GROWTH OF BLACK-LEGGED KITTIWAKE *RISSA TRIDACTYLA* CHICKS IN RELATION TO DELIVERY RATE, SIZE, AND ENERGY DENSITY OF MEALS

PATRICK G.R. JODICE,[1] DANIEL D. ROBY,[2] KATHY R. TURCO,[3] ROBERT M. SURYAN,[4] DAVID B. IRONS,[5] JOHN F. PIATT,[6] MICHAEL T. SHULTZ,[6] DAVID G. ROSENEAU,[7] AND ARTHUR B. KETTLE[7]

[1]*US Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit,*
Clemson University, Clemson, South Carolina, 29634, USA
(pjodice@clemson.edu)
[2]*US Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, Oregon, 97331, USA*
[3]*Institute of Marine Science, University of Alaska, Fairbanks, Alaska, 99775, USA*
[4]*Oregon State University, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, Oregon, 97365, USA*
[5]*US Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska, 99503, USA*
[6]*US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska, 99508, USA*
[7]*US Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, 95 Sterling Highway, Suite 1, Homer, Alaska, 99603, USA*

SUMMARY

JODICE, P.G.R., ROBY, D.D., TURCO, K.R., SURYAN, R.M., IRONS, D.B., PIATT, J.F., SHULTZ, M.T., ROSENEAU, D.G. & KETTLE, A.B. 2008. Growth rates of Black-legged Kittiwake *Rissa tridactyla* chicks in relation to delivery rate, size, and energy density of meals. *Marine Ornithology* 36: 107–114.

The growth rate of chicks is a parameter often used to examine the effects of changes in food availability on reproductive performance of seabirds. We analyzed the relationship of growth rates in Black-legged Kittiwake *Rissa tridactyla* chicks at three colonies in Prince William Sound, Alaska, and three colonies in Lower Cook Inlet, Alaska, to two components of nestling meals that represent diet quantity (meal delivery rate and meal size) and one that represents diet quality (energy density). During this study, kittiwakes appeared to rely on an array of relatively high-lipid prey. Growth rates of alpha and singleton chicks were positively correlated with annual productivity and were best explained by meal delivery rate and meal size; growth rates of beta chicks were not correlated with productivity and were best explained by meal delivery rate alone. The lack of a positive effect of energy density on growth rates was in contrast to results from a companion study that found a moderately positive effect of energy density on kittiwake productivity. Taken together, results from these two studies demonstrate the need to measure both diet quantity and quality to reliably assess the relationships between diet composition, provisioning rates, growth rates, and productivity in seabirds.

Key words: Alaska, Black-legged Kittiwake, diet composition, growth rates, nutritional stress, provisioning rates, *Rissa tridactyla*

INTRODUCTION

Top-down forces can affect the reproductive performance of seabirds, but it is apparent that bottom-up forces, acting through food availability, consistently affect a diverse suite of reproductive parameters within and between seabird species (Cairns 1987, Suryan *et al.* 2006, Piatt *et al.* 2007). The level of food availability for seabirds is controlled by complex interactions of factors that include prey abundance, taxonomic composition of the prey base, prey accessibility, and prey quality. Measures for each of these factors can be obtained or inferred either from diet samples collected from adults and chicks at the colony or from measures of the prey base itself. Diet samples are far easier to collect and therefore much effort has been made to demonstrate that seabird diets are useful and accurate indicators of prey availability (Hatch & Sanger 1992, Davoren & Montevecchi 2003, Le Corre & Jaquemet 2005).

The growth rate of chicks is a parameter commonly used to examine spatial and temporal effects of changes in food availability on the reproductive performance of seabirds (Golet *et al.* 2000, Barrett 2002, Suryan *et al.* 2002). Growth rates provide opportunities to examine trade-offs in resource allocation within growing chicks and can easily be compared both within and between breeding seasons. Cairns (1987) proposed that the relationship between chick growth rates and food availability in seabirds would best be described by a logistic curve, that growth rates would be more responsive to food resources when availability was poor to moderate, and that spatial and temporal differences in growth rates within species would be greater in older chicks. Numerous studies have demonstrated a link between growth rates of seabird chicks and each of the aforementioned factors related to food availability, particularly prey abundance and diet quantity (e.g. Barrett 1994, Lance & Roby 1998, Gill *et al.* 2002). Most often, however, these studies focus on the quantity of food provisioned to chicks. Multiple facets of food availability and the diet are rarely considered simultaneously in a manner that allows for a relative comparison of the effects of the various facets of food availability on growth rates in a natural setting.

Our goal was to assess the relationship between growth rates of Black-legged Kittiwake *Rissa tridactyla* chicks and the quality and quantity of the chick diet at six colonies in two regions of the northern Gulf of Alaska during a four-year period. We measured growth rates of Black-legged Kittiwake chicks and also measured three components of nestling meals: delivery rates, mass, and

energy density. The former two components represent the quantity of the nestling diet, and the latter provides a measure of diet quality. We determined the response of chick growth rates to these three parameters, singly and in combination. We also examined the effect of colony, geographic region, and year on chick growth rates. We conducted these analyses separately based on hatch order (beta chicks compared with alpha and singleton chicks) to determine if both groups responded similarly to meal quantity and quality.

METHODS

Study species and study sites

Black-legged Kittiwakes (hereafter kittiwakes) tend to lay one- or two-egg clutches in Alaska, and chicks remain in the nest until nearly adult size. In the northern Gulf of Alaska, adults forage predominantly by plunge-diving on pelagic schooling fishes such as Pacific herring *Clupea pallasi,* Pacific Sand Lance *Ammodytes hexapterus,* and Capelin *Mallotus villosus.* Prey also include juvenile salmonids, osmerids, juvenile gadids (e.g. Walleye Pollock *Theragra chalcogramma* and Pacific Tomcod *Microgadus proximas*) and euphausiids (e.g. *Thysanoessa* spp.) (Jodice *et al.* 2006b).

