HABITAT QUALITY AND METAPOPULATION DYNAMICS OF BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA*

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SUMMARY

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Neighboring colonies of Black-legged Kittiwakes *Rissa tridactyla* in Chiniak Bay, Alaska, exhibit contrasting long-term trends in productivity and population size that are consistent with variation in habitat quality at a fine spatial scale. Fine-grained reproductive variability of kittiwakes in Chiniak Bay suggests that patchy food abundance does not drive patterns of dispersal, recruitment and colony dynamics within this metapopulation. We found that, among-colonies, variability in productivity was better explained by differences in cliff elevation than by differences in size, age or proximity to Glaucous-winged Gull *Larus glaucescens* colonies. Although lacking direct evidence, we speculate that localized predation may underpin the "elevation effect" for two reasons: anecdotal observations suggest that large aerial predators prefer to roost on and hunt from taller cliffs; and coincident with a marked increase in these predators from historically low levels, the distribution of kittiwakes has shifted from long-established colonies on taller cliffs to newly-formed colonies on shorter cliffs. Regardless of origin, differential productivity can affect population dynamics of seabird colonies either through natal recruitment or by shaping patterns of dispersal between colonies within the wider metapopulation. Performance-based conspecific attraction posits that if chick production is a reliable predictor of habitat quality, then prospective breeders can benefit by preferentially recruiting into colonies with above-average productivity. Despite finding that differences in productivity among kittiwake colonies were predictive of future habitat quality, we found that conspecific attraction could not explain differential population trends of colonies. In contrast, we found that the most important drivers of population dynamics of kittiwake colonies within Chiniak Bay were natal site fidelity and intrinsic differences between colonies that are unrelated to productivity.

Key words: habitat quality, colony dynamics, metapopulation, conspecific attraction, natal fidelity, reproductive variability, population size, black-legged kittiwake, *Rissa tridactlya*, North Pacific.

INTRODUCTION

The ability of individuals to identify and occupy suitable habitat at the time of recruitment into the breeding population can have profound consequences for lifetime reproductive output. Accurate assessment of habitat quality at the time of recruitment is critical for long-lived marine birds, because established breeders typically exhibit high fidelity to colonies, nest sites and mates (Bried & Jouventin 2002). Habitat quality of seabird breeding colonies is shaped by factors such as food resources, abundance of predators and parasites, nesting substrate and microclimate, all of which differ markedly in the spatial and temporal scales over which they operate (Boulinier & Lemel 1996).

Many of these factors (e.g. predator abundance) are poor proxies for habitat quality, because they vary at spatial and temporal scales that are too fine to be easily and accurately assessed. In contrast, previous studies suggest that "prospectors" (any individual seeking a breeding site irrespective of past breeding experience) may use both the presence (Forbes & Kiaser 1994) and productivity (chicks fledged per nest) of conspecifics as a reliable source of "public information" (Danchin *et al.* 1998) regarding habitat quality when making habitat selection decisions. Productivity is readily assessed in cliff-nesting species such as the Black-legged Kittiwake *Rissa tridactyla* (hereafter "kittiwake") and is a good proxy for habitat quality because it is shaped by, and hence integrates, many determinants of habitat quality (Boulinier & Danchin 1997). Moreover, productivity is the most direct indication of fitness (the ultimate currency in which habitat quality should be measured) available to a prospecting seabird.

Food "availability" (i.e. the abundance, distribution and accessibility of prey) is an important driver of productivity and population trends of marine birds (Rindorf *et al.* 2000). This view is supported for kittiwakes in the Gulf of Alaska and Bering Sea because they exhibit concordance in productivity across broad geographic regions (Hatch *et al.* 1993). However, the fact that groups of birds with greatly overlapping foraging areas can and do differ markedly in productivity within a season argues that other more localized factors may also be important determinants of productivity (Danchin 1992b, Parrish 1995, Tims *et al.* 2004, Kildaw *et al.* 2005).

It is generally accepted that seabird colonies are organized by dispersal into larger regional metapopulations (Lebreton *et al.* 2003, Cam *et al.* 2004, Breton *et al.* 2006), but we are only now realizing how variation in productivity at a fine spatial scale affects colony dynamics within metapopulations. The "performance based conspecific attraction" hypothesis (Danchin *et al.* 1998)

proposes that patchy productivity reliably reflects differences in the quality of potential breeding habitats and that prospectors should preferentially recruit into colonies with the highest habitat quality. The use of such public information by individuals making habitat selection decisions can greatly affect patterns of dispersal and colony dynamics within seabird metapopulations (Ray & Gilpin 1991, Danchin *et al.* 1998).

Kittiwakes are small pelagic gulls that breed in discrete colonies on rocky cliffs where they construct conspicuous nests. They are a good model in which to investigate metapopulation processes because their breeding population (nests) and productivity (nest contents) can be readily counted. Like most seabirds, kittiwakes exhibit delayed maturity, high adult survival and low reproductive output (Weimerskirch 2002). In Alaska, kittiwakes first attempt to breed at an average age of five years (DBI unpubl. data), but visit colonies one or more years before recruitment, at which time they have an opportunity to assess habitat quality and compete for potential nesting sites (Cadiou *et al.* 1994).

The objectives of the present paper are threefold. First, we characterize the temporal and spatial patterns of variability in productivity of kittiwakes that breed at 22 discrete colonies within Chiniak Bay, Alaska. Second, we evaluate factors that may explain the differing productivity of kittiwake colonies within Chiniak Bay. Third, we evaluate which of four hypotheses best explains the differing population trends of these colonies. Clearly, the four hypotheses are not mutually exclusive, and all or none of these mechanisms may simultaneously affect colony growth:

- The "conspecific attraction" hypothesis proposes that more productive colonies attract a greater number prospectors and that differential recruitment dictates growth rates of colonies within seabird metapopulations (Danchin *et al.* 1998). It predicts that colony growth will be best related to productivity with a time lag of one year because prospectors locate and secure nest sites in the year preceding their first breeding attempt.
- The "natal philopatry" hypothesis proposes that kittiwake colonies behave as closed populations and predicts that differences in colony growth rates will be driven by chick production with a time-lag of five years, the time it takes fledgling kittiwakes to recruit back into the colony.
- The "cumulative productivity" hypothesis proposes that colony growth is driven by cumulative, lagged effects of productivity from one to six years before the current breeding season, rather than to productivity with a specific time lag of either one or five years.

