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COLONY AND POPULATION DYNAMICS OF BLACK-LEGGED KITTIWAKES IN A HETEROGENEOUS ENVIRONMENT

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Abstract.—Black-legged Kittiwakes (*Rissa tridactyla*) nest at 25 distinct colonies located throughout Prince William Sound that range in size from <20 to >7,000 pairs. Dramatic changes have occurred in the distribution of breeding birds among those colonies during the past few decades (1972–1997). Reproductive success data collected since 1985 confirm that individual colonies are habitat patches of varying quality in space and time. Even with such variation, predictability of habitat quality did occur in short- and long-term (≥3 year) intervals as indicated by significant ($P < 0.05$) relationships between current (t) and previous year's ($t-1$, $t-2$, etc.) reproductive success. Those circumstances provided suitable conditions for testing hypotheses concerning dispersal and recruitment strategies of a long-lived species. Breeding birds responded to both short- and long-term cues and, in general, recruited to the most successful colonies. An apparently lower dispersal propensity and the importance of long-term cues was in contrast to a similar study of kittiwake colonies in France (Danchin et al. 1998). Differences between these studies may be attributed to primary factors controlling habitat quality in Prince William Sound operating in the long-term versus the short-term and the magnitude of scale. Colonies in our study covered a much larger geographic area and therefore, factors such as foraging-site faithfulness, mate retention, and natal philopatry may also have influenced dispersal decisions. Nonetheless, recruitment of kittiwakes in Prince William Sound supported the performance-based conspecific attraction hypothesis, which, in turn, led to an ideal free distribution of breeding birds. Those short-term mechanisms for dispersal and recruitment manifested in a long-term redistribution of nesting kittiwakes from poor breeding conditions in southern Prince William Sound to favorable conditions in northern Prince William Sound. Favorable conditions in northern Prince William Sound were apparently supported by stable or increasing populations of juvenile herring. In contrast, reproductive failures and population declines in southern Prince William Sound were concordant with colonies in the Gulf of Alaska where diets were similar, consisting of primarily capelin (*Mallotus villosus*) and Pacific sand lance (*Ammodytes hexapterus*). Those trends corresponded with the influence of Gulf of Alaska waters in southern Prince William Sound and may have been associated with a reported decline in the abundance of key forage species related to a late 1970s regime shift in the Gulf of Alaska. *Received 30 November 1999, accepted 20 January 2001.*

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The distribution and abundance of animal populations during the breeding season is primarily governed by the quality and availability of suitable habitat. Among central-place foraging species such as colonial seabirds, breeding-habitat quality is a function of both the availability of prey within the animal's foraging range from the colony and the suitability of the breeding site. For seabirds, the quality of foraging habitat is dependent on the distribution, abundance, and species composition of prey within the marine environment (Springer et al. 1984, Hunt et al. 1990), whereas the quality of nesting habitat can be affected by factors such as predation (Clode 1993, Anderson and Hodum 1993, Regehr and Montevecchi 1997) and parasites (Duffy 1983, Danchin and Monnat 1992). Inherent fluctuations in these environmental factors can cause dramatic spatial and temporal variation in the quality of seabird breeding habitat. Therefore, if seabirds select breeding sites on the basis of habitat quality, the distribution and size of colonies should vary in time with those factors affecting quality of the foraging conditions and breeding site.

Dramatic fluctuations in breeding-habitat quality, as measured by reproductive success,

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are common among many seabird populations (Springer et al. 1986, Baird 1990, Danchin and Monnat 1992, Crawford and Dyer 1995, Boulinier and Lemel 1996). Those fluctuations occur at different temporal and spatial scales. Temporal scales of reduced reproductive success may be small, lasting only one or two years, but are more commonly large, lasting many years (Barret et al. 1987, Hatch et al. 1993a) or even decades (Lid 1981, Coulson 1983). Similarly, the spatial scale at which reproductive success is depressed can occur among cliffs within a colony (Danchin et al. 1998), or among colonies (Danchin and Monnat 1992) and regions (Coulson 1983, Harris and Wanless 1997). Small temporal- and spatial-scale declines in reproductive success were often attributed to local factors such as predation or parasites (Danchin and Monnat 1992, Danchin et al. 1998) or reduced local availability of prey items (Baird 1990). In contrast, large-scale failures in reproductive success were often attributed to widespread reductions in prey populations (Coulson 1983, Hatch et al. 1993a, Piatt and Anderson 1996) that, in some cases, appeared to be linked to changes in climate regimes affecting vast oceanic regions (Aebischer et al. 1990, Piatt and Anderson 1996, Anderson and Piatt 1999). Predictability of habitat quality therefore would be a function of scale.

Assuming that individuals are free to move and will seek the highest quality habitat as proposed by the ideal free distribution (Fretwell and Lucas 1970), what cues might colonial birds use to decide when and where to move in an attempt to improve their reproductive success? Previous investigators have proposed that birds may gain information about habitat suitability on the basis of not only their own reproductive success (Chabrzyk and Coulson 1976, Burger 1982, Hass 1998), but also by the presence (Smith and Peacock 1990, Reed and Dobson 1993, Forbes and Kaiser 1994) and reproductive success of conspecifics (Boulinier and Danchin 1997, Danchin et al. 1998, Brown et al. 2000). Recent investigations have lead to a proposal of a conspecific attraction mechanism in which reproductive success is used as a parsimonious assessment of breeding-habitat quality (Boulinier and Danchin 1997, Danchin and Wagner 1997). Danchin et al. (1998) provided the first empirical support for the performance-based conspecific-attraction hypothesis by demonstrating that reproductive success of neighboring pairs of the Black-legged Kittiwake (*Rissa tridactyla*), a colonial seabird, was important in determining whether individuals remained faithful to a colony or dispersed to higher quality habitat. An important pattern behind the observed dispersal of kittiwakes to successful colonies was that although there was significant spatial and temporal variability in habitat quality, the success of a given colony was predictable over time, most significantly from year to year. In this case, breeders or prospectors could expect to improve their chances of reproduction in the following year if they moved to a colony that had high reproductive success during the current year.

