Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*

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ABSTRACT: To better understand how fluctuations in prey abundance may impact seabird reproductive success, we studied short-term changes in prey populations and their effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*, a predator of near-surface-schooling forage fishes. Our fine-scale approach involved a weekly assessment of forage fish abundance and brood-rearing conditions during 4 consecutive years (1996 to 1999) at the Shoup Bay kittiwake colony in Prince William Sound, Alaska. We conducted forage fish surveys from a fixed-wing aircraft to determine weekly prey abundance throughout the known foraging range of breeding kittiwakes. Our results provide clear evidence that short-term fluctuations in prey availability are responsible for dramatic, within-season changes in the breeding conditions of black-legged kittiwakes. Adult kittiwakes often showed immediate response to changes in the prey base by altering prey selection; however, there were instances when kittiwakes selected prey species disproportionate to their availability (typically selecting for Pacific herring *Clupea pallasi* and against Pacific sand lance *Ammodytes hexapterus*). Changes in prey selection often resulted in striking differences in the amount of time required to obtain a load of food. The cascading effects of longer foraging trips was translated into reduced nestling growth and survival. Of the 3 components of energy provisioning to nestlings (meal delivery rate, meal size, and energy density), meal delivery rate had the strongest and most consistent positive effect on nestling growth and survival. Overall, these results demonstrate that complex foraging conditions limit the reproductive success of a central place-foraging species relying on an ephemeral food source. Moreover, we demonstrated that feeding conditions during the first 2 wk of brood-rearing were most critical for survival of the brood. Given the potential for such marked within-season variation in breeding conditions, it is critical that investigators adequately sample throughout the brood-rearing period, or, alternatively, select that portion that is germane to their study.

KEY WORDS: *Rissa tridactyla* · Forage fish abundance · *Clupea pallasi* · *Ammodytes hexapterus* · Prey selection · Nestling provisioning rate · Nestling development

INTRODUCTION

The stochastic nature of prey availability within the marine environment has been theorized as the primary factor shaping seabird life history strategies (Lack

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1968). In general, the lack of a predictable local food source during the breeding season has led Lack (1968) and Ashmole (1971) to suggest that seabirds have adapted to a variable environment by having highly flexible foraging strategies and attempting to raise few young each year during a protracted brood-rearing period. However, among seabird taxa there is considerable variation in the length of brood-rearing, ranging from the extreme life histories with infrequent nestling provisioning (intervals >10 d) and extended brood-rearing periods (up to 90 d or more) for many procellariiformes (shearwaters, petrels, albatrosses; Warham 1990) to larids (gulls and terns) and alcids (guillemots and puffins) which provision their young multiple times per day for a relatively short period (<50 d). Furthermore, it has been noted that differences in meal delivery rates among individual seabirds (including between mates) was greater than among populations, suggesting that food supply at the population level was not the primary cause of variation in foraging success (Ricklefs & Schew 1994, Phillips & Hamer 2000). Therefore, it remains unclear how much of the variation in seabird foraging strategies is related to changes in prey availability at the population level.

Throughout the nestling provisioning period, variation in the foraging activities of adult seabirds may also be related to the demands of nestlings and, therefore, somewhat independent of prey abundance. Several investigators have shown that adult seabirds adjust foraging activities (i.e. provisioning rates) in response to immediate requirements of their nestlings (Ricklefs et al. 1985, Bertram et al. 1996, Hamer & Thompson 1997, Granadeiro et al. 2000). However, other investigators have suggested that the requirements of nestlings did not affect the rate of nestling provisioning by adult seabirds (Galbraith 1983, Ricklefs 1992, Hamer & Hill 1993, Hamer 1994), implying that environmental conditions (e.g. weather or prey abundance) predominantly influenced foraging activities.

Arguably, it may ultimately be environmental conditions, most notably prey abundance, that constrain or provide seabirds the opportunity to adjust their provisioning to meet the requirements of nestlings. Prey abundance is thought to be related to seabird reproductive parameters in a nonlinear fashion (Cairns 1987) such that beyond a threshold or asymptotic value of prey abundance, some reproductive parameters (e.g. clutch size, breeding success, nestling growth and provisioning rate) will not vary (Burger & Piatt 1990, Phillips et al. 1996, Suddaby & Ratcliffe 1997). Beyond this threshold of prey abundance, adult seabirds may have the freedom to adjust provisioning according to demands of nestlings. However, at prey abundances below the threshold, nestling provisioning may be constrained by the ability of adults to obtain a load of food. Discrepan-

cies between studies reporting on factors controlling nestling provisioning in seabirds may, therefore, be a function of differences in prey abundance in relation to this nonlinear association between predator and prey.

Investigators have tested the theory of prey limitation and its effects on seabird reproduction by comparing reproductive parameters among colonies or years using some index or estimate of prey abundance. Often these indices are derived from fisheries catches (Hamer et al. 1993, Monaghan et al. 1994, Crawford & Dyer 1995) or, less frequently, from dedicated prey sampling (Burger & Piatt 1990). Whereas techniques such as these have provided valuable insight into seabird and forage fish relationships on an annual basis, they lack sufficient detail to link a highly mobile predator to a prey base that can exhibit substantial temporal variation on a scale smaller than a 3 mo breeding season. Moreover, because of limited sources for determining forage fish abundance, investigators may be forced to compare prey abundance from sub-surface sampling (e.g. boat-based hydroacoustic or trawl surveys) to diets of a surface-feeding predator. Additionally, the coincidence between at-sea feeding locations of breeding seabirds and locations of prey sampling are assumed with minimal knowledge of the exact feeding locations of breeding birds. In this study we conducted aerial surveys from a fixed-wing aircraft to determine prey abundance, thereby allowing us, within 1 d, to sample prey populations throughout the entire known foraging range (based on radio-tracking studies; Irons 1998, Suryan et al. 2000) of a colony of breeding black-legged kittiwakes *Rissa tridactyla*. To our knowledge, this was the first reported study of a surface-feeding, piscivorous seabird in which the method of assessing prey abundance was comparable to temporal and spatial variation observed from the perspective of the aerial predator. In this study, we assessed weekly changes in prey abundance and determined how short-term variation in forge fish abundance affected prey selection and brood-rearing in this colonial breeding seabird.

MATERIALS AND METHODS

We studied the reproductive and foraging ecology of black-legged kittiwakes during 4 consecutive yr (1996 to 1999) at the Shoup Bay colony (ca. 7000 breeding pairs) in Prince William Sound, Alaska (PWS; Fig. 1). In addition, we determined the abundance of key prey species within the foraging range of breeding birds from Shoup Bay during 3 of the 4 yr (excluding 1996). Our primary goal was to evaluate the ecological relationship between short-term (within-season) changes in prey abundance and kittiwake breeding conditions. We therefore collected data at 7 ± 1 d intervals corre-

sponding to the first 5 wk of brood-rearing (nestlings fledge when ≤40 d). During the first 3 yr, Week 1 began on 1 July, however, in 1999 Week 1 began on 8 July because of delayed breeding chronology.

Forage fish abundance. We used a fixed-wing aircraft to estimate the relative abundance of surface schooling forage fishes (Pacific herring *Clupea pallasi*, and Pacific sand lance *Ammodytes hexapterus*) available to breeding black-legged kittiwakes. Use of aerial surveys to estimate the abundance of forage fishes available to kittiwakes was beneficial compared to boat-based sampling for several important reasons: (1) the entire shoreline within a kittiwake's potential foraging range could be sampled in 1 d, therefore our sampling methodology matched the spatial and temporal scale of the foraging activities of kittiwakes; (2) the aircraft provided observers with a perspective comparable to that of an aerial, near-surface feeding predator like the kittiwake; (3) fish schools often occurred in shoreline waters that were too shallow to operate boat-based hydroacoustic gear; and (4) there was no avoidance of sampling gear by surface-schooling fish.