Our study was conducted at six colonies in the Northern Gulf of Alaska (see Jodice *et al.* 2006b for a study area map); three colonies in Prince William Sound (PWS) and three in Lower Cook Inlet (LCI). The PWS colonies were located at Shoup Bay in northwestern PWS, North Icy Bay in southwestern PWS, and Eleanor Island in central PWS. The area around Shoup Bay is characterized by fjords, bays and inlets. The area around Eleanor Island is characterized by protected bays of larger islands and by open water influences from the northern Gulf of Alaska. The area near north Icy Bay is characterized by fjords, bays and open water influences from the Gulf. Since 1985, the Eleanor Island colony has remained fairly stable (*c.* 220 nests), and the colonies at Shoup Bay (*c.* 7000 nests) and north Icy Bay (*c.* 1800 nests) have increased in size (Suryan & Irons 2001).

The LCI colonies were located at Gull Island in southeastern LCI, East Amatuli Island at the mouth of LCI, and Chisik Island in central LCI. The colony at East Amatuli Island (*c.* 6000 nests) is within a transition zone between the northern Gulf of Alaska and the shallow Cook Inlet estuary. The Alaska Coastal Current enters Cook Inlet via the Barren Islands, creating an upwelling zone along the southeastern Cook Inlet shelf (Burbank 1997, Robards *et al.* 1999). The area nearby the Gull Island colony is characterized by cold, mixed oceanic water with significant freshwater runoff (Robards *et al.* 1999). During the study period, this colony supported *c.* 5000 breeding pairs of kittiwakes, an increase of approximately 20% over the preceding 25 years (Zador *et al.* 1997). In contrast to the two former colonies, the Chisik Island colony is surrounded primarily by stratified, relatively warm estuarine waters (Robards *et al.* 1999). During our study, about 10 000 breeding pairs of kittiwakes bred on Chisik Island, where the population has declined substantially during the past 30 years.

Diet and meals

Details on the determination of diet composition and the measurements of delivery rate, size and energy density of meals can be found in Jodice *et al.* (2006b). Here, we provide a brief description of these determinations and measurements.

Diet composition

We determined diet composition by collecting regurgitations (n = 918) from parent and nestling kittiwakes. We included only regurgitation samples ≥ 3 g in our analyses. Diet samples were seldom collected from the same individuals more than once, and in cases where a second collection occurred, we allowed for at least one week between samples (Suryan *et al.* 2002). Diet samples were not collected from nests where growth rates of chicks were being measured (see below), but were collected from other areas throughout each colony (i.e. center and edge nests). The taxonomic composition of each sample was determined by inspection of whole or partially-digested fish. We estimated standard lengths of partially-digested prey items using a combination of body fragments and otoliths, and we used these data to estimate mass at ingestion. Identifiable prey were categorized into age classes based on documented size–age class relationships. For each regurgitation sample we determined total mass (grams), taxonomic composition by mass (percentage), mass (grams) of each prey species, and mass (grams) of each age class within each prey species. These variables were then used to quantify diet composition by calculating the proportion of the total collected biomass of regurgitation samples from a colony–year that consisted of each prey type (species and age class).

Delivery rates and their component metrics

We measured the number, mass and energy density of meals delivered by parents and used these data to calculate annual means of each metric at each colony. In turn, we used annual means as independent variables in statistical analyses of chick growth rates.

We measured meal delivery rates (MDR), for a total of 545 nest–days, to nestlings (meals nest^{-1} d^{-1}) by observing clustered groups of active nests, or at the Barren Islands, by reviewing video tapes which, during 1996 and 1997, were compared with direct observations to ensure accuracy (Roseneau *et al.* 2000). We included different groups of nests during each observation period, or in cases in which the number of nests within a colony was limited, allowed at least seven days to elapse between watches at the same nest. Observed nests were located throughout each colony to avoid biasing the results. To scale all meal delivery data to the rate of meals nest^{-1} d^{-1}, we multiplied the per-hour MDR for each nest watch by the modal watch duration of 18 hours. We calculated an adjusted meal delivery rate (aMDR) for each colony based on the difference in MDR between one- and two-chick broods and mean brood size at fledging for that colony–year (Jodice *et al.* 2006b).

Meal size was determined from 918 regurgitations collected from nestlings and adults. All samples represented fresh meals, were collected either from chicks aged 10–30 days or from parents raising chicks of that age, and were collected throughout each colony. We distinguished between whole-meal samples (n = 212: regurgitations collected from nestlings immediately following an observed feeding) and random meal samples (n = 255 adult samples and 451 nestling samples: regurgitations for which the probability of collecting an entire meal could not be established). We assessed the differences in size between whole and random meals and between adult random and nestling random meals and developed correction factors that allowed us to pool all meal size data within each colony–year regardless of meal type (Jodice *et al.* 2006b).

Proximate composition analysis of all meal samples was conducted following procedures detailed in Anthony *et al.* (2000) and Jodice

et al. (2006b). As with meal size, we standardized energy density among meal types, which allowed us to pool all energy density data within each colony–year regardless of meal type (Jodice *et al.* 2006b). We assessed differences in energy density between meals collected directly from adults (which we suggest were fresher and hence a better indicator of nestling energy intake) and those collected from nestlings, and between random and whole meals.