The performance-based conspecific-attraction hypothesis provides a theoretical mechanism for individuals to select optimum breeding habitat. However, it remains unclear why some individuals persist in what appears to be suboptimal habitat. Brown et al. (1990) proposed several possible explanations for this occurrence in the context of colony size selection: (1) social costs and benefits of grouping lead to certain colony sizes being optimal for each individual (phenotypic considerations); (2) energetic, temporal, or social constraints limit an individual's ability to sample, assess, and accurately predict habitat quality; (3) individuals are forced by others to suboptimal habitat (despotic distribution; Fretwell and Lucas 1970). Additionally, relocating to a new breeding site may be a complicated task for species, such as many seabirds, that exhibit high longevity, delayed maturation, high mate-retention, and small clutch sizes (typically one or two eggs); presumably, life-history adaptations for breeding in an environment that challenges adults to raise one young during most years (Lack 1967, Cairns 1992).

In this paper, we evaluated factors that may have influenced long-term colony and population dynamics of Black-legged Kittiwakes in Prince William Sound, Alaska. We initially tested nesting-habitat suitability and selection among colonies using the general principles and analytical techniques presented by Danchin et al. (1998). We then increased the spatial scale of our analyses to compare trends in reproductive success and population changes between Prince William Sound regions and colo-

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nies compared to those reported in the Gulf of Alaska. Two important differences exist between our study and that of Danchin et al. (1998). First, overall size and geographic range of our study population was an order of magnitude larger. Secondly, the reproductive success of kittiwakes at certain colonies in Prince William Sound and the Pacific Ocean in general are often low and prone to consistent, widespread breeding failures (Hatch et al. 1993a, Irons 1996), whereas colonies studied by Danchin et al. (1998) rarely failed to produce young.

STUDY AREA AND METHODS

Study area.—Prince William Sound is located along the north coast of the Gulf of Alaska. Two oceanic regimes primarily characterize Prince William Sound; glaciated fjords and an inland sea of sufficient size to allow horizontal cyclonic circulation (Niebauer et al. 1994). The main influx of coastal Gulf of Alaska water into Prince William Sound is through Hinchinbrook Entrance and Montague Strait (Niebauer et al. 1994; Fig. 1). The influence of Gulf of Alaska water and its penetration into Prince William Sound, however, varies seasonally and annually (Niebauer et al. 1994, Cooney 1997). In 1997, 25 Black-legged Kittiwake colonies were active and distributed on cliffs of islands and glacial fjords throughout Prince William Sound (for the purposes of this paper, two small, adjacent colonies in Eaglek Bay were counted as one colony; Fig. 1). Sizes of colonies ranged from <20 to >7,000 nesting pairs.

Population size and breeding success.—Counts of the nesting population of Black-legged Kittiwakes in Prince William Sound were first conducted in 1972 by Isleib and Kessel (1973). There was a 13 year hiatus until 1985, when we began collecting annual breeding-population and productivity data at all colonies in Prince William Sound. We determined breeding-population size by counting nests (i.e. breeding pairs), regardless of contents or an attending adult, in June or early July. We later counted nestlings in early August, just prior to fledging, to estimate annual reproductive success (fledglings per pair). Each colony was divided into plots. Counts of individual plots represented a census of each colony and were repeated until there was a 5% or less error in precision. Observers used binoculars (7 to 10×) and conducted counts from a boat (7.6 m).

We used the same data-collection methods at all colonies and in all years of the study. Results, therefore, are quite precise for reporting trends. However, single counts from a boat are not as accurate as repetitive, land-based counts. To increase the accuracy of our results, we calculated correction factors using repetitive counts of land-based study plots (hereafter referred to as *plots*). Plots were located at four colonies from 1993 to 1997 (actual number of years varied with colony). Two sites represented small island colonies with <500 nests and plots encompassed the entire nesting population (i.e. censuses). The other two sites were medium to large (1,800–7,000 nests) fjord colonies. Eleven to 18 plots containing 162 to 430 nests were counted at those colonies. Plots were checked every three days until nestlings were at least 34 days old and ready to fledge. Plots were considered the most accurate estimate of reproductive success. Therefore, a correction factor was simply the average reproductive success determined from plots divided by reproductive success from boat counts. Two correction factors were developed; one for small colonies (50–1,000 nests; $\bar{x} = 1.230$, SD = 0.172, $n = 4$) located on low-lying islands that were easy to view, and a second for medium to large colonies (>1,000 nests; $\bar{x} = 1.311$, SD = 0.253, $n = 7$) located on cliffs that were difficult to view. No correction was applied at extremely small colonies (<50 nests) where all nests were easily observed.

Statistical Analyses.—Statistical analyses were conducted using SAS software (SAS Institute 1990) and results were considered significant at $\alpha = 0.05$. We used logistic regression to test for differences in the probability of raising a chick (binomial data) among colonies and years. Significance of logistic regression was determined using maximum likelihood estimates. We initially tested for differences in linear relationships among groups of dependent variables using a homogeneity of slopes test. When homogeneity of slopes tests were nonsignificant, we proceeded with an analysis of covariance (ANCOVA). In all cases, we tested for interaction of main effects, and final models were selected by removing, one at a time, effects with the greatest P-value above 0.05. When testing for the effect of reproductive success on the annual multiplication rate of each colony, we used within-year rankings of values to account for relative differences among years (rank 1 = greatest value of each parameter in a given year; Brown et al. 2000). The purpose of the ranking was to standardize values between good and poor years, thereby providing a more accurate description of relative patch quality (Brown et al. 2000). We used linear regression in cases where slopes were heterogeneous among groups of dependent variables (in this case, individual regressions were calculated by group) or if there was only one level of the dependent variable. For comparing means, we used analysis of variance (ANOVA) tests.