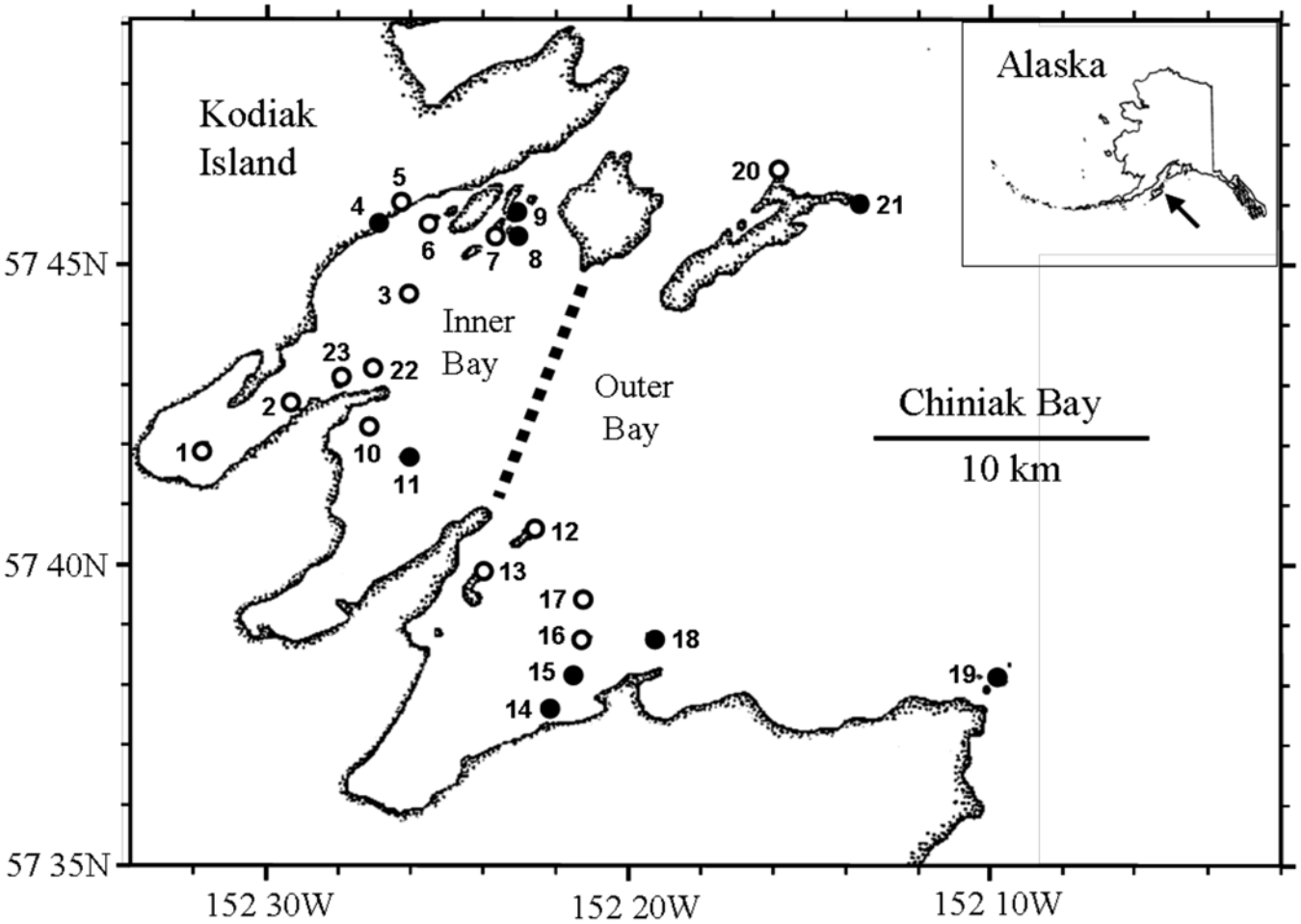

Fig. 1. Distribution of kittiwake breeding colonies in Chiniak Bay, Kodiak Island, Alaska: (1) Mary I., (2) Blodgett I., (3) Puffin I., (4) Gibson Cove, (5) Sealand, (6) Gull I., (7) Crooked I., (8) Kulichkof I., (9) Holiday I., (10) Marathon Rock, (11) Veisoki I., (12) Queer I., (13) Kalsin I., (14) Utesistoi I., (15) Svitlak I., (16) Middle I., (17) Pinnacle Rock, (18) Kekur I., (19) Cape Chiniak I., (20) Long I. Inner, (21) Long I. Outer, (22) Cliff I. and (23) Zaimka I. Filled circles denote colonies present in 1975; open circles represent new colonies formed mainly in the mid-to-late 1980s. Dashed line demarcates inner and outer regions of Chiniak Bay.

We included the cumulative productivity hypothesis in our analyses to identify instances in which apparent support for the philopatry or conspecific attraction hypothesis (or both) is actually a spurious consequence of a more general correlation between productivity and colony growth that exists via another mechanism. For example, cumulative effects of consecutive years of poor productivity might affect population growth by promoting dispersal of breeding adults. Another possibility is that productivity and colony growth may not be causally related. Rather, disturbance by predators might contribute to chronically low productivity over a number of years and, independent of productivity, may also render a colony unattractive to prospectors.

- The "colony-effect" hypothesis proposes that intrinsic characteristics of kittiwake colonies (other than productivity) drive differential rates of colony growth.

METHODS

We studied kittiwakes in Chiniak Bay, on northeastern Kodiak Island, Alaska (Fig. 1), where 22 discrete breeding colonies are located on numerous rocks and small islands, and at two mainland sites. Here, colonies are located in close proximity relative to the maximum potential foraging range of adult kittiwakes [up to 120 km (Suryan *et al.* 2000)]: the bay is only 25 km at its widest point, and many colonies are separated by only a few kilometers.

In all analyses, we exclude data from small transient colonies at Zaimka Island, Cliff Island, and Holiday Island, and from Marathon Rock, because it was first colonized in 1996. In 1975, the time of the first population surveys for seabirds in Chiniak Bay, Kittiwakes bred at 10 discrete colonies. Many new colonies formed in the mid-1980s (Kildaw *et al.* 2005). With the exception of Crooked Island (colonized in 1990), all colonies used in our analyses were established no later than 1988. Therefore, any analyses requiring a six-year time lag for independent variables were restricted to 1994–2005, because 1994 is the earliest year for which all colonies existed for at least six years. In addition, those analyses that required data from a continuous series of years were restricted to nine colonies located within the "inner bay" region (Fig. 1) because in many years preceding 1998, time and weather constraints did not allow a complete census of all nine colonies located in the "outer bay" region (Fig. 1).

