

SURVIVAL AND RECRUITMENT DYNAMICS OF BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA* AT AN ALASKAN COLONY

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ABSTRACT

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Most seabirds breed colonially and exhibit considerable site fidelity over the course of their long lifespans. Initial colony selection can therefore have substantial fitness consequences, but factors contributing to recruitment into colonies and subsequent fidelity remain unclear. We used multi-state capture-recapture models to test several hypotheses related to apparent fledgling survival, probability of recruitment to natal colonies, and apparent post-recruitment survival in Black-legged Kittiwakes *Rissa tridactyla*, using data from individuals banded as chicks and subsequently resighted at a colony in south-central Alaska over a 20-year period. Competitive models suggested that apparent fledgling survival declined throughout our study. This decline was likely driven by intrinsic, cohort-specific processes and was not explainable by post-fledging weather or climate conditions. Independent resightings at other colonies suggest the apparent decline may have been at least partially influenced by permanent emigration (natal dispersal), which occurred more frequently when the colony size was large. Recruitment was primarily age-dependent, with no detectable effects from early life experience or from annual changes in four factors: colony size, colony productivity, climate, or average weather conditions. We estimated an average recruitment age of seven years, which is older than typically reported for Atlantic kittiwake populations and which supports a more conservative life history strategy for kittiwakes in the Pacific. Variation in the apparent survival of recruits was cohort-specific and did not correlate with age or annual changes in the factors listed above. Instead, apparent survival of recruits was best explained by colony size during a cohort's second year, suggesting a degree of negative density dependence in post-recruitment survival or fidelity. This information could prove useful to managers deciding how to allocate resources among small, growing colonies and large, well-established colonies.

Key words: Black-legged Kittiwake, *Rissa tridactyla*, colonial breeding, survival, recruitment, capture-mark-recapture analysis, demographic modeling

INTRODUCTION

Colonial breeding is nearly ubiquitous among seabirds (Coulson 2002). The behavior may provide an informational advantage for birds foraging in a patchy and unpredictable environment (Clode 1993, Buckley 1997, but see Rolland *et al.* 1998), but any such advantage comes at a cost that may be proportional to the size of the colony. Dense colonies can attract seabird predators (Coulson 2002, but see Hernandez-Matias *et al.* 2003) that can substantially influence nest-site choice (Martin 1995, Eggers *et al.* 2006) and breeding success (e.g., Regehr & Montevecchi 1997, Whittham & Leonard 1999). Coloniality can also increase intraspecific competition (Tella *et al.* 2001), risk of ectoparasitism (Møller 1987, Mangin *et al.* 2003), and pathogen transmission (Clancy *et al.* 2006).

Patterns of colony recruitment and fidelity likely reflect life history strategies. The age of recruitment greatly influences lifetime reproductive success (Stearns 1992) but is subject to significant tradeoffs with future reproductive potential (e.g., Reed *et al.* 2008, but see Aubry *et al.* 2011). These tradeoffs may favor different strategies in populations under dissimilar constraints, leading to diverse recruitment patterns. Fitness tradeoffs may also determine fidelity to particular colonies or nest sites following recruitment;

there is some relationship between life expectancy and breeding site fidelity for some seabird taxa (Bried & Jouventin 2002). This relationship suggests that a longer lifespan is associated with a “stay and tolerate occasional costs” strategy, whereas a shorter lifespan is linked to greater variability in breeding site choices from year to year. Colony quality (i.e., the probability of reproductive success for a typical colony member) can be quite variable and may depend on factors such as local foraging-ground characteristics (e.g., Paredes *et al.* 2012, Renner *et al.* 2012) and the degree of inter-colony competition (Cairns 1989, Ainley *et al.* 2003, Grémillet *et al.* 2004); thus, breeding colony choice and subsequent fidelity represent high-stakes decisions for individual birds.

In turn, events occurring at colonies undoubtedly influence population dynamics. Nest-site availability at colonies may limit the number of breeders in a population (e.g., Porter & Coulson 1987). Further, species like the Red-legged Kittiwake *Rissa brevirostris* nest in only a few large colonies so that a single breeding site can contain most of the global breeding population (Byrd & Williams 1993). In these cases, colony success can drive larger population dynamics. Dispersal among colonies could also potentially influence regional population dynamics, both through direct effects on production as well as through alterations to genotype distribution and abundance patterns.

Intrinsic processes clearly play a regulatory role within seabird colonies. Density-dependent relationships between colony size and reproductive success are well-documented (e.g., Hunt *et al.* 1986). Such relationships stem at least partially from localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002), which forces birds nesting in large colonies to forage farther from the colony (Ainley *et al.* 2003, Grémillet *et al.* 2004), presumably at greater cost. Density dependence can also influence recruitment (e.g., Crespin *et al.* 2006). The role of density dependence in breeding site fidelity patterns, however, remains somewhat more enigmatic. In Black-legged Kittiwakes *Rissa tridactyla* (“kittiwake” hereafter), breeding patch success (i.e., success within distinct colony subsections) rather than breeder density is the dominant consideration in movement decisions (Danchin *et al.* 1998). Although new, small colonies can be more productive than large, established colonies, birds may be reluctant to form new colonies (Kildaw *et al.* 2005), suggesting that there are hidden costs

associated with new colony formation or that strong fidelity may sometimes represent an evolutionary trap. We know even less about how extrinsic processes shape colony dynamics, though seabird recruitment patterns have been tied to climate patterns (Crespin *et al.* 2006) and predator density (Finney *et al.* 2003)

Our goal here was to explore return and recruitment dynamics of seabird colonies. We focused on three questions: (1) What factors contribute to the return of fledglings to their natal colony? (2) What influences fledgling recruitment to these colonies? (3) Once recruited, what factors contribute to their continued return? We approached these questions with a suite of specific hypotheses related to apparent fledgling survival, recruitment, and apparent recruit survival of kittiwakes at a south-central Alaskan colony (Table 1). We tested these hypotheses with multi-state capture-mark-recapture (CMR) modeling. Our objectives were to determine whether intrinsic or extrinsic processes drive these vital rates and

TABLE 1
Hypotheses explaining apparent fledgling survival, recruitment, and post-recruitment fidelity in Black-legged Kittiwakes from the Shoup Bay colony in Prince William Sound, Alaska, USA, along with variables and their sources used in multi-state capture-recapture models representing each hypothesis

Hypotheses and variables	Source
Vital rate is a function of cohort-specific factors.	
<i>Carryover effects (fledging survival only)</i>	
Herring spawn activity within colony foraging range during: (1) hatch year, (2) previous breeding season (parental effect)	Moffitt 2016; see McKnight (2017) for details
Modeled age-1 herring abundance in PWS region during: (1) hatch year, (2) previous breeding season (parental effect)	HRMT 2014
<i>Early life experience</i>	
Colony size in cohort’s hatch year	US FWS monitoring data, unpubl. data
Colony productivity in cohort’s hatch year	US FWS monitoring data, unpubl. data
Post-fledging environmental conditions	
Mean first winter* PDO index values	JISAO 2016
Mean first winter ENSO 3.4 index values	ESRL 2016a
Mean monthly modeled first fall**, winter, and spring*** winds in northern Gulf of Alaska (58°N, 147°W)	ESRL 2016b
Mean monthly first winter SST in northern GOA (58°N, 147°W)	ESRL 2016c
<i>Prospecting experience</i>	
Natal colony size at cohort ages 2 or 3	US FWS monitoring data, unpubl. data
Natal colony productivity at cohort ages 2 or 3	US FWS monitoring data, unpubl. data
Vital rate is a function of time-varying factors.	
Natal colony size in current, previous year	US FWS monitoring data, unpubl. data
Natal colony productivity in previous year	US FWS monitoring data, unpubl. data
Environmental conditions in current, previous year (listed above)	JISAO 2016, University of Washington unpubl. data
Vital rate is a function of age (recruitment and post-recruitment fidelity only).	US FWS monitoring data, unpubl. data
Vital rate is constant.	