RESULTS

Spatial and temporal variation in reproductive success.—We first assessed the variation in

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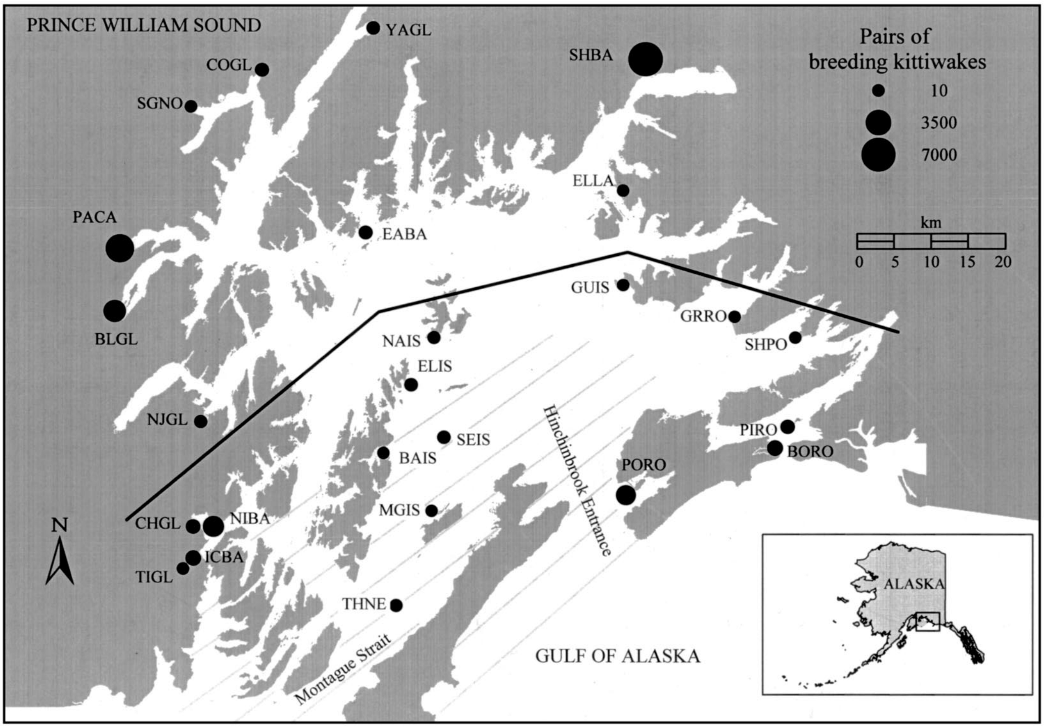

FIG. 1. Location and size (number of pairs in 1997) of Black-legged Kittiwake colonies in Prince William Sound, Alaska. Line depicts division of northern and southern Prince William Sound that was used in some analyses. Northern Prince William Sound comprises those colonies with foraging ranges more likely associated with oceanographic conditions specific to Prince William Sound waters versus Gulf of Alaska (GOA) influences in southern Prince William Sound. Approximate summer influence of Gulf of Alaska waters in Prince William Sound is depicted by diagonal lines. Colonies are identified by a four letter code in this figure and Figure 4 (Bay of Isles, BAIS; Blackstone Glacier, BLGL; Boswell Rocks, BORO; Chenega Glacier, CHGL; Coxe Glacier, COGL; Eaglek Bay, EABA; Eleanor Island, ELIS; Ellamar, ELLA; Gravina Rocks, GRRO; Gull Island, GUIS; Icy Bay, ICBA; Middle Green Island, MGIS; Naked Island, NAIS; Nellie Juan Glacier, NJGL; North Icy Bay, NIBA; Passage Canal, PACA; Pinnacle Rocks, PIRO; Porpoise Rocks, PORO; Seal Island, SEIS; Sheep Point, SHPO; Shoup Bay, SHBA; Surprise Glacier North, SGNO; The Needle, THNE; Tiger Glacier, TIGL; Yale Glacier, YAGL).

breeding-habitat quality by testing the probability (logistic regression) that a pair of kittiwakes would successfully fledge an offspring at different colonies and among years. We detected significant interaction between colony and year ($\chi^2 = 117.49$, df = 302, $P < 0.0001$) and, therefore, analyzed the effects of colony and year separately. The probability of successful reproduction differed among colonies (n = approximately 15,000 to 23,000 pairs per year from 21 to 25 colonies, $\chi^2 > 58.00$, df = 20 and 24, $P < 0.0001$) in every year ($n = 13$). Likewise, the probability of success differed among years (n = approximately 10 to 7,000 pairs per colony during nine to 13 years, $\chi^2 > 4.93$, df = 8 and 12, $P > 0.0264$) within all but 6 colonies (n = approximately 10 to 300 pairs per colony during seven to 13 years, $\chi^2 < 3.27$, df = 6 and 12, $P \geq 0.0706$). Overall, these results support the premise that the probability of reproducing successfully varied among colonies and years.