For each colony–year, we estimated the biomass provisioning rate (BPR: $g\,nest^{-1}\,d^{-1}$) as the product of mean meal delivery rate (meals d^{-1}) and mean meal size (grams). We estimated the energy provisioning rate (EPR: $kJ\,nest^{-1}\,d^{-1}$) as the product of mean meal delivery rate, mean meal size and mean energy density of the meal ($kJ\,g^{-1}$). We obtained a measure of variance for each of these single-point estimates by incorporating the variability inherent in each of the component metrics. The specific technique involved creating a simulation model that randomly selected a data point from each of the component metrics specific to data collected for a given colony–year, multiplying those metrics to estimate BPR and EPR, and then calculating the standard deviation from 1000 runs of the model (Jodice *et al.* 2006b).

Chick growth rates

We measured growth rates of kittiwake nestlings ($g\,d^{-1}$ during the near-linear phase of growth) by periodically weighing chicks. The linear rate of growth is an acceptable measure for intraspecific comparisons of growth rates (Lance & Roby 1998). Each year, *c.* 40 active and accessible kittiwake nests from throughout each colony (i.e. edge and center) were located and marked during the incubation stage. These nests were checked regularly during the hatching period to determine hatching dates. We closely monitored nests until the young fledged or the nesting attempt failed. In the case of two-chick broods, siblings were marked soon after hatching so that individual growth rates could be monitored throughout the nestling period. We weighed both members of two-chick broods. Nestling mass was determined to the nearest one gram using Pesola spring scales beginning within three days of hatching. Thereafter, we weighed nestlings at three- to five-day intervals. To reduce the

risk of premature fledging, measurements were terminated when nestlings reached *c.* 30 days of age. We calculated chick growth ($g\,d^{-1}$) as the slope of the most linear section of the growth curve (60–300 g: Coulson & Porter 1985, Suryan *et al.* 2006). We used chick body mass to delineate the linear phase of growth because chick age was not known precisely for all nests.

Statistical analyses

We used a model selection approach based on the Akaike information criteria (AIC) (Burnham & Anderson 1998) to quantify the effects of meal parameters (each treated as a continuous variable) and region, colony and year (treated as categorical variables) on growth rates of kittiwake chicks (data from east Amatuli Island in1999 were identified as outliers based on regression diagnostics and were omitted from this analysis) (Piatt 2003, Jodice *et al.* 2006b). We analyzed growth rates separately for alpha and singleton chicks combined (*sensu* Suryan *et al.* 2002; hereafter, A-S chicks) and for beta chicks. We developed and tested 11 statistical models (Table 1) and ranked them in terms of the probability of each being the best model to predict growth rates given the data collected and the models tested. We also used a model averaging approach that followed guidelines in Burnham & Anderson (1998) to calculate coefficient and standard error estimates for each variable included

TABLE 1
Statistical models used in a model selection process to identify factors affecting growth rates of Black-legged Kittiwake *Rissa tridactyla* chicks from six colonies in the northern Gulf of Alaska, 1996–1999

Model	Independent variables[a]
1	Meal delivery rate, meal size, energy density
2	Meal delivery rate, meal size
3	Meal delivery rate, energy density
4	Meal size, energy density
5	Meal size
6	Meal delivery rate
7	Energy density
8	Region (Prince William Sound, Lower Cook Inlet)
9	Region, year, region*year
10	Colony
11	Colony, year (colony*year not included because of degrees of freedom limitation)

[a] Analyses were conducted separately for alpha-singleton chicks and for beta chicks.
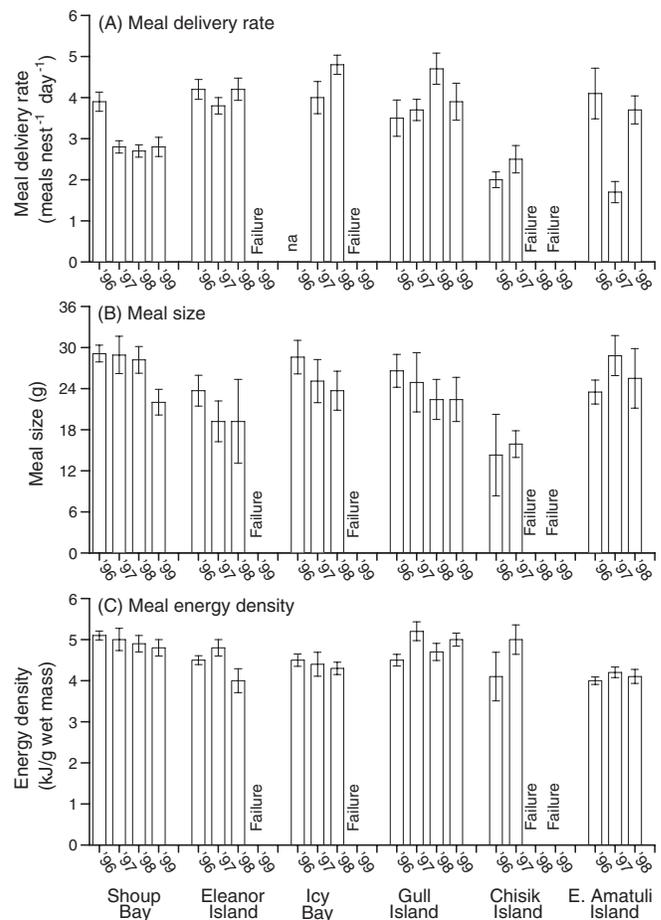
Fig. 1. Annual mean (± standard error) values of (A) meal delivery rate (meals $nest^{-1}\,d^{-1}$), (B) meal size (g), and (C) meal energy density ($kJ\,g^{-1}$ wet mass) measured at six Black-legged Kittiwake *Rissa tridactyla* colonies in the northern Gulf of Alaska, 1996–1999. Data summarized from Jodice *et al.* (2006b). Colony–years with complete reproductive failure are noted; colony–years where data were not collected are noted as "na."

in the 95% confidence set of models. Details of the analytical approach can be found in Jodice *et al.* (2006b). Means and regression coefficients are reported ±1 standard error. Data were transformed as needed, and transformations are noted along with results. Means presented are untransformed data. All analyses were conducted using the SAS software program (version 9.0: SAS Institute, Cary, NC, USA).