* Averaged monthly data from November through February prior to the breeding season

** Averaged monthly data from September and October

*** Averaged monthly data from March through April prior to the breeding season

to evaluate evidence for a more conservative life history strategy in Pacific vs. Atlantic kittiwakes, as has been suggested by other authors (Hatch *et al.* 1993, Golet *et al.* 2004).

METHODS

Ethics statement

Seabird monitoring activities in 2008 were conducted under US Fish and Wildlife Service Region 7 IACUC #2008007.

Focal species

The kittiwake provides an ideal case study to investigate questions regarding natal colony recruitment and fidelity. As such, it has been the focus of numerous studies on breeding habitat selection in marine birds (e.g., Cadiou 1999, Ainley *et al.* 2003, Kildaw *et al.* 2005, Coulson & Coulson 2008). The kittiwake is a small, long-lived, piscivorous gull with a northern circumpolar distribution and a global population size of 17–18 million (Delany & Scott 2006). Kittiwakes are colonial cliff-nesters that rear one, two, or (rarely) three young per breeding season. As in many seabird species, parents share incubation and chick-rearing duties equally (Coulson & Wooller 1984). When breeding patches are successful, both mate (Coulson & Thomas 1985) and nest-site fidelity are high (Danchin *et al.* 1998, Boulinier *et al.* 2008); this facilitates long-term CMR studies. Kittiwake numbers within our study region of Prince William Sound (PWS) fluctuate dramatically: the breeding-season population size ranged from 28 000 to 110 000 from 1989 to 2007 (McKnight *et al.* 2008). Colony occupancy and productivity in PWS are also dynamic—more than 40 colonies were monitored from 1985 to 2012 and during this period, 14 new colonies were initiated while 16 colonies were abandoned (DBI unpubl. data).

Study area

The Shoup Bay kittiwake colony is in northeastern PWS, Alaska (61°10'N, 146°35'W; Fig. 1). Shoup Bay is a small fjord that adjoins the larger Port Valdez fjord with a tidewater glacier that terminates at Shoup Bay's western end. The fjord connects to Port Valdez via

a reversing tidal river that is 0.8 km in length. The kittiwake colony is located primarily on the south-facing side of a rocky island that is 0.4 km in length and 100 m from the mainland. The colony formed sometime after the island emerged from the receding Shoup glacier, which still covered the nesting cliffs in the early 1960s; the colony was well-established by the 1980s and peaked at ~20 000 individual breeders in the early 2000s. Through the early 2000s, the fjord was frequently filled with large icebergs that had calved from the glacier; by the late 2000s, the glacier retreated mostly onto land. Predators at the colony are predominantly avian and include Bald Eagles *Haliaeetus leucocephalus*, Peregrine Falcons *Falco peregrinus*, Northern Ravens *Corvus corax*, Northwestern Crows *Corvus caurinus*, and Black-billed Magpies *Pica hudsonia*. Occasional mammalian predators include American mink *Neovison vison* and wolverine *Gulo gulo*.

Field data collection

Capture/resight sampling

In 1979 and annually from 1988 to 2008, we banded 369 ± 74 (95 % confidence interval (CI)) 12- to 32-day-old kittiwake chicks at the Shoup Bay colony by temporarily removing them from nests by hand. We individually marked chicks with unique color band combinations. From 1992 to 2010, four to eight observers read color bands using binoculars and 60× spotting scopes (hereafter referred to as resighting) during mornings and evenings in May, when breeders were actively building nests. Major breeding patches ($n = 10$) were delineated by cliff features, and birds were resighted within each patch an average of 9.8 ± 0.35 (95 % CI) times within each nesting season.

We evaluated individual breeding status based on the number of times a bird was recorded at a specific nest location. Holding a nest site is the essential condition that affects kittiwake survival, irrespective of reproductive success (Aubry *et al.* 2011), and thus provides a reasonable representation of breeding intent in our survival models. Birds seen at a particular nest site three or more times were considered to be probable breeders ("breeders" hereafter). Birds seen fewer than three times on a single site were noted as probable non-breeders ("non-breeders" hereafter), i.e., they were present but not engaged in intensive nesting behavior. While predation was substantial during some years, the majority of predation affected nestlings and occurred after the period during which we resighted marked individuals at the colony; thus, predation did not appreciably influence breeding status assignments by removing banded breeders prior to their third sighting.

We constructed encounter histories for each individual based on annually summarized encounters and breeding state designations. Each year represented a single occasion in which the individual either was or was not encountered. If encountered, breeding state was designated in the encounter history according to the description above.

Breeding population size and productivity

We included metrics describing colony size and productivity in our modeling to assess the role of intrinsic colony processes in determining vital rate patterns. From 1985 to 2012, we visited the Shoup Bay kittiwake colony twice annually as part of a larger effort to document breeding effort and productivity at all PWS kittiwake colonies. In late May/early June, when birds had begun incubation, we used binoculars to count all active nests (i.e., those attended by

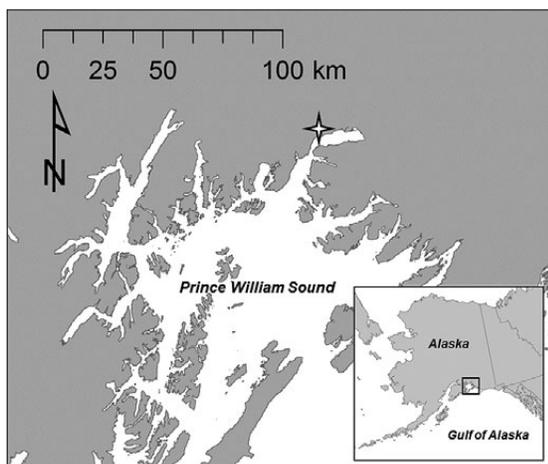


Fig. 1. Location (indicated by star) of the Shoup Bay kittiwake colony in Prince William Sound, Alaska, USA. Inset map shows the location of Prince William Sound within Alaska.

at least one bird) on all faces of the colony from an eight-meter fiberglass boat floating 100–200 m from the cliff faces. We returned in late July/early August each year and used the same method to count chicks and fledglings at a stage of development when most chicks were large enough to be easily visible in the nests. We also included several measures of prey availability: herring spawn activity within foraging range (40 km) of the colony (Moffitt 2016; see McKnight 2017 for details) and modeled age-1 herring abundance for the PWS region (HRMT 2014).