Given the temporal variation in reproductive success, we next tested whether current breeding conditions could be predicted on the basis of successes or failures of previous years. In testing the predictability of reproductive success among years (ANCOVA), we did not detect a colony effect ($F = 1.42$, df = 21, $P = 0.1136$). We did, however, detect a year effect, as indicated by significant interaction between year and reproductive success in previous years ($t-1$, $t-2$, $t-3$, etc.; $F > 1.91$, df = 12, P

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TABLE 1. Relationship (linear regression) between reproductive success (fledglings per pair) in the current (t) and preceding years (t–1, t–2, t–3, t–4, t–5) as an indicator of predictability of breeding habitat quality. Data are presented as P-value (bold type indicates a significant result, $P < 0.05$) followed in parentheses by n (number of colonies), r^2, and F statistic.

t	*t*–1	*t*–2	*t*–3	*t*–4	*t*–5
1986	**0.0001** (20, 0.53, 22.23)				
1987	**0.0126** (20, 0.27, 7.51)	**0.0417** (20, 0.19, 4.74)			
1988	**0.0215** (19, 0.25, 6.27)	0.1716 (19, 0.10, 2.02)	0.1073 (19, 0.13, 2.86)		
1989	**0.0045** (19.0.35, 10.40)	**0.0277** (20, 0.22, 5.64)	**0.0001** (20, 0.57, 27.00)	**0.0073** (20, 0.31, 8.92)	
1990	**0.0001** (23, 0.60, 34.64)	0.0653 (19, 0.17, 3.83)	0.1478 (20, 0.10, 2.27)	**0.0001** (20, 0.71, 49.45)	**0.0037** (20, 0.35, 10.77)
1991	0.0801 (23, 0.13, 3.35)	**0.0074** (23, 0.27, 8.63)	0.1143 (19, 0.13, 2.74)	**0.0385** (20, 0.20, 4.91)	**0.0392** (20, 0.20, 4.87)
1992	**0.0295** (23, 0.19, 5.39)	0.9826 (23, <0.01, <0.01)	0.9038 (23, <0.01, 0.02)	0.4125 (19, 0.04, 0.70)	0.8568 (20, <0.01, 0.03)
1993	0.8415 (22, <0.01, 0.04)	0.4464 (22, 0.03, 0.60)	**0.0002** (22, 0.47, 19.62)	**0.0378** (22, 0.19, 4.89)	0.3734 (18, 0.04, 0.83)
1994	0.3476 (20, 0.04, 0.92)	0.3032 (23, 0.05, 1.11)	0.6942 (23, 0.01, 0.16)	0.5006 (23, 0.02, 0.47)	0.3163 (23, 0.04, 1.05)
1995	**0.001** (22, 0.50, 22.18)	0.0561 (21, 0.16, 4.09)	0.0836 (22, 0.13, 3.29)	0.2603 (22, 0.06, 1.34)	0.1561 (22, 0.09, 2.16)
1996	**0.0011** (21, 0.40, 14.20)	0.1961 (22, 0.08, 1.78)	**0.0039** (21, 0.33, 10.55)	0.8346 (22, <0.01, 0.05)	**0.0143** (22, 0.24, 7.08)
1997	0.1985 (21, 0.08, 1.76)	**0.465** (22, 0.17, 4.45)	0.5804 (22, 0.01, 0.32)	0.7905 (21, <0.01, 0.07)	0.3682 (22, 0.04, 0.84)

< 0.0314). We, therefore, tested the relationship (linear regression) between current and previous years' reproductive success for each year individually. We found the previous year's ($t-1$) reproductive success to be the most consistent predictor of current success, indicating short-term predictability of breeding habitat quality (Table 1). Additionally, however, for ~30% of the years, predictability remained significant up to five years prior ($t-5$) to the current reproductive success (Table 1). In one year, the relationship was significant using reproductive success at 10 years prior ($r^2 = 0.47$, $F = 15.83$, $P = 0.009$, $n = 19$). Hence, breeding-habitat quality was most predictable in the short-term ($t-1$), and during certain periods the predictability remained consistent for five or more years.

The influence of reproductive success on dispersal and recruitment.—We found a highly significant but rather weak relationship ($r^2 = 0.13$) between the short-term response of annual population multiplication rate and previous year reproductive success (Fig. 2). This relationship may have been weakened by two additional factors affecting the population multiplication rate, reproductive success at $t-5$ years and individual colony (ANCOVA; Table 2). Whereas the short-term factor of reproductive success at $t-1$ had the greatest influence ($P = 0.0001$) on population multiplication rate, long-term factors of reproductive success at $t-5$ and colony site were also important ($P < 0.041$). Therefore, we next evaluated the relationship between long-term population trends and reproductive success using the mean annual population change in pairs per year (the slope of linear regression equations fit to population size estimates between 1985 and 1997 for each colony, $n = 25$ colonies) and long-term (8–13 years) mean reproductive success values for colonies. That analysis did show a significant positive relationship (linear regression) with long-term reproductive success explaining 58% of the variation in long-term population change (Fig. 3).

Regional and long-term trends in reproductive success and population change.—Although the reproductive success of individual colonies varied greatly through time, there were particular colonies that showed consistently greater success relative to other colonies (Fig. 4). The most

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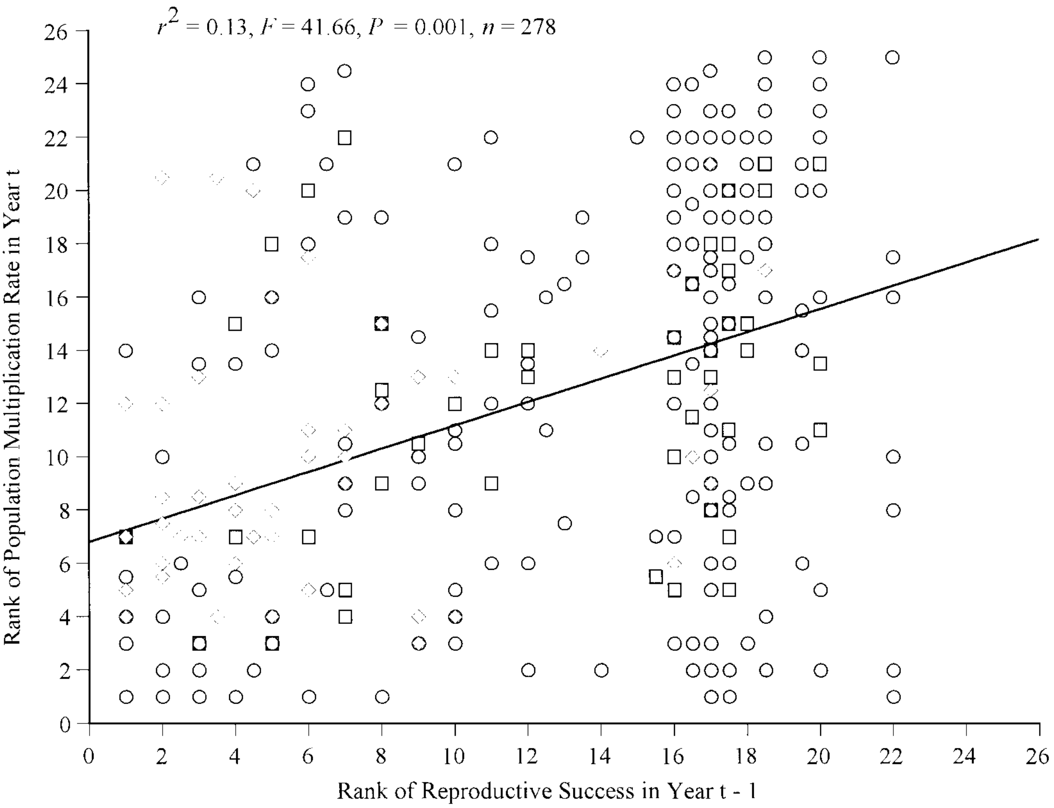