RESULTS

Diet composition and meals

Detailed results of diet composition are presented in Jodice *et al.* (2006b). In brief, Pacific Herring, Pacific Sand Lance, and Capelin comprised *c.* 81% of the biomass of diet items collected for all colony–years. Each of these three prey types has a relatively high lipid content and energy density (Anthony *et al.* 2000). Herring tended to be more common in diets from colonies in PWS, and sand lance was more common in diets from LCI. Capelin was most common in kittiwake diets at E. Amatuli Island (LCI) and least common at Gull Island (LCI) and Shoup Bay (PWS).

Fig. 1 presents annual mean values for delivery rate, size and energy density of meals at each colony. Detailed analyses of these data appear in Jodice *et al.* (2006b), although a brief review is included here. We observed no significant correlations between

delivery rate, size and energy density of the meal when data were pooled across all colonies and years ($|r| < 0.2$ for each pair-wise correlation). Meal delivery rates were consistently low at Chisik Island, were most variable between years at E. Amatuli Island, and least variable between years at Eleanor Island [Fig. 1(a)]. Meal size also was consistently low at Chisik Island, typically high at Shoup Bay, highly variable between years at E. Amatuli Island, and relatively consistent at Gull Island [Fig. 1(b)]. Meal sizes also tended to be higher early in the study period. Energy density was the least variable of the three meal metrics examined [Fig. 1(c)]. Energy density was typically high and relatively stable at Shoup Bay. Unlike meal delivery rate and meal size, energy density at Chisik Island was comparable to that for other colonies. Mean energy density was >4.0 kJ/g wet mass for all colony–years.

The mean annual biomass provisioning rate [Fig. 2(a)] and the energy provisioning rate [Fig. 2(b)] fell into the ranges 29–114 g nest^{-1} d^{-1} and 117–579 kJ nest^{-1} d^{-1} respectively. Interannual variability in BPR and EPR appeared high at Shoup Bay and east Amatuli Island, and relatively low at Gull Island. The BPR and EPR were consistently low at Chisik Island.

Chick growth rates

Growth rates of A-S and beta chicks varied widely between colonies within years and within most colonies between years (Fig. 3).
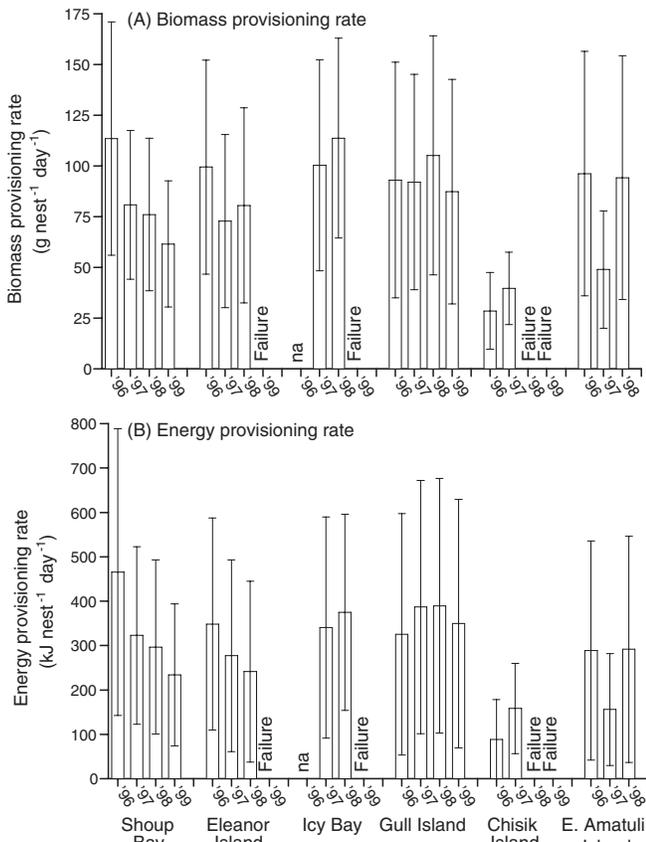
Fig. 2. Annual mean (± standard deviation) of (A) biomass provisioning rates (g nest^{-1} d^{-1}), and (B) energy provisioning rates (kJ nest^{-1} d^{-1}) measured at six Black-legged Kittiwake *Rissa tridactyla* colonies in the northern Gulf of Alaska, 1996–1999. Data summarized from Jodice *et al.* (2006b). Colony–years with complete reproductive failure are noted; colony–years where data were not collected are noted as "na."
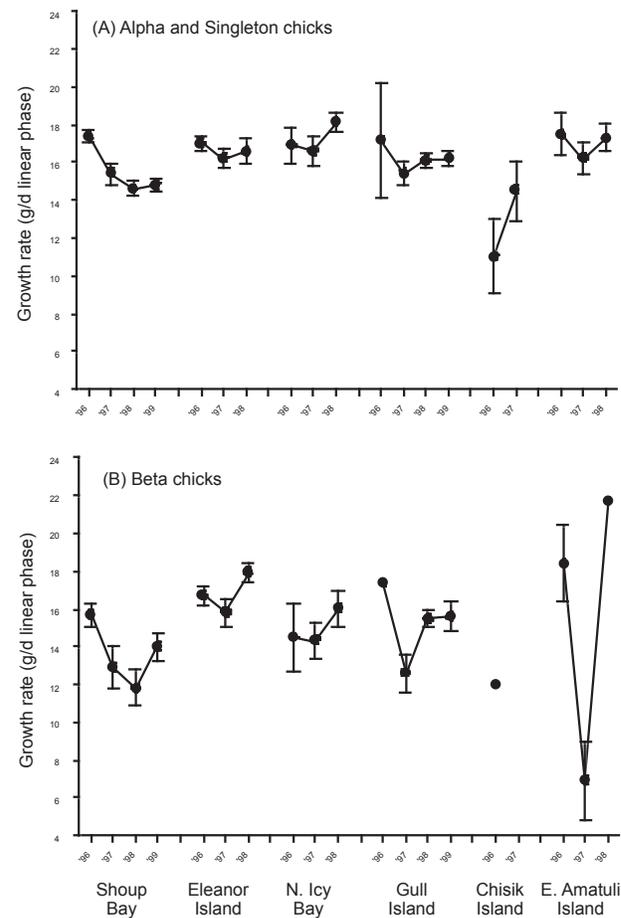
Fig. 3. Annual mean (± standard error) rate of linear growth (g d^{-1}) of (A) alpha-singleton and (B) beta Black-legged Kittiwake *Rissa tridactyla* chicks between 60 g and 300 g body mass at six colonies in the northern Gulf of Alaska, 1996–1999.