Environmental variables

In addition to the metrics described above for breeding kittiwakes, we also considered extrinsic factors that might affect kittiwake survival and recruitment. We suspected that winter conditions were important, although given the Shoup Bay kittiwakes' diverse migratory strategies, choosing a single metric to represent winter posed a challenge. Because kittiwakes migrate in some years but remain in the northern Gulf of Alaska in others (McKnight *et al.* 2011), we hypothesized that birds may face a tradeoff between costs associated with migration and constraints associated with reduced winter day lengths in the high latitudes. Migratory decisions may therefore be made based on local conditions affecting forage efficiency—specifically, wind and sea surface temperature (SST). We therefore used several metrics to represent both winter and spring weather conditions on the northern coastal shelf of the Gulf of Alaska. First, we calculated the mean winter (November–February) Pacific Decadal Oscillation (PDO) index, which is based on the first principal component of monthly SST anomalies in the North Pacific (i.e., north of 20°N) (JISAO 2016). We similarly computed the mean winter El Niño Southern Oscillation (ENSO) index based on a five-month running mean of SST anomalies in the region between 05°N and 05°S and between 170°W and 120°W (ESRL 2016a). Both the PDO and ENSO indices are known to correlate with winter weather patterns in Alaska (Papineau 2001). For an index of fall (September–October), winter (November–February), and spring (March–April) weather conditions on the northern coastal shelf of the Gulf of Alaska, we extracted the monthly modeled wind magnitudes for 59°N, 147°W (ESRL 2016b) and used the average value for each period. We also averaged monthly SSTs for the same region of the Gulf of Alaska from the National Oceanic and Atmospheric Administration's optimally interpolated SST data (ESRL 2016c). We used Z-standardization to center and scale all continuous time- and cohort-varying covariates prior to modeling.

Data analysis

Multi-state modeling

We used multi-state Cormack-Jolly-Seber models (Nichols & Kendall 1995) to test hypotheses about factors governing apparent survival of fledglings, recruitment, and apparent survival of recruits (Table 1) in a kittiwake population. Multi-state modeling allowed us to simultaneously estimate the resighting probability (p), the probability of transitioning between pre-defined states (ψ), and the apparent survival probability (ϕ). We acknowledged that this population was not completely closed and that permanent emigration was possible during our study. Thus, we interpret survival estimates as apparent survival, which reflects a combination of true mortality and permanent emigration from the study colony (i.e., true survival is likely underestimated).

Because the sequence of parameter modeling can affect model selection (e.g., Lawson *et al.* 2017, but see Hadley *et al.* 2007), we followed a consistent modeling scheme whereby we first selected the best structure for “nuisance” parameters before applying those structures in our hypothesis testing. We conducted our analyses in three stages to determine the most parsimonious model structure for p , ψ , and ϕ . In the first stage, we evaluated a set of resighting probability models while allowing a fully general model structure for survival and transition probabilities. During the second stage of analysis, we applied the best resighting structure to a candidate set of transition models with fully state- and time-dependent survival structures to test hypotheses regarding transition probabilities. Finally, in stage three, we used the best resighting and transition probability structures to build candidate models representing hypotheses addressing apparent survival.

Using this general framework, we employed a two-phase approach within each stage of the analysis to evaluate fundamentally different sources of variation in each vital rate. During phase I, we evaluated general sources of variation for each parameter (p , ψ , ϕ) by fitting five alternative models: constant (intercept only), year (as a categorical variable), age or juvenile vs. adult age classes (i.e., all records for that age or age class combined across years), cohort (determined by hatch year), and breeding state, along with any additive and interactive combinations of these factors that were appropriate to the parameter. We further considered that year, cohort, and age effects may interact with breeding state, and that year and cohort may interact with age class. For phase II, we used the best-supported model structure from phase I; however, for the more general model components that were supported in phase I, we substituted explanatory covariates that were consistent with our sub-hypotheses and associated with the best-supported structure (Table 1). For example, if year was supported as a fixed effect in phase I of hypothesis testing, then during phase II, we substituted covariates that varied annually (e.g., colony size) and could provide a biological mechanism for the annual variation supported in phase I.

We performed all demographic modeling using the “RMark” package (Laake 2013) in R (R Core Team 2016) to interface with MARK (White & Burnham 1999). We adjusted Akaike's Information Criterion (AIC) values to the corrected version (AIC_c), which accounts for small effective sample sizes. We assessed goodness-of-fit of the most general model (with p , ψ , and ϕ structures all set to full state- and time-dependence) using the median \hat{c} test in MARK, and we used the test results to calculate a variance inflation factor, adjusting AIC_c values to quasi-AIC_c values (QAIC_c) for the entire model set, as appropriate. We used QAIC_c model selection procedures to evaluate support for competitive models (Burnham & Anderson 1998). We considered any model structure to be competitive if it successfully converged, if the 85 % confidence intervals of beta estimates associated with the model's core hypothesis did not overlap 0.0 (Arnold 2010), and if QAIC_c scores fell within 2.0 units of the best model from the candidate set. We considered a hypothesis to be supported over alternate hypotheses if its model Akaike weight was greater than all other models combined. For models with full annual time-varying structure in both p and ϕ or ψ , we avoided interpretation of parameter estimates for the final time period, during which survival/transition and resight probabilities are confounded in the model likelihood. We report 95 % confidence intervals for real parameter estimates as the 2.5 (lower) and 97.5 (upper) percentiles of bootstrapped ranges (10000 iterations), calculated using the logit back-transformed beta coefficients. Finally, we performed a sensitivity analysis on each model set to determine the effect

of different variance inflation factors on top model support. This was done by recalculating and comparing each QAIC_c value using variance inflation factors of 1.0, 1.5, 2.0, 2.5, and 3.0.

Model construction

We performed two separate analyses (detailed in the sections below) on two different variations of the data set: 1) an analysis to test hypotheses regarding fledgling survival and recruitment using all records; and 2) an analysis to test hypotheses regarding apparent post-recruitment survival (a combination of true survival and fidelity), which omitted individuals that failed to recruit.

1. Apparent fledgling survival and recruitment

To test hypotheses regarding apparent fledgling survival and recruitment (i.e., permanent transition from the pre-breeder state to the breeder state), we constructed models with data from chicks banded in 1991 and 1995–2006 ($n = 5090$). Using 2006 as our end year ensured that all birds were at least four years of age during the final year of resighting; 90 % of returning chicks from the 1991–1999 cohorts ($n = 1329$) had returned at least once by age four. In every year a bird was detected, we assigned it to one of two states: “pre-recruits”, which included chicks and any birds present but not documented as breeders in the current or previous years, or “recruits”, which included birds classified as breeding during the current or previous year. To facilitate modeling, we simulated the release of all birds as age-1 pre-recruits to eliminate the mathematical gap between the banding year (age 0) and the earliest possible sighting for most birds (age 2); age-1 returns were negligible ($n = 8$ of 5090 individuals). Cohort-specific covariates (e.g., colony size during the hatch year) were included as individual covariates with a common value applied to all members of a cohort. In addition to investigating age effects (e.g., one year old, two years old, etc.), we also assigned birds to one of two age classes in each year (juvenile = 0–2 years; adult = 3+ years), acknowledging that the transition between age classes occurred before most individuals returned to the colony for the first time. This distinction allowed us to calculate separate parameter estimates for fledglings in their first two years of life. The juvenile survival estimates thereby represented the cumulative probability of apparent survival associated with the first two years combined, and detection probabilities from juvenile birds reflected the joint probability of detection and first return to the colony, assuming survival. We fixed the following two parameters to zero to improve estimation: (1) the probability of transitioning from a breeder to a pre-recruit, and (2) survival and resighting probabilities for missing cohorts (i.e., 1992–1994 when intensive chick banding did not occur). Because 95 % of all recruiting individuals had recruited by age 12, we also fixed the probability of transitioning from pre-recruit to a recruit to 0.0 after age 12. The transition from pre-recruit to recruit was calculated via maximum likelihood estimation in MARK, and the probability of remaining within a state was calculated via subtraction.