FIG. 2. Relationship between the population multiplication rate of Black-legged Kittiwakes in year t ($N[t]/N[t-1]$) and reproductive success (fledglings per pair) in year $t-1$. Values are plotted as ranks for both x and y axes (with rank 1 equal to the greatest value). The data are separated into three categories based on colony size; <500 pairs (circles), 500–1,499 (squares), ≥1,500 (diamonds).

TABLE 2. Results of ANCOVA tests of variables affecting the annual multiplication rate in population size of breeding kittiwakes. The independent variables included colony, year (*t*), and reproductive success (RS, fledglings per pair) in previous years *t*–1 to *t*–6.

Independent variables	df	*F*	*P*
Colony	23[a]	1.66	0.0425
Year	6[b]	0.09	0.9975
RS in year *t*–1	1	28.78	0.0001
RS in year *t*–2	1	3.58	0.0609
RS in year *t*–3	1	2.62	0.1084
RS in year *t*–4	1	0.83	0.3649
RS in year *t*–5	1	4.27	0.0410
RS in year *t*–6	1	<0.01	0.9762
Model	35	2.88	0.0001

[a] Sufficient data were available for this analysis at 24 of the 25 colonies.

[b] The annual multiplication rate for 1991–1997 (n = 7) were used such that a RS value at *t*–6 was available for each year (the first year of this study was 1985).

successful colonies were large colonies located in the northern region of Prince William Sound. Additional analysis (ANCOVA) confirmed that reproductive success was positively affected by colony size and distance from the Gulf of Alaska (Table 3). To further evaluate these regional trends, we divided colonies throughout Prince William Sound into northern and southern regions as shown in Figure 1. Annual reproductive success was significantly greater (ANOVA; F = 31.54, df = 1, P = 0.0001) in north versus south Prince William Sound (Fig. 5A). In support of the significant ''distance from the Gulf of Alaska'' effect, a comparison with colonies in the Gulf of Alaska indicated that reproductive success in southern Prince William Sound was more similar to colonies in the Gulf of Alaska than colonies in northern Prince William Sound (Fig. 5A). Coincident with those regional differences in reproductive success,

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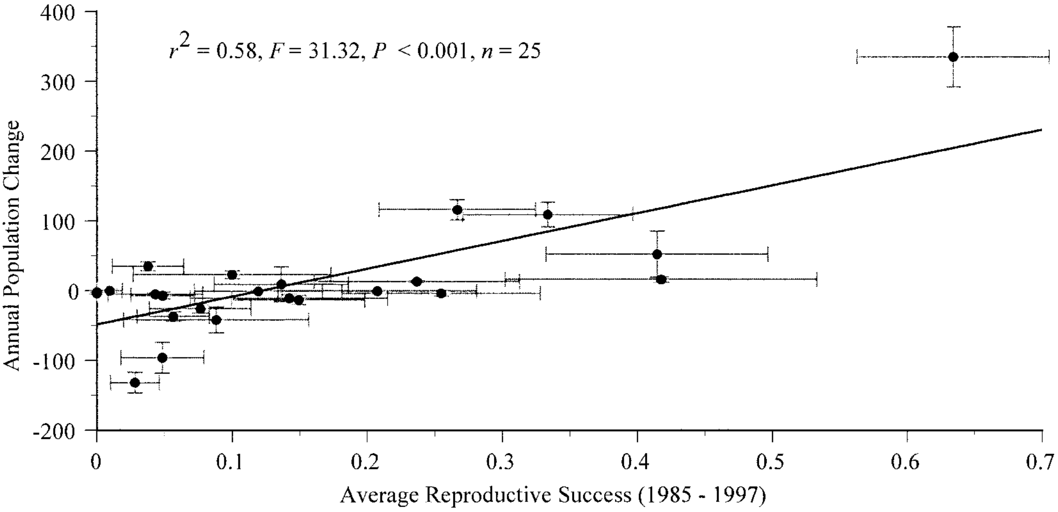

FIG. 3. Relationship (linear regression) between the annual population change ±SE (pairs per year, from linear regression equations fit to annual population size estimates for each colony) and the average reproductive success ±SE (fledglings per pair) for Black-legged Kittiwakes between 1985 and 1997.

population trends were divergent between northern and southern Prince William Sound (Fig. 5B). The population size in the north increased whereas that in the south declined, such that 70% of the kittiwake population nested in the north during the latter years of the study. The majority of the population, however, did not always occur in the northern region. In the mid-1980s the population was distributed equally between north and south, whereas in 1972 the trend was reversed—most of the kittiwake population (70%) was in southern Prince William Sound (Fig. 5B).