The annual means of A-S chick growth rates differed between the colonies ($F_{5,10} = 4.1$, $P = 0.03$), but not between the years ($F_{3,10} = 0.2$, $P = 0.8$). The A-S chick growth rates were greater at north Icy Bay, Eleanor Island and east Amatuli Island as compared with Chisik Island (Tukey post-hoc test: $P < 0.05$). We observed no difference in growth rates of beta chicks between colonies ($F_{5,9} = 0.7$, $P = 0.6$) or between years ($F_{3,8} = 1.9$, $P = 0.2$). Growth rates of A-S chicks were positively correlated with those of beta chicks, although only moderately so ($r = 0.51$, $P = 0.03$; Fig. 3). Annual productivity [see Jodice *et al.* (2006b), here defined as number of chicks fledged per nest structure] was positively correlated with annual growth rates of A-S chicks ($r = 0.48$, $P = 0.03$) across all colony–years, but not with growth rates of beta chicks ($r = –0.01$, $P = 0.9$).

Some temporal trends in the growth rates of A-S chicks were identified. For example, growth rates declined from 1996 to 1997 at all colonies except Chisik Island [Fig 3(a)]. Growth rates at Chisik Island, which were the lowest recorded, showed an opposite pattern to all other colonies and increased between 1996 and 1997. Growth declined further between 1997 and 1998 at Shoup Bay, but other colonies showed improvement. As with growth rates of A-S chicks, growth rates of beta chicks declined between 1996 and 1997 at all colonies, then increased or remained stable between 1997 and 1998, except at Shoup Bay, where rates declined [Fig. 3(b)]. Interannual variability in A-S chick growth rates was least at Eleanor Island (CV = 2.4%), greatest at Chisik Island (19.4%) and intermediate (4.1–8.2%) at the remaining colonies. Interannual variability in beta chick growth rates ranged between 6.2% and 12.9% at Eleanor Island, Gull Island, Shoup Bay, and north Icy Bay, but was *c.* 50% at east Amatuli Island.

Diet and growth rates

The model that best explained the variability in growth rates of A-S chicks included meal delivery rate and meal size (i.e. the biomass provisioning rate); that model was 2.0 times more likely (ratio of AIC_c weights for first and second ranked models; Table 2) to be the best as compared with the next-highest-ranked model in the candidate set (meal delivery rate, meal size and energy density). The 95% confidence set of models contained just these two models, and the variability in A-S growth explained by them ranged from 72% to 75%. Colony, region and year did not appear in any of

the models within the 95% confidence set. Table 3 presents the coefficient estimates (± unconditional standard errors) for variables contained in the 95% confidence set of models. The ratios of the unconditional standard errors to the coefficient estimates for both meal delivery rate and meal size indicate that each of these variables positively affected growth rates of the A-S chicks. In contrast, the unconditional standard error for energy density was relatively large as compared with its coefficient estimate, suggesting that this variable had no effect on growth rates of A-S chicks.

The 95% confidence set for growth rates of beta chicks included three models, each of which included meal delivery rate (Table 2). The variability in growth rates of beta chicks explained by the three models in the 95% confidence set ranged from 49% to 56%. Colony, region and year did not appear in any of the models within the 95% confidence set. The ratios of the unconditional standard error to the coefficient estimate for meal delivery rate indicates that this variable positively affected growth rates of the beta chicks (Table 3). In contrast, the unconditional standard errors for both meal size and energy density were relatively large as compared with their coefficient estimates, suggesting that neither variable affected the growth rates of beta chicks.