To calculate the average recruitment age, we first used estimates from the best-supported model to calculate a cumulative transition probability, γ , which gave the probability that a bird would recruit to the breeding population at or before age j , according to

$$\gamma_j = \sum_{i=1}^j [\psi_j * \prod_{i=1}^{j-1} (1 - \psi_i)]$$

where γ is the probability that a bird would recruit to the breeding population at or before age j . The calculated value γ is also the probability that recruitment at a given age was conditional both

on not recruiting during any prior year and on survival. The age at which cumulative recruitment probability first surpasses 0.5 represents the average recruitment age, ω , of the sampled cohorts.

We also assessed the probability of survival to the average recruitment age. To do this, we used the coefficients from the best-supported model to calculate the cumulative probability, η , of pre-recruits surviving to the average age of recruitment, ω , for each cohort k , according to

$$\eta_k = \prod_{A=0}^{\omega_k} \varphi_A$$

We then calculated the geometric mean of these cumulative probabilities over all cohorts that reached the mean recruitment age during the study in order to approximate the mean probability of recruitment.

2. Apparent post-recruitment survival

We used resighting data from only the 1991 and 1995–2004 cohorts to test hypotheses regarding apparent post-recruitment survival (a combined measure of survival and fidelity); members of later cohorts were less likely to have recruited by the time resighting ceased in 2010. Further, we were interested solely in factors associated with apparent survival following recruitment to the colony (i.e., not natal fidelity *per se*), so we included only those individuals that eventually recruited to the Shoup Bay colony ($n = 997$) in the modeled data set. In this separate apparent-survival analysis that included only successful recruits, we identified three breeding states: “pre-recruit” (as described above), “breeder” (observed three times on the same nest site), and “non-breeder” (a former breeder observed fewer than three times on a single nest site). We released all individuals as two-year-olds to facilitate estimation, for reasons described above. Because the modeled data set included only eventual recruits, we lost little information in eliminating records of pre-recruit returns at age 2, as the number of reported two-year-old breeders was negligible ($n = 5$ of 997 individuals). Parameter estimates for the first modeled time period therefore represented cumulative probabilities across a three-year period. Once again, we assigned each bird sighting as either a juvenile or adult, as defined previously. This distinction allowed us to separate the recruitment probability of three-year-olds from that of older birds. As in the fledgling survival analysis, we fixed several parameters to improve model estimation: we fixed all impossible transition probabilities to 0.0 (e.g., non-breeder to pre-recruit), all survival probabilities of pre-recruits to 1.0, and all survival and resight probabilities for missing cohorts to 0.0. Transition probabilities between states were determined via maximum likelihood estimation, while the probabilities of remaining within a state were determined via subtraction.

Assessing permanent emigration

Our data did not allow us to estimate post-recruitment fidelity directly. However, we conducted a cursory assessment of permanent emigration, using independent resighting work from two time periods within the larger study period to provide context for apparent survival estimates. To this end, we used ancillary resighting data, which were collected using comparable methods, from other PWS colonies (1997–1999; DBI unpubl. data) and from the new Valdez pipeline terminal dock colony (2007; dock is less than 10 km from the Shoup Bay colony) to assess the relative degree of emigration in the 1990s vs. the 2000s. We calculated the proportion of each cohort with

members aged 5–11 that were observed nesting outside of Shoup Bay over a three-year period (1997–1999) and at the pipeline terminal colony in 2007. We chose age 11 as the cutoff because annual banding began in 1988 at the Shoup Bay colony; birds in this cohort would have been 11 years old in 1999. We then calculated the percentage of the pipeline terminal group that had never been detected at the Shoup Bay colony; a similar calculation was not possible for the 1997–1999 group, as some members carried only cohort-specific marks and were not individually distinguishable from other members of their cohorts.

RESULTS

Colony size and productivity

The size of the Shoup Bay colony ranged from 8400–19000 actively breeding kittiwakes during this study. It peaked in 2002 and declined to 14400 active breeders by 2010. Productivity (defined as the number of chicks per nest) varied widely during the same period, from a maximum of 0.62 in 1996 to a minimum of 0.00 in 2009, with a general decline over time (Fig. 2).

Apparent fledgling survival and recruitment

Of chicks banded in the 1991 and the 1995–2006 cohorts, 35 % ± 6 % (95 % CI) of each cohort was documented at least once at the Shoup Bay colony in the years following fledging, and 20 % ± 6 % of the 1991 and the 1995–2004 cohorts (i.e., birds that were at least age 6 during the last year of resighting) were detected breeding at their natal colony.

Apparent fledgling survival appeared to be driven by factors shared among members of a cohort. After we adjusted all AIC_c to QAIC_c with the estimated variance inflation factor $\hat{c} = 2.13$, the best-supported model structure for resighting probability included the additive effects of breeding state and age class ($w_i > 0.99$; Table S1 in Appendix 1, available on the website), and the best-performing model structure for transition probability contained only an age effect ($w_i > 0.99$; Table 2). The top-ranked general model of apparent fledgling survival included an interaction between age class and cohort ($w_i > 0.99$; Table S2), indicating that apparent fledgling survival is influenced by events that affect cohorts independently (e.g., events occurring during a sensitive age or immediately after the hatch year). Hypotheses involving time-varying factors were not supported; apparent fledgling survival was

not closely linked to annual variations in colony characteristics or environmental conditions. Of the models reflecting our specific cohort-based hypotheses, the top-ranked model included a negative effect of hatch-year population size ($w_i > 0.99$; Table 3). However, none of the models reflecting specific cohort-based hypotheses outperformed the general cohort structure. Apparent survival of fledglings generally declined over cohorts from a peak of 0.81 (95 % CI 0.73–0.87) for the 1995 cohort down to 0.23 (95 % CI 0.10–0.47) for the 2005 cohort. However, once individuals reached adulthood, apparent survival was variable, with no obvious trend and with a mean annual survival of 0.82 (0.77–0.87; Fig. 3). The cumulative probability of survival to age 7 (average modeled recruitment age) for the 1991 and 1995–2003 cohorts (i.e., birds were at least seven years of age during the final resighting effort in 2010) was 0.23 (95 % CI 0.17–0.31).

The resight probability was 0.53 (95 % CI = 0.47–0.57) for pre-recruitment adults and 0.81 (0.77–0.83) for post-recruitment adults, whereas the resight probability for juveniles was 0.09 (0.08–0.10) for pre-recruits and 0.27 (0.24–0.29) for two-year-old breeders. The probability of recruitment peaked between ages 5 and 6 at 0.21 (0.17–0.25), then declined until age 10, when the cumulative probability of recruitment had reached 0.69 (Fig. 4). The average recruitment age was seven years old.