Fig. 1. Location of the Shoup Bay black-legged kittiwake colony in Prince William Sound, Alaska (61° 10′ N, 146° 33′ W). The maximum foraging range of kittiwakes breeding at Shoup Bay is depicted by the dashed polygon. Also shown is the flight path (•••) used during aerial surveys to determine weekly abundance of surface schooling forage fishes within the foraging range of breeding kittiwakes

Aerial surveys included all shoreline waters within the maximum known foraging range of adult kittiwakes from the Shoup Bay colony (Suryan et al. 2000; Fig. 1). We restricted our surveys to nearshore waters because, in 8 yr of study, nearly all foraging by kittiwakes (D.B.I. & R.M.S. unpubl. data) and other seabirds in PWS (Maniscalco et al. 1998) occurred within 1 km of the shoreline. Aerial surveys were conducted during 11 of the 20 wk of our 4 yr study and survey effort ranged from 219 to 1043 $km^2 wk^{-1}$ (Table 1). The relative density of prey species was consistent among locations within our study area and, therefore, occasions of variable shoreline coverage should not affect our results. Typically, 1 to 3 surveys of the entire study area were conducted each week.

Herein we describe the basic methodology for conducting aerial surveys; for a more detailed description see Brown et al. (2002). Transects were surveyed from a float plane (Cessna 185) at approximately 204 $km h^{-1}$. A single transect line was surveyed parallel to the shore and was broken only in areas of high school density, where the area was circled to ensure complete counts of schools. The preferred altitude range was 274 to 366 m based on ability to discriminate fish
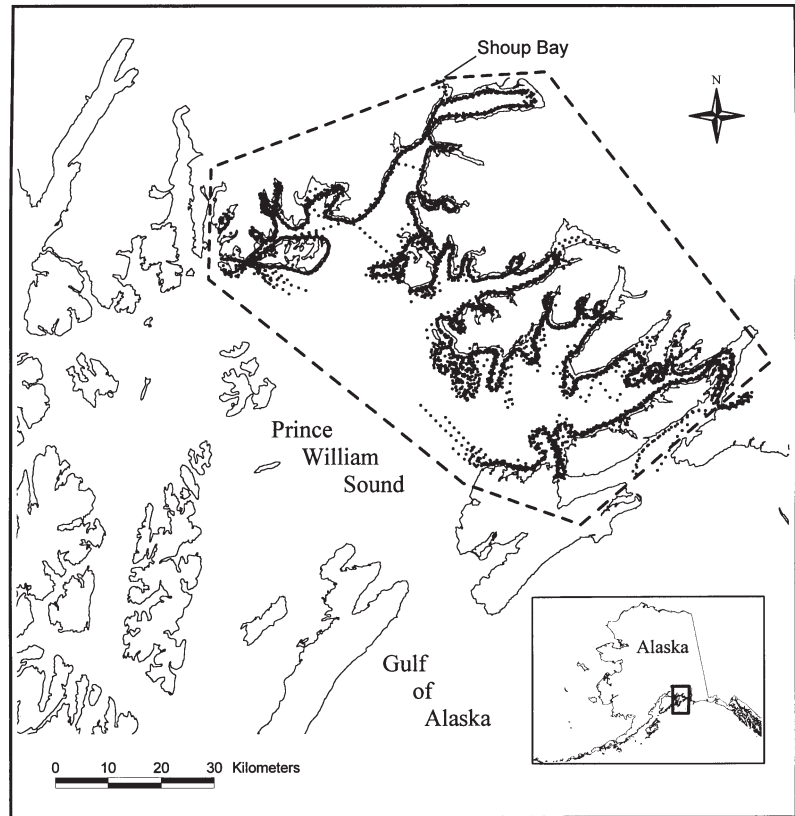
school size. An altitude of 305 m provided a swath width of 325 m, using a fixed angle of 30°, and allowed distinction of the smallest school observed (<10 m^2 surface area). We conducted all observations from the right side of the plane using a modified line transect survey method. Fish schools were counted and their surface area was estimated using a sighting tube. Observers used school characteristics (e.g. shape, size, location) to identify fish species. The accuracy of species identification was 96.1 % for herring and 80.4 % for sand lance, based on discriminate function analyses

Table 1. Weekly aerial survey effort (km^2) to determine the species composition and density of surface-schooling forage fishes within the foraging range of breeding black-legged kittiwakes at Shoup Bay, Alaska

Year	Week				
	1	2	3	4	5
1996	–	–	–	–	–
1997	–	–	219	277	–
1998	558	501	668	683	1043
1999	843	698	890	261	950

using boat-based sampling of fish schools concurrent with aerial surveys.

Kittiwake diets. We collected diet samples from nestlings weekly throughout the chick-rearing period, beginning soon after the first nestlings hatched. In total, we collected 758 regurgitations representing 18 wk during 4 breeding seasons. The nest was our sampling unit, therefore regurgitations from alpha and beta chicks were combined in final analyses. Samples were rarely collected from the same brood in one year and, if so, the collection dates were separated by at least 1 wk and were therefore considered independent.

The species of prey were determined using otoliths, morphological characteristics, scales, and bones. We present the taxonomic composition of diet as both % occurrence and % mass. We used % occurrence to relate foraging trip duration to the spatial distribution of prey (i.e. the proportion of foraging trips when a particular prey type was obtained) and % mass to determine the relative contribution of each prey type to nestling growth.

Previous investigations in PWS and the northern Gulf of Alaska indicated that not only prey species, but also age class may be an important parameter affecting the nutritional quality of prey (Anthony et al. 2000) and the foraging patterns, reproductive success (Suryan et al. 2000), and energy expenditure of adult kittiwakes (Roby et al. 2000, Jodice et al. 2002). Therefore, were used otolith lengths to determine age classes of herring and sand lance, the 2 species known to be primary prey for kittiwakes at the Shoup Bay colony (Irons 1992, Suryan et al. 2000). Otoliths were measured to the nearest 0.01 mm using an ocular micrometer. Age classes of herring were inferred from modes of frequency distributions for otolith lengths (1 to 2 mm for young-of-year [YOY] and 2 to 3 mm for 1-yr-old; Suryan et al. 2000). Age classes of sand lance were also determined using modes of frequency distributions for otolith lengths ($\leq$1.9 mm for YOY and >1.9 for 1+ yr-old), which were consistent with classifying YOY sand lance as typically <100 mm (Robards et al. 1999).

The quantity of food that a nestling receives is a function of feeding frequency and meal size (g). We used radio-tagged adult kittiwakes to estimate feeding frequency and report these values as the number of meals d^{-1} or 'meal delivery rates'. We used weekly regurgitation samples as indices to meal size. An opportunistic collection of a regurgitation is an index of size because the transfer of food between the parent and nestling was not observed. Therefore, we do not know if the sample represents a partial or complete feeding or the elapsed time since feeding. Because of incomplete feedings and partial digestion of the meal between feeding and collection, the regurgitate sizes are undoubtedly biased low compared to the true meal size. They should, nonethe-

less, provide an index of relative change in meal size among weeks. Regurgitations were weighed to the nearest 0.1 g on an electronic balance before freezing.

We calculated the weekly energy density (kJ g^{-1}) of chick regurgitates as the % mass contribution of each prey item and published energy values for whole forage fishes collected within our study area and nearby regions in PWS (Anthony et al. 2000). Using this technique, we were able to quantify the energy content of nearly 100% of most samples. For the few samples containing a portion of unidentified material or a prey item with an unknown energy density value, we assumed the energy content of the unknown portion (typically <25%) was equal to the identified portion. This index of energy density is potentially biased high compared to that of the actual bolus fed to the nestling because partial breakdown or digestion could occur between the time the prey is captured and when it is delivered to the nestling.