We use annual counts of kittiwake nests and broods as indices of abundance and productivity of individual colonies. In all years, broods were counted in early August just before fledging of the earliest-hatched nestlings in the bay. In most years, nest counts were conducted in late June during the middle of the incubation period for kittiwakes; however, between 1989 and 2002, inclusive, colony surveys were limited to a single, pre-fledging count of nests and broods in early August. All counts were made using 8×–10× binoculars and tally counters from an open skiff or small boat (less than 10 m) at a distance of 40–150 m from the cliff. We defined a "nest" as any site with a palm-sized or larger disk of nesting material. During brood surveys, we kept separate counts for broods of one, two, or three chicks and also tallied "fledged" chicks observed roosting on the cliff face or on the water near the colony. We defined productivity for each colony as total nestlings divided by total nests. Although counts of nests and chicks are somewhat biased measures of the size and productivity of kittiwake colonies (Kildaw *et al.* 2005), our analyses require only that these biases are consistent among colonies within each year.

Statistical analyses

All statistical analyses were performed using SAS 9.1 (SAS Institute, Cary, NC, USA). Linear statistical models—analysis of variance (ANOVA) and analysis of covariance (ANCOVA)—were fit using proc GLM and the least-squares method. We assessed assumptions of normality and homogeneity of variance by examining residuals from global models (all parameters included) and found no serious departures.

When evaluating a suite of candidate models within an information–theoretic framework (Burnham & Anderson 2002), we used Akiake's Information Criteria adjusted for small sample sizes (AIC_c). AIC_c weights, w_i, the probability that a candidate model is the best given the data and the suite of models evaluated and we identified a 90% confidence set of best-fitting models (models accounting for 90% of cumulative w_i), renormalized w_i to sum to 1 within this set and used model averaging to compute parameter estimates, standard errors and confidence intervals.

Spatial and temporal patterns of productivity

We assessed spatial and temporal variability in habitat quality by comparing kittiwake productivity among colonies and years with an ANOVA model that treated year as a blocking factor. Missing data for outer bay colonies precluded analysis of all colonies over all years of the study. Instead, we conducted separate analyses for inner (nine colonies) and outer regions (nine colonies) of Chiniak Bay using data only from years for which counts were available from all colonies within the inner (n = 18 years; 1988–2005) and outer (n = 9 years; 1990, 1998–2005) regions respectively.

We tested for predictability of productivity of individual colonies across years using an autocorrelation analysis (proc CORR) that computes a single correlation coefficient for each time lag from $t - 1$ through $t - 6$ years. We restricted this analysis to nine inner bay colonies that had a complete time series of productivity data from 1988 through 2005.

We generated autocorrelation functions for both productivity and standardized productivity (standardized within each year by subtracting the mean productivity of all colonies in a given year). Standardizing raw productivity controls for considerable interannual variability observed for kittiwakes in Chiniak Bay [see Fig. 2(a)] that may swamp more subtle relative differences in productivity among colonies.

Determinants of productivity

We used AIC and multi-model inference to investigate factors responsible for contrasting productivity among kittiwake colonies in Chiniak Bay. In this analysis, the productivity of each of the 18 colonies was first standardized to control for interannual variability in productivity (by subtracting mean productivity of all colonies in a given year), and was then averaged over nine years (1990, and 1998–2005) for which data were available from all colonies within Chiniak Bay. We did not run separate analyses on inner and outer sections of Chiniak Bay (and thereby make use of the longer time series available for inner bay colonies), because the sample size in this analysis was limited to one data point for each colony

(n = 18). We evaluated 15 models representing all possible *n*-way combinations of the following four factors:

- Colony age (old vs. young)—included as a predictor variable because kittiwake colonies that formed in the mid-to-late 1980s in Chiniak Bay displayed greater productivity and growth rates than did long-established colonies (Kildaw *et al.* 2005). Also, previous research indicates that productivity of older kittiwake colonies may be diminished by higher levels of ectoparasites (Danchin 1992a) or enhanced by older, more-experienced breeders (Coulson 1966, Coulson & Porter 1985).
- Colony size (nest count, log-transformed to normalize residuals)—included as a predictor variable because colony size may affect productivity through effects of density on intraspecific competition for nests and food and on prevalence of parasites and disease (reviewed by Wittenberger & Hunt 1985).
- Gull abundance (low vs. high)—presence or absence of an adjacent breeding colony of Glaucous-winged Gulls *Larus glaucescens* may affect kittiwake productivity directly through predation or indirectly through mobbing and harassment of aerial predators that are a threat to both species.
- Cliff height (maximum elevation of the breeding cliff)—the preference of large-bodied aerial predators to roost and hunt from high perches can negatively affect the productivity of kittiwake colonies located on taller cliffs either directly, by harassment, and indirectly by creating disturbances that smaller, more abundant Northwestern Crows *Corvus caurinus* and Black-billed Magpies *Pica pica* can exploit.

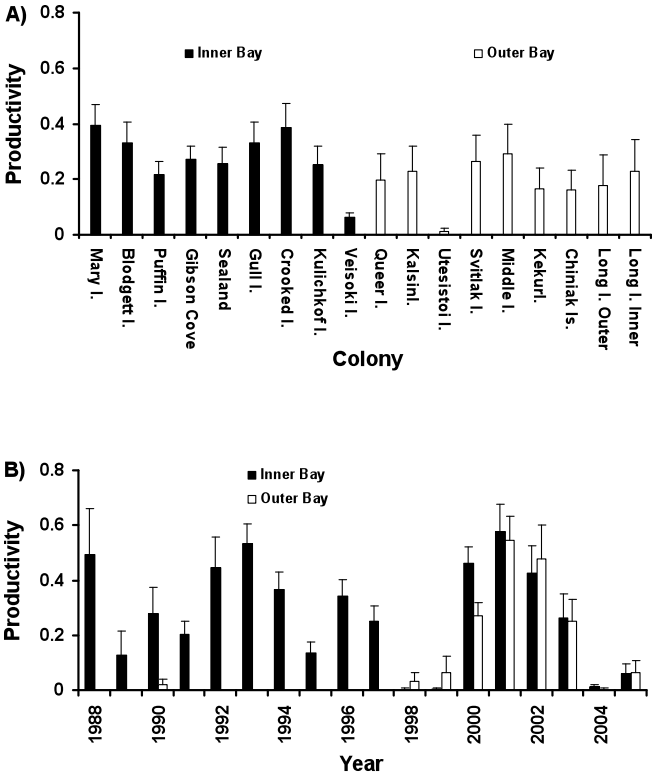

Fig. 2. Productivity (chicks fledged per nest) of kittiwake colonies in Chiniak Bay is variable in both space and time. Productivity varies (A) between the colonies (spatial variation) in the inner region of the bay and (B) between the years (temporal variability) in both the inner and outer regions.

