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Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey

Abstract Populations of the pigeon guillemot (*Cepphus columba*) and other piscivores have been in decline for several decades in the Gulf of Alaska and Bering Sea, and a decline in abundance of lipid-rich schooling fishes is hypothesized as the major cause. We tested this hypothesis by studying the breeding biology of pigeon guillemots during 1995–1999 while simultaneously measuring prey abundance with beach seines and bottom trawls. Our study area (Kachemak Bay, Alaska) comprises two oceanographically distinct areas. Populations of a lipid-rich schooling fish, Pacific sand lance (*Ammodytes hexapterus*), were higher in the warmer Inner Bay than in the colder Outer Bay, and sand lance abundance was higher during warm years. Populations of low-lipid content demersal fishes were similar between areas. Chick survival to age 15 days was 47% higher in the Inner Bay (high-lipid diet) than in the Outer Bay (low-lipid diet), and estimated reproductive success (chicks fledged nest^{-1}) was 62% higher in the Inner Bay than in the Outer Bay. Chick provisioning rate (kJ chick^{-1} h^{-1}) increased with the proportion of sand lance in the diet (r^2=0.21), as did growth rate (g day^{-1}) of younger (beta) chicks in two-chick broods (r^2=0.14). Pigeon guillemots in the Inner Bay switched to demersal prey during years of below-average sand lance abundance, and these birds reacted to 38-fold interannual changes in sand lance abundance with reductions in beta chick growth rates, with no decline in beta chick survival. In contrast, the proportion of nests experiencing brood reduction in the Outer Bay (demersal diet) increased >300% during years of below-average demersal abundance, although demersal fish abundance varied only 4-fold among years. Our results support the hypothesis that recovery of pigeon guillemot populations from the effects of the *Exxon Valdez* oil spill is limited by availability of lipid-rich prey.

Keywords Climate · *Exxon Valdez* · Food limitation · Junk food hypothesis · Seabird

Introduction

The pigeon guillemot (*Cepphus columba*) is a semicolonial seabird of the auk family (Alcidae) that has been one of the species affected by a widespread decline in populations of piscivorous seabirds and pinnipeds in the Bering Sea and Gulf of Alaska. The best census data for the species in the Gulf of Alaska are from Prince William Sound, where populations have declined approximately 72% between 1972 and 1989–1993 (Agler et al. 1999). This decline was partly due to the *Exxon Valdez* oil spill, which immediately killed approximately 500–1,500 pigeon guillemots in the Sound (5–14% of the estimated overall decline; Piatt et al. 1990). Populations in oiled areas had not recovered as of 1998 (Irons et al. 2000; Golet et al. 2002).

However, pigeon guillemot populations in the region may have also been affected by changes in fish abundance due to decadal-scale climate variability. Water temperatures in the Gulf of Alaska oscillate between cold and warm regimes that are associated with decadal-scale shifts in the location of the Aleutian atmospheric low (the Pacific Decadal Oscillation [PDO]; Mantua et al. 1997; Hare and Mantua 2000). A shift to a warm water regime in 1977 resulted in a >90% decline in populations of capelin (*Mallotus villosus*), a lipid-rich schooling fish, and a >250% increase in populations of

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lipid-poor demersal fishes (mostly Gadidae and Pleuron-ectidae; Anderson and Piatt 1999). This dramatic ecosystem change apparently cascaded through higher trophic levels, as the proportion of capelin and other lipid-rich fishes in diets of piscivorous birds and mammals declined, and populations of these high trophic level consumers declined as much as 95% (Piatt and Anderson 1996; Kuletz et al. 1997; Merrick et al. 1997; Agler et al. 1999). A subsequent regime shift in the late 1980s did not return the Gulf of Alaska food web to a pre-1977 state (Springer 1998; Hare and Mantua 2000).

One hypothesis to explain these population declines holds that the energy density (kJ g^{-1}) of low-lipid demersal fishes is inadequate to meet the energetic demands of birds and mammals, even when these fish are abundant (the "junk food" hypothesis; Piatt and Anderson 1996; Merrick et al. 1997; Rosen and Trites 2000). This is an attractive explanation for the decline in pigeon guillemots, since the proportion of Pacific sand lance (*Ammodytes hexapterus*), a lipid-rich schooling fish, in chick diets declined concurrent with the population decline, and sand lance were replaced in diets by a variety of low-lipid demersal fishes (Hayes and Kuletz 1997). Furthermore, natural or oil spill-caused declines in sand lance abundance have been hypothesized to constrain recovery of guillemot populations from the impact of the *Exxon Valdez* by limiting the ability of the population to replace oil-killed individuals (Golet et al. 2002). Captive feeding experiments with tufted puffins (*Fratercula cirrhata*), black-legged kittiwakes (*Rissa trydactyla*) and Steller sea lions (*Eumetopias jubatus*) support the junk food hypothesis (Kitaysky et al. 1999; Romano 2000; Rosen and Trites 2000). These studies have found that even when diets of high- and low-lipid fish contain the same amount of energy, piscivores fed the low-lipid diet experience reduced growth, reduced lipid reserves and elevated levels of corticosterone stress hormones. However, these experiments used diets comprising solely a gadid (walleye pollock *Theragra chalcogramma*) for low-lipid treatments. Diets of piscivores in the wild typically comprise a mixture of low- and high-lipid prey (Hatch and Sanger 1992; Merrick et al. 1997; Suryan et al. 2000), so captive-rearing experiments using single-species diets may overestimate the importance of high-lipid prey. Piscivores also possess a variety of behavioral and physiological traits (e.g., flexible foraging effort, variable duration of offspring rearing) that serve as buffers against variable food supply in the wild (Cairns 1987a; Burger and Piatt 1990; Monaghan et al. 1994; Uttley et al. 1994). Field studies of the response of free-ranging piscivores to variability in abundance of high-lipid and low-lipid prey are needed to further understanding of the links between ocean climate variability and the population ecology of high trophic level predators. However, few studies have simultaneously measured prey abundance and demography of piscivores in the high-latitude North Pacific.