Kittiwake foraging trip length, meal delivery rates, and energy provisioning index. Between 1996 and 1999 we captured and radio-tagged 136 adult kittiwakes. Of these, 108 successfully reared young for at least a portion of the season and were included in our analyses ($\bar{x}$ = 22 d, range = 2 to 31 d). Birds were removed from the sample when their nestlings were lost or reached 31 d, the age at which growth measures were terminated and beyond which adult nest attendance changed considerably (R.M.S & D.B.I. unpubl. data). Adult black-legged kittiwakes were captured at their nests, usually during incubation, using a noose-pole (Hogan 1985) or leg-noose (Benson & Suryan 1999). Radio transmitters (164 to 167 MHZ, 9 g Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA) were attached to 15–40 birds yr^{-1}. Transmitters were secured ventrally to the base of the tail feathers using methods described by Anderson & Ricklefs (1987) and Irons (1998). Radio-tagged birds were distributed throughout the colony and their ages ranged from 4 to 21 yr (D.B.I. unpubl. data).

We monitored the 24 h presence of radio-tagged kittiwakes with a remote data logging system. The system consisted of a VHF receiver (R4000, ATS) linked to a data collection computer (DCC II, ATS). The receiver and DCC were powered by a 12 V deep cycle battery that was charged using a 3.3 A photovoltaic panel. A 2-element antenna was connected to the receiver and pointed directly at the colony from a hill at a distance of 0.5 km and at an elevation approximately the same as the top of the colony. The signal reception range was approximately 1.0 km. Activities of adult kittiwakes within 1.0 km of the colony were predominantly nest attendance, occasionally roosting away from the nest, and very rarely foraging (based on pers. obs. and radio-tracking studies; Irons 1992, Suryan et al. 2000). For each transmittered bird, 3 frequencies were pro-

grammed into the DCC, 1 optimal and 2 'bracket' frequencies (1 each at 2 kHz above and below the optimal to ensure continued reception in the event of frequency drift or if the optimal frequency was misjudged during testing). A reference transmitter was placed on the colony and its regular occurrence in the data file signified the receiving system was operating properly. Also, 2 'dummy' frequencies, (i.e. frequencies at least 10 kHz away from those of deployed transmitters) were programmed into the DCC to detect interference signals that could record on a portion or all of the transmitter frequencies thereby falsely indicating the presence of a bird. Each frequency was scanned for 20 s to maximize the detection of a bird while reducing the total scan time to <45 min for all frequencies.

Based on radio-tracking studies of kittiwakes in PWS (Irons 1992, Suryan et al. 2000), we know that adults provisioning young rarely leave the colony for >45 min without feeding, and that feeding typically does not occur during hours of darkness (R.M.S. & M.K. pers. obs). Therefore, foraging trips were defined as absences >45 min occurring between 04:00 and 24:00 h. The average trip duration was calculated for each radio-tagged adult that was currently provisioning 1 or 2 nestlings. Because trip duration and, hence, the number of trips per week can vary considerably among birds, a weekly mean trip duration was calculated for each bird, then a grand mean of all birds was calculated for that week (each bird contributed equally to the weekly mean).

Although only 1 adult per pair was radio-tagged, we were able to estimate the number of meals delivered to nestlings in 1 d (meal delivery rate) by assuming nestlings were fed by the radio-tagged adult when it arrived and by the mate when the radio-tagged bird departed. Whereas this type of mate exchange data from the DCC is far more extensive than what can be obtained by direct observation, the true number of feedings can only be determined by direct observation (not all mate exchanges are followed by feeding of the nestling). Therefore, we also conducted direct observations of nestling feeding frequency each year and used these data to check and calibrate exchange rate data collected with the DCC. These observations occurred from 04:00 to 24:00 h on 4 to 5 d yr^{-1} and included 8 to 10 kittiwake pairs with nestlings observation d^{-1}. Each pair had at least 1 clearly marked adult (black dye [Nyanzol D], red dye [Rhodomine B-base], or color leg bands) allowing observers to easily detect changes in nest attendance and record whether subsequent feedings followed. We then culled the maximum number of daily exchanges (i.e. feedings) in the DCC data for a given year to the maximum number of daily feedings detected during direct observations. We tested results of these 2 methods by conducting direct observations of nestling feeding frequency for a subsample of nests

containing a radio-tagged adult. These 2 methods produced results that were within 5% on average ($\bar{x} = 3.0$ and 2.9 deliveries d^{-1}, SE = 0.28 and 0.30, n = 13 for direct observations and DCC data, respectively).

We calculated a weekly energy provisioning index as the product of meal delivery rate, regurgitate size, and energy density. Each of these 3 components of energy provisioning were weekly means with associated variances. We therefore used Monte Carlo simulations with 1000 repetitions to develop means ±95% confidence intervals (CI) for energy provisioning indices. A Monte Carlo simulation involved randomly generating a population (n = 1000) of each component based on a normal distribution with a mean and 95% CI for that component. A random value was then selected from each population of the 3 components and multiplied to produce a value for the energy provisioning index. This simulation was repeated 1000 times to produce the final means and associated error for energy provisioning indices.

Nestling growth and survival. Prior to hatching, we selected 60 to 100 nests containing eggs for measuring chick growth rates. These nests were located throughout the colony and included relative proportions of 1 and 2 egg clutches equal to the colony average at the time of selection. We checked eggs within these nests daily to determine hatch dates. Alpha and beta nestlings were individually marked with colored ink the day of hatching, then soon after with a numbered US Fish and Wildlife leg band to identify individual chicks. We began measuring nestlings within 3 d of hatching, thereafter they were weighed at 4 d intervals, and mass was determined to the nearest 1 g using either 100, 300, or 500 g Pesola spring scales. Measurements were terminated when nestlings reached 30 ± 1 d, to reduce the risk of causing premature fledging. We completed final measures on at least 37 broods yr^{-1}, except in 1998 when nestling mortality was particularly high (n = 17 broods). We fit logistic and Gompertz nonlinear models to the growth data for each nestling. Logistic growth curves provided the best fit to the data and were used in all years. Parameters of growth determined from logistic curves included the inflection point (I), growth rate constant (K), asymptote (A), and the maximum instantaneous growth rate ($AK/4$). Parameter estimates from each nestling were averaged to represent growth for a given year. In 2 of the years, 1997 and 1998, few beta nestlings survived to fledge, therefore the growth parameters reported herein include only alpha and single nestlings.

When foraging conditions deteriorate such that adults are unable to obtain sufficient quantities of food for nestlings, the beta nestlings often suffer the greatest consequences (Gill et al. 2002). Therefore, we used beta nestlings to evaluate the effect of changes in

the foraging environment on nestling survival. Beta nestlings used in survival analysis were from the same broods as alpha chicks used for growth rate measures. Nests were checked every 4 d and the presence or absence of individually marked beta nestlings was noted. Survival was calculated as the proportion of nestlings alive from one week to the next (i.e. a weekly survival rate is reported rather than a cumulative rate).