Determinants of colony growth

We used AIC and multi-model inference to assess the influence of past productivity on the rate of colony growth ($N_t / N_{(t-1)}$). This analysis was restricted to nine inner bay colonies, because it required an uninterrupted data series and the dependant variable was restricted to the 1994–2005 time frame (providing a time lag of up to six years for some independent variables). We evaluated four hypotheses that potentially explain colony dynamics within kittiwake metapopulations—conspecific attraction, natal philopatry, cumulative productivity and colony-specific growth—by modeling the dependant variable, colony growth, as a function of 15 *n*-way combinations of four explanatory variables (described below) that were each associated with one particular hypothesis. Because our four hypotheses are not mutually exclusive, we evaluated all of their possible combinations to accommodate the possibility that colony growth might be best explained by additive effects of a combination of factors. In addition to the 15 base models, we generated seven models that included two interaction variables (also described below) to account for potential interactive effects of current and past productivity on the growth rate of kittiwake colonies. Interaction terms were added only to models that included the associated main effect and to models that initially contained no more than two variables. For this analysis, we standardized colony growth and all continuous predictor variables across years by subtracting the annual mean of all colonies from the value for each colony in a given year. Standardization across years removes the need to include year as a factor in our models and at the same time controls for considerable interannual variability in both the growth and productivity of colonies that could otherwise mask among-colony variability in these parameters.

Our four explanatory variables and two interaction terms were these:

- Productivity in year t – 1—Standardized productivity of a colony in the preceding breeding season. The conspecific attraction hypothesis proposes that productivity is a reliable indicator of habitat quality. It predicts that more productive colonies will attract a disproportionate number of prospectors and will exhibit greater rates of growth when those prospectors recruit into the colony the following year.
- Effective productivity in year $t - 5$—Standardized "effective" productivity of a colony five years before the current breeding season. The natal philopatry hypothesis predicts that more productive colonies will exhibit greater colony growth when fledged chicks recruit back into the population with a time lag of five years (DBI unpubl. data). We computed effective productivity by adjusting raw productivity values by the ratio of colony size between year $t - 5$ (fledging year) and $t - 1$ (year preceding recruitment) to compensate for changes in colony size between fledging and recruitment that can modulate the effect of a cohort of juvenile kittiwakes on colony growth—a cohort of recruits of a given size will have a smaller effect on the growth of a colony that has increased in size between fledging and recruitment than one that has decreased in size.
- Mean productivity in years $t - 1$ through $t - 6$—Standardized productivity averaged across time lags of $t - 1$ through $t - 6$ years. The cumulative productivity hypothesis predicts that colony growth will be more strongly correlated with productivity integrated over several years than with productivity at any specific time lag.

- Colony—A categorical predictor variable that accommodates intrinsic differences among kittiwake colonies and that may be responsible for differential colony growth.
- Mean productivity in year t * productivity in year $t-1$ and mean productivity in year t * effective productivity in year $t-5$—Following the suggestion of Suryan & Irons (2001), we included in our analysis interactions between the mean productivity of all colonies in the current breeding season and the productivity of individual colonies in years $t-1$ and $t-5$. Poor productivity in the current year can diminish the effects of past productivity on colony growth because prospectors faced with poor early-season breeding conditions may defer recruitment until the following year. Furthermore, poor productivity is associated with reduced breeding propensity of established breeders (Danchin 1992b) and diminished maintenance and retention of failed nests (Hatch & Hatch 1988). Both of these factors add variability to the apparent size and growth rate of colonies that potentially mask effects of other factors on colony growth.

Our use of AIC and multi-model inference to identify the factors that drive the growth rate of kittiwake colonies in Chiniak Bay contrasts greatly with analyses used in two previous studies of colony dynamics of Black-legged Kittiwakes (Danchin *et al.* 1998, Suryan & Irons 2001). For the sake of direct comparison of results, we performed additional analyses on our data using the methods of the earlier authors:

- Danchin *et al.* (1998) modeled the growth of subcolonies of kittiwakes ("cliffs") located within six neighboring kittiwake colonies in France as a function of year, colony and productivity in years $t-1$ through $t-4$. They did not standardize productivity or growth data, opting for raw values instead. Also, we added productivity in year $t-5$ to our ANCOVA model to account for delayed age of first breeding of kittiwakes in the North Pacific, and we did not consider any interactions between main effects (with both year and colony included as class variables, interactions could not be computed because of a lack of replication).
- Suryan & Irons (2001) modeled the growth rate of 25 kittiwake colonies in Prince William Sound (PWS), Alaska, using dependent variables year, colony, and five measures of productivity at time lags of $t-1$ through $t-6$ years. To emulate their analysis, we first ranked values of each productivity and growth variable within each year (to standardize data across years) and then performed an ANCOVA on those ranks. We did not include year as a factor in the model, because when data are ranked to standardize across years, any year effect is eliminated.

RESULTS

Spatial and temporal patterns of productivity

We determined that productivity, an indicator of breeding habitat quality, exhibited spatial and temporal heterogeneity: significant effects of colony [$F_{8,134} = 4.89$, $P < 0.0001$, Fig. 2(a)] and year [$F_{17,134} = 8.23$, $P < 0.0001$, Fig. 2(b)] on productivity of inner bay kittiwake colonies (nine colonies, 18 years) indicated that habitat quality varied in both space (among colonies) and time (among years). A comparable analysis of outer bay colonies (nine colonies, nine years) indicated that productivity varied in time [$F_{8,64} = 10.78$, $P < 0.0001$, Fig. 2(b)], but not space ($F_{8,64} = 1.64$, $P = 0.13$, Fig. 2(a)].

