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Reproductive success of kittiwakes and murre in sequential stages of the nesting period: Relationships with diet and oceanography



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ABSTRACT

Reproductive success is one of the most easily-measured and widely studied demographic parameters of colonial nesting seabirds. Nevertheless, factors affecting the sequential stages (egg laying, incubation, chick-rearing) of reproductive success are less understood. We investigated the separate sequential stages of reproductive success in piscivorous black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murre (*Uria lomvia*) using a 36-year dataset (1975–2010) on the major Pribilof Islands (St. Paul and St. George), which have recently had contrasting population trajectories. Our objectives were to evaluate how the proportion of successful nests varied among stages, and to quantify factors influencing the probability of nest success at each stage in each island. We modeled the probability of nest success at each stage using General Linear Mixed Models incorporating broad-scale and local climate variables, and diet as covariates as well as other measures of reproduction such as timing of breeding and reproductive output in the previous year and previous stage. For both species we found: (1) Success in previous stages of the breeding cycle and success in the prior year better explained overall success than any environmental variables. Phenology was also an important predictor of laying success for kittiwakes. (2) Fledging success was lower when chick diets contained oceanic fish found farther from the colonies and small invertebrates, rather than coastal fish species. (3) Differences in reproductive variables at St. Paul and St. George islands did not correspond to population trends between the two islands. Our results highlight the potential importance of adult condition and annual survival to kittiwake and murre productivity and ultimately, populations. Adult condition carrying over from the previous year ultimately seems to drive annual breeding success in a cascade effect. Furthermore, condition and survival appear to be important contributors to population dynamics at each island. Therefore, adult condition and survival prior to breeding, and factors that influence these parameters such as foraging conditions in the non-breeding season, may be important datasets for understanding drivers of seabird demography at the Pribilof Islands.

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1. Introduction

Seabirds are widely touted as “indicator species” for the state of the marine ecosystem (Furness and Camphuysen, 1997; Montevecchi, 1993; Piatt et al., 2007). Several characteristics are proposed to make them useful indicators: they are top predators, they are conspicuous central place foragers during the breeding season, many species are widespread and common, and as a group they exploit different aspects of the marine system (i.e., fish vs. plankton, surface vs. depth, nearshore vs. offshore) (Einoder, 2009).

Reproductive success (chicks fledged per nest start) is one of the most easily-measured and widely studied demographic parameters of

colonial nesting seabirds (e.g., Dragoo et al., 2012; Mavor et al., 2008) even though for long-lived species, its relative contribution to population trends is often minimal (Schmutz et al., 1997; Schmutz and Byrd, 2004). Variation in seabird breeding success is often used as an indicator of changes in the marine environment because success is widely assumed to be “mediated through the food web” (e.g., Ainley et al., 1995; Byrd et al., 2008a; Frederiksen et al., 2005). Proximate causes of success or failure during different stages of seabird nesting cycles differ, however, because these cycles extend over several months and energetic constraints vary over this period (Shaffer et al., 2003).

Reproductive failure may occur during any one of three separate sequential stages: the nest building period (for those species that build nests), the incubation period, and the chick-rearing period. Prior to egg laying, seabirds are not tied to the nest site and have only themselves to feed. Laying failure may be related to breeding experience of the individual (Coulson, 1966),

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climate conditions prior to incubation (Quillfeldt, 2001), or nutritional condition of the adult (Kitaysky et al., 2010), which could theoretically be influenced by either reproductive expenditure during the previous breeding season or foraging conditions leading up to egg production in the current season [or unavailability of habitat – e.g., auklets (Bedard, 1969); gannets (Nelson, 1980)]. During incubation and chick-rearing, in contrast, adult birds are constrained by incubation or chick-feeding duties and have both decreased foraging range and increased energetic demands to raise young (Golet et al., 2000). Egg loss can result from predation or abandonment by the parent, either because the egg was not viable or because of food supply limitations during the laying or incubation period (e.g., Hatch and Hatch, 1990; Wanless and Harris, 1992). Finally, chick loss may result from storm events, predation, or the adult's inability to provide sufficient food resources to the chick during this energetically intensive period (e.g., Baird, 1990; Gill and Hatch, 2002; Hatch and Hatch, 1990). Given success or failure during each nesting stage may be affected by different aspects of the marine environment, understanding when breeding loss occurs and how each stage of reproduction relates to environmental factors are crucial to using seabirds as bioindicators.

Relationships between seabird demography and local and regional climate variables are largely affected by life history traits and colony location (review by Sydeman et al., 2012). Accordingly, the degree in climatic responsiveness of seabirds may reflect different tradeoffs between survival and reproduction (Coulson, 2002). For instance, although many studies have found relationships between climate variables and seabird productivity (Sydeman et al., 2012), others are weak (Satterthwaite et al., 2012), and population trajectories do not necessarily match patterns in reproductive success (Murphy et al., 1991). Some seabird species are more flexible in that they can adapt foraging in response to changes in the environment, masking effects on some breeding parameters (Piatt et al., 2007). For instance, kittiwakes can compensate for low food supply by increasing foraging range and effort, resulting in low interannual variation in chick growth rates despite variable foraging conditions (Kitaysky et al., 2000). Similarly, murrelets can increase foraging effort or feeding rates to maintain relatively constant levels of fledging success when facing low prey density (Harding et al., 2007) or a handicapped mate (Paredes et al., 2005). Of course, seabirds' ability to compensate for low food availability is limited; in extremely poor food years (i.e., El Niño events in the Southeastern hemisphere; Duffy, 1990), nest failure can occur at any stage of reproduction, leading to very low or zero reproductive success.

In general, though, changes in ocean conditions often correlate with seabird productivity and prey availability in a variety of marine habitats (Byrd et al., 2008a; Wolf et al., 2009; Watanuki and Ito, 2012); therefore changes in climatic variables (e.g., SST, PDO) are expected to affect seabird demography via food supply. Studies examining the relationships between prey availability and seabird productivity can use concurrent measures of foraging effort and prey abundance and distribution, but this is logistically a difficult task. Alternatively, seabird diets, which are a function of both prey availability and foraging effort, may be useful for exploring how the marine food web mediates seabird population processes (Connan et al., 2008).

We investigated the separate sequential stages of reproductive success in piscivorous black-legged kittiwakes (*R. tridactyla*) and thick-billed murrelets (*U. lomvia*) using a 36-year dataset (1975–2010) on the Pribilof Islands in the Bering Sea, Alaska. We had two primary objectives: (1) evaluate whether the proportion of successful nests varied among nesting stages and between islands, and (2) quantify factors influencing the probability of nest success at each stage. For the latter, we hypothesized that different stages would be responsive to different cues in the environment; we

modeled three stages of nest success using (a) previous nesting stage reproductive output (assumed to be related to body condition which was not measured), (b) climate variables (broad-scale and local indices) likely to influence foraging conditions, and (c) seabird diet.

2. Study area and species

The Pribilof Islands are located in the Southeastern Bering Sea (~57°N, 169°W) near the edge of the continental shelf. St. Paul Island is approximately 65 km north of St. George Island and is closer to the southern extent of the winter sea ice, whereas St. George Island is closer to the edge of the continental shelf than St. Paul Island. The area along the shelf break is a region of high productivity that supports large numbers of forage fishes, marine mammals, and seabirds (Springer et al., 1996).

