 3 1998 | Neptune Bay 1995 ^a | Yukon Island | | Outer Seldovia 1 | | Outer Seld. 2 | | Inner Seldovia 1 | | Inner Seld. 2 1998 ^a |
|---------------------------------------|----------------------|-------------------|------|------|-------------|-------------------|---------------------|----------------------------------|-------------------|------|------------------|------|-------------------|-------------------|-------------------|-------------------|------------------------------------|
| | | 1995 ^a | 1996 | 1997 | 1999 | 1998 ^a | 1999 ^a | | 1996 ^a | 1997 | 1997 | 1997 | 1998 ^a | 1997 ^a | 1998 ^a | 1997 ^a | |
| Total schooling fish | 41.1 | 83.4 | 46.1 | 74.1 | 79.6 | 55.2 | 77.8 | 20.0 | 2.9 | 1.9 | 21.1 | 14.8 | 11.1 | | 0.8 | | 9.6 |
| Sandeels ^d | 39.1 | 83.4 | 44.2 | 67.7 | 79.6 | 55.2 | 76.6 | 19.3 | | 1.0 | 21.1 | 14.1 | 11.1 | | | | 3.8 |
| Capelin ^{b,e} | | | 1.9 | | | | | | | | | 0.4 | | | 0.8 | | |
| Salmonids ^f | 2.0 | | | 0.4 | | | | 0.7 | 2.9 | 1.0 | | | | | | | 1.0 |
| Unidentified schooling fish | | | | 6.0 | | | 1.2 | | | | | | | | | | 4.8 |
| Total demersal fish | 53.6 | 10.9 | 49.8 | 11.0 | 20.4 | 44.8 | 19.3 | 53.3 | 94.1 | 87.6 | 66.8 | 66.8 | 66.7 | 92.3 | 90.0 | | 91.3 |
| Gadoids ^{b,g} | | | | 0.4 | | | | | 1.5 | | 1.4 | 1.2 | | | | | |
| Sculpins ^h | 5.3 | | 6.8 | 1.2 | | | 1.8 | 6.7 | 4.4 | 3.8 | 7.0 | 12.4 | 22.2 | 29.0 | 9.2 | | 4.8 |
| Blennies ⁱ | | | | | | | | | | | | | | | | | |
| Gunnels ^j | 42.4 | 9.7 | 28.4 | 1.2 | 17.5 | 29.3 | 7.0 | 29.6 | 26.5 | 8.6 | 5.6 | 6.4 | 11.1 | 15.4 | 16.2 | | 34.6 |
| Prickleback, eelblennies ^k | 5.3 | 1.1 | 10.4 | 4.8 | 2.9 | 8.6 | 6.4 | 12.6 | 7.4 | 18.1 | | 1.2 | 1.0 | 30.1 | 50.0 | | 30.8 |
| Arctic shanny ^{o,l} | | | | | | 3.4 | | | | 4.8 | | 1.6 | 2.0 | | | | 1.0 |
| Ronquils ^{b,m} | | | 0.7 | 0.4 | | | | | 8.8 | 3.8 | | | | | | | |
| Unidentified blennies | | | 1.2 | 1.6 | | | | | 1.5 | 30.5 | | 3.2 | 3.0 | 13.3 | 9.2 | | 5.8 |
| Total blennies | 47.7 | 10.9 | 40.8 | 7.9 | 20.4 | 41.4 | 13.4 | 42.2 | 44.1 | 65.7 | 5.6 | 14.4 | 17.2 | 58.7 | 75.4 | | 72.1 |
| Flatfish ⁿ | | | 0.7 | 0.7 | | 4.1 | | 4.4 | 4.4 | 9.5 | 32.4 | 32.4 | 18.2 | 2.4 | 6.2 | | 2.9 |
| Rockfish ^o | | | | | | | | | | 1.9 | | | | | | | |
| Greenlings ^{b,p} | | | 0.2 | | | | | 2.9 | | | | | | | | | |
| Unidentified demersal fish | 0.7 | | 1.2 | 0.4 | | 3.4 | | 36.8 | 6.7 | 6.7 | 16.9 | 6.4 | 9.1 | 2.1 | 5.4 | | 11.5 |
| Total invertebrates | 2.0 | | | | | | | | | | | 8.8 | | 1.4 | | | 1.0 |
| Hermit Crabs ^q | | | | | | | | | | | ^c | 8.4 | 2.0 | 1.4 | | | 1.0 |
| Shrimp ^r | 2.0 | | | | | | | | | | | | | | | | |
| Unidentified invertebrates | 3.3 | 5.7 | 4.1 | 3.2 | | | 2.9 | 26.7 | 2.9 | 10.5 | 15.5 | 0.4 | 5.1 | 6.3 | 3.1 | | 2.9 |
| Unidentified | 151 | 175 | 412 | 249 | 103 | 58 | 171 | 135 | 68 | 105 | 71 | 250 | 99 | 286 | 130 | | 104 |