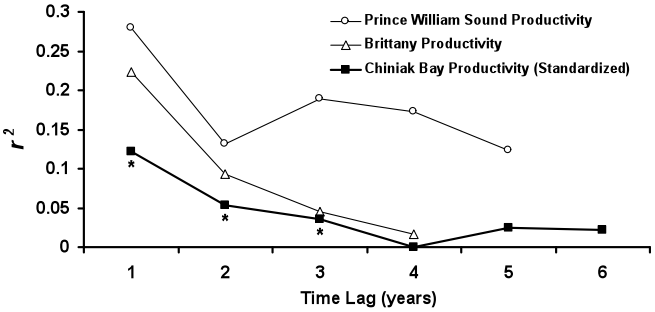

Fig. 3. Standardized productivity (departure from annual mean number of chicks fledged per nest) of kittiwake colonies is predictable for up to three years in Chiniak Bay and is even better autocorrelated in Prince William Sound, Alaska, and Brittany, France. Data for Chiniak Bay (CB) are from nine inner bay colonies between 1990 and 2005 and are derived from a sample size of ranging from 124 to 143 colony–years. Data from studies in Prince William Sound (PWS), Alaska, and from Brittany, France are presented for comparison; however, significant correlations are not indicated. Data for PWS were computed as the mean r^2 of between eight and 12 annual r^2 values (derived from approximately 20 colonies) as presented in Suryan & Irons (2001). Brittany data are taken directly from Danchin *et al.* (1998) and were derived from between 125 and 205 "cliff–years" of data. Asterisks indicate significant ($P < 0.05$) autocorrelations in Chiniak Bay.

TABLE 1
A summary of the 90% confidence set[a] of general linear models that best explain the relative productivity of 18 kittiwake breeding colonies in Chiniak Bay, Alaska, in nine years: 1990, and 1998 through 2005

Model	K	r^2	RSS	MLL	AIC_c	ΔAIC_c	w_i
Elevation	3	0.48	0.082	48.5	–89.33	0.0	0.64
Elevation, age	4	0.50	0.079	48.9	–86.68	2.6	0.17
Elevation, size	4	0.48	0.082	48.5	–85.97	3.4	0.12
Global model	6	0.51	0.077	28.4	–37.21	52.1	0.00

[a] Cumulative w_i of 0.90. The model set is presented in descending order of w_i and was extracted from an initial set of 15 models that included all possible n-way combinations of four explanatory variables—two continuous variables [maximum elevation of kittiwake breeding cliff (Elevation) and size of kittiwake colony (Size)] and two categorical variables [presence of neighboring Glaucous-winged Gull colony (GWGU: yes vs. no) and age of the kittiwake colony (Age: old vs. young)].

K = number of parameters in the model, including parameters for intercept and error terms; r^2 = coefficient of determination: proportion of variability in relative productivity explained by model; RSS = residual sum of squares from regression model; MLL = maximized log-likelihood of model; AIC_c = Akaike's Information Criterion adjusted for small sample size; ΔAIC_c = departure of AIC_c from that of the best model; $w_i = AIC_c$ weight, the probability a given model is the best of the suite of models considered.

We next assessed the degree to which habitat quality of a colony in one year could be predicted from productivity in previous years and found that productivity was significantly correlated only between adjacent years ($r^2 = 0.15$, $P < 0.05$). However, when we controlled for interannual variability by standardizing productivity relative to the mean in each year, we found that habitat quality of a colony (relative to all others) was correlated ($P < 0.05$) and predictable for up to three years into the future (Fig. 3).

Determinants of productivity

We used AIC and multi-model inference to determine the factors that best explained differences in standardized productivity of 18 kittiwake colonies averaged over nine years. We evaluated 15 general linear models representing all possible *n*-way combinations of four predictor variables, but the 90% confidence set comprised just three models. The best-fitting model included only "elevation" and carried approximately two thirds of the total AIC_c weight ($w_i = 0.64$; Table 1). The remaining two models in the confidence set added parameters without improving the maximum log-likelihood; these more complex models and their additional parameters are therefore not supported by the data. Thus, the 90% confidence set collapses down to a single best model—elevation—that explains 48% of the variation in the mean standard productivity of a colony (Table 1). We generated model-averaged estimates for all parameters included in the 90% confidence set of models (using w_i of the full confidence set) and found that only elevation had a confidence interval that did not bound zero (Table 2). Productivity was negatively related to maximum cliff height (Fig. 4) and decreased by 0.08 chicks/nest for each 10 m increase in cliff height (Table 2).

TABLE 2
Model-averaged parameter estimates (θ), standard errors (SEs), and 95% confidence intervals (CIs) derived from the 90% confidence set of models that best explain relative productivity of kittiwake breeding colonies in Chiniak Bay, Alaska, between 1994 and 2005

Parameter	θ	SE	95% CI
Intercept[a]	0.173	0.049	0.076 to 0.270
Elevation	–0.008	0.002	–0.012 to –0.003
Age			
Old	0.006	0.009	-0.013 to 0.024
Young[a]	—	—	—
Size	1×10^{-7}	6×10^{-6}	-6×10^{-6} to 6×10^{-6}

[a] Estimates for young colonies are represented by the intercept.

Determinants of colony growth

We employed AIC and multi-model inference to determine whether natal philopatry, conspecific attraction, cumulative productivity or colony-specific growth best explains population dynamics (standardized growth rate) of colonies within Chiniak Bay. The

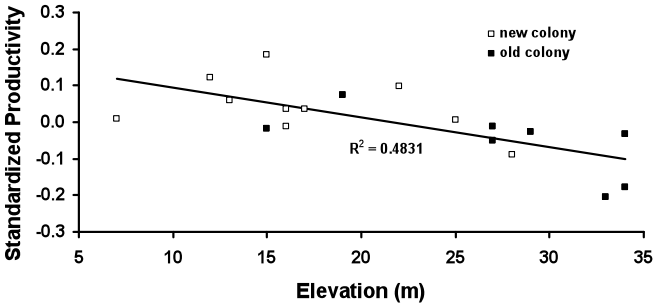

Fig. 4. Negative relationship between maximum height of a breeding cliff and standardized productivity (chicks fledged per nest) of 18 kittiwake colonies in Chiniak Bay (Standardized Productivity = 0.0081 (Elevation) + 0.10, $r^2 = 0.48$). Data points represent the mean of standardized productivity values for each colony in the years 1990 and 1998 through 2005—years for which data were available for all 18 colonies. Old and new colonies have the same linear relationship; thus, the varying productivity of old and new colonies reported in Kildaw *et al.* (2005) is an effect of elevation rather than of age.