Statistical analyses. By comparing the relative abundance of available prey (herring and sand lance) obtained from aerial surveys to the diets of kittiwakes, we determined if kittiwakes selected prey in proportion to its availability. We quantified prey selection using resource selection equations provided by Manly et al. (1993; Design I with known proportion of available resource units) for 10 wk during 1997 to 1999, when concurrent collection of prey abundance and kittiwake diet data occurred. Selection ratios ($\hat{w}_i$) for herring and sand lance were calculated as:

$$\hat{w}_i = o_i / \pi_i \tag{1}$$

where o_i is proportion of used resource units (regurgitations) containing 100% of prey item i and π_i is proportion of available resource units for prey item i from aerial surveys (e.g. $m^2\ km^{-2}$ of herring/[$m^2\ km^{-2}$ for herring + sand lance]). A standardized selection ratio was also calculated using the formula:

$$B_i = \hat{w}_i \Big/ \sum_{i=1}^{I} \hat{w}_i \tag{2}$$

so that selection ratios add to 1 and can be interpreted as the probability that resource unit i would be selected if each type of resource unit were equally available. The standard error (SE) for selected proportion of resource unit i (o_i) was calculated as:

$$SE(o_i) = \sqrt{o_i(1 - o_i)} / u_+ \tag{3}$$

where u_+ is the total number of used resource units (regurgitations). Confidence intervals (CI) for o_i were then calculated as:

$$95\%\ CI = o_i \pm Z_{\alpha/2} SE(o_i) \tag{4}$$

where $Z_{\alpha/2}$ is the percentage of the normal distribution that is exceeded with the probability $^{\alpha}/_2$ ($\alpha = 0.05$ and a Bonferroni adjustment was used). A log-likelihood test was used to determine if selection was significantly different than availability and calculated as:

$$\chi^2 = 2\sum_{i=1}^{I} u_i \log_e[u_i / (u_+ \pi_i)] \tag{5}$$

If the results of the log-likelihood test were significant, then positive or negative selection could be determined if the lower CI for the selected proportion of resource unit i (o_i) was greater (positive) or lesser (negative) than the proportion available (π_i).

We compared weekly and annual means using analysis of variance (ANOVA) for data that met assumptions of parametric statistics, otherwise we conducted ANOVA tests on ranked data. In analyzing data from radio-tagged birds, the sample unit was an individual adult, therefore weekly means for each adult represented 1 sample for that week. In many cases an individual adult contributed to the mean of multiple weeks of a season. The occurrence of the same individuals in calculating weekly means may violate assumptions of independence in statistical tests if, in fact, the variable being analyzed is more dependent on the individual bird than temporal changes in environmental conditions. However, preliminary analyses indicated that environmental conditions were the primary control of foraging activities. Additionally, less than half of the radio-tagged kittiwakes were represented in all weeks of a given year. Therefore repeated measures ANOVA was inappropriate for most data and, if used, sample sizes would be severely reduced. For 2-sample comparisons of means, we used a nonparametric Chi-squared approximation which produces p-values equivalent to a Mann-Whitney U-test (SAS Institute Inc. 1990).

We tested for relationships between nestling age and date on the foraging activities of adult kittiwakes using partial correlation analysis; a method that controls for interaction between variables (e.g. nestling age and date; Zar 1984). We used chi-squared or G-tests to statistically compare the proportion of nestlings surviving among weeks and years. To evaluate whether individual components of energy provisioning effected nestling survival, we used logistic regression. We included all main effects plus interaction terms in initial regression models. All analyses were conducted using SAS software (SAS Institute Inc. 1990). Results were considered significant at an α of 0.05, and SE are reported unless otherwise noted.

RESULTS

Forage fish abundance versus kittiwake diets

In most years, the abundance of forage fishes varied markedly among the weeks of chick-rearing (Fig. 2a–c). Likewise, the diets of kittiwakes often showed distinct within-season changes in prey selection. For example, in 1997 a dramatic reversal in the abundance of herring and sand lance in surface schools between Week 3 and Week 4 was directly reflected in kittiwake diets (Fig. 2a,e). In 1998 the abundance of herring and sand lance also varied among weeks; however, the relative abundance of these 2 prey items remained fairly consistent. Concordantly, we did not observe a dramatic change in the relative proportion of herring or sand lance

selected by kittiwakes. However, the birds did select herring in significantly ($p < 0.001$) greater proportion to its abundance relative to sand lance during Weeks 2 and 5 (Fig. 2b,f; Table 2). In the following year, 1999, we again detected a distinct within-season change in the relative abundance of herring and sand lance in surface schools. Selection of prey species by kittiwakes also varied, ranging from selection for sand lance ($p < 0.025$) during the first week to selection for herring ($p < 0.005$) during the last week, with selection proportional to availability ($p > 0.05$) during the interim period (Fig. 2c,g, Table 2). Overall, during half the sampling periods adult kittiwakes responded to short-term changes in prey availability by selecting primary prey species in proportion to its availability. However, when prey selection was disproportionate to abundance, kittiwakes most often selected for herring and against sand lance (Table 2).

Kittiwake diets and foraging activities

Adult kittiwakes captured over 15 different species of prey (Appendix 1), however, herring or sand lance consistently dominated the diets, and short-term changes in abundance of those 2 items appeared to have the greatest effect on foraging activities. Whereas most nestling regurgitations contained herring and/or sand lance (n = 610 of 778), both prey items infrequently occurred (10%) within the same sample. Therefore, adult kittiwakes most often obtained exclusively herring or sand lance during each foraging trip. In 1996, as kittiwakes made more foraging trips for sand lance ($G_3 = 16.33$, $p < 0.001$) and fewer trips for herring ($G_4 = 114.32$, $p < 0.001$), their weekly foraging trip durations significantly increased ($F_{3,53} = 9.89$, $p < 0.0001$; Fig. 2d,h). A similar occurrence was observed
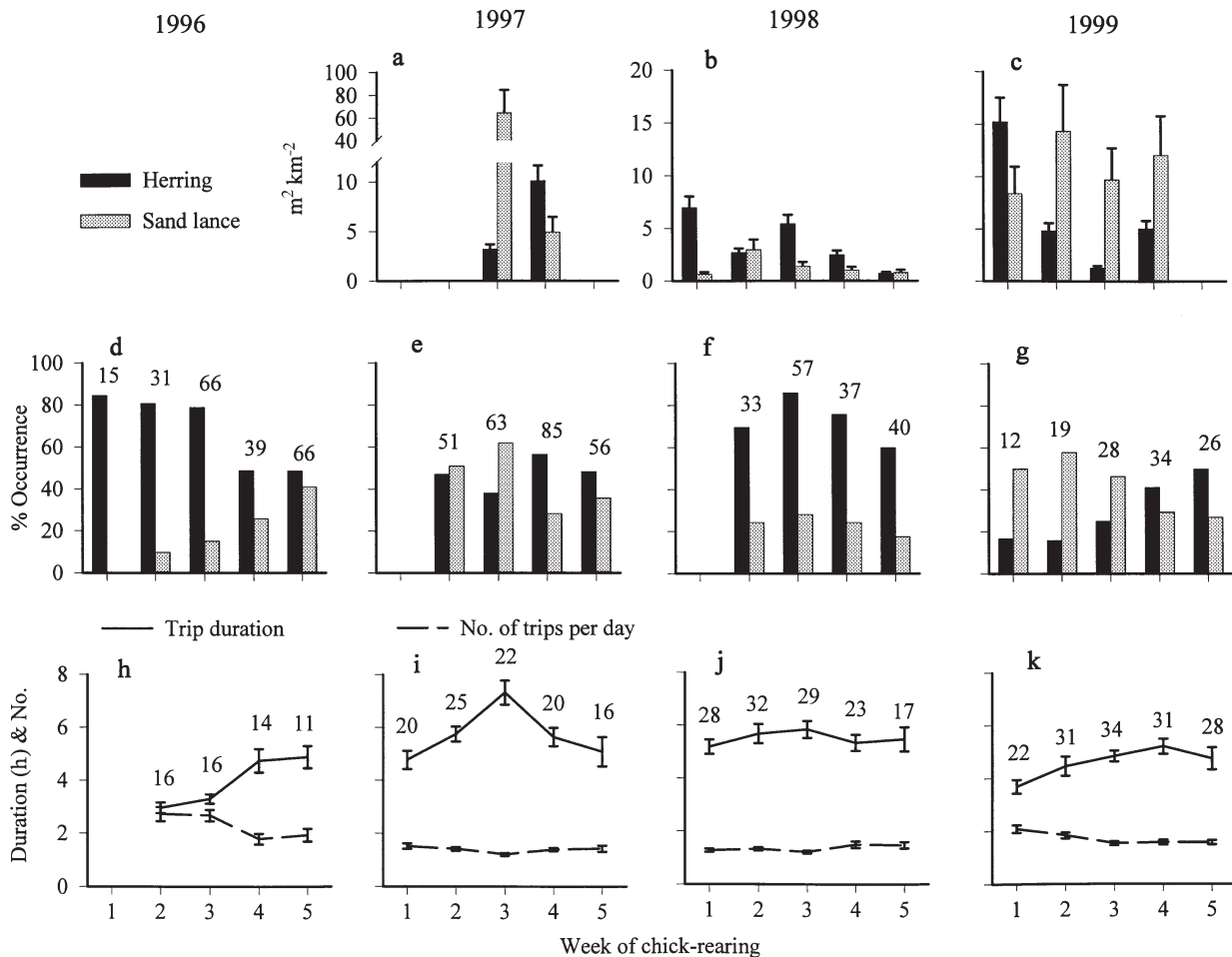