^aObservations made from boats. ^bThese identifications were not used in 1995, and these groups could not be reliably distinguished during boat observations.^cMay have been present this year, but not identified. ^d*Ammodytes hexapterus*; ^e*Gadidae*; ^f*Cottidae*; ^g*Mallotus villosus*; ^h*Salmonidae*; ⁱ*Blenniodae*; ^j*Pholidae*; ^k*Lumpenus* spp.;^l*Stichaeus punctatus*; ^m*Bathymaster signatus*; ⁿ*Ronquilus jordani*; ^o*Pleuronectidae*; ^p*Sebastes* spp.; ^q*Anomura*; ^rDecapoda.

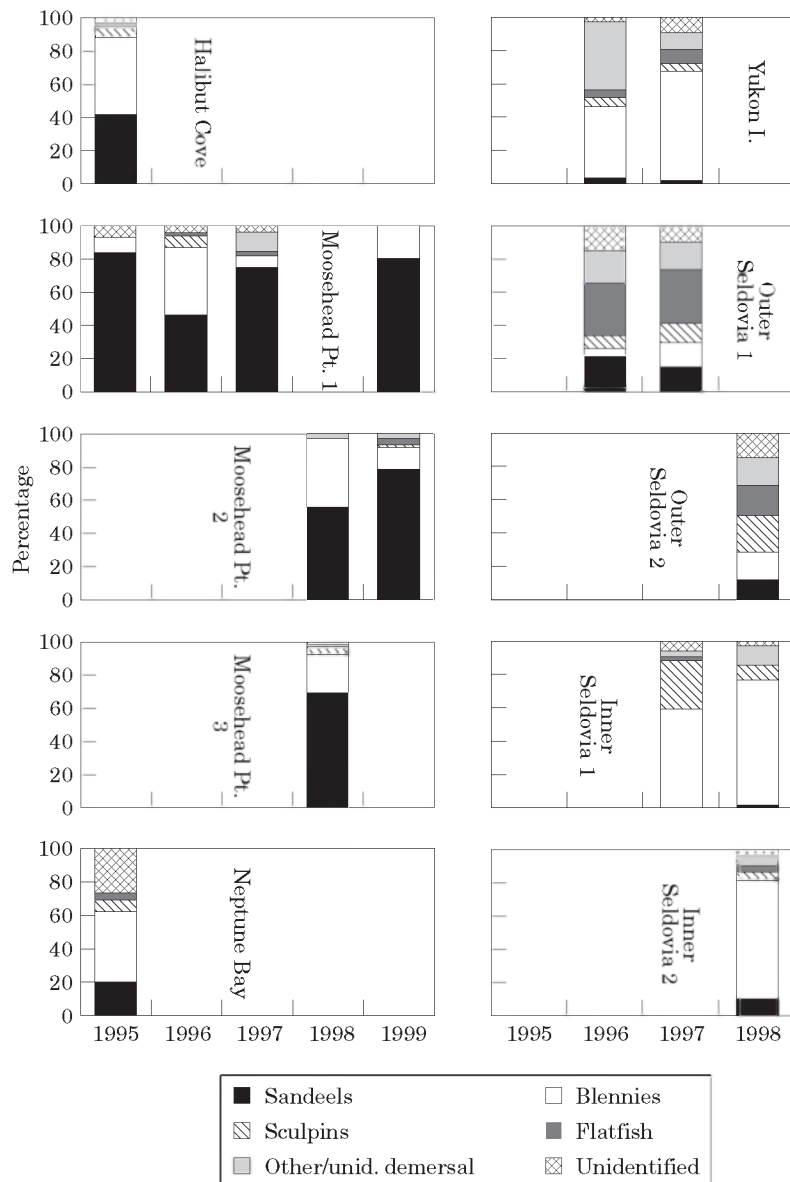


Figure 2. Composition of pigeon guillemot nestling diet at ten colonies in Kachemak Bay, Alaska, 1995–1999. Diets were significantly different among colonies in all years, and inter-annual differences were significant at Moosehead Pt no. 1 and 2, Outer Seldovia no. 1, and Inner Seldovia no. 1. See Results for details.