DISCUSSION

Spatial and temporal variation and predictability in reproductive success.—Danchin et al. (1998) demonstrated that breeding site selection of Black-legged Kittiwakes in Brittany, France, fit the performance-based conspecific-attraction hypothesis because habitat quality was patchy and patch quality was predictable from one year to the next, although predictability faded after the first year. Similarly, our results demonstrate that the 25 kittiwake colonies located throughout Prince William Sound were habitat patches of varying quality, and habitat quality was predictable from one year to the next. In contrast to the results of Danchin et al. (1998), however, we found that predictability of habitat quality did not always fade with time, but sometimes remained for multiple years. Such differences between our studies probably resulted from the fact that although significant short-term (annual) variation in habitat quality existed among colonies in Prince William Sound, many colonies exhibited consistently high or low reproductive success in the long-term (Fig. 4). Hence, habitat quality for kittiwakes in Prince William Sound showed some long-term predictability, which appeared to influence dispersal and settling decisions of breeding birds.

The influence of reproductive success on dispersal and recruitment.—Danchin et al. (1998) found that high local reproductive success always led to a net recruitment of new breeders the following year and, conversely, low reproductive success led to a net emigration of breeders. In addition, individuals were less likely to emigrate if the reproductive success of neighboring birds was high and more likely to emigrate if success of neighbors was low. Those results provide strong support for a performance-based conspecific attraction mechanism in the formation and growth, as well as extinction, of breeding colonies. Is a similar mechanism responsible for the dynamics of kittiwake colonies in Prince William Sound? We detected a short-term relationship between local reproductive success and population change; how-

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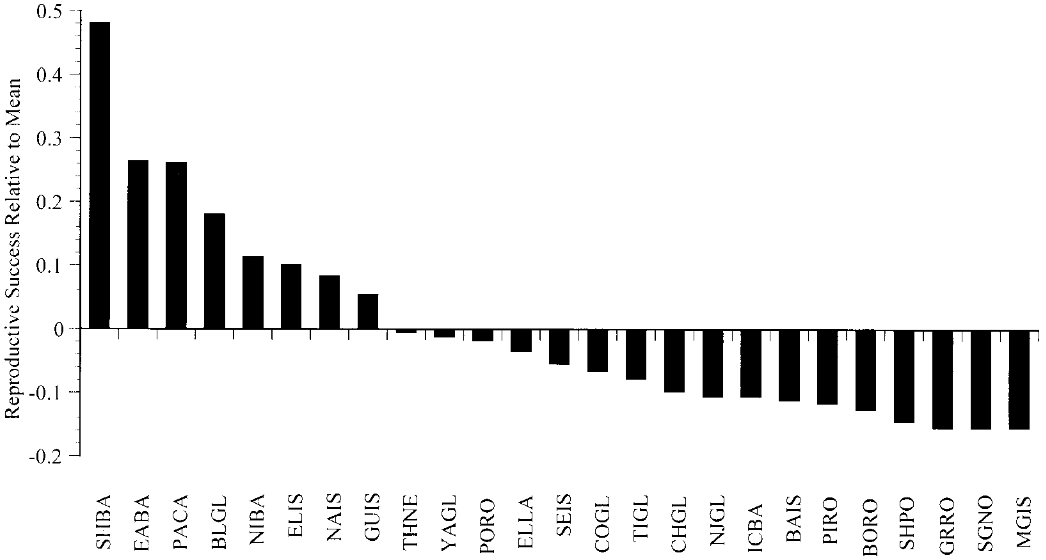

FIG. 4. Reproductive success of individual Black-legged Kittiwake colonies relative to the overall mean (0.15 fledglings per pair) during 1985 to 1997.

ever, we also found that long-term effects of reproductive success at $t-5$ and colony location were important factors. Indeed, we detected a very strong relationship between long-term rate of change in colony size and local reproductive success. Kittiwakes in Prince William Sound were, in fact, recruiting to the most successful colonies, and colonies with poor reproductive success were decreasing in size. These trends could result from colonies operating as closed populations. In fact, the significant effect of reproductive success at $t-5$ (the mean age at first breeding for kittiwakes at Shoup Bay; Suryan et al. 2000b) on colony multiplication rate suggests a potentially high degree of natal philopatry. At the colony level, natal philopatry may be sufficiently high to affect

TABLE 3. Variables associated with high reproductive success (fledglings per pair) of kittiwake colonies (ANCOVA). Variables included year, colony size (number of breeding pairs), and distance from the Gulf of Alaska (GOA; shortest distance over water between colony and nearest boundary between Prince William Sound and the Gulf of Alaska).

Independent variables	df	*F*	*P*
Year	12	1.93	0.0308
Size	1	6.26	0.0129
Distance from GOA	1	9.69	0.0020
Model	14	2.78	0.0007

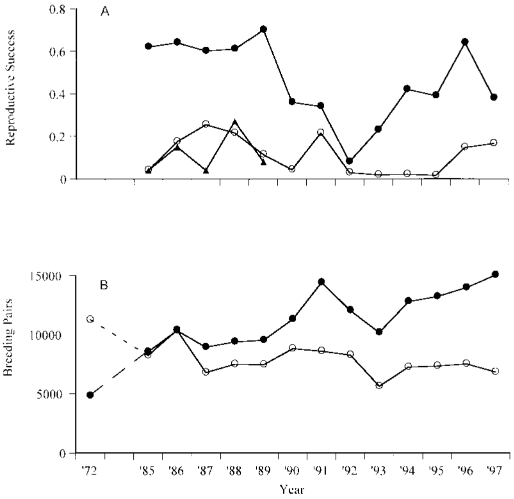

FIG. 5. (A) Reproductive success (fledglings per pair) from Black-legged Kittiwake colonies in north (filled circles) and south (open circles) Prince William Sound (see Fig. 1 for demarcation) during 1985 to 1997 and the Gulf of Alaska during 1985 to 1989 (triangles; Hatch et al. 1993a). (B) The number of breeding pairs in northern and southern Prince William Sound. Population counts of all colonies were first conducted in 1972 then resumed in 1985.