We also examined the simple relationships of chick growth rates to BPR and EPR. Positive relationships occurred between the A-S chick growth rate and BPR (11.6 ± 0.05 * BPR: $F_{1,16} = 29.6$, $P < 0.0001$, $R^2 = 0.65$), between A-S chick growth rate and EPR (12.3 ± 0.009 * EPR: $F_{1,16} = 14.9$, $P = 0.001$, $R^2 = 0.48$), between beta chick growth rate and BPR (7.9 ± 0.08 * BPR: $F_{1,15} = 7.2$, $P = 0.02$, $R^2 = 0.32$) and between beta chick growth rate and EPR (10.3 ± 0.012 * EPR: $F_{1,15} = 3.0$, $P = 0.10$, $R^2 = 0.17$).

DISCUSSION

Growth and provisioning rates

Flexibility in nestling growth rates, and the ability to temporarily arrest growth, are adaptive responses to variable feeding conditions that allow seabirds to optimize growth under unpredictable foraging conditions confronting adults, thereby enhancing a chick's probability of fledging (Schew & Ricklefs 1998). The response of seabird growth rates to the delivery rate, size and quality of the

---

TABLE 2
Model-selection statistics for growth rate of Black-legged Kittiwake *Rissa tridactyla* chicks from six colonies in the northern Gulf of Alaska, 1996–1999[a]

Independent variables	K[b]	ΔAIC$_c$	AIC$_c$ weight	Cumulative sum of AIC$_c$ weights
Alpha-singleton chicks				
Meal delivery rate, meal size	4	0.00	0.657	0.657
Meal delivery rate, meal size, energy density	5	1.42	0.323	0.980
Beta chicks				
Meal delivery rate	3	0.00	0.473	0.473
Meal delivery rate, energy density	4	0.56	0.357	0.831
Meal delivery rate, meal size	4	2.87	0.113	0.944

[a] Models are ranked from most to least plausible given the data collected and the models tested, but only those models from Table 1 that were included in the 95% confidence set of models are presented.

[b] The number of estimable parameters, +1 for intercept, +1 for residual variance of the estimator.

AIC = Akaike information criteria.

meals provisioned by parents has rarely been explored within the same study. Other attempts to compare these relationships over the range of colonies (n = 6) and years (n = 4) that we examined appear to be lacking.

The model that best explained the variability in annual growth rates of A-S chicks in our study included meal delivery rate and meal size. Both variables were positively related with growth rates and estimates of coefficients, and the standard errors indicated that each variable had a strong effect. The ranking of models for growth rates of beta chicks was less clear, although the first- and second-ranked models, and the estimates for coefficients and standard errors from those models, each indicated a strong positive response of growth rate of beta chicks to meal delivery rate. The BPR explained more of the variability in the growth rates of A-S and beta chicks than did the EPR. Hence, meal delivery rate and meal size each played a decisive role in determining growth rates of kittiwake chicks across regions, colonies and years.

In kittiwakes, there is strong evidence that growth rates respond positively to increased food at the nest, although the relative contributions of food quantity and quality are not always clear. For example, Gill *et al.* (2002) demonstrated that supplemental food provided directly to the parents increased the growth rates of kittiwake chicks and eliminated differences in growth between alpha and beta chicks. Furthermore, growth rates of alpha and beta chicks in that study were two of the 10 most sensitive variables with respect to supplemental feeding. It is likely that the response in growth to supplemental feeding was an effect of food quantity and not food quality, although the latter cannot be ruled out because quality was not measured. Barrett and Runde (1980) also found that slower growth and lower productivity of kittiwakes in Norway were associated with decreased food availability (with a contributing effect of predation on productivity). The implication, given a decrease in local forage fish stocks, was that food quantity was the driving factor (Barrett & Runde 1980). Suryan *et al.* (2002) examined temporal variation in kittiwake growth at a weekly scale at Shoup Bay, Alaska, and found a strong relationship with meal delivery rates.

TABLE 3
Coefficient estimates and standard errors for variables contained in 95% confidence sets of models used to examine growth rates of Black-legged Kittiwake *Rissa tridactyla* chicks (alpha-singletons, betas) at six colonies in the northern Gulf of Alaska, 1996–1999

Independent variable	Coefficient and standard error estimate[a]	
	Alpha-singleton chicks	Beta chicks
Meal delivery rate	1.22±0.46 (averaged)	2.63±0.68 (averaged)
Meal size	0.19±0.05 (averaged)	–0.09±0.15 (single)
Energy density	–0.78±0.54 (single)	–0.22±1.40 (single)

[a] The term "averaged" indicates that the variable appeared in more than one model from the 95% confidence set (Table 2) and that the coefficient and standard error estimates were calculated by model averaging (Burnham & Anderson 1998). The term "single" indicates that the variable appeared in just one model from the 95% confidence set (Table 2) and that the coefficient and standard error estimates were taken directly from that model.

Energy density, a strong indicator of diet quality, did not appear to strongly affect the growth rates of either A-S or beta chicks in our study (Tables 2 and 3). Furthermore, the simple linear regression models of growth rate for A-S and beta chicks that included EPR each explained 30%–50% less variability than the BPR model did. However, rearing experiments with captive chicks have clearly demonstrated the benefits of high-quality prey to seabird nestling development. Romano *et al.* (2006) found that kittiwake and Tufted Puffin *Fratercula cirrhata* nestlings fed prey of high energy density and high lipid:protein ratios experienced faster growth, greater fat reserves upon fledging and greater energy utilization efficiency as compared with nestlings fed an equal biomass of low-quality prey. Similarly, Kitaysky *et al.* (2006) found that captive Red-legged Kittiwake *Rissa brevirostris* chicks fed low-lipid diets had retarded growth and increased corticosterone levels. Finally, Golet *et al.* (2000, 2002) and Litzow *et al.* (2002) showed that various aspects of growth in Pigeon Guillemot *Cepphus columba* chicks from PWS and LCI responded positively to higher lipid diets.