Moosehead Pt ($p < 0.05$). Sandeel c.p.u.e. in 1998 differed significantly among months ($F = 10.8$, 2 d.f., $p < 0.001$) and colonies ($U = 281$, 45 d.f., $p < 0.01$); catches were greater in August than June, and greater at Moosehead than at Seldovia. We did not detect seasonal differences in sandeel c.p.u.e. in 1999 ($H = 4.88$, 2 d.f., $p = 0.09$). When data from all years were combined, mean c.p.u.e. of seines was greater in the inner bay (199 ± 60) than the outer bay (130 ± 78 ; $t = 2.91$, 387 d.f., $p < 0.01$).

The composition of beach seine catches was predominantly age 1+ sandeels (80%) and Pacific herring

(*Clupea harengus pallasii*; 10%). In July and August of 1996–1999, “forage” size herring were present in 57% of the seines in Halibut Cove, 13% at Moosehead Pt, 22% in Neptune Bay, 6% at Yukon I., 25% in Outer Seldovia, and 2% in Inner Seldovia Bay.

We caught 2330 forage-size fish in bottom trawls. The most common taxa were flatfish (40% of total), blennies (31%), sculpins (10%), and 19% other. Hexagrammids (52%) and gadoids (38%) comprised most of the “other” category. Mean total August c.p.u.e. (Fig. 4) varied among years (1996 = 18 ± 3 ; 1997 = 73 ± 23 ;

Table 2. Variability in diet composition among pigeon guillemot colonies during 1995–1999 in Kachemak Bay, Alaska. See Methods for details.

| Year | n (colonies) | n (meals) | G | df | p |
|------|-----------------|--------------|-------|----|-------|
| 1995 | 3 | 409 | 140.6 | 4 | 0.001 |
| 1996 | 3 | 474 | 105.6 | 4 | 0.001 |
| 1997 | 4 | 754 | 758.2 | 12 | 0.001 |
| 1998 | 5 | 417 | 291.1 | 12 | 0.001 |
| 1999 | 2 | 267 | 13.7 | 2 | 0.001 |

Table 3. Inter-annual variability in diet composition at pigeon guillemot colonies during 1995–1999 in Kachemak Bay, Alaska. See Methods for details.

| Colony | n (years) | n (meals) | G | df | p |
|----------------------|--------------|--------------|-------|----|-------|
| Moosehead no. 1 | 4 | 854 | 289.6 | 9 | 0.001 |
| Moosehead no. 2 | 2 | 211 | 16.6 | 2 | 0.001 |
| Yukon I. | 2 | 171 | 3.6 | 2 | 0.17 |
| Outer Seldovia no. 1 | 2 | 257 | 12.3 | 4 | 0.02 |
| Inner Seldovia no. 1 | 2 | 381 | 23.5 | 2 | 0.001 |

Table 4. Seasonal variability in diet composition at pigeon guillemot colonies during 1995–1998 in Kachemak Bay, Alaska. See Methods for details.

| Colony | Year | n (subsets) | n (meals) | G | df | p |
|-------------------|------|----------------|--------------|------|----|-------|
| Moosehead no. 1 | 1995 | 3 | 165 | 2.6 | 2 | 0.27 |
| | 1996 | 3 | 395 | 31.2 | 4 | 0.001 |
| | 1997 | 3 | 239 | 0.4 | 2 | 0.82 |
| Moosehead no. 2 | 1998 | 2 | 56 | 1.6 | 1 | 0.21 |
| Moosehead no. 3 | 1998 | 2 | 84 | 6.0 | 2 | 0.049 |
| Neptune Bay | 1995 | 3 | 99 | 8.2 | 4 | 0.9 |
| Outer Seld. no. 1 | 1997 | 2 | 226 | 0.5 | 4 | 0.98 |
| Inner Seld. no. 1 | 1997 | 2 | 268 | 1.8 | 2 | 0.41 |
| | 1998 | 2 | 126 | 0.4 | 1 | 0.54 |