St. George and St. Paul Islands together comprise one of the largest breeding concentrations of marine birds in the North Pacific, estimated to exceed 2 million individuals (Hickey and Craighead, 1977). Both islands are approximately equal in size but St. George Island has more extensive cliff nesting habitat and an order of magnitude more ledge-nesting seabirds than St. Paul Island (Hickey and Craighead, 1977). Black-legged kittiwakes and thick-billed murrelets are the most abundant species of piscivorous seabirds on the Pribilofs, where they nest in mixed colonies with red-legged kittiwakes (*Rissa brevirostris*) and common murrelets (*Uria aalge*). The total population of black-legged kittiwakes at St. Paul (~15,000 individuals) and St. George (~72,000 individuals) for 2005 was calculated based on Hickey and Craighead (1977) counts and trend rates reported by Byrd et al. (2008b). The two islands also support substantially different numbers of breeding thick-billed murrelets: St. George=1,500,000, St. Paul=57,000 (Hickey and Craighead, 1977; modified using Byrd et al. (2008b)). Reproductive success of kittiwakes and murrelets at the Pribilof Islands is presumed to be related mostly to prey availability, as nest predation for ledge-nesting birds at both islands is minimal (Byrd et al., 2008a).

3. Materials and methods

3.1. Data collection

Reproductive success was estimated each year on St. Paul and St. George islands, 1975–2010, by recording the status (i.e., presence of nest structure, egg or chick) of nests on systematically-selected plots within the viewable population (see Byrd, 1989; Byrd et al., 2008a; Hunt et al., 1981). Prior to 1989 (except in 1984), nests monitored were not grouped into plots or plot-specific data were not available, and nests were treated as a simple random sample. In subsequent years plots were used as single-stage cluster samples, to more accurately represent the variance. Data collection consisted of photographing or drawing each plot and numbering nest sites on the photograph or drawing so individual sites could be identified and followed throughout the nesting cycle. For kittiwakes, nest sites were considered active only when new plant material was added within that season. Since murrelets do not build nests, the appearance of an egg constituted an active site (therefore, laying success could not be estimated for murrelets as it was for kittiwakes). Numbered sites typically were checked every three to five days throughout the incubation and chick-rearing periods to estimate loss of reproductive potential during the laying (kittiwakes only), egg, and chick stages of the nesting cycle. Nests were monitored until chicks departed the cliffs (fledged). Hatch dates were estimated as the mid-points between the date the egg was last seen and the date the chick was first observed. Nests were monitored in the same areas each year, with substantial overlap in individual nests and plots, but

Table 1

Sample sizes used for analyses of seabird reproductive success and diets of black-legged kittiwakes (BLKI) and thick-billed murre (TBMU) from the Pribilof Islands, 1975–2010. Numbers of nests are those with a known fate (successful or laying, egg or chick loss) at the end of the season. Diet samples represent those collected during the chick-rearing period only and exclude years with < 6 samples.

Year	Species	St. George Island		St. Paul Island	
		Reproductive success (# nests)	Diet (# samples)	Reproductive success (# nests)	Diet (# samples)
1975	BLKI	–	–	185	118
1975	TBMU	–	–	–	–
1976	BLKI	34	31	127	55
1976	TBMU	–	6	47	17
1977	BLKI	110	60	157	129
1977	TBMU	51	21	102	20
1978	BLKI	229	52	203	70
1978	TBMU	90	23	114	16
1979	BLKI	146	–	158	23
1979	TBMU	–	–	–	–
1980	BLKI	106	–	–	–
1980	TBMU	–	–	–	–
1981	BLKI	102	10	–	–
1981	TBMU	88	–	–	–
1982	BLKI	–	–	–	–
1982	TBMU	–	–	–	–
1983	BLKI	–	–	–	–
1983	TBMU	–	–	–	–
1984	BLKI	49	67	92	29
1984	TBMU	55	31	27	20
1985	BLKI	154	12	428	–
1985	TBMU	253	–	360	–
1986	BLKI	155	38	554	–
1986	TBMU	388	–	624	–
1987	BLKI	126	–	506	23
1987	TBMU	377	11	792	–
1988	BLKI	85	28	204	48
1988	TBMU	195	36	317	12
1989	BLKI	59	–	351	–
1989	TBMU	326	–	346	–
1990	BLKI	95	–	369	–
1990	TBMU	286	–	325	–
1991	BLKI	99	–	–	–
1991	TBMU	269	–	–	–
1992	BLKI	98	65	511	7
1992	TBMU	360	–	475	–
1993	BLKI	113	11	–	8
1993	TBMU	318	–	–	–
1994	BLKI	113	–	–	–
1994	TBMU	322	–	–	–
1995	BLKI	57	–	–	–
1995	TBMU	269	–	–	–
1996	BLKI	95	–	280	–
1996	TBMU	243	–	356	–
1997	BLKI	105	9	301	30
1997	TBMU	297	–	293	–
1998	BLKI	75	39	299	30
1998	TBMU	160	–	246	–
1999	BLKI	76	13	290	–
1999	TBMU	243	–	434	–
2000	BLKI	110	9	289	–
2000	TBMU	364	–	546	–
2001	BLKI	95	–	360	–
2001	TBMU	382	38	482	–
2002	BLKI	113	–	343	–
2002	TBMU	371	–	265	–
2003	BLKI	121	–	349	22
2003	TBMU	418	19	425	–
2004	BLKI	158	–	425	–
2004	TBMU	310	7	386	–
2005	BLKI	161	7	543	–
2005	TBMU	590	–	177	–
2006	BLKI	255	–	479	9
2006	TBMU	574	52	316	–
2007	BLKI	67	–	483	–
2007	TBMU	729	18	627	–
2008	BLKI	179	36	388	33
2008	TBMU	327	75	337	355

Table 1 (continued)

Year	Species	St. George Island		St. Paul Island	
		Reproductive success (# nests)	Diet (# samples)	Reproductive success (# nests)	Diet (# samples)
2009	BLKI	169	24	422	22
2009	TBMU	307	237	351	193
2010	BLKI	199	51	366	35
2010	TBMU	363	200	370	77

varying enough to achieve desired sample sizes. Sample sizes of nests and diet samples in each year are shown in Table 1.

Kittiwake diet samples were collected from captured or shot adults attending the cliff breeding colonies or from chicks handled in their nests. Adult and chick diets were combined as in previous studies (e.g., Decker et al., 1995; Hunt et al., 1996; Renner et al., 2012; Sinclair et al., 2008) because it is not possible to distinguish between the two, given kittiwakes store prey in their crops for several hours before regurgitating it to the young. For both species, we only included diet data collected during the chick-rearing period (21 June–22 September) because our previous analysis and others (Hunt et al., 1981; Renner et al., 2012) have indicated significant differences across different stages of the breeding period and because we only had data from outside the chick period in a few years. We used the same samples analyzed in Renner et al. (2012) with two exceptions: (1) we eliminated years with less than six samples (Duffy and Jackson, 1986), resulting in the exclusion of two years data at each island for each species, and (2) we included samples collected in 2005 and 2010, which became available after the former analysis was conducted. Because sample collection, prey processing and identification for kittiwake samples were identical to Renner et al. (2012), we have not repeated the details here.

Murre chick diet samples were obtained from bill loads or ledge drops by adult murre and regurgitations by chicks. Bill load samples included actual collections as well as observations made through spotting scopes during either formal nest observations or incidental observations while monitoring nests for reproductive success data. For collected bill loads, ledge drops, and chick regurgitations (1975–1978, 1984, 1987, 1988), samples were preserved, and identified in the laboratory following procedures used for kittiwake samples (Renner et al., 2012). For bill load observations (1999–2010), prey items were identified visually in the field to the lowest taxonomic level possible by the observer as adults carrying bill loads arrived at nest sites to feed chicks. When identifications could not be made or were in question for any reason, prey were classified as “unknown fish”, “unknown invertebrate”, or “unknown prey”. All entirely unknown prey were excluded from further analysis.