Fig. 2. Changes in the weekly abundance of Pacific herring and Pacific sand lance (school surface area density, $m^2 \ km^{-2}$, a–c) and percent frequency of occurrence (d–g) of these primary prey items fed to black-legged kittiwake nestlings during 4 yr (1996 to 1999) at the Shoup Bay colony, Alaska. Aerial surveys to determine prey abundance were not conducted in 1996. Weekly mean (±SE) foraging trip duration (h) and number of trips d^{-1} of radio-tagged adult kittiwakes (h–k) were determined using automated data loggers. Survey effort to determine prey abundance is provided in Table 1, otherwise weekly sample sizes are provided above each graph

in 1997 during Week 3; more foraging trips for sand lance (G_3 = 19.53, p < 0.001) corresponded to the greatest foraging trip durations ($F_{4,98}$ = 6.61, p < 0.0001; Fig. 2e,i). In 1999, however, the opposite occurred; as kittiwakes gradually made more trips for herring (G_4 = 101.57, p < 0.001) and fewer trips for sand lance (G_4 = 21.42, p < 0.001) the duration of their foraging trips also gradually increased ($F_{4,141}$ = 4.75, p = 0.0013; Fig. 2g,k). The third year of our study, 1998, was the only season where kittiwakes made consistently more trips for 1 prey item throughout the chick-rearing period (Fig. 2f). Accordingly, foraging trip durations among weeks were relatively consistent ($F_{4,124}$ = 0.55, p = 0.7013, df = 4; Fig. 2j).

The age class of herring consumed by kittiwakes varied annually with either 1-yr-old or YOY fish dominating alternating years. Primarily 1-yr-old herring were consumed in 1996 (86%, n = 56 otoliths) and 1998 (76%, n = 89 otoliths), whereas YOY herring were taken in 1997 (93%, n = 42 otoliths) and 1999 (88%, n = 43 otoliths). Nearly all sand lance consumed during the 4 yr were YOY (97%, n = 527 otoliths).

Effect of nestling age and brood size on kittiwake foraging activities

Nestling age had little influence on the foraging activities of adult kittiwakes. Foraging trip duration and meal delivery rate was only weakly affected by nestling age and date of chick-rearing (partial correlation with date, r < 0.1950), and those relationships that were significant (p < 0.05; 4 of 8 correlations) contained very large sample sizes (n > 312). Furthermore, brood size also showed little effect on foraging activities, when it was a factor. In only 1 (1996) of 4 yr did 2-chick broods compose >28% of the broods of radio-tagged birds. A comparison of weekly trip duration, number of trips d^{-1}, and meal delivery rates between adults with 1- and 2-chick broods produced only 1 significant result (χ^2_1 = 4.220, p = 0.040, n = 21 one-chick and 7 two-chick nests) for comparisons spanning 9 wk during 2 yr. These results demonstrate that intra-annual variation in foraging activities of adult kittiwakes were primarily influenced by factors other than nestling age and brood size. Therefore, we did not consider nestling age and brood size in subsequent analyses.

Meal delivery rates, regurgitate size, and energy density

Of the 3 components of energy provisioning, the greatest variation was detected in meal delivery rates and regurgitate size, with less variation in energy density. As adult kittiwakes required varying amounts of time to obtain a load of food, the number of trips they completed in 1 d also varied ($F_{3-4,53-141} \geq 2.43$, p ≤ 0.05; Fig. 2h,i,k). Indeed, meal delivery rates varied significantly among weeks in years when foraging trip durations also varied (1996, 1997 and 1999; Table 3). We also detected significant variation in

Table 2. Resource selection results for herring (HERR) vs sand lance (SALA) where π_i is the proportion of available resource units for prey item i from aerial surveys, u_i is the number of used resource units (regurgitations) containing only prey item i, o_i is the proportion of used resource units (regurgitations) containing prey item i followed by the upper and lower confidence interval (CI) with a Bonferroni adjustment, B_i is the standardized resource selection probability function (selection probabilities sum to 1). Significance tests were calculated using log-likelihood and are reported with significant χ-square values marked in bold text and the results shown as a significant positive (+) or negative (–) selection for a particular prey species

	π_i	u_i	o_i	Lower CI	Upper CI	B_i	χ_1^2	Selection
1997 Week 3								
HERR	0.048	19	0.358	0.229	0.488	0.918	**49.866**	+
SALA	0.952	34	0.642	0.512	0.771	0.082		–
1997 Week 4								
HERR	0.672	45	0.682	0.569	0.794	0.511	0.030	
SALA	0.328	21	0.318	0.206	0.431	0.489		
1998 Week 2								
HERR	0.473	21	0.808	0.656	0.959	0.824	**12.386**	+
SALA	0.527	5	0.192	0.041	0.344	0.176		–
1998 Week 3								
HERR	0.797	40	0.851	0.749	0.953	0.592	0.907	
SALA	0.203	7	0.149	0.047	0.251	0.408		
1998 Week 4								
HERR	0.709	23	0.852	0.718	0.986	0.702	3.031	
SALA	0.291	4	0.148	0.014	0.282	0.298		
1998 Week 5								
HERR	0.474	21	0.808	0.656	0.959	0.823	**12.290**	+
SALA	0.526	5	0.192	0.041	0.344	0.177		–
1999 Week 1								
HERR	0.645	2	0.25	0.050	0.550	0.155	**5.184**	–
SALA	0.355	6	0.75	0.450	1.050	0.845		+
1999 Week 2								
HERR	0.253	3	0.214	0.001	0.429	0.447	0.113	
SALA	0.747	11	0.786	0.571	1.001	0.553		
1999 Week 3								
HERR	0.117	5	0.313	0.085	0.540	0.775	4.341	
SALA	0.883	11	0.688	0.460	0.915	0.225		
1999 Week 4								
HERR	0.295	13	0.591	0.385	0.796	0.776	**8.276**	+
SALA	0.705	9	0.409	0.204	0.615	0.224		–

the size of regurgitates among weeks in a given year resulting from, with few exceptions, an increase in regurgitate size with chick age (i.e. week of season, Table 3). Although the size of the regurgitates varied considerably, the energy density (kJ g^{-1}) of individual regurgitates remained relatively consistent, varying significantly in only 2 (1996 and 1997) of the 4 yr (Table 3). The greater overall energy density of regurgitates during 1996 and 1998 was because the herring consumed during these years were 1-yr-old which had a greater energy value than the YOY herring consumed in 1997 and 1999. Therefore, the multiplicative

effects of weekly changes in meal delivery rates and regurgitate sizes were most responsible for the considerable variation in the index of daily energy supplied to nestlings (Table 3).