In this paper we relate the breeding biology of pigeon guillemots to spatial and temporal variability in oceanography and prey abundance. Our study area (Kachemak Bay, Alaska) is bisected into two oceanographically distinct sections by the Homer Spit, and the two sections support distinct fish communities (Abookire et al. 2000). As a result, guillemots in the Inner Bay feed their chicks mostly sand lance (59% of meals), while guillemots in the Outer Bay feed their chicks mostly low-lipid demersal fishes (94% of meals; Litzow et al. 2000). By working in the two parts of the bay we could study the reproductive response of pigeon guillemots to differences in food availability while controlling for confounding temporal effects and effects operating over large spatial scales (hundreds of kilometers). Specifically, we tested two hypotheses. We tested the prediction of the junk food hypothesis that the high lipid content of sand lance should increase reproductive success for pigeon guillemots with access to these prey. A possible disadvantage of schooling prey not accounted for in the junk food hypothesis is that midwater fishes may be more variable in abundance than demersal fishes (Bradstreet and Brown 1985; Cairns 1987b). We therefore tested the hypothesis that switching between sand lance and demersal prey allows pigeon guillemots to moderate the effects of below-average sand lance abundance. On the basis of past work we expected the effects of diet quality to be more noticeable in younger (beta) chicks than in older (alpha) chicks (Ainley et al. 1990a; Shultz and Sydeman 1997; Cook et al. 2000). We tested our hypotheses with data on fish abundance from beach seines and bottom trawls, and data on the rate of energy flow to the nest, chick growth and survival rates, duration of chick rearing, and reproductive success.

Materials and methods

Study area

Kachemak Bay (59°35′N, 151°19′W) is located on the east shore of lower Cook Inlet, Alaska. The bay is bisected into oceanographically distinct inner and outer sections by the Homer Spit (Fig. 1). The Outer Bay is dominated by input from the Gulf of Alaska and is well mixed and relatively cold and saline, while the Inner Bay is influenced by river runoff and tends to be more stratified, warmer, and less saline (Abookire et al. 2000). During summer 1996–1998 median monthly surface temperatures averaged 0.9°C higher, and median monthly surface salinity averaged 3.1 PSU lower, in the Inner Bay (Abookire et al. 2000). Pigeon guillemots nest in approximately 30 small colonies of 2–15 nests each and in numerous solitary sites on the south shore of Kachemak Bay. Radio-tagged pigeon guillemots in the area foraged only within the part of the bay they nested in (Litzow et al., unpublished data), so we consider Inner Bay and Outer Bay colonies to represent independent foraging habitats.

Prey abundance

We measured prey abundance with trawls and seines set in areas where guillemots from study colonies were observed foraging. Detailed methods for our measurements of fish abundance are reported elsewhere (Robards et al. 1999a; Abookire et al. 2000; Litzow et al. 2000). We measured sand lance abundance with catch per unit effort (CPUE; fish set^{-1}) in 226 beach seines set every 2 weeks at ten sites around guillemot colonies during chick rearing. We made a single set at each site during a given tide stage

and sampled from 16 June to 25 July in 1995 and from 1 June to 8 August in 1996–1999 (n=18 sets in 1995, 46 in 1996, 60 in 1997, 57 in 1998, and 45 in 1999). We classified sand lance ≥80 mm total length as "forage size", as these are the size classes fed to guillemot chicks (Litzow et al. 2000).

We measured demersal fish abundance with bottom trawl CPUE (fish 1,000 m^{-2}). We classified *Lumpenus* pricklebacks 80–200 mm total length and other demersal fish 80–150 mm total length as forage size (Litzow et al. 2000). We excluded hexagrammids and gadids from trawl data because these fishes account for <1% of chick diets in Kachemak Bay (Litzow et al. 2000). Bottom trawls were conducted once each year during mid-August (n=11 sets in 1996, 13 in 1997, 14 in 1998, and 11 in 1999).

We related sand lance abundance during 1996–1998 to previously published average July-August sea surface temperature (SST) from the Inner and Outer Bay (Abookire et al. 2000). We also used 1999 SST data that were collected using identical methods (A. Abookire, personal communication).

Nestling diet composition

Pigeon guillemots carry single fish in their bills when provisioning chicks, and usually rest on the water in front of the colony before delivering to the nest, making prey identification relatively easy. We collected diet data for at least 1 year at each of ten guillemot colonies (Fig. 1). 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 hours) in 1995. Each nest was watched

Fig. 1 Location of pigeon guillemot (*Cepphus columba*) study nests and colonies in Kachemak Bay, Alaska. *Stars* indicate colonies where provisioning watches occurred

for at least 14 h (n=15 nests). From 1996 to 1999 we conducted all day watches (0600–2200 hours; n=10 nests in 1996, 18 in 1997, 18 in 1998, 8 in 1999). Provisioning adults were observed from anchored boats (using binoculars) or from blinds (using telescopes), and each chick meal was identified to the lowest possible taxonomic level.