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population multiplication rate; however, we have some evidence to refute the possibility of colonies strictly operating as closed populations. We have observed banded kittiwakes recruit to non-natal colonies and occasional dramatic increases in the size of some colonies could not be explained by local fledgling production alone (Suryan et al. 2000b). Hence, we believe that short-term mechanisms of recruitment described by Danchin et al. (1998), Brown et al. (2000), and others are operating within the kittiwake population in Prince William Sound, but it appears that such mechanisms may be operating on a longer temporal scale. Population change at colonies spread over larger geographic regions such as Prince William Sound may be more dependent upon recruitment of new breeders rather than dispersal of established breeders.

The relatively frequent occurrence of stable or increased colony size following a year of poor reproductive success (Fig. 2) provided circumstantial evidence that emigration of established breeders was not as prevalent, recruitment to failing colonies was more common in Prince William Sound than reported by Danchin et al. (1998), or both. Indeed, strong evidence for site faithfulness of established breeders to the Shoup Bay colony in Prince William Sound was observed by Golet (1999). This is not surprising because Shoup Bay was the most productive colony in Prince William Sound. Strong site-faithfulness by breeding kittiwakes was also observed by Coulson and Nève de Mèvergnies (1992) during their long-term study of a productive colony. Our study, however, is not the first to suggest kittiwakes showed a relatively high degree of site faithfulness to a colony with poor reproductive success. Hatch et al. (1993b) also indicated there was no strong evidence of emigration at a long-time failing colony in the Gulf of Alaska, resighting probability was high (>0.98), and the population decline could be explained by adult mortality alone.

Why would kittiwakes remain faithful or recruit to a failing colony? Aside from simply a paucity of suitable habitat, which may not be that uncommon during certain periods in the Gulf of Alaska, Brown et al. (1990) offered three possible explanations. One explanation was that individuals were limited in their ability to accurately assess and predict habitat quality. We can refute that explanation with some certainty because habitat quality was predictable in the short and long-term, and kittiwakes first bred when four to five years old (Suryan et al. 2000b). Individuals should, therefore, have sufficient cues and time to select good breeding habitat. Instead, we believe it is more likely that individuals nest in suboptimal habitat because they may be inferior competitors for optimal sites (despotic distribution; Fretwell and Lucas 1970), habitat choice represents an individual's phenotypic quality (Brown et al. 1990), or both. Apparent differences in emigration propensity between our study and Danchin et al.'s (1998) may be phenotypic and related to differences in life-history strategies between Atlantic and Pacific Ocean populations. Pacific Black-legged Kittiwakes live longer and typically experience lower annual reproductive success than Atlantic kittiwakes (Hatch et al. 1993b, Golet et al. 1998). These life-history characteristics, in addition to frequent and widespread breeding failures of Pacific kittiwakes (Hatch et al. 1993a, Murphy et al. 1991), may lead to a more conservative dispersal strategy for breeding birds that are already established at a colony compared to the population studied by Danchin et al. (1998) where individuals ''vote with their feet'' by moving to more productive locations.

A confounding issue in comparing emigration propensity between these studies, however, is the magnitude of geographic scale. In Brittany, all colonies were within a 20 km radius, and dispersal was considered among cliffs within colonies as well as among colonies. In contrast, colonies in Prince William Sound covered a 70 km radius and we only considered dispersal among individual colonies; therefore required dispersal distances could range from 6 to140 km. Would Danchin et al. (1998) have found similar results if kittiwakes in Brittany had to disperse over a greater range to find better breeding habitat? If prey availability is the primary factor limiting reproductive success of seabirds (Ashmole 1963, Birkhead and Furness 1985, Barrett et al. 1987, Furness and Monaghan 1987, Monaghan et al. 1992) and successful foraging often requires learned strategies that result in fidelity to particular feeding areas (Becker et al. 1993, Weimerskirch et al. 1993, Irons 1998), then moving to a distant colony may involve the cost of having to learn new for-

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aging strategies. Another cost of moving could involve mate retention. Kittiwakes exhibit a high degree of mate fidelity (Hatch 1993b, Coulson 1972) and successful chick rearing requires proper coordination between adults (Irons 1992). The possibility of losing a compatible mate, therefore, also may influence decisions to relocate to a more distant breeding site. Movements of birds among cliffs or colonies may be more common if individuals can continue to maintain pair bonds and use their traditional foraging areas (or if prey is plentiful thereby eliminating the need for local knowledge of foraging conditions) as may have been the case in Danchin et al.'s (1998) study. For many colonies in Prince William Sound and for Middleton Island (Hatch et al. 1993b), kittiwakes would not be able to use traditional foraging areas if they moved to a more successful colony.

An additional factor that may have weakened the relationship between population multiplication rate and reproductive success at $t-1$ in Prince William Sound compared to Brittany is early-season breeding condition and its effect on breeding attempts. Ainley et al. (1990) noted the potential importance of good early-season prey availability for attracting immigrants and promoting breeding attempts in a rather unsuccessful colony of South Polar Skuas (*Catharacta maccormicki*), a long-lived seabird that exhibits varying degrees of site faithfulness, similar to Black-legged Kittiwakes. In Prince William Sound, kittiwakes could have dispersed or recruited to a colony on the basis of the previous year's success, but failed to build nests because of poor early season prey availability and were, therefore, not included in our population estimates. Because the primary factors affecting kittiwake reproductive success in Brittany were not related to prey and occurred during the nestling period (Danchin et al. 1998), early-season prey abundance may have contributed much less to variation in the number of breeding attempts compared to Prince William Sound.