The lack of a strong relationship between energy density and growth rate in our study may be a result of the relatively narrow and high range (4.0–5.2 kJ/g wet mass) over which energy density was measured during the course of our study (Jodice *et al.* 2006b). The high energy density was consistent with the diet described earlier, consisting predominantly of three high-lipid forage fish: Pacific Herring, Pacific Sand Lance and Capelin. Kittiwakes in other portions of their range often encounter prey of lower energy density (Jodice *et al.* 2006b). It appears that the colonies we examined were supported by relatively high-quality prey between 1996 and 1999, and our opportunity to examine the effects of a low-quality diet on chick growth rates was therefore limited.

A comparison of growth rates from our study with those from elsewhere in Alaska where kittiwake growth has been measured similarly suggests that chicks in PWS and LCI (with the possible exception of Chisik Island) were not experiencing poor conditions for growth. The mean of the annual mean growth rates across all colony–years in our study was 16.1 g d⁻¹ for A-S chicks and 15.0 g d⁻¹ for beta chicks. Growth rates of kittiwakes nesting on Middleton Island in 1996 and 1997 were *c.* 14.0 g d⁻¹ and 11.3 g d⁻¹ for alpha and beta chicks respectively (Gill *et al.* 2002). At St. George Island, kittiwake growth between 1976 and 1981 ranged from 10.3 g d⁻¹ to 13.8 g d⁻¹, all chicks combined (Springer *et al.* 1986). The growth rates reported from Middleton Island during the late 1990s and from St. George Island were considered to be low and were attributed to low food availability (Springer *et al.* 1986, Hatch *et al.* 1993). In contrast, growth rates similar to or higher than those we measured are also reported from Alaska [e.g. *c.* 17 g d⁻¹ for kittiwake chicks at Bluff (Bering Sea coast) between 1978 and 1988 (Murphy *et al.* 1991)].

Although study year did not appear in any of the models within the 95% confidence set, we observed, within regions, interannual shifts in growth rates that coincided with shifts in diet composition. For example, growth rates declined at all colonies in PWS between 1996 and 1997. That decline coincided with declines in the delivery rate and size of chick meals and with a decline in the proportion of age 1+ Pacific Herring in the diet (Jodice *et al.* 2006a, 2006b). The proportion of herring in the diet rebounded from 1997 to 1998 at all three PWS colonies, although perhaps too late in the season at Shoup Bay to benefit parents or chicks. Meal delivery rates also rebounded between 1997 and 1998 at north Icy Bay and

Eleanor Island, as did growth rates. The importance of 1+ herring to kittiwakes in PWS has been noted previously, and it has been suggested that the combination of size, energy density, lipid content and schooling behavior (i.e. ease of capture) are what make herring a preferred prey during chick-rearing (Suryan *et al.* 2002; Jodice *et al.* 2006a, 2006b). In LCI, interannual shifts in meal delivery rate, meal size and diet composition were less concordant than they were in PWS, implying that foraging conditions outside PWS were more variable between colonies.

Kittiwakes nesting in LCI and PWS during this study foraged primarily on an array of relatively high-quality prey, and chicks at most colonies during most years experienced growth rates that were comparable to those measured at other kittiwake colonies in Alaska. Spatial and temporal variability in prey availability determined the annual BPR, predominantly through meal delivery rate, and BPR was, in turn, primarily responsible for variation in chick growth rates. Kittiwake productivity in the same colonies and years was similarly affected by the BPR, although a moderate, positive effect of prey quality was also observed [i.e. colony–years with the highest measures of energy density also experienced very high productivity (Jodice *et al.* 2006b)]. Taken together, results from this study and from Jodice *et al.* (2006b) demonstrate the need to measure both the quantity and quality components of diet to gain a better understanding of growth rates and productivity in seabirds and ultimately to assess the link between environment and fitness.

ACKNOWLEDGEMENTS

REFERENCES

ANTHONY, J.A., ROBY, D.D. & TURCO, K.R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* 248: 53–78.

BARRETT, R.T. 1994. Prey harvest, chick growth, and production of three seabird species on Bleiksoy, North Norway, during years of variable food availability. In: Montevecchi, W.A. (Ed). Studies of high latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Ottawa: Canadian Wildlife Service Special Publication. pp. 20–26.

BARRETT, R.T. 2002. Atlantic Puffin *Fratercula arctica* and Common Guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. *Marine Ecology Progress Series* 230: 275–287.

BARRETT, R.T. & RUNDE, O.J. 1980. Growth and survival of nestling Kittiwakes *Rissa tridactyla* in Norway. *Ornis Scandinavica* 11: 228–235.

BURBANK, D.C. 1997. Circulation studies in Kachemak Bay and lower Cook Inlet. In: Trasky, L.L., Flagg, L.B. & Burbank, D.C. (Eds). Vol. 3. Environmental Studies of Kachemak Bay and lower Cook Inlet. Anchorage, AK: Alaska Department of Fish and Game.

BURNHAM, K.P. & ANDERSON, D.R. 1998. Model selection and multimodel inference: a practical information–theoretic approach. New York: Springer-Verlag. 488 pp.

CAIRNS, D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–267.

COULSON, J.C. & PORTER, J.M. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* 127: 450–466.

DAVOREN, G.K. & MONTEVECCHI, W.A. 2003. Signals from seabirds indicate changing biology of Capelin stocks. *Marine Ecology Progress Series* 258: 253–261.