We measured diet composition as the proportion (by number) of sand lance in the diet.

Chick provisioning rates

Pigeon guillemots provision chicks at a lower rate when they are newly hatched or nearly fledged (Drent 1965; Emms and Verbeek 1991), so we only included nests with chicks aged 8–30 days in calculations of delivery rate (meals chick^{-1} h^{-1}) and energy provisioning rate (kJ chick^{-1} h^{-1}).

We visually estimated fish length relative to the length of a pigeon guillemot bill, in multiples of half bill-lengths. In order to calibrate our visual estimates of meal length we collected chick meals during 1996–1998 and measured the bill length (gape to tip) of six adult pigeon guillemots from Prince William Sound (mean=43.2 mm). The length of collected meals (mean=128 mm, SD=39 mm, n=79) was significantly greater than visual length estimates generated with this standard for bill length (mean= 115 mm, SD=32 mm, n=2167; t_{2244}=3.54, P<0.001). We therefore corrected our visual estimates upwards by multiplying them by 128/115. We estimated energy provisioning rates by converting length to mass with length-weight regressions from fish caught in trawls and seines (Table 1). We translated the resulting mass estimates into meal energy content using published values for prey taxa energy density. Energy density was calculated by averaging values for every species in a particular prey group that was sampled in appropriate size classes in the cited references (Table 1; Van Pelt et al. 1997; Robards et al. 1999b; Anthony et al. 2000). This method provides an unbiased comparison of the energy content of diets containing different prey taxa (Emms and Verbeek 1991). We included date in our calculations in situations when information on seasonal change in energy density was available.

Chick growth rates and reproductive success

We visited nests every 5 days to determine the fate of eggs and chicks and to weigh chicks with spring-loaded scales. During 1997 and 1998 we visited nests every 2 days after chicks were >30 days old so that we could accurately estimate fledging age. Chicks were assigned a rank based on their age: alpha (the older of a two-chick brood), beta (the younger in a brood) or singleton (when only one egg in a clutch hatched). Because of the cryptic nature of nests, we often discovered nests only after chicks had hatched. In these situations we estimated age for chicks ≤10 days old based on flattened wing chord, using measurements from a set of known-age chicks for comparison (G. Divoky, personal com-
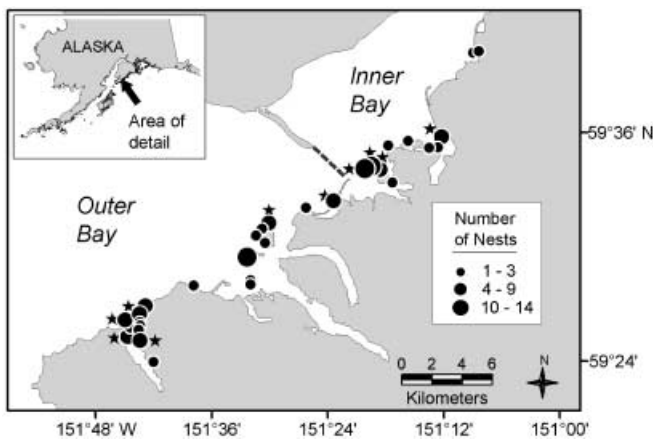
Table 1 Regressions of mass (y) on length (x) and wet mass energy density values used in estimating the energy content of pigeon guillemot nestling diets. Sources: *a* Robards et al. (1999b); *b* Anthony et al. (2000); *c* Van Pelt et al. (1997)

Prey group	Scientific name	Regression	kJ g^{-1}	Source
Pacific sand lance (July)	*Ammodytes hexapterus*	$y=(2\times10^{-6}x)^{3.1224}$	5.25	a
Capelin	*Mallotus villosus*	$y=(3\times10^{-7}x)^{3.684}$	5.04	b
Pacific sand lance (August)	*Ammodytes hexapterus*	$y=(2\times10^{-6}x)^{3.1224}$	5.02	a
Prickleback	*Lumpenus* spp.	$y=(4\times10^{-6}x)^{2.8977}$	4.76	b
Gunnel	Pholidae	$y=(8\times10^{-7}x)^{3.2825}$	4.69	b
Ronquil	*Ronquilus jordani, Bathymaster signatus*	$y=(3\times10^{-6}x)^{3.177}$	4.11	b
Sculpin	Cottidae	$y=(1\times10^{-5}x)^{3.0128}$	4.10	b
Salmonid	Salmonidae	$y=(6\times10^{-6}x)^{3.0781}$	4.04	b
Gadid	Gadidae	$y=(7\times10^{-6}x)^{3.0241}$	3.31	b
Flatfish	Pleuronectidae	$y=(9\times10^{-6}x)^{3.0354}$	3.28	b
Greenling	Hexagrammidae	$y=(2\times10^{-6}x)^{3.3399}$	3.16	b,c

munication). Age explained 83% of variability in wing length of known-age chicks in this age range. We used growth rate (slope of linear regression of mass on age) of chicks age 5–20 days for comparisons of chick growth (Emms and Verbeek 1991).