TABLE 3
Summary of the 90% confidence set[a] of general linear models that best explain the standardized growth rate—that is, departure of growth rate from the annual mean—of nine kittiwake breeding colonies in Chiniak Bay, Alaska, between 1994 and 2005 (n = 106 colony–years)

Model	K	r^2	RSS	MLL	AIC_c	ΔAIC_c	w_i
EProd5, Colony	11	0.31	6.60	147.1	–269.5	0.00	0.47
EProd5, Colony, Prod1	12	0.31	6.61	147.1	–266.8	2.71	0.12
EProd5, Colony, Prod1–6	12	0.31	6.62	147.0	–266.6	2.87	0.11
EProd5, Colony, MeanProd*EProd5	12	0.31	6.62	147.0	–266.6	2.87	0.11
EProd5, Prod1	4	0.17	7.96	137.2	–266.0	3.45	0.08
Global model	15	0.31	6.59	147.2	–259.1	10.36	0.00

[a] Cumulative AIC weights w_i of 0.90. The model set is presented in descending order of AIC weights (w_i) and was extracted from an initial set of 19 models that included selected combinations of six explanatory variables (see Methods): colony, standardized productivity in year $t - 1$ (Prod1), standardized effective productivity in year $t - 5$ (EProd5), mean standardized productivity of a colony for time lags of one to six years before the current breeding season (Prod1 – 6), and interactions between mean productivity of all colonies in the current year with Prod1 and with EProd5 (MeanProd * Prod1 and MeanProd * EProd5).

K = number of parameters in the model, includes intercept and error parameters; r^2 = coefficient of determination: proportion of variability in relative growth explained by model; RSS = residual sum of squares from regression model; MLL = maximized log-likelihood of model; AIC_c = Akaike's Information Criterion adjusted for small sample size; ΔAIC_c = departure of AIC_c from that of the best model; $w_i = AIC_c$ weight, the probability a model is the best given the suite of models considered.

best fitting model included predictors "Colony" and "Effective Productivity in year $t - 5$" (EProd5) and carried approximately one half of the total AIC weight ($w_i = 0.47$; Table 3). Closer inspection of Table 3 reveals that adding parameters to the "Colony, EProd5" base model does not improve the maximum log-likelihood of any more complex model. Thus, our data do not support the more complex models, nor the additional parameters they contain, and our 90% confidence set collapses down to strongly support the base model ($w_i = 0.81$). Despite strong AIC support, our "best" model explains only 31% of the variation in standardized colony growth ($r^2 = 0.31$). We model-averaged all parameters included in the 90% confidence set of models across the full confidence set and determined that only parameters associated with individual colonies and EProd5 have confidence intervals that do not bound zero (Table 4). Standardized annual growth rate varies among colonies—the fastest growing colony exceeded the slowest by 0.33 units (33% annually)—and was positively related to standardized chick production in year $t - 5$. An increase in productivity of 0.10 chicks/nest produces an increase in standardized growth of roughly 7% (Table 4).

To facilitate direct comparison of our results with those of two previous studies of colony dynamics in kittiwakes (Danchin *et al.* 1998, Suryan & Irons 2001), we analyzed our data using alternative methods. We performed an ANCOVA on unmodified productivity and growth data (after Danchin *et al.* 1998) and found that colony growth varied among years ($P < 0.0001$), but was unrelated to productivity in any previous year (all $P > 0.05$, Table 5). We then performed an ANCOVA on productivity and growth data that was first standardized by ranking observations within each year (after Suryan & Irons 2001) and found that colony growth was unrelated to productivity at any time lag (Table 6).

TABLE 4
Model-averaged parameter estimates (θ), standard errors (SEs), and 95% confidence intervals (CIs) for parameters included in the 90% confidence set of models that best explain the relative population growth of kittiwake breeding colonies in Chiniak Bay, Alaska, between 1994 and 2005

Parameter	θ	SE	95% CI
Intercept[a]	–0.16	0.09	–0.34 to 0.02
Colony			
Blodgett I.	0.23	0.11	0.02 to 0.44
Crooked I.	0.26	0.11	0.04 to 0.48
Gibson Cove	0.07	0.10	–0.13 to 0.27
Gull I.	0.36	0.11	0.14 to 0.58
Kulichkof I.	0.01	0.10	–0.19 to 0.21
Mary I.	0.12	0.11	–0.09 to 0.33
Puffin I.	0.31	0.10	0.10 to 0.51
Sealand	0.08	0.10	–0.12 to 0.28
Veisoki[a]	—	—	—
Prod1	0.05	0.10	–0.14 to 0.24
EProd5	0.69	0.15	0.39 to 0.99
Prod1 – 6	–0.01	0.05	–0.11 to 0.09
MeanProd * EProd5	–0.02	0.11	–0.23 to 0.19

[a] Parameter estimate for Veisoki Island is represented by the intercept.

DISCUSSION

Patterns of kittiwake productivity in Chiniak Bay indicated that kittiwake colonies represent habitat patches where quality is variable in both space and time and that the relative quality of these patches in the future can be predicted from current conditions. Moreover, the spatial scale of heterogeneity is as fine-grained as 2 km and is many times smaller than the maximum potential foraging range of a breeding kittiwake (80–120 km; Suryan *et al.* 2000, Daunt *et al.* 2002, Bull *et al.* 2004)

A central paradigm in seabird ecology is that food abundance is the most important determinant of productivity and population trends. In support of this idea, Alaskan kittiwakes display striking patterns

TABLE 5
Results from an analysis of covariance model[a] that emulates an analysis presented by Danchin *et al.* (1998) for kittiwake colonies in Brittany, France

Parameter	df	MS	*F*	*P*
Year	11	0.297	3.07	0.002
Colony	8	0.071	0.74	0.66
Prod1	1	0.053	0.55	0.46
Prod2	1	0.040	0.41	0.52
Prod3	1	0.345	3.57	0.06
Prod4	1	0.157	1.62	0.21
Prod5	1	0.037	0.39	0.53
Error	81	0.096		

[a] We found significant effects only for Year on the growth rate (N_t / N_{t-1}) of kittiwake colonies. Our analysis was based on a sample of 106 colony–years of observations from nine colonies located in Chiniak Bay, Alaska, between 1994 and 2005.