1998=21 ± 5; 1999=26 ± 8; $F=3.53$, 3 d.f., $p=0.02$). Pairwise comparisons showed that c.p.u.e. was greater in 1997 than in every other year ($p<0.05$). In 1997 abundance increased significantly by month ($H=9.6$, 2 d.f., $p<0.01$) such that catches were greater in August than in early July. We detected no seasonal effect in 1998 ($H=4.5$, 2 d.f., $p=0.11$). Catch composition varied among colonies in 1997 ($G=78.9$, 4 d.f., $p=0.001$) and 1998 ($G=113.8$, 4 d.f., $p=0.001$). We did not detect a difference in total c.p.u.e. among colonies in 1996 ($t=1.3$, 5 d.f., $p=0.24$), 1997 ($F=0.02$, 2 d.f., $p=0.99$), or 1998 ($t=0.28$, 18 d.f., $p=0.78$). When data for all years

Table 5. Variability in diet composition among pigeon guillemot nests (within colonies) in Kachemak Bay, Alaska, 1995–1997. See Methods for details.

| Year | Colony | n (nests) | n (meals) | G | df | P |
|------|----------------|--------------|--------------|-------|----|-------|
| 1995 | Halibut Cove | 3 | 150 | 20.41 | 4 | 0.001 |
| 1995 | Moosehead Pt | 3 | 114 | 9.06 | 2 | 0.01 |
| 1996 | Moosehead Pt | 6 | 235 | 75.07 | 10 | 0.001 |
| 1997 | Moosehead Pt | 3 | 117 | 1.02 | 2 | 0.59 |
| 1997 | Outer Seldovia | 4 | 169 | 79.57 | 9 | 0.001 |
| 1997 | Inner Seldovia | 4 | 228 | 16.36 | 6 | 0.01 |

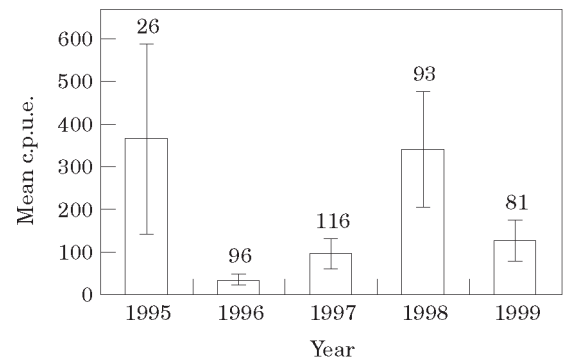


Figure 3. Inter-annual variability in sandeel abundance: mean c.p.u.e. (numbers of fish per seine set) of age 1+ sandeels in beach seines at Kachemak Bay, Alaska, 1995–1999. Inter-annual differences are significant ($F=3.87$, 4 d.f., $p<0.01$). Sample sizes (number of sets) above columns, error bars ± 1 s.e.

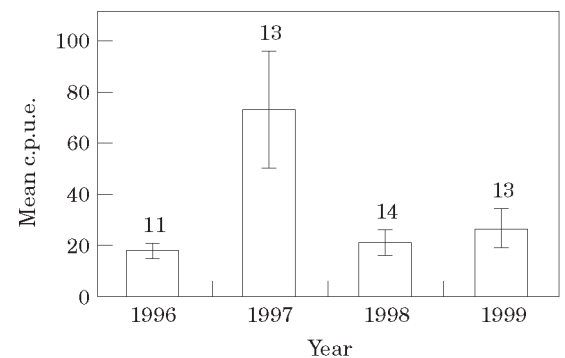


Figure 4. Inter-annual variability in demersal fish abundance: mean c.p.u.e. (numbers of fish per 1000 m² trawled) of demersal fish in bottom trawls at Kachemak Bay, Alaska, 1996–1999. Inter-annual differences are significant ($F=3.53$, 3 d.f., $p<0.02$). Sample sizes (number of sets) above columns, error bars ± 1 s.e.

were combined, we detected no difference in trawl c.p.u.e. between the inner bay (36 ± 6) and outer bay (34 ± 15; $t=1.73$, 49 d.f., $p=0.09$).