We used the Mayfield method (Johnson 1979) to estimate nesting success. We used a mean value for incubation length (31 days; Ewins 1993). Chicks may fledge any time post-30 days (Ewins 1993), and since it is difficult to determine whether chicks older than 30 days have fledged or been depredated, we calculated survival to age 30 days. To account for age dependant mortality we calculated separate survival estimates for chicks age 1–15 days and 16–30 days. We make statistical comparisons of reproductive success in terms of five parameters: clutch size, proportion of eggs surviving incubation, proportion of surviving eggs that hatched, proportion of chicks surviving to age 15 days, and proportion of chicks surviving 16–30 days. We also present estimates of reproductive success (chicks fledged nest^{-1}) that are the product of these five parameters. Reproductive success during the study was also affected by nest predation. Since predators typically removed the entire contents of nests, we used the incidence of brood reduction as a measure of reproductive success independent of predation. We defined brood reduction as situations where a beta chick died or disappeared from a nest while the alpha survived. Every case of brood reduction that we observed occurred when chicks were ≤20 days old, so we estimated the incidence of brood reduction as the Mayfield daily survival rate of beta chicks age 0–20 days in nests with surviving alpha chicks.

Statistical analysis

Daily survival rates estimated from the Mayfield method were compared with a Z-test (Johnson 1979). When provisioning data were collected more than once from a single nest in one year we averaged data from different watches before analysis. We did not detect an effect of chick age on provisioning rate for chicks age 8–30 days (linear regression; $F_{1,38}=0.22$, $r^2=0.01$, $P=0.65$), so we ignored the effect of age in subsequent analyses.

Multiple beach seine sets made at a single site violate assumptions of independence, so we treated individual sets as subsamples with nested ANOVA (Zar 1999). We tested for year differences using year, site, and set(site) as factors, and tested for area differences using area, site(area) and set(site) as factors. Bottom trawls were set only once at each site in each year, so we used only used a nested approach for our test of area differences. Our 5-year study did not provide adequate power to use a regression approach to examine the annual-scale response of pigeon guillemot breeding biology to variability in prey abundance, so we used a categorical approach. When ANOVA indicated significant differences in CPUE among years we compared breeding parameters during years of above-average and below-average CPUE for the dominant prey type in each study area. Classification of years as "above average" and "below average" was judged superior to statistical pairwise comparisons for purposes of defining food abundance categories because the extremely high variability in CPUE data and the logistical difficulty of conducting seines and trawls meant that we could only detect extremely large pairwise differences. By classifying years as above- and below-average for each prey type we were able to use all of our breeding biology data in tests for response to variability in food supply. Each year was classified as above- or below-average through comparison with the interannual grand mean of log (x+1) transformed CPUE for each prey type. CPUE data were log-transformed to correct for heteroscedasticity, and because the dietary functional response of pigeon guillemots shows a logarithmic relationship with variability in abundance of preferred prey (Litzow et al. 2000). One-tailed tests were used for the junk food hypothesis and for tests of the effects of declining food abundance, since in both cases hypotheses made directional predictions. All other tests were two-tailed. All proportional data used in regression analysis were arcsine-transformed to satisfy assumptions of normality. We set α=0.05, and we report all means ±1 SE.
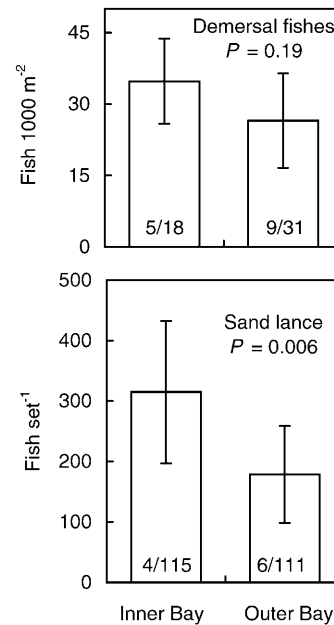

Fig. 2 Food availability for breeding pigeon guillemots in two areas of Kachemak Bay, Alaska, 1995–1999. Catch per unit effort (CPUE) is from beach seines for sand lance, bottom trawls for demersal fishes. Sample sizes at base of columns are number of sites / number of individual sets. Data are grand means of average CPUE at different site-years in the two areas, *error bars* ±1 SE. *P*-values are from nested ANOVA

Results

Prey availability

We caught 56,037 forage-size sand lance and 936 forage-size demersal fish. The most common demersal fishes in trawls were rock sole (*Pleuronectes bilineatus*), yellowfin sole (*P. asper*), crescent gunnels (*Pholis laeta*), northern ronquils (*Ronquilus jordani*), arctic shannies (*Stichaeus punctatus*), and flathead sole (*Hippoglossoides elassodon*). Sand lance CPUE was 76% higher in the Inner Bay than in the Outer Bay (Fig. 2; nested ANOVA, $F_{1,224}=7.63$, $P=0.006$). We failed to detect a significant area difference in CPUE of all demersal fishes (Fig. 2; nested ANOVA, $F_{1,47}=1.79$, $P=0.19$), although sampling effort (49 sets) limited the power of this comparison.