TABLE 6
Results from an analysis of covariance model[a] that evaluated eight variables that may affect within-year rankings of the growth rate [$N_t / N_{(t-1)}$] of kittiwake colonies: year, colony, and within-year ranks of productivity (chicks fledged per nest) with time lags of one to six years (RankProd1 – 6)

Parameter	df	MS	*F*	*P*
Colony	8	10.64	1.81	0.09
RankProd1	1	0.14	0.02	0.88
RankProd2	1	1.34	0.23	0.63
RankProd3	1	13.34	2.26	0.14
RankProd4	1	9.54	1.62	0.20
RankProd5	1	5.52	0.94	0.34
RankProd6	1	14.48	2.24	0.13
Error	91	5.89		

[a] This model replicates one presented by Suryan & Irons 2001 for kittiwake colonies in Prince William Sound, Alaska. Our analysis was based on a sample of 106 colony-years of observations from nine colonies located in Chiniak Bay, Alaska, between 1994 and 2005. Interactions could not be included in this model because of a lack of replication.

of regional concordance in productivity (Hatch *et al.* 1993) that is thought to arise through the action of bottom-up effects of marine conditions acting over a large spatial scale. As a corollary, regional differences in productivity and population trends of kittiwake colonies that do have exclusive foraging areas (Ainley *et al.* 2003) within PWS, Alaska, reflect differences in marine habitat and forage fish communities between the northern and southern regions (Suryan & Irons 2001).

The food paradigm predicts that seabirds in neighboring colonies that have greatly overlapping foraging ranges should share common food resources (via scramble competition) and experience comparable breeding success. We observed fine-grain patchiness of kittiwake productivity among colonies within Chiniak Bay that contradicts this prediction. While high levels of prey abundance have the potential to restrict kittiwake foraging trips to within 5 km of their nests (Hamer *et al.* 1993, Suryan *et al.* 2000) and thereby segregate foraging areas of adjacent colonies, abundant food should at the same time produce consistently high productivity across all colonies. Moreover, given a situation in which food is locally abundant at only some colonies, kittiwakes in adjacent colonies could readily include these food "hotspots" in their foraging travels with minimal additional energetic expense. The only possible mechanism by which food abundance could produce the fine-grained patchiness observed in the quality of kittiwake habitat within Chiniak Bay, is if abundant predictable food resources could be monopolized, through interference competition, by breeders from a nearby colony (see discussions by Lewis *et al.* 2001, Ainley *et al.* 2003, Tims *et al.* 2004). Thus, we argue that while food abundance might drive regional population trends in kittiwakes, patchy food abundance is an unlikely explanation for the fine-scale variability in kittiwake productivity observed in Chiniak Bay.

Several other factors have the potential to affect kittiwake productivity in a localized fashion: predation (Gilchrist 1999), bird quality (Coulson & Thomas 1985, Coulson & Fairweather 2001) ectoparasitism (Danchin *et al.* 1998), nest site quality (Nettleship 1972, Potts *et al.* 1980) and localized weather conditions (Aebischer 1993). Lacking data to test these possibilities directly, we assessed four characteristics that differed noticeably between colonies and potentially affected kittiwake productivity through mechanisms unrelated to food.

We found that elevation best explained among-colony variability in kittiwake productivity observed within Chiniak Bay, and we argue that large-bodied aerial predators, namely Bald Eagles *Haliaeetus leucocephalus,* Peregrine Falcons *Falco peregrinus,* and Common Ravens *Corvus corax* may be responsible for depressed productivity of kittiwakes that nest on taller cliff faces in two ways. First, anecdotal observations suggest that these predators prefer higher cliffs as hunting perches and roosts (SDK pers. obs.). Taller perches may allow for greater diving velocity that many raptors depend upon to surprise prey, and higher cliffs can generate stronger updrafts that may increase hunting efficiency or allow aerial predators to hunt on days with marginal wind speed (Gilchrist *et al.* 1998, Massaro *et al.* 2001), or both. In addition to having a direct effect on kittiwake productivity through predation of eggs and chicks, large aerial predators can have indirect effects by creating disturbances that are exploited by abundant facultative predators (Parrish 1995), such as the Northwestern Crow and Black-billed Magpie. Second, the formation and rapid expansion of new kittiwake colonies on lower-elevation cliffs in Chiniak Bay (Kildaw *et al.* 2005) occurred in the midst of rapid expansion of the Bald Eagle population on Kodiak Island (Zwiefelhofer 2002) and the recovery of the Peregrine Falcon from brink of extinction in the early 1970s (Ambrose *et al.* 1988, Paine *et al.* 1990). Unlike circumstances in Britain, where kittiwakes colonized shorter cliffs at a time of general population expansion (Coulson 1963), kittiwakes in Chiniak Bay colonized short cliffs in conjunction with a dramatic exodus of birds from established colonies on taller cliffs (Kildaw *et al.* 2005). Together, these observations suggest that direct and indirect effects of large-bodied predators may have prompted the relocation of kittiwakes from established colonies on tall cliffs to the refuge of shorter cliffs, where they continue to experience greater productivity. Thus, the apparent effect of age on productivity and growth of colonies in Chiniak Bay (Kildaw *et al.* 2005) might be explained by the differing elevations of the cliffs occupied by old and new colonies (Fig. 4).

PATCHY PRODUCTIVITY AND POPULATION DYNAMICS: FOUR HYPOTHESES

Regardless of habitat quality differences between kittiwake colonies in Chiniak Bay, theory predicts that differential productivity between neighboring seabird colonies should drive differential colony dynamics. We evaluated four hypotheses, each of which addresses a specific mechanism by which differential productivity could shape colony dynamics within the Chiniak Bay metapopulation.

Conspecific attraction hypothesis

The conspecific attraction hypothesis proposes that where habitat quality is patchy but predictable from one year to the next, prospective breeders can assess productivity in the pre-recruitment year as a reliable indicator of habitat quality (Danchin *et al.* 1998) and should preferentially recruit into high-productivity colonies.

In contrast to comparable studies in Brittany, France (Danchin *et al.* 1998), and PWS, Alaska (Suryan & Irons 2001), we found that the rate of colony growth was at best only weakly influenced by its productivity in the previous year. Differing spatial scales of the three analyses may have contributed to differing results: kittiwake colonies in PWS were distributed across a much larger region (more than 100 km) than was the case for either Chiniak Bay or Brittany (both approximately 20 km). Moreover, the French study was more fine-grained than either Alaskan study because it was conducted at a subcolony spatial scale (data were collected from several cliff sections within each colony with plots ranging in size from 11 to 121 nests). Thus, the whole-colony analyses adopted in the two Alaskan studies smoothed over subcolony variability in chick production and growth that was captured in the French analyses.