Factors affecting reproductive success.—We identified size and location of colony as important correlates of reproductive success. Large colonies in northern Prince William Sound were the most successful. That suggests that sufficient prey were available near those colonies to promote high reproductive success. Why small colonies in northern Prince William Sound tended to have poor reproductive success, however, is unexplained. It is unlikely that prey is a limiting factor at some of those small colonies because the foraging ranges of birds from some small and large colonies overlap (cf. Suryan et al. 2000b fig. 1, to Fig. 1 of this article). This second limiting factor is probably avian predators. Bald Eagles (*Haliaeetus leucocephalus*), Common Ravens (*Corvus corax*), and Peregrine Falcons (*Falco peregrinus*) often cause partial or total reproductive failure at kittiwake colonies throughout Prince William Sound (D. Irons and R. Suryan unpubl. data). The relative effect of predation at small to medium-size colonies would, in part (social facilitation may also be important), explain why small colonies often fail when neighboring large colonies succeed. The effect of ''predator swamping'' at large colonies has also been described for other colonial nesting birds (Gochfeld 1982, Wilkinson and English-Loeb 1982).

Breeding conditions in northern Prince William Sound, 1972–1997.—The redistribution of breeding kittiwakes from southern to northern Prince William Sound since 1972 and greater reproductive success in the north since at least 1985 imply that breeding conditions have improved in the north relative to the south on a decadal time scale. Reproductive success at Shoup Bay, the most successful colony in northern Prince William Sound, is most closely associated with the availability of juvenile Pacific herring (*Clupea pallasi*; Golet 1999, Suryan et al. 2000a). Juvenile herring also appear to be the primary prey of kittiwakes at Passage Canal, the second most successful colony in northern Prince William Sound (Suryan et al. 2000b). Juvenile herring are most often located in shallow bays, particularly in northern and southwestern Prince William Sound (Brown et al. 1999, Stokesbury et al. 2000). In addition, herring spawn biomass increased two- to three-fold during the 1980s (Alaska Department of Fish and Game unpubl. data), indicating a large increase in the availability of juvenile herring during that time. Therefore, favorable breeding conditions for kittiwakes in northern relative to southern Prince William Sound over the past couple decades probably resulted from an increase in abundance of their primary prey item.

Breeding conditions in southern Prince William Sound, 1972–1997.—Since 1972, the kittiwake

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population in southern Prince William Sound has declined by 40%, and reproductive success has been consistently poor at large and small colonies during at least the latter part of this period. As in the north, reproductive success of southern colonies is closely associated with the availability of prey (Suryan et al. 2000a,b). However, in contrast to a primarily herring diet in the north, diets of kittiwakes in southern Prince William Sound were frequently dominated by Pacific sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*; Suryan et al. 2000a,b). Diets of kittiwakes in southern Prince William Sound appear to be more similar to those reported for the Gulf of Alaska (Hatch et al. 1993a) than in northern Prince William Sound. This pattern is consistent with the influence of Gulf of Alaska waters near southern colonies (Fig. 1). Moreover, as in southern Prince William Sound, kittiwake colonies in the Gulf of Alaska experienced poor reproductive success during at least the late 1980s and early 1990s (Fig. 5A), which was attributed to reduced prey availability (Hatch et al. 1993a).

Environmental factors affecting prey abundance.—The reduced availability of forage fishes appears to have led to long-term declines in breeding success and population sizes of kittiwakes and other piscivorous seabirds in the Gulf of Alaska (Hatch et al. 1993a, Springer et al. 1993, Piatt and Anderson 1996). Direct causes of reduced forage-fish populations are not always identifiable, but in some cases have been linked to changes in oceanographic conditions (Springer et al. 1984, Harris and Wanless 1990, Hunt et al. 1990). In the Gulf of Alaska, there was an abrupt change from colder than average water temperature (sea surface, 150 m, and 250 m depth) during the 1970s to warmer than average temperature during the 1980s (Royer 1989, 1993). This change in ocean climate was associated with a reorganization of community structure in the Gulf of Alaska (Anderson and Piatt 1999). Community reorganization in the Gulf of Alaska involved a precipitous decline in the standing stock of important forage species (pandalid shrimp and capelin) in favor of increased abundance of predatory species (cod, pollock [Gadidae], and flatfishes [Pleuronectidae]). This change in community organization is thought to be responsible for the dramatic declines in piscivorous bird and mammal species during the same time period (Anderson and Piatt 1999). Fluctuations in upper ocean temperature regularly occur on the decadal scale in the Gulf of Alaska (Favorite and McLain 1973, Xiong and Royer 1984, Royer 1989, Royer 1993); however, it is unknown whether changes in trophic structure also occur during those different ocean regimes. Nonetheless, these broad-scale changes in ocean conditions provide evidence that long-lived marine animals, such as kittiwakes, may face cyclic periods of widespread reproductive failures that may influence dispersal strategies of breeding adults.

Summary.—The population dynamics of kittiwakes in Prince William Sound generally fit the theoretical dispersal and recruitment models of performance-based conspecific attraction (Danchin et al. 1998), a mechanism leading to an ideal free distribution of the breeding population (Fretwell and Lucas 1970). Discrepancies between our study and that of Danchin et al. (1998) were primarily of scale. Whereas Danchin et al. (1998) reported habitat quality was primarily controlled by parasitism and predation that occurred in annual or biennial cycles, habitat quality in Prince William Sound appeared to be governed by primarily prey availability that showed decadal trends despite annual fluctuations. Hence, Danchin et al. (1998) concluded that kittiwakes in Brittany, France, relied on short-term cues in making dispersal and settling decisions at relatively small spatial scales (within colonies and among nearby colonies). We concur that short-term cues likely influenced kittiwake recruitment decisions in Prince William Sound, however, long-term cues were also important and we had some indication that individuals may be less likely to disperse at large spatial scales solely on the basis of short-term cues.

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