Sand lance CPUE varied 38-fold among years (Fig. 3; nested ANOVA, $F_{4,212}=3.58$, $P=0.008$). Log-transformed sand lance CPUE was above average in 1995, 1998, and 1999, and below average in 1996 and 1997. CPUE for all demersal fishes as a group varied 4-fold among years (Fig. 3; ANOVA, $F_{3,45}=3.49$, $P=0.02$). Log-transformed demersal CPUE was above average in 1997 and below average in 1996, 1998 and 1999.

Interannual variability in sand lance abundance was apparently driven by variability in ocean climate; CPUE increased with increasing SST (Fig. 4; ANCOVA of area and SST, SST: $F_{1,5}=11.22$, $P=0.02$). We did not detect a
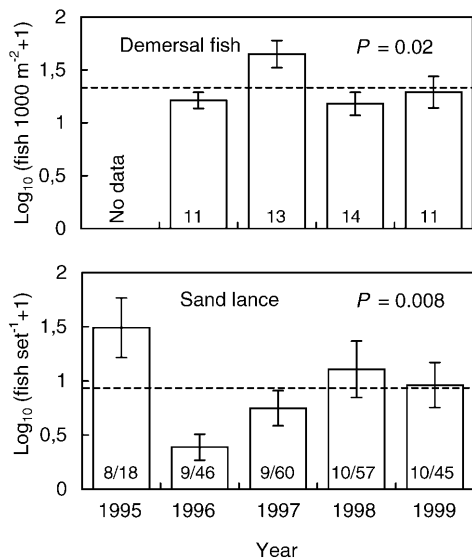
Fig. 3 Interannual variability in CPUE of sand lance and demersal fishes in Kachemak Bay, Alaska, 1995–1999. Note log scales. Dashed lines indicate interannual means used to classify years for tests of response of pigeon guillemots to variability in food supply. Sample sizes given at base of demersal fish columns are the number of bottom trawl sites; one set was made at each. Sample sizes given at base of sand lance columns are number of beach seine sites / total number of sets. *Error bars* ±1 SE
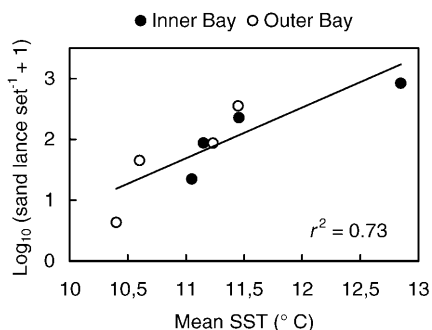

Fig. 4 The effect of variable sea surface temperature (SST) on sand lance abundance (log-transformed CPUE in beach seines). Each point represents annual data from one study area. Temperature data are July–August averages during 1996–1999 (Abookire et al. 2000; A. Abookire, personal communication). ANCOVA showed a significant SST effect on CPUE (*P*=0.02)
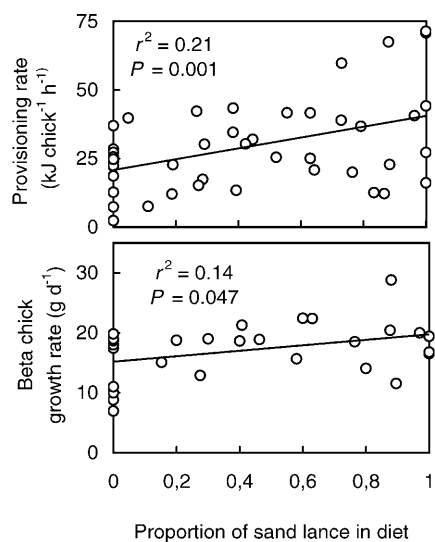

Fig. 5 The effect of high-lipid prey on nestling provisioning and growth rates. Growth rates are for beta chicks age 5–20 days. Fourteen data points lie on the y-axis in the *top panel*, 12 in the *bottom panel*

similar relationship between SST and demersal CPUE ($F_{1,5}$=0.73, *P*=0.43).

Breeding biology in relation to diet

Estimated chick provisioning rates (kJ chick^{-1} h^{-1}) increased with the proportion of sand lance in the diet (Fig. 5; linear regression, *n*=46 nests, r^2=0.21, *P*=0.001). This increase in provisioning rate was due to the high caloric value of sand lance, as we failed to detect increases in prey delivery rate (linear regression, *n*=46 nests, r^2=0.02, *P*=0.38), or estimated meal mass (demer-

sal fish = 10.6±0.3 g, sand lance = 9.9±0.4 g, t_{819}=1.38, *P*=0.16).

Growth rates of beta chicks also increased with the presence of sand lance in the diet (Fig. 5; linear regression, *n*=28, r^2=0.14, *P*=0.02). There was no area effect on growth rates of alpha and singleton chicks as a group; mean and standard error were identical for the two areas (18.3±0.6 g day^{-1}). However, beta chick growth was 37% higher in the sand lance diet area (Inner Bay = 18.9±0.6 g day^{-1}; Outer Bay = 13.8±1.4 g day^{-1}; one-tailed t_{59}=3.66, *P*<0.001). Average growth rate of all chicks in this study (17.7±0.4 g day^{-1}) was 9% greater than the average growth rate (16.2±0.8 g day^{-1}) from five studies reviewed by Golet et al. (2000; one-sample t_{160}=3.93, *P*=0.0001).