We speculate that our results differ from earlier studies for two additional reasons. First, although statistically significant, the predictability of productivity across years was not strong ($r^2 = 0.15$) and was weaker than that observed in the two previous studies (Fig. 3). Second, kittiwakes in Chiniak Bay (Fig. 2) and PWS (see Fig. 5 in Suryan & Irons 2001) exhibited far greater interannual variability in productivity relative to those in Brittany, France (see Table 2 in Danchin 1992b). Given a combination of high variability in productivity from year to year and weak predictability of productivity between years, current productivity may be a relatively unreliable indicator of habitat quality in Chiniak Bay.

Rejecting the conspecific attraction hypothesis contradicts evidence suggesting that conspecific attraction likely contributed to the rapid

growth of newly formed kittiwake colonies in Chiniak Bay in the mid-to-late 1980s (Kildaw *et al.* 2005). The discrepancy between past and present studies may result from the different focus of the two analyses.

The present study excludes data from colonies less than seven years old because we required time-lagged productivity data for our analyses. In contrast, the former study used data from the inception of each colony. Thus, the period of formation and rapid expansion of new colonies (1985–1994) is not contemporary with the time frame of analyses conducted in the present study (1994–2005). That lack of contemporaneousness implies that the contribution of conspecific attraction to colony dynamics in kittiwake metapopulations may be context-dependant.

Natal philopatry hypothesis

We found that above-average chick production in one year tends to induce above-average colony growth when those same chicks reach breeding age five years later. Thus, our results support the natal philopatry hypothesis, in that juveniles recruited back into their colony of origin. Our results are surprising given the small spatial extent of Chiniak Bay (approximately 20 km maximum distance between inner-bay colonies) and high levels of both natal and breeding dispersal observed for kittiwakes in France (Danchin 1992b, Danchin *et al.* 1998).

Natal philopatry shapes the colony dynamic of kittiwakes in PWS, where colonies are distributed at a much larger spatial scale (approximately 100 km) and where large regional differences in breeding success between inner and outer regions of PWS were attributed to differences in food resources between areas (Suryan & Irons 2001). Our results do not rule out the occurrence of natal and breeding dispersal among colonies; rather, we conclude that any net imbalance in the exchange of dispersing individuals between colonies is insufficient to overcome the strong signal of natal philopatry on colony growth.

Cumulative productivity hypothesis

We found that a colony's cumulative productivity (productivity averaged from year $t - 1$ through $t - 6$) is a poor predictor of the rate of colony growth, which suggests that the high interannual variability in productivity typical of kittiwakes in the North Pacific (Hatch *et al.* 1993) appears not to extend the time scale over which prospectors make recruitment and habitat selection decisions. Our rejection of the cumulative productivity hypothesis strengthens the natal fidelity hypothesis by discounting an alternative explanation for our results—that is, that a strong correlation between colony growth and productivity in year $t - 5$ (evidence for natal fidelity) might arise because growth of a generally productive kittiwake colony will be correlated with productivity at all time lags.

Colony effect

Kittiwake colonies within Chiniak Bay displayed intrinsic differences in growth rate that could not be attributed to any measure of productivity included in our analysis. Danchin *et al.* (1998) and Suryan & Irons (2001) also identified colony-specific growth in their respective analyses. Unlike hypotheses related to productivity, the colony effect does not lend itself to a mechanistic interpretation. Thus, we are left to conclude that some unidentified factor (besides chick production) varies among kittiwake colonies and shapes colony growth by affecting rates of recruitment or dispersal (or both) of either young birds or established breeders.

Unexplained variability in colony growth

Despite strong AIC support for our best model, the model explained less than one third of the variability observed in the growth rate of kittiwake colonies in Chiniak Bay. While some of the residual variability is attributable to measurement error (imprecise indices of colony growth and productivity) and to (random) sampling error, we have likely overlooked one or more important drivers of kittiwake dispersal, recruitment and survival that ultimately affect population dynamics of kittiwake colonies in this system.

Factors considered in our analysis eliminate a number of potential explanations for residual variability. We accounted for all sources of spatial (colony-specific) variability by including colony as a factor in our analysis, and we neutralized temporal (among-year) variability by standardizing colony growth and productivity relative to annual means. Therefore, residual variability can arise only from year-to-year departures of a colony's standardized growth rate from its long-term mean. For example, while variation in the breeding propensity of adult kittiwakes can affect nest counts and apparent growth rates of kittiwake colonies, among-colony variation in breeding propensity does not contribute to residual variability in our analysis because this variability is already "captured" by the inclusion of "colony" as a factor. Similarly, interannual variability in mean breeding propensity of all colonies does not contribute to residual variability in our model because standardization strips year-to-year variability from our data. Only variability in breeding propensity that affects the departure of a colony's growth rate from its long-term mean will contribute to residual variability in our analysis.

Suryan & Irons (2001) reported greater unexplained variability in colony growth than did Danchin *et al.* (1998); the former authors speculated that it might have been driven by much greater interannual variability in the productivity of kittiwake colonies in the North Pacific as compared with Europe. They suggested that poor early-season breeding conditions in a given year might reduce nest-building propensity of newly recruited individuals and thereby contribute to residual variability in their analysis. We explicitly addressed this scenario in our analyses by including interactions between current and past productivity, and yet we were left with even greater residual variability than either previous study [we could not directly compare residual variability between studies (r^2 was not reported in the earlier studies)]. When we used our data to emulate analyses of the two prior studies, we found no effect of past productivity on colony growth at any time lag.

It is noteworthy that the drivers of kittiwake colony dynamics that we identified in the present study would have been "missed" had we adopted the data analysis methods of either of the previous studies. The key difference in the analyses of these three studies was our approach to data standardization. The analysis of Danchin *et al.* (1998) had the least residual variability, despite addressing a finer spatial scale without the benefit of standardization—consistent productivity across the years of their study introduced less "noise," and thus they detected a strong signal of conspecific attraction. In contrast, Suryan & Irons (2001) encountered considerable interannual variability in kittiwake productivity and colony growth rates in PWS and opted to standardize their data across years by ranking productivity and growth data within each year. We, too, standardized variability in productivity and growth across years, but instead of ranking, we computed deviations from annual means. This mode of standardization is more efficient (discards less information) than ranking because it preserves not only the

relative ranking, but the magnitude of the differences between colonies within years. We believe that our strategy for data analysis was better suited to detect signal from background noise than were the strategies employed by the two previous studies (Danchin *et al.* 1998, Suryan & Irons 2001).

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