Our sensitivity analysis on the variance inflation factor revealed no

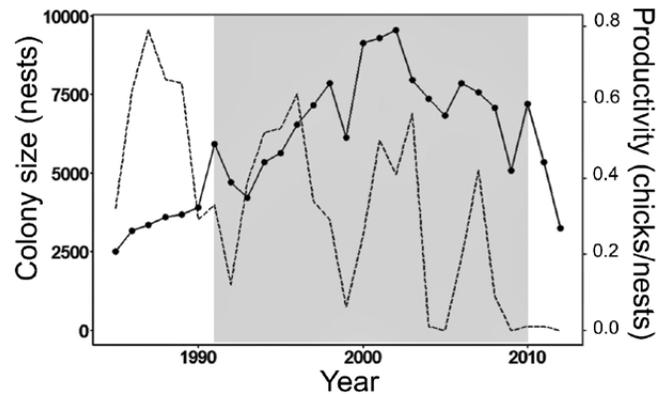


Fig. 2. Total nests (left axis; solid line) and productivity measured as total chicks divided by total nests (right axis; dotted line) at the Shoup Bay kittiwake colony in Prince William Sound, Alaska, 1985–2012. Gray box denotes the time period assessed in the present study

TABLE 2

Fledgling survival and recruitment modeling: recruitment probability. Performance of competing models exploring the best general structure for multi-state models estimating the probability of state transition (ψ), where states were pre- vs. post-recruitment, for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound, Alaska, 1991–2008

Model*	Hypothesis	$\Delta QAIC_c$	w_i	K
Recruitment probability varies ...				
$\Psi_{(age)}$... among ages only.	0.00	> 0.99	51
$\Psi_{(time)}$... among years only.	160.24	< 0.01	57
$\Psi_{(cohort)}$... among cohorts only.	230.67	< 0.01	57
$\Psi_{(constant)}$	Recruitment probability does not vary.	293.75	< 0.01	40

* Model structure for resight probability was set to the best competing structure (recruitment state + age class) and survival was set to general state and time dependence (by year). Model weights are denoted by w_i and K represents the number of estimable parameters in each model, adjusted for any parameters that were fixed during analysis. $\Delta QAIC_c$ values reflect ΔAIC_c values adjusted according to a median \hat{c} estimate of 2.13.

change in model selection outcomes for variance inflation factors between 1.5 and 3.0.

Apparent post-recruitment survival

Factors shared among members of a cohort also drove apparent post-recruitment survival, which incorporates both true survival and colony fidelity. After we adjusted all AIC_c to $QAIC_c$ based on

a variance inflation factor of $\hat{c} = 1.76$, the best-supported model structure for resighting probability included the additive effects of breeding state and time ($w_i > 0.99$; Table S3). The best-performing model structure for transition probability contained the interactive effects of breeding state and year ($w_i > 0.99$; Table S4). The top-ranked variability structure in apparent survival included the additive effects of breeding state and cohort ($w_i = 0.94$; Table S5), which supports our hypothesis that post-recruitment apparent

TABLE 3
Fledgling survival and recruitment modeling: apparent survival probability. Performance of competing multi-state models testing hypotheses to explain the observed cohort effect on apparent survival (φ ; survival + fidelity) of Black-legged Kittiwakes banded as chicks at the Shoup Bay colony, Prince William Sound (PWS), Alaska, 1991–2008, with the top-ranked general model (italicized) included for reference

Model ^a	Hypothesis	$\Delta QAIC_c$	w_i	K
Apparent survival varies ...				
$\varphi_{(age\ class * cohort)}$... between age classes and among cohorts, with a different cohort pattern between age classes.	-78.47	n/a	41
$\varphi_{(age\ class * HY\ pop\ size)}$... between age classes and by hatch year colony size, with a different colony size pattern between age classes.	0.00	> 0.99	19
$\varphi_{(age\ class * pre-HY\ herring\ spawn)}$... between age classes and by herring spawn activity within colony foraging range in breeding season prior to hatch, with a different herring spawn pattern between age classes (parental effect).	68.40	< 0.01	19
$\varphi_{(age\ class * HY\ herring\ spawn)}$... between age classes and by herring spawn activity within colony foraging range during hatch season, with a different herring spawn pattern between age classes.	68.40	< 0.01	19
$\varphi_{(age\ class * age\ 2\ pop\ size)}$... between age classes and by colony size during the cohort's second year, with a different colony size pattern between age classes.	73.12	< 0.01	19
$\varphi_{(age\ class * HY\ age\ 1\ herring)}$... between age classes and by PWS-modeled age-1 herring abundance in hatch year, with a different herring pattern between age classes (parental effect).	79.75	< 0.01	19
$\varphi_{(age\ class * pre-HY\ age\ 1\ herring)}$... between age classes and by PWS-modeled age-1 herring abundance in breeding season prior to hatch, with a different herring pattern between age classes (parental effect).	79.76	< 0.01	19
$\varphi_{(age\ class * age\ 3\ pop\ size)}$... between age classes and by colony size during the cohort's third year, with a different colony size pattern between age classes.	87.70	< 0.01	19
$\varphi_{(age\ class * age\ 3\ prod)}$... between age classes and by colony productivity during the cohort's third year, with a different productivity pattern between age classes.	98.22	< 0.01	19
$\varphi_{(age\ class * AHY\ spring\ winds)}$... between age classes and average spring winds in the northern GOA following the cohort's first winter, with a different wind pattern between age classes.	105.08	< 0.01	19
$\varphi_{(age\ class * HY\ prod)}$... between age classes and by colony productivity during the cohort's hatch year, with a different productivity pattern between age classes.	115.61	< 0.01	19
$\varphi_{(age\ class * first\ winter\ winds)}$... between age classes and by average hatch year winter winds in the northern GOA, with a different wind pattern between age classes.	126.79	< 0.01	19
$\varphi_{(age\ class * AHY\ PDO)}$... between age classes and by the PDO value from the cohort's first winter, with a different PDO pattern between age classes.	128.37	< 0.01	19
$\varphi_{(age\ class * age\ 2\ prod)}$... between age classes and by colony productivity during the cohort's second year, with a different productivity pattern between age classes.	129.63	< 0.01	19
$\varphi_{(age\ class * HY\ PDO)}$... between age classes and by the PDO value from the winter prior to the cohort's hatch, with a different PDO pattern between age classes.	133.52	< 0.01	19
$\varphi_{(age\ class * HY\ fall\ winds)}$... between age classes and by average hatch year fall winds in the northern GOA, with a different wind pattern between age classes.	134.11	< 0.01	19
$\varphi_{(age\ class * first\ winter\ SST)}$... between age classes and by average hatch year winter SST in the northern GOA, with a different SST pattern between age classes.	136.90	< 0.01	19

^a Asterisks denote interactive models, which include both additive and interactive effects. Model structure for resight probability was set to the best-competing structure (recruitment state + age class, where the states were pre- vs. post-recruitment), and transition model structure was set to the best-competing structure from transition modeling (age). For further explanation of column headings, see footnote in Table 2.

survival is driven by factors shared among a cohort. The analysis did not support hypotheses that apparent survival was a function of age or temporal variation. Of the models reflecting specific cohort-based hypotheses, the top-ranked model included a term for the colony size during the cohort's second year ($w_i = 0.74$; Table 4). Models containing a term for population size for the cohort's second or third year, by which time 63 % and 85 %, respectively, of all individuals that eventually returned had been detected at the colony, had a combined Akaike weight of 0.99.