3.2. Data analysis

3.2.1. Diet datasets

Because the diet data used in this paper were not collected and analyzed consistently in all years (e.g., biomass data collected in some but not all years, some prey items identified to species while others only to genus or family, etc., and some murre bill loads identified only by field observation), we were limited in our diet data metric to either numerical abundance (how many individuals of a prey type were in each sample) or frequency of occurrence (how many samples contained a given prey type, regardless of quantities). Both measures have potential biases: abundance data underemphasize the importance of fish and other larger diet items (a bird may eat only a few larger fish but many smaller invertebrates), whereas frequency of occurrence does not account for

differences in the quantities of prey items across samples (a sample containing a single individual is treated the same as a sample containing hundreds of individuals) and thus may under-emphasize the importance of more numerous diet items. Fortunately, the measures are identical for murre chick samples, because adults carry only one prey item to the chick. Our previous analyses with this dataset (Renner et al., 2012) indicated consistent conclusions with both measures. We used frequency of occurrence for this study because it simplified the analysis and our ability to reclassify prey groupings; also, more years of diet data were available in this format.

Prior to the analyses, prey items were grouped into nine taxonomic groups representing the major prey types [walleye pollock (*Theragra chalcogramma*), Pacific sandlance (*Ammodytes hexapterus*), myctophids (family Myctophidae), capelin (*Mallotus villosus*), all fish combined, squid, amphipods, euphausiids, and all invertebrates combined]. All unidentified gadids were assumed to be walleye pollock, as the only other identified gadid (Pacific cod *Gadus macrocephalus*) occurred in just two years and in < 1% of samples. It would have been preferable to further separate all invertebrate prey to the species level, as euphausiids, amphipods and squid are known to have species-specific distributional differences (Sinclair et al., 1999; Benoit-Bird, pers. comm.) but species identification of invertebrates were not available in all years, especially for murre chick diet.

3.2.2. Climate datasets

Details of the final climate, reproductive and diet variables chosen as fixed effects in our models are shown in Table 2. For climatic

variables, we considered a wide range of local and regional variables that could affect prey availability and thus nesting success of seabirds. While atmospheric variability is believed to drive primary production, secondary production, forage fish recruitment, and ultimately, predator demographic parameters in the Bering Sea (see Renner et al., 2012 for detailed discussion), this can happen through direct and indirect effects on predators, and there is increasing decoupling at each sequential level of the food chain. As apex predators, seabirds are several steps removed from physical climate variables, and the marine system is complex enough that we had little *a priori* means to choose specific variables to investigate. Therefore, as in Renner et al. (2012), we cast a wide net of available climate time series, but then we reduced these by evaluating for multicollinearity and when two or more variables were highly correlated ($r \geq 0.60$; e.g., multiple datasets for sea surface temperature were considered), we removed the variables with the most missing data. We further limited our selection to those shown by previous studies to be correlated with seabird productivity (e.g., sea surface temperature and ice retreat index), as well as those for which we could hypothesize a direct mechanistic link to seabird demography (e.g., wind mixing would affect prey distribution on a short time scale, and strong wind events could directly destroy nests or kill chicks). We had two major limitations in our choice of climate variables. First, almost all of the available climate datasets are measured/integrated at an annual scale, which is not ideal for our intent to understand seabird processes occurring at a less-than-annual time scale (e.g., within a season). Second, in spite of having what is viewed widely as a tremendously long-term dataset, statistical power considerations severely limited our ability to test multiple variables in our very complicated model sets and we were forced to limit the scope of this paper. While climate variables may

Table 2
Environmental (or climatic), reproductive and diet variables, and their abbreviations, used in analyses of reproductive success of black-legged kittiwakes and thick-billed murrelets at the Pribilof Islands.

Variable		Description
Climate		
Summer wind mixing index	WM	Defined as mean daily wind speeds cubed at 10 m height at 57°N, 169°W (just east of the Pribilof Islands), averaged over the period 1 June–31 August (data from the NOAA Bering Climate website, http://www.beringclimate.noaa.gov).
Strong wind event index	WS	Defined as the number of days with wind speeds in excess of 9 m/s (same location/time period as wind mixing; data from the NOAA Bering Climate website).
Regional summer SST	SST	Longer time series for regional index of average sea surface temperature over the Eastern Bering Sea shelf during the summer breeding season (June through August), based on NOAA's extended reconstructed SST data over the approximate trawl survey region (inshore of approximately 200 m depth contour between 55°N and 61°N).
Spring ice retreat index	IRI	Defined as the number of days with ice cover after 15 March in the vicinity of Mooring 2 site (56.9°N, 164.1°W) as a proxy for the timing of ice retreat from the southeast Bering Sea shelf (data from the NOAA Bering Climate website, http://www.beringclimate.noaa.gov).
Pacific Decadal Oscillation Index (PDO)	PDO	November–March large-scale index related to climate variability in the eastern Bering Sea. Monthly values obtained from the Joint Institute of the Atmosphere and Oceans, University of Washington (http://jisao.washington.edu/pdo/PDO.latest).
Arctic Oscillation Index (AO)	AO	January–March large-scale index related to climate variability in the eastern Bering Sea. Monthly values obtained from NOAA, National Weather Service, Climate Prediction Center (http://www.cpc.ncep.noaa.gov/).
Reproductive		
Laying success	LS	The proportion of nest starts that had at least one egg laid for a given plot at each island each year. Variable used only for black-legged kittiwake models predicting hatching success.
Hatching success	HS	The proportion of nests with eggs that had at least one egg hatch for a given plot at each island each year. Variable used for thick-billed murre and black-legged kittiwake models predicting fledging success.
Fledging success	FS	The proportion of nests with chicks that had at least one chick fledge for a given plot at each island each year.
Previous year success	PYS	The proportion of successful nests (at least one chick fledged) in the previous year for a given plot at each island each year.
Timing	TIM	Annual mean hatch date at each island by Julian date.
Diet		
Pollock	POLL	Frequency of occurrence of pollock in chick (murrelets) and adult/chick (kittiwakes) diet.
Sandlance	SAND	Frequency of occurrence of sandlance in chick (murrelets) and adult/chick (kittiwakes) diet.
Myctophid	MYCT	Frequency of occurrence of myctophids in chick (murrelets) and adult/chick (kittiwakes) diet.
Capelin	CAPE	Frequency of occurrence of capelin in chick (murrelets) and adult/chick (kittiwakes) diet.
All fish	FISH	Frequency of occurrence of all fish combined in chick (murrelets) and adult/chick (kittiwakes) diet.
Squid	SQD	Frequency of occurrence of squid in chick (murrelets) and adult/chick (kittiwakes) diet.
Amphipod	AMPH	Frequency of occurrence of amphipods in chick (murrelets) and adult/chick (kittiwakes) diet.
Euphausiids	EUPH	Frequency of occurrence of euphausiids in chick (murrelets) and adult/chick (kittiwakes) diet.
NMDS axis 1	NMDS	Axis 1 from NMDS ordination of adult/chick diet of kittiwakes from Renner et al. (2012).

influence success of top predators with a time lag as their effects may be mediated through lower trophic levels, we chose not to investigate these relationships because they were recently explored in another publication (see Zador et al., 2013).