Nestling growth, and survival

There were 2 distinctive trends observed in nestling growth rates; growth of chicks was consistent throughout the year (either relatively fast [1996] or slow [1998]) or growth was inconsistent (slow initially then fast

Table 3. Weekly mean (SE, n) values for delivery rate (meals d^{-1}), size (g), and energy density (kJ g^{-1}) of regurgitates and an energy provisioning index (kJ d^{-1}) for kittiwake nestlings at the Shoup Bay colony during 1996 through 1999 in Prince William Sound, Alaska. Energy provisioning index, a product of delivery rate, size, and energy density, was calculated using Monte Carlo simulations (1000 repetitions) and presented as means (±95% confidence intervals). Like symbols denote means that are significantly different (p < 0.05) within years

	Week 1	Week 2	Week 3	Week 4	Week 5	F	p
Meal delivery rate							
1996		5.54* (0.40, 16)	5.31‡ (0.25, 16)	4.08*,‡ (0.37, 14)	4.13 (0.48, 11)	5.14[a]	0.0034
1997	3.16* (0.19, 20)	2.83 (0.14, 25)	2.37* (0.13, 22)	2.79 (0.10, 20)	2.55 (0.20, 16)	3.95[b]	0.0052
1998	2.83 (0.09, 28)	2.81 (0.14, 32)	2.43 (0.13, 30)	2.66 (0.17, 23)	2.88 (0.24, 18)	1.58[b]	0.1825
1999	3.73*,‡ (0.18, 21)	3.65‡ (0.15, 30)	3.38 (0.09, 34)	3.21*,‡ (0.12, 30)	3.19‡ (0.13, 28)	4.42[a]	0.0022
Regurgitate size							
1996	6.21*,‡ (1.47, 15)	7.32‡,** (0.64, 32)	10.03+,# (0.85, 69)	15.83*,‡,+ (2.22, 26)	21.63‡,**,# (2.20, 54)	15.55[b]	0.0001
1997		10.20*,‡,‡ (0.91, 40)	18.73* (1.67, 51)	18.70‡ (1.43, 66)	23.88‡ (2.10, 53)	11.89[b]	0.0001
1998		11.90*,‡,‡ (1.56, 26)	22.53* (2.44, 38)	27.65‡ (3.60, 22)	20.45‡ (2.19, 36)	5.95[b]	0.0008
1999	4.53*,‡,‡ (1.58, 12)	9.95** (1.36, 19)	14.31* (2.06, 28)	16.34‡ (2.26, 17)	18.62‡,** (1.96, 19)	9.68[b]	0.0001
Energy density							
1996	5.45 (0.24, 13)	5.52*,‡ (0.13, 31)	5.43‡,** (0.10, 65)	4.88*,‡ (0.17, 38)	5.07‡,** (0.11, 60)	6.93[b]	0.0001
1997		4.29 (0.09, 51)	4.45*,‡ (0.08, 63)	4.06* (0.06, 84)	4.07‡ (0.08, 54)	6.50[b]	0.0003
1998		5.13 (0.14, 33)	5.49 (0.08, 57)	5.41 (0.12, 36)	4.93 (0.15, 41)	1.98[b]	0.1184
1999	4.16 (0.23, 12)	4.52 (0.14, 19)	4.04 (0.11, 28)	4.14 (0.14, 33)	4.11 (0.17, 26)	2.26[b]	0.0673
Energy provisioning index							
1996		224 (53.9)	289 (58.3)	316 (114.0)	452 (154.9)		
1997		125 (26.4)	197 (41.5)	211 (35.3)	248 (64.0)		
1998		178 (51.5)	300 (74.6)	394 (119.9)	290 (88.9)		
1999	75 (48.3)	164 (51.6)	195 (59.7)	221 (68.3)	243 (60.5)		

[a]ANOVA; [b]ANOVA conducted on ranked values

[1997] or fast initially then slow [1999]; Fig. 3). In general, annual trends in foraging trip duration and, to a lesser extent, energy provisioning index supported these yearly growth patterns (except for 1998 in the case of energy provisioning). However, the absolute index values did not fully explain differences in nestling growth among years. In 1996, relatively short foraging trips and high energy provisioning index throughout chick-rearing (Table 3) resulted in the greatest maximum instantaneous growth rate and asymptotic weight measured during the 4 years (Table 4). In 1997, long foraging trips and low energy provisioning indices during mid-chick-rearing were associated with reduced initial growth (delayed growth curve inflection point). This period of reduced growth was followed by high energy provisioning during late chick rearing, increased growth, and a greater asymptotic weight of nestlings, in contrast to 1999 when the opposite trend was observed (Tables 3 & 4). Maximum instantaneous growth rate and asymptotic weight were lowest in 1998, consistent with long foraging trips throughout chick-rearing and low energy provisioning during the Weeks 2 and 5, although energy provisioning during Weeks 3 and 4 was surprisingly high (primarily because of large regurgitate sizes during these weeks; Table 3).

Survival of beta chicks varied among weeks during 3 of the 4 years (Table 5). Overall, the first 2 wk of brood-rearing appeared most critical to survival, 84% (n = 96) of beta and 61% of alpha chick mortality occurred before the third week. The typically greater survival of older nestlings confounded the relationship between nestling provisioning variables and survival when all
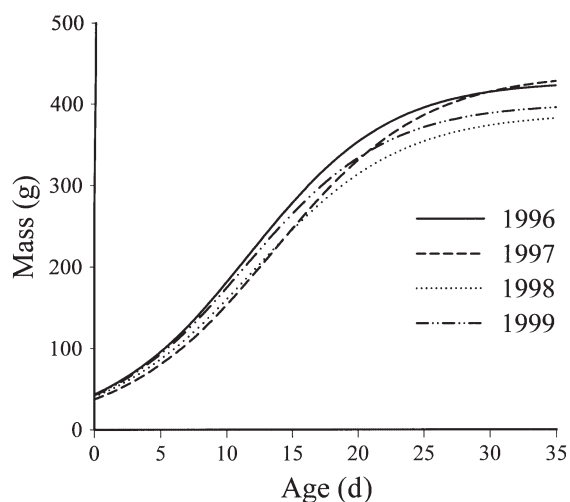
Table 4. Annual parameter means (SE) for logistic growth models fitted to body mass (g) of individual kittiwake nestlings (α and single chicks only) during 1996 through 1999 at the Shoup Bay colony, Prince William Sound, Alaska. Like symbols denote parameter means that are significantly different (p < 0.05) among years. K = growth rate constant; I = inflection point (d), A = asymptote (g); $AK/4$ maximum instantaneous growth rate (g d^{-1})

	1996 (n = 55)	1997 (n = 37)	1998 (n = 17)	1999 (n = 48)	F	p
K	0.187 (0.003)	0.175 (0.006)	0.179 (0.008)	0.187 (0.005)	1.63[a]	0.1843
I	11.63* (0.20)	13.51*,** (0.51)	11.95 (0.40)	11.37** (0.28)	7.22[b]	0.0001
A	427.5*,** (5.0)	437.6†,‡ (11.8)	388.2*,† (9.2)	400.2**,‡ (6.7)	7.07[b]	0.0002
$AK/4$	19.7*,**,† (0.3)	18.6* (0.4)	17.2** (0.5)	18.4† (0.4)	6.49[b]	0.0004

[a]ANOVA; [b]ANOVA conducted on ranked values

weeks were included; the only significant effects were week, year, and a week × year interaction (logistic regression; $\chi^2_1 > 4.38$, p = 0.036, n = 165). Therefore, we focused on early chick-rearing by evaluating the effect of provisioning variables on survival during the first 2 wk. In this analysis, trip duration, meal delivery rate, regurgitate size and the energy provisioning index significantly affected nestling survival ($\chi^2_1 > 9.11$, p < 0.002, n = 96); trip duration and regurgitate size were negatively related to survival, whereas meal delivery rate and energy provisioning index were positively related to survival. Small regurgitates were likely associated with high survival because regurgitate size and trip duration were positively related during this period (r = 0.94, p = 0.057, n = 4). Overall, survival of beta nestlings was lowest during 1997 and 1998 (Table 5), consistent with the greater initial foraging trip durations during those years, indicating prey was difficult to obtain.