Pre-recruit resight probabilities were lower and spanned a wider range (0.45–0.80) than those of post-recruits (0.70–0.94). Non-breeders had greater resight probabilities than breeders, likely owing to the more stringent observation criteria for breeders, though the confidence intervals overlapped substantially. Juvenile transition probabilities (0.11–0.55) were greater and more variable than those of adults (0.02–0.23). The colony size at age 2 had a negative influence on a cohort's apparent post-recruitment survival (Fig. 5).

Our sensitivity analysis on the variance inflation factor revealed no change in model selection outcomes for variance inflation factors between 1.0 and 2.5.

Emigration assessment

At least some part of the decline in apparent survival at the Shoup Bay colony was likely caused by declining fidelity, as dispersal appears to have increased since the 1990s, including among established breeders. Only $1.6\% \pm 1.5\%$ (95 % CI) of the chicks banded in the 1988–1994 Shoup Bay colony cohorts were detected nesting at any other PWS colony between 1997 and 1999. In contrast, our single visit to the Valdez pipeline terminal colony in 2007 revealed that at least $3.1\% \pm 0.7\%$ (95 % CI) of the 1996–2003 Shoup Bay cohorts had established nests at that colony. Further, 38 % of these nesters had never been resighted at the Shoup Bay colony following banding, whereas 11 % had previously bred there; the remainder had been observed roosting at the Shoup Bay colony.

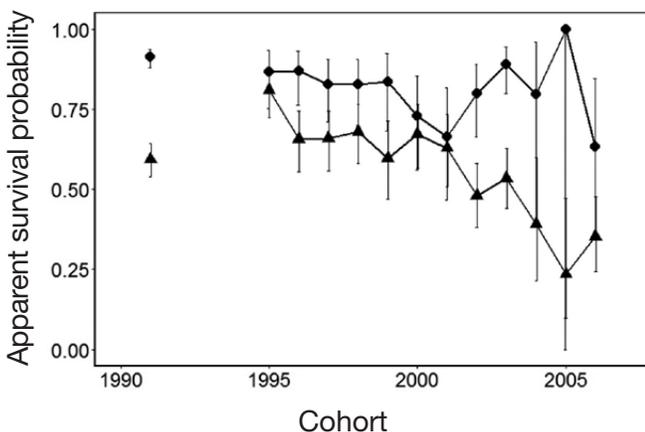


Fig. 3. Apparent survival probabilities (φ ; survival + fidelity) of juveniles (age 0–2; triangles) and adults (age 3+; circles) by cohort from the top-ranked multi-state survival model ($\varphi \sim$ age class \times cohort, $p \sim$ breeding state [pre-recruit vs. recruit] + age class, $\psi \sim$ age) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony in Prince William Sound in 1991 and 1995–2006. Error bars denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10 000 iterations).

Data accessibility

Manipulation and encounter history data is available from the Dryad Digital Repository (McKnight *et al.* 2019).

DISCUSSION

Trends in apparent fledgling survival: Evidence for increased dispersal over time

Estimating post-fledgling survival rates is challenging because of kittiwakes' tendency to remain at sea for the first two years of life and because of their propensity for dispersal from the natal colony (e.g., Coulson & Coulson 2008). Coulson & Ouellet (1988) estimated an overall survival rate of 0.34 from fledging until

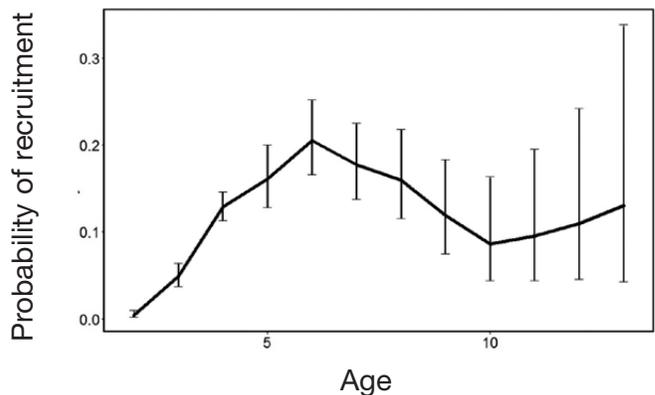


Fig. 4. Recruitment probabilities from the top-ranked multi-state model of apparent fledgling survival ($\varphi \sim$ age class \times cohort, $p \sim$ breeding state [pre-recruit vs. recruit] + age class, $\psi \sim$ age) for Black-legged Kittiwakes banded as chicks at the Shoup Bay colony in Prince William Sound in 1991 and 1995–2006. Error bars denote the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10 000 iterations).

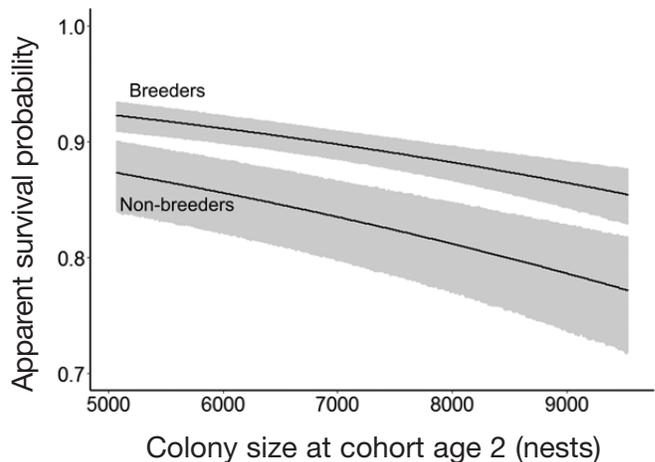


Fig. 5. Effect of natal colony size on the apparent survival of recruits from the top-ranked multi-state model explaining recruit fidelity to the natal colony as a function of natal colony size at age 2 in Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony in Prince William Sound. The two states, breeders and post-recruitment non-breeders, are denoted by the solid black lines; the gray shading denotes the 2.5 and 97.5 percentiles of bootstrapped estimate distributions (10 000 iterations).

recruitment for individuals at a well-studied British colony, while Porter & Coulson (1987) reported that 11 % of each cohort returned to breed at the same colony. Our cumulative probability of survival (0.23, 95 % CI = 0.17–0.31) through the average age of recruitment was slightly less than that of Coulson & Ouellet (1988); this difference likely reflected the younger recruitment age in Atlantic kittiwakes (age 4.5: Coulson 1966, Wooller & Coulson 1977, Link *et al.* 2002) compared to birds in our study (age 7). Survival to recruitment age can also be influenced by both hatch order and the duration of the rearing period (Cam *et al.* 2003), which we were unable to account for in this work. Further, realized recruitment, which reflects the integration of both survival and the transition to a breeding state, can be a function of factors affecting survival prior to recruitment (Cam *et al.* 2005). Our approach assessed both components simultaneously; however, we suggest that, in the absence of such cohort-specific survival effects, recruitment is primarily age-dependent.