3.2.3. Statistical methods

We modeled the probability of success at each nesting stage with a separate model for each stage. We evaluated the effects of several variables: (1) prior reproductive output (previous colony-wide stage and year success) and timing of nesting, (2) environmental variables likely to influence foraging conditions (Table 1), and (3) diet sampled during the chick period. We used Generalized Linear Mixed Models (GLMM) to compare the importance of several variables for predicting the response (nest success or failure) at 3 stages in the nesting cycle for kittiwakes and in 2 stages for murre. Our candidate models took the form of

$$\Pr(y_i = 1) = \text{logit}^{-1}(\alpha_{01jk[i]} + \alpha_{02h[i]} + \beta_0 + \beta_1 X_{1[i]} + \beta_2 X_{2[i]} + \dots + \beta_n X_{n[i]} + \varepsilon_{[i]})$$

for $i = 1, \dots, n$ nests,

The response, $\Pr(y_i = 1)$, i.e., the probability of nest success, was modeled as a binomial random variable with a logit link for 3 responses: laying success (the probability of at least one egg being laid; kittiwakes only), hatching success (the probability of at least one egg hatching), and fledging success (the probability of at least one chick fledging successfully). The errors, $\varepsilon_{[i]} \sim N(0, \sigma^2)$, had independent normal distributions with mean zero and standard deviation σ . The random intercepts $\alpha_{01} \sim N(\mu = 0, \sigma^2_{jk})$, for $j = 1, \dots, n$ plots in $k = 2$ islands, and $\alpha_{02} \sim N(\mu = 0, \sigma^2_h)$, for $h = 1, \dots, n$ years were used to model the nonindependence of nests within plots, subset i.e., statistically nested, within two islands, crossed with year effects. For fixed effects, we estimated coefficients (β_1, \dots, β_n) for several ocean and diet variables ($X_1 \dots X_n$; Table 1) to quantify the importance of these variables for predicting the mean response $\Pr(y_i = 1)$.

For many years some or all covariate data were not available, so data from these years had to be eliminated. Because climate data were available for most of the years when we had reproductive success data, but diet data were available for fewer (and different) years, we ran climate and reproductive parameters in the same model sets and diet separately.

We followed Bolker et al. (2009) and Grueber et al. (2011) procedures for fitting GLMMs. For variables that were not normally distributed (IRI and SST), we attempted several data transformations to improve the distribution. Additionally, we used models with nonlinear splines for these covariates; neither approach improved the distribution or fit of models with IRI and SST.

We centered all covariates to improve interpretation of the relative strength of parameter estimates (Grueber et al., 2011). Centering changed the interpretation so that the intercepts were no longer the expected value when the predictor=0 on the original scale, but the expected value when the covariate was at its mean. For some variables, e.g., Julian date, there was no meaningful zero point (Julian hatch dates ranged from 181 to 230), which was another reason for centering variables.

For the climate and reproductive parameter modeling, we formulated 51–60 candidate models a priori to obtain balanced model sets. We model-averaged parameter estimates to account for model uncertainty (Bolker et al., 2009; Burnham and Anderson, 2002) using the natural-average method, where a parameter estimate for each predictor is averaged only over the models in which that predictor appears and is weighted by the summed weights of these models (Burnham and Anderson, 2002). The relative importance of variables was determined by summing the

Akaike weights across all models in which the variable occurs (Burnham and Anderson, 2002). We also evaluated confidence intervals for model-averaged parameter estimates; we considered variables with 90% confidence intervals that did not overlap with zero to be significant predictors of the response.

We ran univariate diet models because we were interested in whether individual diet variables predicted nest success. Because diet data were limited to the chick-rearing period, we used diet parameters to model only fledging success for both species. Detailed results of all model selection and model-averaged parameter estimates are included in online supplementary appendices (Tables A.1–A.14).

We evaluated between-island differences in total nest success, with a univariate model using Island only as a fixed effect, where

$$\Pr(y_i = 1) = \text{logit}^{-1}(\alpha_{01j[i]} + \alpha_{02h[i]} + \beta_0 + \beta_1 \text{Island})$$

To test whether success stages on both islands was correlated, we used Pearson correlations.

All analyses were conducted using program R (R Development Core Team, 2012).

4. Results

4.1. Thick-billed murre

During the 36 years of the study, the proportion of successful murre nests was higher on St. George Island (prop. success=0.512) than on St. Paul Island (prop. success=0.442, $n = 18,465$ nests, $Z = 9.52$, $p < 0.001$). The proportion of successful nests varied among stages with most loss occurring during the egg period (Figs. 1 and 2).

4.1.1. Hatching success

The probability of hatching success was lower on St. Paul Island ($P_{\text{success}} = 0.560$, 90% CI=0.542–0.579) than on St. George Island ($P_{\text{success}} = 0.617$, 90% CI=0.583–0.649), and 90% confidence intervals do not overlap indicating this difference was significant. In addition, hatching success was significantly correlated between islands ($r_s = 0.466$, $p = 0.016$).

For the climate and reproductive parameter models ($n = 26$ years with complete data), several models tied for the best models ($\Delta\text{AIC} < 2$). Previous year success was the most important predictor of hatching success of thick-billed murre: it occurred in all competing models and was the only statistically significant fixed effect (Table 3). Higher hatching success followed higher success in the previous year. No climate variables were significant predictors of murre hatching success.

4.1.2. Fledging success

The probability of fledging success was not significantly different on St. Paul Island ($P_{\text{success}} = 0.818$, 90% CI=0.802–0.832) than on St. George Island ($P_{\text{success}} = 0.847$, 90% CI=0.820–0.871). Fledging success was not correlated between islands ($r_s = -0.183$, $p = 0.372$).

Timing of nesting and hatching success were the most important predictors of fledging success for the climate and reproductive parameter models showing high importance values and statistical significance (Table 3). Fledging success was higher with higher hatching success and earlier timing of breeding. Although the best model for fledging success also included the strong wind event index, wind index was not a significant predictor.

Hatching success was included in all diet models predicting fledging success because it was a significant predictor in climate and reproductive modeling. The best diet model also included myctophids, which was a significant negative predictor of fledging