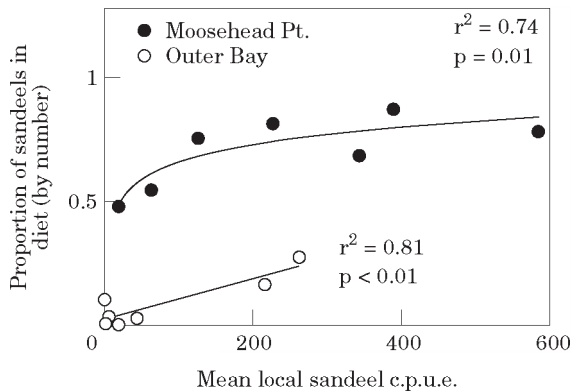


Figure 5. The functional dietary response of pigeon guillemots to variability in sandeel abundance: regression of chick diet composition against local age 1+ sandeel c.p.u.e. in Kachemak Bay, Alaska. Each dot represents data from one year at a single colony. Upper line is best fit regression for Moosehead Pt data, lower line is best fit for outer bay colonies. Replication at Moosehead Pt was primarily temporal; three colonies were sampled four times, twice and once, respectively. Replication at the outer bay was mostly spatial; three colonies were sampled once and two were sampled twice.

Comparisons of chick diets and fish abundance

At Moosehead Pt, where sandeels dominated diets, there was a significant non-linear relationship between the proportion of sandeels in the diet and local sandeel c.p.u.e. (Fig. 5, linear regression of ln-transformed data, $n=7$, $r^2=0.74$, $p=0.01$). Diets at Moosehead Pt reflected sandeel abundance only on a local scale; we found no relationship between the proportion of sandeels in the diets at these colonies and bay-wide c.p.u.e. (ln-transformed data, $n=7$, $r^2=0.38$, $p=0.14$, power=0.96). We can therefore conclude that diets at Moosehead Pt were not correlated (at $r \geq 0.86$) with age 1+ sandeel c.p.u.e. at the meso-scale of Kachemak Bay (Toft and Shea, 1983). We cannot rule out the possibility that diets were coupled with c.p.u.e. at this larger spatial scale with a lower correlation coefficient.

At the outer bay, where sandeels were a minor part of the diet, the relationship between diet and local c.p.u.e. was best described by a linear equation (Fig. 5, $n=7$, $r^2=0.81$, $p<0.01$). We lacked data at high levels of abundance that would allow us to draw a complete curve for these other colonies, so were unable to conclude that the functional relationship between sandeel abundance and consumption at these colonies was fundamentally different than that at Moosehead Pt. However, the magnitude of the functional response at Moosehead Pt was clearly different from that at other colonies; pigeon guillemots at Moosehead delivered higher proportions of sandeels at similar levels of availability.

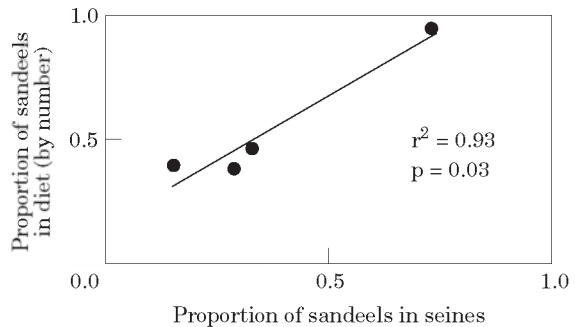


Figure 6. Dietary response of pigeon guillemots to seasonal variability in sandeel abundance: regression of chick diet composition against the proportion of age 1+ sandeels in beach seine catches at Moosehead Pt throughout summer, 1996. Data are from all-day chick provisioning watches and beach seines set within four days of watches. Each dot represents one sampling period: 2–6 July, 22–25 July, 31 July–4 August and 10–12 August.

Diets exhibited significant seasonal variability only at Moosehead Pt in 1996 and 1998, the only two years of significant seasonal variability in sandeel c.p.u.e.. The proportions of sandeels in diets and beach seine catches were significantly related ($n=4$, $r^2=0.93$, $p=0.03$) through the season at Moosehead Pt in 1996 (Fig. 6), but diet composition and c.p.u.e. were not ($n=4$, $r^2=0.63$, $p=0.21$, power=0.72). Diet watches and seine sets were not synchronized well enough to allow robust seasonal comparisons in other cases.