DISCUSSION

Aerial surveys proved successful in determining the abundance of near-surface schooling forage fishes available to breeding kittiwakes at a time and spatial scale that could not have been captured using slow-moving vessel surveys or generalized fisheries data. Our results demonstrated that short-term fluctuations in prey availability was an important factor affecting kittiwake diets, foraging trip durations and, subsequently, the provisioning, growth, and survival of their nestlings.

Fig. 3. Logistic growth curves fit to body mass increments of α and single nestlings of black-legged kittiwakes breeding at Shoup Bay, Prince William Sound, Alaska. Curves depict annual growth patterns for 1996 to 1999 and were drawn using values of model parameters presented in Table 3

Table 5. Weekly and annual survival rates (SE) of nestlings during 4 breeding seasons of black-legged kittiwakes at Shoup Bay, Prince William Sound, Alaska. Weekly survival rates are the proportion of beta chicks that survive between 2 consecutive weeks. Annual survival is the proportion of beta chicks that survive to Week 5

	Week				χ^a_3	p	Annual[b]
	1–2	2–3	3–4	4–5			
1996 n = 30	0.93 (0.046)	0.75 (0.083)	0.95 (0.048)	1.00 (0)	10.14	< 0.025	0.65
1997 n = 29	0.41 (0.093)	0.67 (0.142)	0.75 (0.164)	1.00 (0)	84.94	< 0.001	0.21
1998 n = 24	0.46 (0.104)	0.82 (0.122)	0.56 (0.176)	0.75 (0.216)	64.77	< 0.001	0.17
1999 n = 13	0.92 (0.077)	0.83 (0.112)	1.00 (0)	0.80 (0.133)	2.86	> 0.200	0.62

[a]Chi-squared analysis was conducted to allow for occasional cells containing zeros (i.e. no mortality)
[b]G-test for annual difference in survival, $G_3 = 22.18$, p < 0.001

Prey selection versus availability

We demonstrated that changes in prey selected by black-legged kittiwakes was often a response to short-term fluctuations in prey abundance. Kittiwakes, however, did not always select prey species in proportion to their relative abundance. In half of the time periods we considered, kittiwake selected prey disproportionate to its abundance, usually selecting for herring and against sand lance. It is not immediately clear why such selective pressure for herring occurred. Perhaps the schooling characteristics of the 2 species differed such that herring were easier to capture than sand lance. Nonetheless, the greater occurrence of herring (particularly 1-yr-old) relative to sand lance in the diets of kittiwakes at Shoup Bay is typically associated with shorter foraging trip durations and greater reproductive success (Suryan et al. 2000). Therefore, under some circumstances, kittiwakes at Shoup Bay appear to be selecting prey that is most beneficial to reproductive success. Although it is unknown whether this selection is a result of choice by foraging kittiwakes or differential capture vulnerability of prey.

Seasonal variation in prey selection also has been documented for a variety of other seabirds including cape gannets *Morus capensis* (Berruti et al. 1993), double-crested cormorants *Phalacrocorax auritus* (Neuman et al. 1997), blue petrels *Halovaena caerulea* (Chaurand & Weimerskirch 1994), king penguins *Aptenodytes patagonicus* (Adams & Klages 1987), and gentoo penguins *Pygoscelis papua* (Adams & Klages 1989, Kato et al. 1991). In these examples dietary changes were presumed to result either from changes in species composition of available prey occurring within the birds' primary foraging grounds (Adams & Klages 1989, Kato et al.

1991, Neuman et al. 1997) or from different prey assemblages encountered when switching between alternate foraging areas (Brown & Klages 1987, Chaurand & Weimerskirch 1994). These studies suggested that seabirds varied their prey consumption in concert with changes in available prey. However, without adequately sampling the prey base, it was not known if breeding birds were consuming the most abundant prey species or if they were selecting prey disproportionate to its abundance. Discriminatory prey choice has been demonstrated in other studies of upper-trophic level aquatic predators for which there was an independent measure of prey abundance. For example, in diets of cormorants *Phalacrocorax carbo*, Suter (1997) showed that roach *Rutilus rutilus* were over-represented, and whitefish *Coregonus* sp. were under-represented relative to their abundance. Likewise, Lawson et al. (1998) successfully demonstrated that harp seals *Phoca groenlandica* preferentially selected capelin in offshore waters and arctic cod *Boreogadus saida* in nearshore waters by comparing prey consumed by seals and fish species collected in trawls. Therefore, an independent measure of prey availability is critical to determine whether prey selection is consistent with availability or, instead, if predators are exhibiting positive or negative selective pressure within multispecies prey populations.

Factors affecting nestling provisioning

Two competing hypotheses exist on the regulation of nestling provisioning; provisioning is determined by demands of the chick (e.g. Ricklefs et al. 1985, Hamer 1994, Bertram et al. 1996) or by environmental conditions (e.g. Galbraith 1983, Hatch 1984, Uttley et al. 1994). Our results demonstrated that both hypotheses appear to be supported, depending on which components of energy provisioning were considered. In all years, with few exceptions, regurgitate size increased with nestling age, indicating adult kittiwakes responded to the needs and ability of nestlings to consume larger quantities of food as they grew. However, we also found that nestling age and brood size had little effect on meal delivery rates. Instead, within-season changes in prey abundance or selection were mostly responsible for weekly variation in foraging trip durations. The final component of energy provisioning, energy density of prey, was likewise controlled by extrinsic factors rather than intrinsic decisions by for-

aging kittiwakes. Overall, foraging trip duration, and hence meal delivery rate, appeared to be the dominant component of energy provisioning in controlling nestling growth and survival, suggesting that environmental conditions were most responsible in controlling nestling provisioning during our study. Under these foraging conditions our data support Lack's (1968) hypothesis that adults work near maximum capacity for a given resource abundance and that brood size and growth rate are adjusted accordingly.

Prey abundance and the ability to buffer young

Cairns (1987) proposed that the relationship between seabird reproductive parameters and prey abundance could be represented by sigmoidal response curves. The premise of the curves is that the reproductive parameters of seabirds will be affected by changes in prey abundance up to a point, the asymptote, beyond which reproductive parameters do not respond to increased prey abundance (Cairns 1987, Monaghan 1996). The position of the asymptote relative to prey abundance will differ among reproductive parameters, indicating that some parameters are more sensitive to prey abundance than others. This difference in sensitivity is attributed to the ability of adult seabirds to alter their foraging effort to compensate for changes in prey availability, thereby buffering their young from these changes (Burger & Piatt 1990). In order for this buffering effect to occur, prey abundance must be approaching or be beyond a theoretical asymptote. During our study, prey abundance appeared to be near or beyond the asymptote in 2 of the 4 years, 1996 and 1999. During 1996, kittiwake foraging trip duration doubled in response to a change in diet during the last 2 wk of chick-rearing; however, there was no detectable change in nestling survival or growth. Prey abundance, therefore, appeared to be beyond the asymptote. Initially in 1999, prey appeared to be sufficiently abundant to support high beta chick survival and moderate early season nestling growth. However, chicks ultimately reached a low fledging weight in this year, indicating prey had declined to levels below the asymptote for optimal nestling growth. This was not true during 1997 and 1998, when changes in the foraging activities of adult kittiwakes in response to fluctuating prey availability (or consistently low prey availability in 1998) resulted in effects on nestling survival and growth. This indicated that in 1997 and 1998 prey abundance was in the critical range where adults could not buffer their young from limited prey resources. Indeed, aerial surveys in 1998 demonstrated that the abundance of both herring and sand lance was very low. Prey abundance in 1997 and

1999 appeared relatively high even though survival and growth was hindered in 1997 and fledging weight was low in 1999. However, few of the herring consumed in those 2 years were 1-yr-old, the prey identified as most critical to successful reproduction at the Shoup Bay colony (Suryan et al. 2000).