Boulinier & Danchin (1997) proposed that when the environment quality is patchy but breeding patch quality is stable and predictable, the optimal recruitment strategy has two parts: (1) prospecting before choosing to recruit to a patch and then (2) retaining or abandoning nest sites based on the patch's overall reproductive success rather than the individual's own breeding success. Indeed, individuals who prospect a patch prior to breeding may enjoy greater initial reproductive success (Schjørring *et al.* 1999), which likely influences the trajectory of future reproductive success (Cam *et al.* 2002) and thus patch fidelity. Unfortunately, we did not assess breeding success in this work and were therefore unable to account for it in our exploration of post-recruitment dynamics. When colony or patch quality is predictable, better-quality colonies or patches likely recruit through conspecific attraction (e.g., Oro & Ruxton 2001), performance-based conspecific attraction (Danchin *et al.* 1998), or natal philopatry (in which young birds recruit to the colony from which they successfully fledged, implying that it was of reasonably good quality). Varying degrees of natal philopatry

have been observed in many colonial birds (e.g., Thibault 1993, Aebischer 1995, Pyk *et al.* 2013, but see Coulson & Coulson 2008). One contributing factor appears to be the age of the colony: during the initial years of colony development, growth is dependent on immigration alone until the first generations of chicks produced at the colony have reached maturity (e.g., Pyk *et al.* 2013). Following this phase, colony growth is contingent upon some combination of natal philopatry and immigration.

Crespin *et al.* (2006) found a suggestion of negative density dependence in return rates (i.e., apparent survival was not corrected for imperfect detection) for the Common Murre *Uria aalge*, which may indicate a reduction in natal philopatry at large colonies. We found a similar suggestion in kittiwakes at the Shoup Bay colony: hatch-year colony size was the best predictor of apparent fledgling survival after the general cohort-varying model structure. This means that as colony size increases, new recruits may not have access to the best patches. Such limitation is likely responsible for slower growth in large colonies compared to small colonies (e.g., Porter & Coulson 1987, Chapdelaine & Brousseau 1989). In large colonies, dispersal away from the natal colony may then become the better strategy over philopatry. Steiner & Gaston (2005) documented greater reproductive success in Thick-billed Murres *Uria lomvia* that dispersed from their natal colony, presumably owing to a greater choice in mates and nest sites.

Such strategic dispersal likely contributed to the decline in apparent survival of fledglings that we observed at the Shoup Bay colony. Recruits from Shoup Bay were very rare at other PWS colonies in the late 1990s but were fairly common during a survey at a single neighboring colony in 2007, suggesting an increase in dispersal from Shoup Bay over that time period. Such a decline in natal philopatry could have further reduced recruitment to the Shoup Bay colony through negative feedback on immigrants. The number of non-breeders, including pre-recruits, attending a seabird colony can be a relatively good indicator of the colony's quality to other prospectors

TABLE 4
Post-recruitment survival modeling: apparent survival probability. Performance of competing multi-state models testing hypotheses to explain the observed cohort effect on apparent survival (φ ; survival + fidelity) of post-recruitment breeders and non-breeders (determined by nest-site attendance) for Black-legged Kittiwakes banded as chicks at and eventually recruiting to the Shoup Bay colony, Prince William Sound, Alaska, 1991–2006, with the top-ranked general model (breeding state + cohort; italicized) included for reference

Model ^a	Hypothesis	ΔQAIC_c	w_i	K
Apparent survival probability of recruits varies ...				
$\varphi_{(\text{state} + 2\text{Y pop size})}$... between breeding states and by colony size in a cohort's second year.	0.00	0.74	73
$\varphi_{(\text{state} + 3\text{Y pop size})}$... between breeding states and by colony size in a cohort's third year.	2.42	0.22	73
$\varphi_{(\text{state} + \text{HY pop size})}$... between breeding states and by colony size in a cohort's hatch year.	6.69	0.03	73
<i>$\varphi_{(\text{state} + \text{cohort})}$</i>	<i>... between breeding states and among cohorts.</i>	8.74	0.01	82
$\varphi_{(\text{state} + \text{HY PDO})}$... between breeding states and by winter PDO value prior to a cohort's hatch year.	14.67	< 0.01	73
$\varphi_{(\text{state} + \text{AHY PDO})}$... between breeding states and by winter PDO value in a cohort's hatch year.	15.96	< 0.01	73
$\varphi_{(\text{state} + \text{HY Prod})}$... between breeding states and by colony productivity in a cohort's hatch year.	16.96	< 0.01	73
$\varphi_{(\text{state} + 3\text{Y Prod})}$... between breeding states and by colony productivity in a cohort's third year.	17.01	< 0.01	73
$\varphi_{(\text{state} + 2\text{Y Prod})}$... between breeding states and by colony productivity in a cohort's second year.	17.29	< 0.01	73

^a Model structures for resight and transition probability were set to the best-competing structures (state + time and state \times time, respectively; asterisk denotes interactive model). For further explanation of column headings, see footnote in Table 2, except that ΔAIC_c values were adjusted according to a median \hat{c} estimate of 1.76.

(Klomp & Furness 1990, Cadiou 1999); such non-breeders may contribute to a population's resilience by filling nest sites left vacant during periods of high adult mortality (Porter & Coulson 1987). The presence of natal pre-recruits at a colony would be an even better indicator of a colony's quality than the presence of late-stage chicks because chicks have some ability to buffer the effects of low food quality temporarily (Dahdul & Horn 2003), but they may suffer greater post-fledging mortality than well-fed counterparts. Szostek *et al.* (2014) found that Common Tern *Sterna hirundo* immigrants were attracted strongly by local recruits and pre-recruits at the colony. If such attraction also occurs in kittiwakes, then declining numbers of pre-recruits at the Shoup Bay colony could have had a negative effect on colony growth that was disproportionate to their actual numbers.

Pacific vs. Atlantic life history differences

Local adaptation may be responsible for apparent differences in kittiwake life-history strategies between the two ocean basins. Atlantic kittiwakes enjoy greater and more stable productivity compared to Pacific counterparts (Hatch *et al.* 1993) and exhibit reduced adult survival: 0.78–0.88 for Atlantic kittiwakes (Coulson & Wooller 1984, Coulson & Thomas 1985, Aebischer & Coulson 1990, Oro & Furness 2002, Ponchon *et al.* 2018) compared to 0.92–0.94 for Pacific kittiwakes (Hatch *et al.* 1993, Golet *et al.* 2004). However, survival estimates generated from single-site CMR studies should always be viewed with caution (Ponchon *et al.* 2018). The recruitment age we estimated for the Shoup Bay kittiwakes provides more evidence of this strategic difference. Our estimate of seven years agrees with the maturation age estimated using a different method for kittiwakes at a nearby (within 200 km) Gulf of Alaska colony that is located near the continental shelf break (Vincenzi *et al.* 2013). Together, these estimates stand in sharp contrast to a much younger maturation age of four to five years observed in Atlantic kittiwakes (Coulson 1966, Wooller & Coulson 1977, Link *et al.* 2002). Further study is needed to determine whether the contrast stems directly from biological differences or if it reflects greater freedom to spend time prospecting prior to breeding in longer-lived Pacific populations.

Patterns of juvenile mortality may shape tradeoff strategies (Goodman 1984, Young 1990), while patterns in adult mortality likely result from these strategies. Variable juvenile survival to adulthood can favor a “bet-hedging” strategy among iteroparous organisms, particularly when nest sites are limited (Sæther *et al.* 1996) or where the cost-savings associated with reduced reproductive effort during a vulnerable time may afford young adults a greater chance of surviving to take part in future reproductive opportunities. This delayed investment may lead to the tradeoff often seen between longevity and maturation age (e.g., Wooller & Coulson 1977, Orell & Belda 2002, Reed *et al.* 2008, Aubry *et al.* 2009). On one hand, early maturity can lead to greater probability of surviving to maturity, shorter generation time, and increased lifetime fitness. Such early maturation, however, may require a sacrifice of growth, fecundity, or offspring quality and may not be advantageous when bet-hedging is the optimal approach. Given its potential fitness tradeoffs, maturation age may be sensitive to selective pressure and thus may rapidly respond to local conditions (Stearns 1992). Alternatively, delayed maturation may reflect more time spent in prospecting potential colonies and breeding patches. This investment could lead to fitness payoff, as prospecting can improve initial breeding success (Schjorring *et al.* 1999) and overall fitness (Cam *et al.* 2002), though it may incur a survival cost via increased food competition during the prospecting period (Bosman *et al.* 2013).