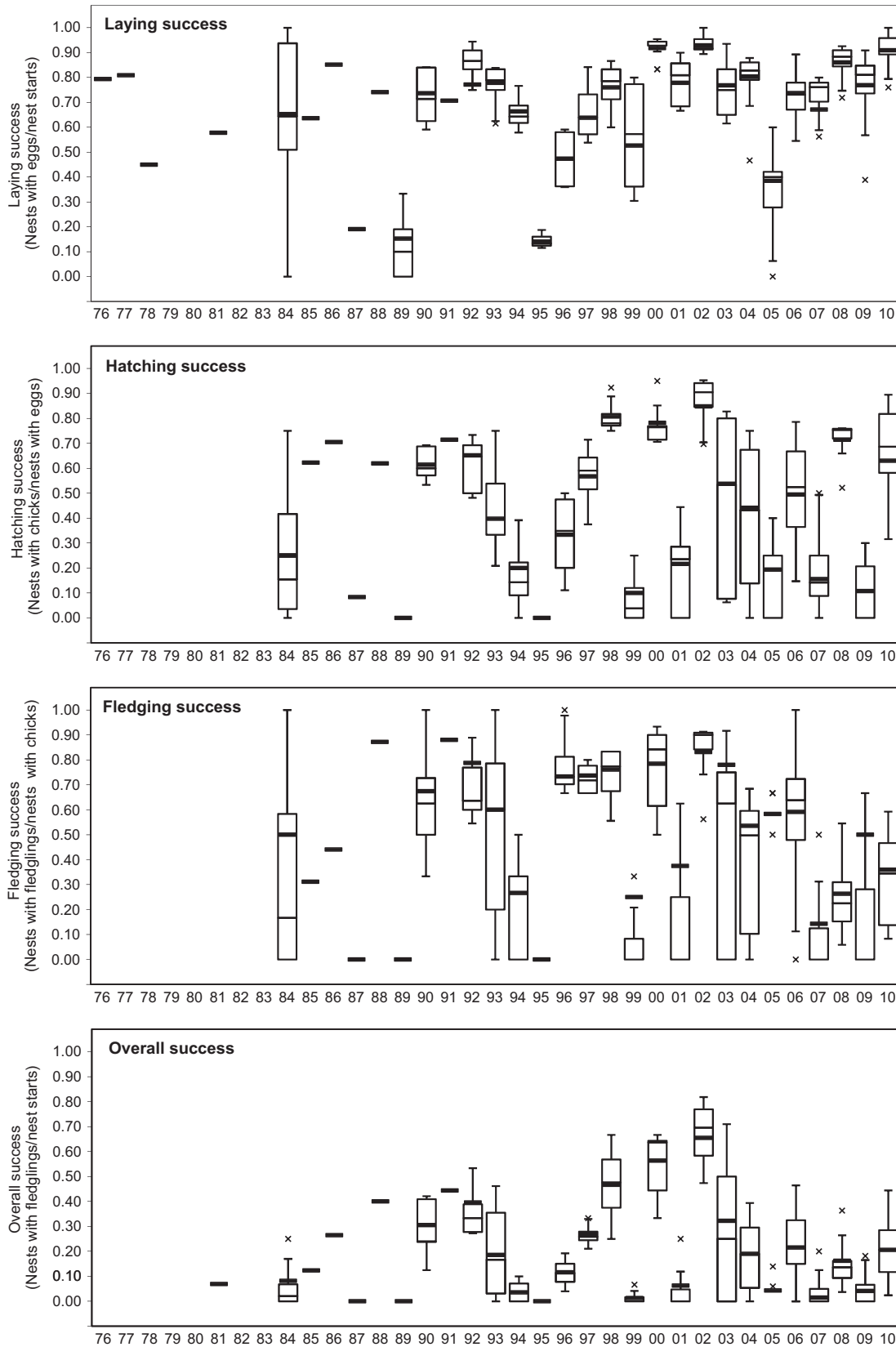


Fig. 1. Success of black-legged kittiwakes at St. George Island, Alaska in 1976–2010. Thick horizontal lines represent total annual success calculated across all nests each year. Box plots are calculated using annual success rates in each plot as the sample unit: boxes represent first and third quartiles, whiskers are 1.5x the interquartile range (IQR), and “x” shows outlier plots beyond 1.5xIQR. Years with no data for individual plots have no box plots.

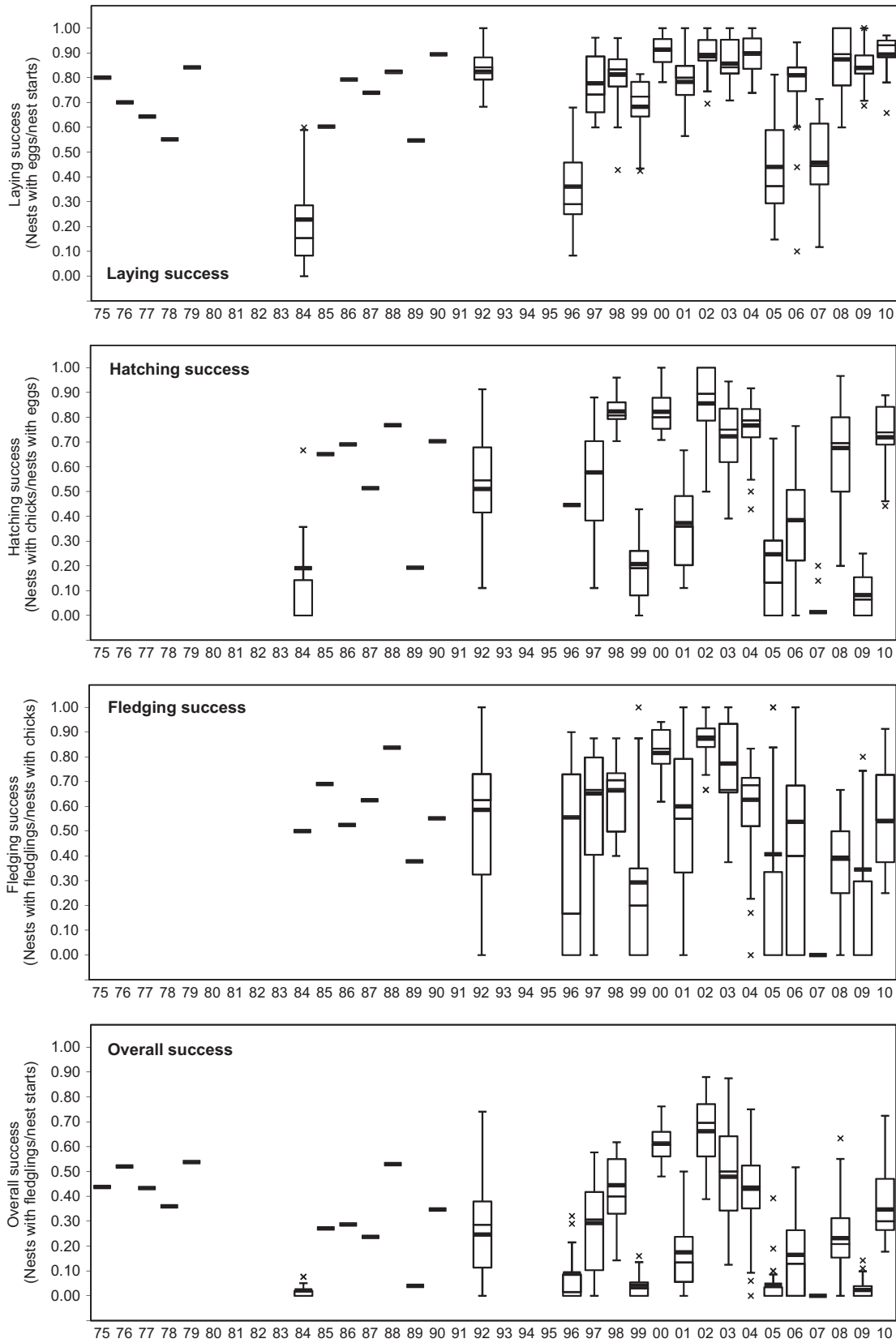


Fig. 2. Success of black-legged kittiwakes at St. Paul Island, Alaska in 1975–2010. Thick horizontal lines represent total annual success calculated across all nests each year. Box plots are calculated using annual success rates in each plot as the sample unit: boxes represent first and third quartiles, whiskers are 1.5x the interquartile range (IQR), and “x” shows outlier plots beyond 1.5xIQR; years with no data for individual plots have no box plots.

Table 3

Significant predictors of laying, hatching and fledging success of thick-billed murres and black-legged kittiwakes at St. Paul and St. George Islands, Alaska. Results are based on presence in top models ($\Delta AIC < 2$), high relative importance based on AIC weights and model-averaged parameter estimates with 90% confidence intervals not overlapping with zero.

Reproductive stage	Thick-billed murre	Black-legged kittiwake
Laying success	No data	Timing (–)
Hatching success	Previous year success (+)	Previous year success (+) Laying success (+)
Fledging success	Hatching success (+) Timing (–) Myctophid (–)	Hatching success (+) Amphipod (–)

success (Table 3). These results may be spurious, however, because myctophids were rarely found in murre chick diets in the Pribilofs (only in one year for St. George Island and two years for St. Paul Island).