Trawl c.p.u.e. increased bay-wide through the summers of 1997 and 1998, and was higher in 1997 than in other years, but there were no concurrent seasonal or inter-annual increases in the proportion of demersal fish in diets at any colony. There were no differences between 1996 and 1997 in trawl catch composition at Outer Seldovia Bay, although diets were significantly different between years in this area. We did not conduct trawls in Inner Seldovia Bay, but mean c.p.u.e. of sculpins in seines declined from 1997 to 1998 in this area ($1997=1.9 \pm 0.7$; $1998=0.3 \pm 0.2$, $U=717$, 45 d.f., $p<0.01$).

Spatial differences in diet did not reflect spatial differences in demersal fish abundance. There was no relationship between the proportion of demersal fish in diets and local trawl c.p.u.e. either at all colonies ($n=8$, $r^2=0.06$, $p=0.54$, power>0.99), or at colonies with $\geq 50\%$ demersal fish in the diet ($n=5$, $r^2=0.05$, $p=0.72$, power=0.95). Considering separate taxonomic groups of demersal fish, there was no relationship between trawl c.p.u.e. and proportions in the diet for blennies ($n=8$, $r^2=0.19$, $p=0.28$, power=0.99), flatfish ($n=8$, $r^2=0.15$, $p=0.11$, power=0.97) or sculpins ($n=8$, $r^2=0.03$, $p=0.68$, power>0.99).

Discussion

Chick diets as temporal monitors

Cephus guillemot diet composition often varies within and between years, especially with respect to the proportion of schooling fish in the diet (Ainley *et al.*, 1990; Ewins, 1990; Barrett and Anker-Nilssen, 1997; Hayes and Kuletz, 1997). Diets accurately reflected sandeel abundance around the Moosehead Pt colonies on both an annual scale (Fig. 5) and a seasonal scale (Fig. 6). The dietary functional response of pigeon guillemots to temporal changes in sandeel abundance appears to be non-linear, as has been observed for other alcids (Piatt, 1987, 1990).

Pigeon guillemots in the outer bay also fed sandeels to their chicks in proportions that were related to abundance, but sandeels comprised a smaller proportion of diets at these colonies than at Moosehead Pt over similar levels of local sandeel abundance. Diet specialization by individual *Cephus* guillemots is well known (Drent, 1965; Cairns, 1981; Kuletz, 1983). We hypothesize that the increased dependence on sandeels at Moosehead Pt is the result of pervasive specialization at these colonies in response to higher average levels of sandeel availability in the inner bay.

Chick diets at larger *Cephus* colonies tend to be dominated by a single schooling fish species (Ainley *et al.*, 1990; this study), and may provide accurate indications of temporal changes in abundance of these species. Sandeels (Ammodytidae) are often a major component of *Cephus* diets (Ewins, 1990; Oakley and Kuletz, 1996). These fish are an important prey of birds, fish, and mammals in the North Pacific and the North Atlantic (Bradstreet and Brown, 1985; Field, 1988; Furness, 1990; Robards *et al.*, 1999b), but little information of their abundance is available in areas where they are not the target of a human fishery. Because nestling meals may be identified visually, guillemot diet data are relatively easy to gather and may provide a useful index of sandeel abundance in situations when stock assessment data are not available.

A problem in using seabirds (and *Cephus* guillemots in particular) as monitors of temporal variability in fish abundance is the issue of scale (Hunt *et al.*, 1991). Anecdotal evidence suggests that pigeon guillemots forage within 2–6 km of their colony (Drent, 1965; Kuletz, 1983). We found that diets at Moosehead Pt reflected trends in sandeel abundance only at the micro-scale of the colony area, although the power of our analysis was inadequate to conclusively demonstrate that diets are de-coupled from fish abundance at meso-scales. Seabird species with short foraging ranges are likely to be influenced by small scale fluctuations in food abundance (Montevecchi and Berruti, 1991), and

inferences about fish abundance made from the diet of a single *Cephus* guillemot colony are necessarily uncertain if applied to an area beyond the foraging range of birds from that colony (but see Montevecchi and Myers, 1995).