Over all years of the study, chick survival to age 15 days was 47% higher in the Inner Bay (sand lance diet) than in the Outer Bay (demersal diet; *Z*=3.75, one-tailed *P*<0.001), and estimated reproductive success was 62% higher in the Inner Bay (0.47 chicks fledged nest^{-1}, *n*=115) than in the Outer Bay (0.29 chicks fledged nest^{-1}, *n*=136). Daily survival rates of beta chicks were higher in the Inner Bay (0.998±0.002, *n*=36) than in the Outer Bay (0.971±0.002, *n*=45; *Z*=3.72, one-tailed *P*<0.001). This difference in survival rate produced strong spatial patterns in brood reduction, which was observed in 3% of Inner Bay two-chick nests (*n*=36) and 36% of Outer Bay nests (*n*=45). Chicks in the Inner Bay also fledged an average of 3 days younger than chicks in the Outer Bay (Inner Bay = 35±0.5 days; Outer Bay = 38± 0.6 days; t_{64}=3.24, one-tailed *P*=0.001). We detected no area difference in clutch size, egg survival, the proportion of surviving eggs that hatched or survival of chicks age 16–30 days (one-tailed *P*>0.25).
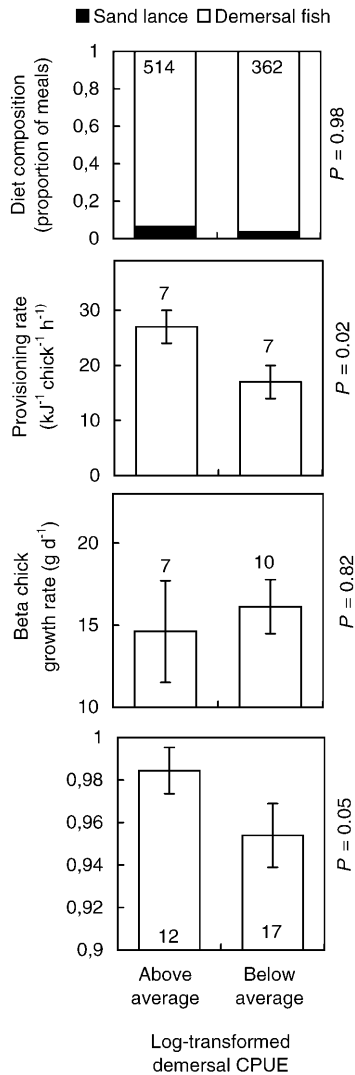
Fig. 6 Response of pigeon guillemots feeding on demersal prey to interannual variability in prey abundance: Outer Kachemak Bay breeding parameters in years of above-average (1997) and below-average (1996, 1998, 1999) demersal fish abundance. *P*-values are one-tailed, error bars ± 1 SE

Fig. 7 Response of pigeon guillemots feeding on sand lance to interannual variability in prey abundance: Inner Kachemak Bay breeding parameters in years of above-average (1995, 1998, 1999) and below-average (1996, 1997) sand lance abundance. *P*-values are one-tailed, *error bars* ±1 SE

Responses to temporal prey variability

Pigeon guillemots in the two areas reacted to low food availability with adjustments to different breeding parameters. In the Outer Bay sand lance were rarely fed to chicks, and parents did not increase the proportion of sand lance in chick diets when demersal abundance declined; demersal fish actually made a larger contribution to diets during years of below-average demersal CPUE (Fig. 6; Fischer exact test, one-tailed *P*=0.98). Estimated provisioning rates fell 37% in the Outer Bay during below-average demersal years (Fig. 6; t_{16}=2.30, one-tailed *P*=0.02). We did not detect a decline in beta chick growth rates (Fig. 6; t_{15}=0.47, one-tailed *P*=0.82), although we recognize the low statistical power of this comparison. Brood reduction did increase significantly during below-average years; beta chick daily survival
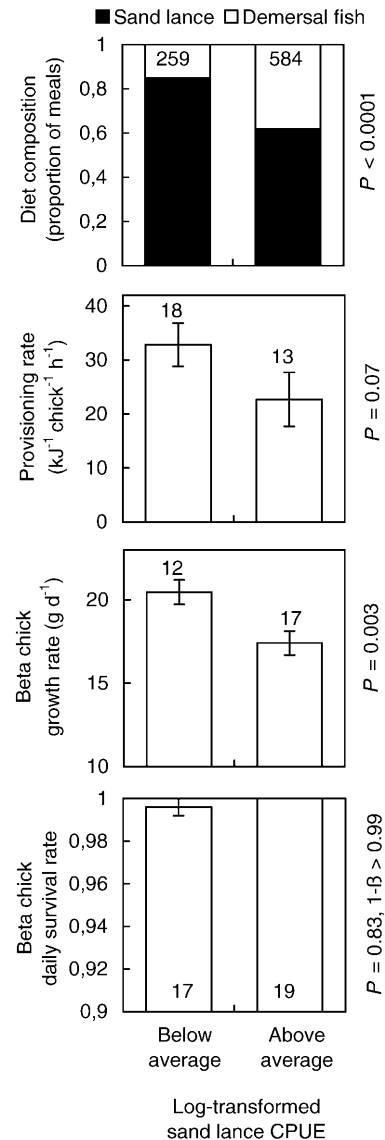
rates decreased 3% during below-average demersal years (Fig. 6; *Z*=1.65, one-tailed *P*=0.05). This decline in daily survival was large enough that the incidence of brood reduction increased from 17% during the above-average demersal year (*n*=12 nests) to 53% during below-average years (*n*=17 nests).