Energy provisioning, nestling growth, and survival

It is unclear why trends in energy provisioning were not entirely consistent with patterns of nestling growth, particularly in instances when energy provisioning rate was relatively high yet chick growth remained low (e.g. Weeks 3 and 4 in 1998; Table 3). Instead, patterns in foraging trip duration and its effect on feeding frequency appeared to be more consistent with nestling growth. These results suggest that feeding frequency was a critical component of energy provisioning, possibly overshadowing total daily energy delivered under some circumstances. Postnatal energetic studies conducted by Roby et al. (2000) provided similar results, but at larger time scales, for black-legged kittiwakes in Prince William Sound and Cook Inlet. Their analyses of annual mean values for 5 yr at 6 colonies demonstrated that food provisioning rate had the greatest effect on nestling growth and that feeding frequency explained most of the variation in energy provisioning rate (Roby et al. 2000). In these situations, of the primary factors controlling postnatal development (energy intake, digestive capacity, digestive efficiency, energy storage, and maximum rate of tissue development), the growth of kittiwake nestlings may be most limited by digestive efficiency and/or energy storage capacity when meal delivery rate is low yet total energy delivered remains high. Unfortunately, there is little information in the literature addressing feeding frequency independent of diet quantity or quality (energy density) and its effect on avian postnatal development. In general, the digestive and assimilation efficiencies of neonatal birds are poor relative to adults (Karasov 1990, Obst & Diamond 1992, Weathers 1992, Caviedes-Vidal & Karasov 2001) and, given adequate food supplies, may be a key factor limiting postnatal growth (Ricklefs 1969, Caviedes-Vidal & Karasov 2001). Experimental studies in domestic animals provide some evidence that increasing feeding frequency while holding other variables constant can improve digestibility of organic matter and protein (Shabi et al. 1999) and affect blood metabolites (Eicher et al. 1999). In a broader context of the effects of feeding frequency, Lemon & Barth (1992) demonstrated that experimentally controlling search time of foraging zebra finches *Taeniopygia guttata* resulted in a positive relationship between feeding frequency and repro-

ductive success, even though food abundance was held constant. Although these studies did not specifically address tissue growth and development, they do provide some evidence that increased feeding frequency independent of quantity may promote postnatal development.

Less frequent provisioning of kittiwake nestlings associated with changes in prey selection and longer foraging trip durations also resulted in reduced beta survival during the first 2 wk of chick-rearing. Regehr & Montevecchi (1997) also reported reduced survival of kittiwake nestlings as a result of within-season changes in prey consumption. Although they did not explicitly address early nestling survival, their data and those of Lance & Roby (1998) and Gill et al. (2002) showed the greatest percent mortality occurred during the first 2 wk of brood-rearing. Their results and ours are consistent with the ability of kittiwake nestlings to assimilate and store a limited amount of food in 1 feeding, particularly during early development. Since very young nestlings can only accept a relatively small amount of food, it may be even more critical for them to be fed frequently during the first 2 wk of development.

Appendix 1. Prey consumed by black-legged kittiwakes breeding at the Shoup Bay colony in Prince William Sound, Alaska. The diet composition (% occurrence above % mass) is presented for Weeks 1 to 5 of the chick-rearing period during the 4 yr (1996 to 1999) of our study. Weekly sample sizes are shown in parentheses (n = no. of regurgitations)

Prey species	1996					1997					1998					1999				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
	(15)	(31)	(66)	(39)	(66)	(0)	(51)	(63)	(85)	(56)	(0)	(33)	(57)	(37)	(40)	(12)	(19)	(28)	(34)	(26)
Pacific herring	84.6	80.7	78.8	48.7	48.5	–	47.1	38.1	56.5	48.2	–	69.7	86.0	75.7	60.0	16.7	15.8	25.0	41.2	50.0
Clupea pallasi	53.0	68.3	52.9	46.8	41.6	–	37.1	34.5	48.8	47.9	–	61.0	68.2	66.6	59.2	12.1	11.5	21.9	37.7	33.7
Pacific sand lance	–	9.7	15.2	25.6	40.9	–	51.0	61.9	28.2	35.7	–	24.2	28.1	24.3	17.5	50.0	57.9	46.4	29.4	26.9
Ammodytes hexapterus	–	11.5	11.8	15.4	33.9	–	44.5	54.7	30.8	33.4	–	20.6	13.9	15.9	13.2	23.2	53.8	34.8	20.4	22.1
Capelin	–	–	4.5	2.6	1.5	–	7.8	3.2	8.2	1.8	–	6.1	3.5	5.4	12.5	–	21.1	17.9	23.5	23.1
Mallotus villosus	–	–	4.4	1.3	2.6	–	9.1	3.2	10.7	0.5	–	1.7	4.8	2.5	5.9	–	26.1	17.1	19.5	22.6
Salmon sp.	7.7	–	–	5.1	4.6	–	5.9	1.6	–	3.6	–	6.1	10.5	5.4	15.0	25.0	10.5	21.4	5.9	3.8
Oncorhynchus sp.	25.7	–	–	5.9	3.5	–	4.6	1.0	–	2.3	–	2.5	5.8	3.8	8.9	30.0	5.0	11.8	1.7	1.1
Offal	15.4	9.7	10.6	28.2	18.2	–	3.9	4.8	7.1	8.9	–	9.1	3.5	5.4	15.0	8.3	–	10.7	14.7	23.1
Oncorhynchus sp.	7.7	7.9	8.7	22.6	10.3	–	4.0	3.7	3.4	8.0	–	14.3	1.7	4.8	7.2	1.6	–	7.7	6.9	13.5
Salmon eggs	–	–	1.5	5.1	18.2	–	–	1.6	2.4	5.4	–	–	1.8	8.1	10.0	–	5.3	–	5.9	7.7
Oncorhynchus sp.	–	–	0.9	1.4	3.7	–	–	2.6	0.4	0.7	–	–	1.3	1.8	5.7	–	0.6	–	0.5	2.6
Walleye pollock	–	3.2	–	–	1.5	–	–	–	–	–	–	–	–	–	–	8.3	5.3	7.1	11.8	–
Theragra chalcogramma	–	1.2	–	–	0.3	–	–	–	–	–	–	–	–	–	–	3.5	2.9	4.3	11.8	–
Pacific tomcod	–	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	8.3	–	3.6	–	3.8
Microgadus proximus	–	–	–	–	–	–	–	–	–	–	–	–	4.0	–	–	2.9	–	2.5	–	2.8
Saffron cod	–	–	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleginus gracilis	–	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Flatfish	–	–	–	–	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleuronectidae	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crested sculpin	–	–	–	2.6	–	–	2.0	1.6	7.1	–	–	–	–	–	8.3	–	–	–	–	–
Blepsias bilobus	–	–	–	0.1	–	–	0.7	0.4	5.9	–	–	–	–	–	26.7	–	–	–	–	–
Smelt	–	–	–	–	–	–	–	–	–	–	–	–	5.4	–	–	–	–	–	–	–
Osmeridae	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–
Eulachon	–	–	–	–	–	–	–	–	–	–	–	–	5.4	–	–	–	–	–	2.9	3.8
Thaleichthys pacificus	–	–	–	–	–	–	–	–	–	–	–	–	2.3	–	–	–	–	–	1.6	1.6
Slender eelblenny	–	–	–	–	–	–	–	–	–	–	–	–	2.7	–	–	–	–	–	–	–
Lumpenus fabricii	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–
Pacific sandfish	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–
Trichodon trichodon	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–
Unidentified	38.5	41.9	43.9	30.8	18.2	–	–	–	–	–	–	–	2.7	–	–	–	–	–	–	–
	13.6	11.1	19.2	6.6	3.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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