4.2. Black-legged kittiwake

During the 36 years of the study, the proportion of successful kittiwake nests was higher on St. Paul Island (prop. success=0.234) than on St. George Island (prop. success=0.1696; $n=13,212$, $Z=8.22$, $p < 0.001$). Most of the nests were lost in the first two stages, but in contrast to murres, even in the fledging stage, a high proportion of the remaining nests failed (Figs. 3 and 4).

We analyzed data from 27 years in climate and reproductive parameter models of black-legged kittiwakes and 22 years in diet models. Years with missing covariate data were excluded.

4.2.1. Laying success

The probability of laying success was not significantly different on St. Paul Island ($P_{\text{success}}=0.677$, 90% CI=0.651–0.702) than on St. George Island ($P_{\text{success}}=0.611$, 90% CI=0.532–0.684). Laying success was significantly correlated between islands ($r_s=0.723$, $p < 0.001$).

In climate and reproductive models, timing of breeding occurred in the top two competing models (and all models with an AIC weight > 0) and was the only significant predictor of laying success (Table 3). Timing and laying success were inversely related, with a higher probability of laying success in years with earlier nest initiation dates. No climate variables were significant predictors of laying success.

4.2.2. Hatching success

The probability of hatching success was not significantly different on St. Paul Island ($P_{\text{success}}=0.454$, 90% CI=0.415–0.493) than on St. George Island ($P_{\text{success}}=0.410$, 90% CI=0.311–0.527). Hatching success was significantly correlated between islands ($r_s=0.812$, $p < 0.001$).

In climate and reproductive models, laying success and previous year success were both important variables for predicting hatching success of black-legged kittiwakes. The two variables comprised the single top model that had 98% of the weight of the model set and both were statistically significant predictors of hatching success (Table 3). Hatching success was high in years when laying success was high and when overall reproductive success in the previous year had been high.

4.2.3. Fledging success

The probability of fledging success was not significantly different on St. Paul Island ($P_{\text{success}}=0.610$, 90% CI=0.564–0.651) than on St. George Island ($P_{\text{success}}=0.522$, 90% CI=0.438–0.604).

Fledging success was significantly correlated between islands ($r_s=0.700$, $p < 0.001$).

Because laying success and hatching success were positively correlated ($r=0.576$, $p < 0.0001$), we included only hatching success in our fledging model set. In climate and reproductive models, hatching success was the most important variable for predicting fledging success: it appeared in all models with an AIC weight > 0 and was a statistically significant predictor of fledging success (Table 3). Higher fledging success was predicted by higher hatching success. A number of other climate and reproductive variables appeared in competing models predicting fledging success but none were significant.

In diet models, hatching success was included in all models because it was a significant predictor of fledging success in climate and reproductive models. The best model also contained frequency of amphipods in diet, which was a significant predictor of kittiwake fledging success (Table 3). Fledging success was higher when frequency of amphipods in diets was lower.

5. Discussion

5.1. Reproductive stages for each species

Our findings for both kittiwakes and murres suggest that annual reproductive outcome is most strongly related to conditions occurring prior to the nesting season. Colony-wide probability of success in the earlier stages was always the best predictor for those individuals proceeding to the next sequential stage: colony-wide laying success predicted individual hatching success, and colony-wide hatching success predicted individual fledging success. In addition, previous year's success was the single most important predictor for hatching success. This pattern indicates a cascade effect, in which overall breeding success is dictated by success early in the season, which in turn is driven by success in the previous year. This temporal autocorrelation, likely a function of adult condition, could be explained by two not mutually exclusive hypotheses. First, a relationship between adult condition in year zero and year one could be due to autocorrelation in environmental and foraging conditions (e.g., Zador et al., 2013). Second, costs associated with reproductive output in one year may determine future reproductive output. If high success in year one was due to good foraging conditions, whereby the adults incurred little stress, they should be in good condition for year two. We could also predict the opposite relationship if merely the effort of reproduction is a great cost. Life-history theory assumes costs associated with reproduction, and that these costs should be seen in a trade-off between current-year reproductive effort and future reproductive success (e.g., Bell and Koufopanou, 1986; Charnov and Krebs, 1974; Lessells, 1991; Reznick, 1985; Stearns, 1989; Williams, 1966). Reproductive costs may be incurred in any of the three sequential stages, egg production, incubation or chick-rearing (Monaghan and Nagar, 1997). High costs in one or more of these stages in a given year should decrease survival or reproductive performance (in subsequent stages in the same year or in subsequent years). For example, Milonoff et al. (2004) showed goldeneyes that reared chicks had lower productivity the following year than those that failed during incubation. Indeed, in reduced food conditions, kittiwakes and murres at the Pribilofs Islands appear to accept potential long-term costs (e.g., adult survival) to successfully rear chicks (Harding et al., 2013; Paredes et al., 2014). In addition, the cost of breeding in a year with poor food supply may also carry over to the following year, thereby diminishing reproductive performance in the next year for surviving birds (Kitaysky et al., 2000; Moss et al., 2009). For seabirds with only 1–2 eggs, this often leads to nest failure;