Gill & Hatch (2002) proposed that the differences between the two populations may be driven by differences in food availability rather than local adaptation. However, several lines of evidence suggest that food is not as limiting within PWS as it may be elsewhere in Alaska. Kittiwake colonies within 10 km of the Shoup Bay colony that were geographically restricted to the same general foraging area grew and produced chicks during the Shoup Bay colony's decline (McKnight 2017), suggesting that food limitation was not the proximate cause. Instead, predation may have a greater influence on productivity in this region (McKnight 2017) compared to oceanic colonies such as the Pribilof Islands in the Bering Sea (DBI unpubl. data), where predation is minimal (Byrd *et al.* 2008) and where food is likely more limiting (e.g., Harding *et al.* 2013). Combined with the contrast between Alaskan and western Atlantic kittiwake recruitment ages, the fact that our recruitment age agreed closely with that of a Gulf of Alaska colony experiencing different prey and predator dynamics may reflect a true phenotypic difference in life history strategy between Pacific and Atlantic populations.

Density dependence in apparent survival of recruits

We have long been aware of the role of negative density dependence in population regulation (e.g., Hassell 1975). In seabirds, this dependence is evident in the negative relationship between colony size and reproductive success (e.g., Hunt *et al.* 1986), which at least partially reflects a direct cost of large colony size in the form of localized prey depletion (e.g., Lewis *et al.* 2001, Forero *et al.* 2002). Nest-site limitation can also dampen population growth potential when poorer sites (i.e., those that produce few fledglings) are used at high population densities (Kokko *et al.* 2004). Somewhat counterintuitively, nesting success can also exhibit positive density dependence if the decreased predator defense activity required by individuals allows for an increase in foraging effort, although this effect can be countered by increased intraspecific aggression towards unattended nestlings (Ashbrook *et al.* 2010). In our study, we have revealed another expression of negative density dependence: apparent survival of recruits was lower when natal colony size was large early in life (Fig. 5). This reduction was likely due in part to the increased dispersal of established breeders when the colony was at its largest, as suggested by the larger numbers of Shoup Bay emigrants detected in 2007 compared to the late 1990s.

Many species exhibit high site fidelity following recruitment (e.g., Atwood & Massey 1988, Coulson & Nève de Mévergnies 1992, Pyle *et al.* 2001, Kokko *et al.* 2004), with few established breeders switching colonies (e.g., Aebischer 1995). Emigration is not well understood but may occur more regularly when a colony or breeding patch is declining in quality (e.g., Martínez-Abraín *et al.* 2003), producing few chicks (e.g., Danchin & Monnat 1992), or experiencing a series of cumulative disturbances (Fernández-Chacón *et al.* 2013). Site fidelity in Atlantic kittiwakes is known to be strongly tied to both individual and conspecific reproductive success within the nesting patch (Danchin *et al.* 1998, Boulonier *et al.* 2008, Ponchon *et al.* 2015, Ponchon *et al.* 2017). Once dispersal begins, emigration can accelerate rapidly, suggesting that declining attendance may trigger other breeders to leave as well (Martinez-Abraín *et al.* 2003).

Nest site limitation may have contributed to emigration of recruited breeders in our work. If young recruits tend to establish nest sites on the periphery of the colony, peripheral nests established when the colony is small may become centrally located as the colony grows around them. Centrally located nests tend to have greater quality

(e.g., safety from predators) than nests at the periphery (Hamilton 1971, Vine 1971, Wittenburger & Hunt Jr. 1985, Kharitonov & Siegel-Causey 1988, but see Descamps *et al.* 2009 and Minias *et al.* 2012). Therefore, young individuals that recruited when the Shoup Bay colony was small may have eventually possessed nests in higher quality patches than individuals recruiting when the colony was large; greater success in these higher quality patches, in turn, may have led to greater fidelity (e.g., Danchin *et al.* 1998).

Dispersal of established breeders from productive colonies is uncommon among kittiwakes (e.g., Coulson & Nève de Mévergnies 1992); our relatively large apparent survival estimates for recruits (> 0.75) support this theme. When established breeders disperse, they tend to recruit to other existing colonies. Kildaw *et al.* (2005) documented a “threshold of reluctance” to establish new colonies, even though new colonies can be highly productive. Dispersal to new, unoccupied nesting areas may simply present too many risks for the average breeder: unknown factors include predator dynamics, long-term food availability, and microclimate effects, whereas existing colonies provide copious information to potential recruits regarding food abundance and nest safety (Forbes & Kaiser 1994). However, decreasing productivity at the Shoup Bay colony in the later years of our study may have signaled to breeders that patch quality was becoming less predictable, causing them to employ the “dispersal following patch failure” strategy (Boulinier & Danchin 1997). Frederiksen & Bregnballe (2001) found that productivity affected recruitment age in Great Cormorants *Phalacrocorax carbo sinensis*, where individuals waited longer to recruit after seasons of poor productivity. We found no such relationship for the Shoup Bay kittiwakes, potentially due to the ease of dispersal to more promising colonies within the PWS system. Dispersal of breeders may have become even more feasible after the establishment of nearby (i.e., within 10 km) colonies in Port Valdez beginning in the late 1990s. This was likely exacerbated by declining habitat quality at the Shoup Bay colony due to post-glacial successional changes in vegetation that may have benefited predators. Because any birds nesting within Port Valdez must travel into Valdez Arm and its associated fjords to forage, we suspect that foraging grounds overlap almost completely (but see Ainley *et al.* 2003), which would make a move more feasible for birds that are already familiar with feeding conditions in the area.

CONCLUSION

Given the recent and dramatic decreases in seabird populations around the globe (Palczy *et al.* 2015), understanding recruitment and emigration patterns is important not only for successful population management but also for the effective use of seabirds as ecosystem indicators (e.g., Cairns 1988, Piatt *et al.* 2007). In this work, we identified that intrinsic processes may drive apparent survival in fledglings and recruits at an Alaska seabird colony and that declines in apparent survival likely reflect greater dispersal when colony sizes are larger. This fidelity/colony size relationship could be a useful consideration for managers, as small, growing colonies may represent a better long-term investment for conservation projects than large, established colonies. Additionally, our results allowed us to estimate the average age of first reproduction for this population. Our estimate agreed with that calculated for another Pacific colony, and both were several years older than recruitment ages calculated for Atlantic populations. This strengthens the argument that Pacific kittiwakes follow a more conservative life history strategy than their Atlantic counterparts, which may confer

added resilience against the increased frequency or magnitude of short-term environmental perturbations associated with ecosystem change. Finally, while this study addresses a single colony of a single species, it provides demographic parameter estimates that can be applied in parameterizing models of population dynamics. Such models can provide us with valuable insights and realistic predictions about future dynamics in changing marine systems.

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