Another problem is that the diets of polyphagous seabirds may not track all prey taxa equally well (Cairns, 1987a; Montevecchi, 1993). Although demersal fish populations exhibited significant seasonal and annual fluctuations in abundance, this variability was usually not reflected in pigeon guillemot diets. In one instance of inter-annual change in demersal fish diet composition (at Outer Seldovia Bay no. 1), different nest sites were active in the colony in each year. Pigeon guillemots tend to re-use the same nest site from year to year (Drent, 1965; Nelson, 1991), so it is likely that we were observing different individuals in each year at this colony, and the observed differences in diet composition may have been due to individual differences in diet preference. In the other instance (at Inner Seldovia Bay no. 1), a decline in sculpins in the diet reflected a decline in local abundance of this family, which establishes that in some instances *Cephus* guillemot nestling diets may accurately monitor changes in demersal fish populations. However, in light of the other possible explanations for inter-annual changes in the proportion of demersal fish in nestling diets (e.g. changes in the breeding population of a colony that introduce new patterns of prey preference), we suggest that care must be taken in drawing conclusions about trends in demersal fish abundance from *Cephus* guillemot diets.

Why did pigeon guillemot diets consistently reflect temporal changes only in sandeel abundance? Fluctuations in prey abundance may not affect some of the biological parameters we routinely measure at colonies because adult seabirds may be able to adjust time budgets to maintain steady food intake and reproductive success over a wide range of prey densities (Burger and Piatt, 1990; Monaghan *et al.*, 1994; Zador and Piatt, 1998). Until prey abundance falls below some threshold level, diets and reproductive parameters may be insensitive to changes in prey abundance (Cairns, 1987a; Piatt, 1987; Phillips *et al.*, 1996). At Kachemak Bay, sandeel abundance varied an order of magnitude within and between years, which is not unusual for this pelagic schooling fish (Blackburn and Anderson, 1997). In contrast, demersal fish abundance changed by less than an order of magnitude within and between years, which is not unusual for demersal species (e.g. Abookire and Norcross, 1998). Thus, it may be that fluctuations in sandeel abundance were reflected in pigeon guillemot diets only because they were of sufficient magnitude to cross a lower threshold below which pigeon guillemots were unable to maintain maximal rates of sandeel predation.

Chick diets as spatial indicators

Diets showed a general concordance with spatial differences in sandeel abundance. Sandeels were most abundant in the inner bay, and pigeon guillemot diets in the inner bay were consistently richer in sandeels than those in the outer bay. Similarly, the proportion of sandeels in diets at outer bay colonies was a function of local c.p.u.e. (Fig. 5). However, pigeon guillemots in different parts of the bay responded differently to similar levels of sandeel abundance (see above), so we could not accurately predict spatial differences in sandeel c.p.u.e. from diets alone. We found spatial variability in the catch composition of demersal fish in every year of the study, but the proportions of major demersal taxa in colony diets never reflected these spatial differences. The statistical power of our regressions was adequate (≥ 0.95) for us to conclude that there was no spatial relationship between diet composition and bottom trawl catch composition. Demersal fish abundance varied among colonies only in 1998, and then the area with the greatest local abundance of these fish, Moosehead Pt, also had the colonies with the lowest proportion of demersal fish in the diet. Finally, herring were common around our study colonies, and comprise up to 20% of chick diets elsewhere in Alaska (Oakley and Kuletz, 1996), but we never observed herring in pigeon guillemot diets.

If local prey availability does not always account for spatial variability in *Cephus* guillemot diets, then what does? We suggest two possible explanations: (i) diets reflect differences in abundance on a spatial scale that this study did not detect, or (ii) spatial variability in diet actually results from prey specialization by individuals or colonies. We found specialization at the nest level to be pervasive (Table 2), even in situations where a single prey species dominated diets at a colony (e.g. Moosehead Pt no. 1 in 1995). We also found evidence that specialization occurs at the colony level. At the two colonies where mostly different nest-sites were observed in different years there was either no difference in diet composition (Yukon I.) or a characteristically high proportion of one taxon in both years (flatfish at Outer Seldovia Bay no. 1). It is possible that foraging adults share information about the location of prey near colonies (Hunt *et al.*, 1991) or exhibit high fidelity to colony-specific foraging sites (Kuletz, 1983), leading to a similarity of diets within colonies. Alternatively, chicks may acquire a preference for the prey fed to them by adults, as has been demonstrated in western gulls (*Larus occidentalis*; Annett and Pierotti, 1999), thereby leading to continuing specialization for that prey by recruits that return to breed at the same colony.

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