Pigeon guillemots in the Inner Bay more than doubled the proportion of demersal fish in chick diets during years of below-average sand lance abundance (Fig. 7; Fischer exact test, one-tailed *P*<0.0001). Mean provisioning rate in the Inner Bay was 31% lower during years of below-average sand lance abundance, but this decline was marginally non-significant (Fig. 7; t_{23}=1.52, one-tailed *P*=0.07). There was a 15% decline in beta chick growth rates during below-average sand lance

years (Fig. 7; t_{27}=2.98, one-tailed P=0.003). However, declines in food abundance did not reduce beta chick survival in this area; we observed brood reduction once during years of above-average sand lance abundance (n=17 nests), and never during below-average sand lance years (n=19 nests; Z=1.00, one-tailed P=0.83; Fig. 7). These results allow us to rule out an effect similar to that observed in the Outer Bay with statistical power (1-β)>0.99.

Discussion

This study supports the hypothesis that scarcity of lipid-rich schooling fish has negatively affected pigeon guillemot populations in the Gulf of Alaska. The presence of sand lance in the diet was associated with higher rates of energy delivery to the nest, higher chick growth rates, shorter duration of chick rearing, improved chick survival, decreased brood reduction and increased reproductive success. An additional benefit was seen in a buffered response to annual-scale variability in prey abundance. Individuals with access to abundant sand lance switched to demersal fishes when sand lance were scarce, and reacted to declines in food availability with adjustments to a less critical breeding parameter (beta chick growth rate) than did non-switching individuals feeding primarily on low-energy demersal fishes (brood reduction).

Differences in prey abundance in our study were correlated with variability in ocean climate. We found that warmer SST resulted in increased sand lance abundance (Fig. 4), and the spatial differences in sand lance abundance that we observed have previously been linked to spatial differences in oceanography (Abookire et al. 2000). By demonstrating a link between pigeon guillemot reproductive success and oceanographically mediated patterns in the abundance of high-lipid prey, this study supports the hypotheses that food limitation has adversely affected pigeon guillemot populations in the Gulf of Alaska since 1977, and that natural or oil spill-related reductions in sand lance abundance have constrained recovery of guillemot populations that were harmed by the *Exxon Valdez* oil spill. Because our study was correlative, we cannot rule out other area differences, such as other differences in foraging ecology or differences in parental quality, that may have contributed to differences in guillemot breeding biology. However, there is some evidence that one potential confounding factor, predation, did not drive differences in breeding biology. Most egg losses in the study were due to predation, so our failure to find area differences in egg survival suggests that nest predation was fairly constant between areas.

Benefits of high-lipid prey

Dietary energy content is often the limiting factor for seabird breeding success (Drent and Daan 1980). Birds may regulate the rate of energy provisioning to nestlings through adjustments to three variables: meal mass, meal energy density (kJ g^{-1}), and meal delivery rate (Orians and Pearson 1979; Roby 1991). We did not find an effect of diet composition on meal delivery rate or meal mass. Since sand lance energy density is up to 1.7 times greater than that of the demersal fish species that pigeon guillemots preyed on in this study (Table 1), provisioning rate (kJ chick^{-1} h^{-1}) was influenced by the proportion of sand lance in the diet. Diet composition explained 21% of variability in provisioning rate and 14% of variability in beta chick growth rate (Fig. 5). These are strong effects, considering that other factors may affect both provisioning rate (e.g., prey abundance, chick age, brood size, and parental experience) and chick growth (e.g., meal delivery rate, degree of hatch asynchrony; Cook et al. 2000; Drent 1965; Emms and Verbeek 1991; Roby 1991; Sydeman and Emslie 1992; Shultz and Sydeman 1997). Pigeon guillemots at colonies without access to abundant schooling fish were apparently unable to make adjustments to prey delivery rates or meal size in order to compensate for the low energy content of available prey. Thus, below some threshold of high-lipid prey availability, pigeon guillemots are apparently unable to achieve maximal rates of chick provisioning.

Average chick growth rate in this study was 9% greater than the average of growth rates from five other studies (Golet et al. 2000), suggesting that foraging conditions were relatively good during our study, and that our conclusions regarding the impact of low-lipid diets are conservative. Our findings corroborate previous research showing that pigeon guillemots specializing on high-lipid schooling prey have higher reproductive success than individuals within the same colony that provision mostly with demersal fishes (Kuletz 1983; Golet et al. 2000).

Given the apparent advantages of a diet rich in midwater prey, why would pigeon guillemots choose to nest in areas without access to these prey? While *Cepphus* chick diets are occasionally dominated by lipid-rich fishes (Ewins 1990; Golet et al. 2002), diets are more typically composed of lipid-poor demersal fishes (Drent 1965; Cairns 1981, 1987b; Ainley et al. 1990b; Emms and Verbeek 1991; Barrett and Anker-Nilssen 1997). One advantage of low-lipid demersal fishes may be their temporal predictability. Interannual variability in sand lance abundance (38-fold) was greater than that of all demersal fishes as a group (4-fold) although our 5-year study was not long enough for a statistical comparison of interannual variability in the two groups. Others have speculated that demersal fish abundance varies less among years than midwater fish abundance (Bradstreet and Brown 1985; Cairns 1987b), but we are not aware of any other study that has measured annual variability of the two prey groups. Decadal-scale variability is also probably greater for midwater fish species, which may disappear from regional food webs for decades (Anderson and Piatt 1999) resulting in breeding failure, increased adult mortality, and population declines in seabird spe-

cies that rely on midwater prey (Blake 1986; Crawford and Dyer 1995; Barrett 1996; Piatt and Anderson 1996). Alternately, predation on demersal fishes may release *Cepphus* guillemots from competition with other piscivorous auks, which mostly prey on midwater fishes (Bradstreet and Brown 1985). Finally, some pigeon guillemots may be forced to nest in poor foraging areas due to a shortage of adequate nest sites in areas with abundant schooling prey (Cairns 1992).