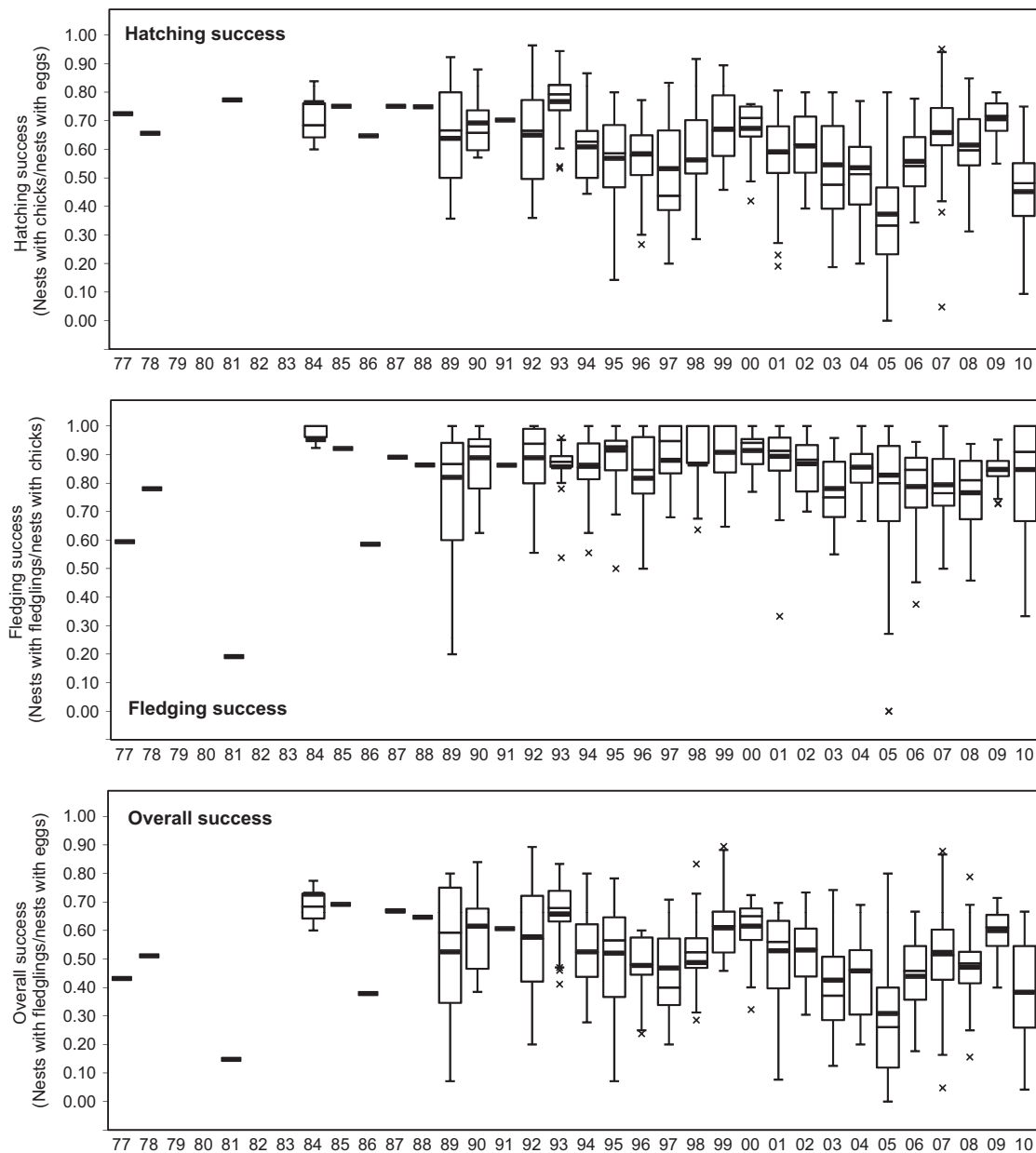


Fig. 3. Success of thick-billed murres at St. George Island, Alaska in 1977–2010. Thick horizontal lines represent total annual success calculated across all nests each year. Box plots are calculated using annual success rates in each plot as the sample unit: boxes represent first and third quartiles, whiskers are 1.5x the interquartile range (IQR), and “x” shows outlier plots beyond 1.5xIQR; years with no data for individual plots have no box plots.

unlike e.g., most waterfowl species, which can adjust clutch size in relation to body condition or stress (e.g., Erikstad et al., 1993), seabirds will forego a breeding attempt, or abandon a breeding attempt once initiated, if the consequences (presumably to adult condition/survival) are too great (e.g., Chastel et al., 1995).

Alternatively, environmental variation on the scale of the whole summer (which is all we have available for climate variables) may be most relevant to seabird reproductive success, which would imply that whole summers are good or bad for reproductive success. If this is the case, we would expect that hatching success would be a good predictor of fledging success, for example, because both components would be experiencing the same condition. Correlation with prior year also may not connote carryover effects, but instead could simply mean that if the conditions are the same between years, then reproductive success is about the same. Variation in environmental and reproductive parameters may not be continuous, but instead change may occur after a

threshold is crossed from one relatively stable environmental state to another (e.g., a regime shift, Mantua et al., 1997).

5.2. Timing

Timing of breeding was the most important predictor of laying success for kittiwakes. Similarly, Shultz et al. (2009) found timing explained 78% of variability in laying success and 94% of the variability in total reproductive success in kittiwakes in the Gulf of Alaska. Many studies have shown that across a wide range of bird families, individuals breeding earlier do better than individuals breeding later in a given season (e.g., Hipfner, 1997). Better body condition in adult birds likely leads to both earlier breeding and higher laying success (Faivre et al., 2001).

Elevated stress levels (as measured by corticosterone, CORT) may result in a delayed time of breeding (Schoech et al., 2009) or reduced return rate of individuals (Goutte et al., 2010 for

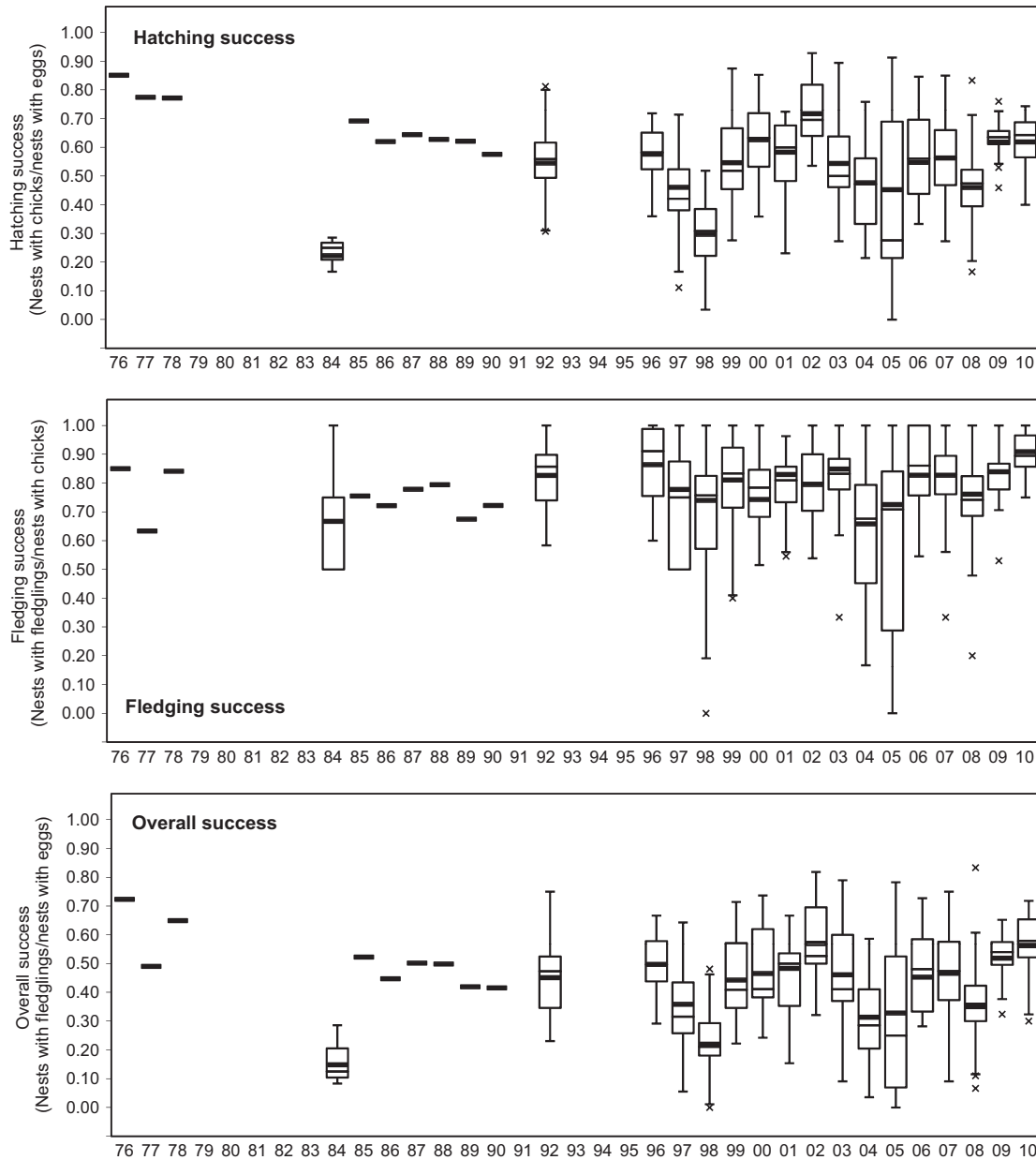


Fig. 4. Success of thick-billed murres at St. Paul Island, Alaska in 1976–2010. Thick horizontal lines represent total annual success calculated across all nests each year. Box plots are calculated using annual success rates in each plot as the sample unit: boxes represent first and third quartiles, whiskers are 1.5x the interquartile range (IQR), and “x” shows outlier plots beyond 1.5xIQR; years with no data for individual plots have no box plots.

kittiwakes) the following breeding season. Similarly, delayed egg-laying can be associated with high stress during the incubation stage and low laying success (Kitaysky et al., 2010) and overall productivity (Verhulst and Nilsson, 2008). Shultz et al. (2009) indicated that in the Gulf of Alaska, timing of breeding in kittiwakes was driven by amount of pre-lay food availability rather than timing of peak food, suggesting that timing of nest initiation was dictated by energetic constraints early in the season rather than anticipation of future food supplies (see also Sorensen et al., 2009).