GILL, V.A., HATCH, S.A. & LANCTOT, R.B. 2002. Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla. Ibis* 144: 268–283.

GOLET, G.H., KULETZ, K.J., ROBY, D.D. & IRONS, D.B. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. *Auk* 117: 82–91.

GOLET, G.H., SEISER, P.E., MCGUIRE, A.D., ROBY, D.D., FISCHER, J.B., KULETZ, K.J., IRONS, D.B., DEAN, T.A., JEWETT, S.C. & NEWMAN, S.H. 2002. Long-term direct and indirect effects of the "Exxon Valdez" oil spill on Pigeon Guillemots in Prince William Sound, Alaska. *Marine Ecology Progress Series* 241: 287–304.

HATCH, S.A. & SANGER, G.A. 1992. Puffins as samplers of juvenile Pollock and other forage fish in the Gulf of Alaska. *Marine Ecology Progress Series* 80: 1–14.

HATCH, S.A., BYRD, G.V., IRONS, D.B. & HUNT, G.L. Jr. 1993. Status and conservation of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds). The status, ecology, and conservation of marine birds in the North Pacific. Ottawa: Canadian Wildlife Service Special Publication. pp. 140–153.

JODICE, P.G.R., ROBY, D.D., SURYAN, R.M., IRONS, D.B., TURCO, K.R., BROWN, E.D., THEDINGA, J.F. & VISSER, G.H. 2006a. Increased energy expenditure in a seabird in response to higher food abundance. *Marine Ecology Progress Series* 306: 283–293.

JODICE, P.G.R., ROBY, D.D., TURCO, K.R., SURYAN, R.M., IRONS, D.B., PIATT, J.F., SHULTZ, M.T., ROSENEAU, D.G., KETTLE, A.B. & ANTHONY, J.A. 2006b. Assessing the nutritional stress hypothesis: the relative influence of diet quantity and quality on seabird productivity. *Marine Ecology Progress Series* 325: 267–279.

KITAYSKY, A.S., KITAISKAIA, E.V., PIATT, J.F. & WINGFIELD, J.C. 2006. A mechanistic link between chick diet and decline in seabirds? *Proceedings of the Royal Society of London B* 273: 445–450.

LANCE, B.K. & ROBY, D.D. 1998. Diet and postnatal growth in Red-legged and Black-legged kittiwakes: an interspecies comparison. *Colonial Waterbirds* 21: 375–387.

LE CORRE, M. & JAQUEMET, S. 2005. Assessment of the seabird community of the Mozambique Channel and its potential use as an indicator of tuna abundance. *Estuarine, Coastal and Shelf Science* 63: 421–428.

LITZOW, M.A., PIATT, J.F., PRICHARD, A.K. & ROBY, D.D. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* 132: 286–295.

MURPHY, E.C., SPRINGER, A.M. & ROSENEAU, D.G. 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactyla*) at a colony in western Alaska. *Journal of Animal Ecology* 60: 515–534.

PIATT, J.F. 2003. Response of seabirds to fluctuations in forage fish density: can seabirds recover from effects of the *Exxon Valdez* oil spill? In: Piatt, J.F. (Ed). Response of seabirds to fluctuations in forage fish density. Final Report to *Exxon Valdez* Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region). Anchorage, AK: US Geological Survey, Alaska Science Center. pp. 132–171.

PIATT, J.F., HARDING, A.M.A., SHULTZ, M., SPECKMAN, S.G., VAN PELT, T.I., DREW, G.S. & KETTLE, A.B. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352: 221–234.

ROBARDS, M., PIATT, J.F. & ROSE, G.A. 1999. Maturation, fecundity, and intertidal spawning of Pacific Sandlance in the northern Gulf of Alaska. *Journal of Fish Biology* 54: 1050–1068.

ROMANO, M., PIATT, J.F. & ROBY, D.D. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. *Waterbirds* 29: 407–524.

ROSENEAU, D.G., KETTLE, A.B. & BYRD G.V. 2000. Barren Island seabird studies. Final Report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163J). Homer, AK: US Fish and Wildlife Service Alaska Maritime National Wildlife Refuge.

SCHEW, W.A. & RICKLEFS, R.E. 1998. Developmental plasticity. In: Starck, J.M. & Ricklefs, R.E. (Eds). Avian growth and development: evolution within the altricial–precocial spectrum. New York: Oxford University Press. pp. 288–304.

SPRINGER, A.M., ROSENEAU, D.G., LLOYD, D.S., MCROY, C.P. & MURPHY, E.C. 1986. Seabird response to fluctuating prey availability in the eastern Bering Sea. *Marine Ecology Progress Series* 32: 1–12.

SURYAN, R.M., IRONS, D.B., BROWN, E.D., JODICE, P.G.R. & ROBY, D.D. 2006. Site-specific effects on productivity of an upper trophic-level marine predator: bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. *Progress in Oceanography* 68: 303–328.

SURYAN, R.M. & IRONS, D.B. 2001. Colony and population dynamics of Black-legged Kittiwakes in a heterogeneous environment. *Auk* 118: 636–649.

SURYAN, R.M., IRONS, D.B., KAUFMAN, M., BENSON, J., JODICE, P.G.R., ROBY, D.D. & BROWN, E.D. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake (*Rissa tridactyla*). *Marine Ecology Progress Series* 236: 273–287.

ZADOR, S.G., HARDING, A.M.A., PIATT, J.F., OCHIKUBO, L. & NIELSEN A.A. 1997. Monitoring populations and productivity of seabirds at colonies in lower Cook Inlet, Alaska, 1995. US Geological Survey Final Report to Minerals Management Service, Anchorage, AK.