Prey switching as a buffer against temporal variability in food supply

In spite of the high interannual variability in sand lance abundance, pigeon guillemots nesting at the Inner Bay (sand lance diet, switching to demersal fish) were less susceptible to the effects of decreased food abundance than pigeon guillemots at the Outer Bay (entirely demersal diet). Sand lance and demersal fish abundance fluctuated asynchronously during the study (Fig. 3), which would make switching to demersal fishes during years of low sand lance abundance a particularly effective strategy. Guillemots may also have buffered against temporal variability in food supply with behavior not measured in this study, such as flexible time-activity allocation (Burger and Piatt 1990).

Evidence that prey switching can act as an efficient buffer for seabirds against declines in the abundance of preferred prey is equivocal, and maintenance of some threshold amount of lipid-rich fish in the diet may be a key factor. Thus black-legged kittiwakes in Norway and Alaska were able to maintain high reproductive success by switching among alternate lipid-rich prey (Barrett et al. 1987; Suryan et al. 2000). Common and thick-billed murres (*Uria aalge* and *U. lomvia*) in Canada were able to maintain constant reproductive success when the proportion of lipid-rich capelin in chick diets declined from ~75% to 12–45% (for common) and 20–30% to ~3% (for thick-billed; Bryant et al. 1999). Conversely, other species in California and Norway (pelagic cormorant *Phalacrocorax pelagicus*, pigeon guillemot, Atlantic puffin *Fratercula arctica*) suffered large declines in reproductive success when lipid-rich fish were not available to replace scarce preferred prey (Ainley et al. 1995; Barrett 1996).

We found that pigeon guillemots were well described by the Cairns (1987a) model of response to variable prey abundance, which hypothesizes that breeding seabirds should respond to increasingly severe food shortages with modification of increasingly critical reproductive parameters. Pigeon guillemots feeding mostly on lipid-rich sand lance suffered reduced beta chick growth rates during years of below-average sand lance abundance, but did not experience a decline in beta chick survival (Fig. 7). Although there was some evidence that provisioning rates for this group declined during years of below-average sand lance abundance (Fig. 7), the decline was not as severe as that experienced by the low-

lipid diet group in years of below-average demersal abundance (Fig. 6). This more food-limited group experienced a decline in beta chick survival rate (Fig. 6) that resulted in a >300% increase in the proportion of nests experiencing brood reduction during years of below-average demersal abundance – 3 out of the 4 years that demersal fish abundance was measured during the study. This increase in brood reduction is consistent with beta starvation as a result of alpha chicks taking the majority of meals delivered to a nest during food shortages, as has been demonstrated for black guillemots (*Cepphus grylle*; Cook et al. 2000).

Pigeon guillemot populations and ocean climate

Spatial differences in physical oceanography between Inner and Outer Kachemak Bay created spatial differences in fish abundance and community composition (Abookire et al. 2000). These differences in fish distribution led to differences in pigeon guillemot diet (Litzow et al. 2000), which in turn produced geographic differences in reproductive success (this study). Thus, we demonstrate a link between ocean climate and pigeon guillemot demography, supporting the hypothesis that changes in fish abundance due to temporal variability in oceanography have adversely affected pigeon guillemot populations in the Gulf of Alaska since the 1977 PDO regime shift. The link between pigeon guillemots and oceanography is also demonstrated by the effect of temporal variability in SST on the abundance of high-lipid prey (Fig. 4).

Sand lance populations are apparently higher in Inner Kachemak Bay because the combination of nutrient input from rivers and increased stratification results in increased primary production (Abookire et al. 2000). Our findings that guillemot reproductive success was higher in a warm area and that sand lance were more abundant during warm years complement studies of interannual climate variability in southeast Alaska (Paul et al. 1991; Paul and Coyle 1993) and the Sea of Okhotsk (Kitaysky and Golubova 2000). These studies have shown that the meso-zooplankton prey of lipid-rich schooling fishes are more abundant during warm years than during cold years, and that piscivore reproductive success increases as a result.

Although several hypotheses have been advanced, the mechanisms linking fish populations with decadal-scale climate variability are not currently understood (Mantua et al. 1997; Anderson and Piatt 1999; Hare and Mantua 2000; Mueter and Norcross 2000). The complexity of this problem is highlighted by an apparent paradox: while both high-lipid prey abundance and piscivore reproductive success were higher in warm spatial regimes (this study) and during warm annual regimes (Kitaysky and Golubova 2000; this study), warm decadal-scale PDO regimes are associated with population declines of high-lipid fishes and piscivores (Anderson and Piatt 1999).

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