For murres, although we found no relationship between timing and hatching success (the earliest stage measured in this study), timing was a good predictor of fledging success. This suggests that pre-egg laying food conditions appear to have little effect on the timing of breeding of murres. Instead, murre timing may be driven by conditions later in the breeding season that favor chick survival. Regular et al. (2009) found that breeding chronology in common

murres in the Atlantic was related to food availability for chicks, such that hatching coincided with peak capelin abundance. There might be some advantages to chick survival to hatch earlier (that were not seen in the egg stage) such as seasonal variation in food conditions (Shultz et al., 2009). Alternately, it is possible that we did not detect an effect in hatching success because the ratio of noise to signal was too high (especially given we had no measure of laying success). Variation in murre timing was half that of kittiwakes, both in our study and in the Gulf of Alaska (Shultz et al., 2009). An alternative explanation is that such low variation in murre timing may be due to social reasons, such as selection pressure to synchronize with neighbors (Benowitz-Fredericks and Kitaysky, 2005).

We found no strong correlations between timing of either species and any of the regional or local environmental variables in our models. Shultz et al. (2009) found that kittiwake timing and laying success were related to sea surface temperature, with

earlier laying and higher laying success in colder years when forage fish were more abundant. In the Pribilofs, Byrd et al. (2008a) indicated that *detrended* kittiwake timing was inversely correlated with sea ice extent and winter sea surface temperature (neither of the two detrended). Detrending is typically used when a variable distorts or masks a variable of interest and Byrd et al. (2008a) suggested it was useful to emphasize high frequency interannual variability over interdecadal variability. We feel it was not warranted here because timing was not correlated with any of the other climate covariates, and because when timing was removed from our model, the other variables did not improve the fit. Further, Byrd et al. (2008a) found no relationships between timing and other measures of sea ice or temperature, leading us to infer what they found was a weak relationship.

5.3. Environmental variables

We found little evidence that any local or regional current-year climate variables were useful predictors of reproductive output at any stage. Although the top models ($\Delta AIC < 2$) occasionally contained an inconsistent suite of climate variables, all had parameter estimates with 90% confidence intervals overlapping zero. This is an apparent contradiction to previous studies (Table 4), which all used different subsets of the data and different analytical techniques. However, several lines of reasoning suggest to us that relationships described earlier were either weak or spurious. First, they are sometimes contradictory. Satterthwaite et al. (2012) found a *weak positive* relationship between sea surface temperature and overall reproductive success of kittiwakes in the Pribilofs using these same datasets. Using two different subsets of years, Springer (1992) and Byrd et al. (2008a) both reported a *negative* relationship with sea surface temperature. Using yet another subset of the same data, Decker et al. (1995) and Lloyd (1985) reported none at all with current-year sea surface temperature. Second, most earlier studies ran simple correlations on point estimates of mean reproductive success (but see Satterthwaite et al., 2012 and Zador et al., 2013).

We were able to reproduce some of these earlier findings by running multiple simple correlations on our expanded dataset (Table 4), but not many others after adding more years. In fact, these relationships completely “go away” using our single-model approach accounting for individual nest and plot level effects, as well as all of the possible interacting reproductive and environmental variables. Our results strongly suggest that the outcome of previous year success was a better predictor of each stage of reproductive success than any environmental variables. Clearly changes in the environment are likely to affect foraging conditions and effort allocation in seabirds but relationships with fertility do appear to be straightforward. We propose that the condition of adults at the end of a breeding attempt might carry on across sequential nesting stages, masking any weak relationship with environmental variables in a given year.

Our modeling approach has two points of caution that may have lessened our precision in detecting relationships with environmental variables. First, model averaging increases standard error estimates for parameters to account for model uncertainty. This would make us less likely to call a variable “significant” based on its confidence interval overlapping with zero (if parameter estimates were not averaged across the entire model suite). Second, our modeling approach requires data to be present for every variable for each year, so 9 years with incomplete data for one or more climate variables were discarded, mostly earlier in the dataset.

A major difficulty in modeling ecological data and trying to define climatic predictors is the huge suite of time series with potentially weak mechanistic links (see Renner et al., 2012 for discussion). Our model sets were very large for even a 36-year study. Therefore we were forced to limit our models to include only climatic variables from the current year. Zador et al. 2013 found lagged effects (up to two years) of environmental forcing mechanisms with indices of Pribilof seabird productivity combined across species, and Lloyd (1985) found that kittiwake success on St. George Island was negatively correlated with sea surface temperature lagged one and two years.

Table 4

Literature review of relationships between climatic variables and breeding success of black-legged kittiwakes and thick-billed murrets at the Pribilof Islands. Sources and specifics of climate datasets vary among studies (i.e., Byrd et al., 2008 and Satterthwaite et al., 2012 use different datasets for “Spring SST”). Positive (+) and negative (–) signs show significant positive and negative relationships, respectively; signs with “SG” or “SP” indicate a relationship found only for St. George or St. Paul. All studies use correlation analysis except Satterthwaite et al. (2012). Results from this study are pairwise Spearman rank correlations ($P < 0.1$) shown for comparison with other similar analyses.

Species	Source	Years	Success parameter	Annual SST	Winter SST	Spring SST	Summer SST	Ice	PDO	Wind speed
Black-legged	Satterthwaite et al., 2012	1985–2009	Overall			+	None	–	+	
Kittiwake	Byrd et al., 2008a	1975–2005	Overall		None	–SG ^a	None	+ ^{SG}		
	Springer, 1998	1976–1995	Overall	+SG ^b						
	Decker et al., 1995	1975–1990	Overall	None						
	Springer, 1992	1976–1990	Overall	–						
	Springer, 1991	1976–1990	Overall	–						
	Lloyd, 1985	1976–1984	Overall	None ^{SG}			None ^{SG}			– ^{SG}
	This study (correlations)	1975–2010	Laying		None	None	None	None	None	None
	This study (correlations)	1975–2010	Hatching		None	None	+	None	None	None
	This study (correlations)	1975–2010	Fledging		+	+	+	–	+ ^{SP}	+ ^{SG}
	This study (correlations)	1975–2010	Overall		None	+ ^{SP}	+	None	None	None
Thick-billed	Byrd et al., 2008a	1975–2005	Overall		None	– ^{SG}	–	None		
Murre	Decker et al., 1995	1975–1990	Overall	–						
	Lloyd, 1985	1976–1984	Overall	None ^{SG}			None ^{SG}			None ^{SG}
	This study (correlations)	1975–2010	Hatching		None	None	None	None	None	None
	This study (correlations)	1975–2010	Fledging		None	– ^{SG}	– ^{SP}	None	None	+ ^{SP}
	This study (correlations)	1975–2010	Overall		None	– ^{SG}	None	None	None	None

^a Detrended dataset only.

^b Analysis is divided into two atmospheric regimes based on low pressure state (1976–1989) or high pressure state (1990–1995); in each state, seabird productivity is higher in warmer years.

5.4. Diet variables

Success of murres and kittiwakes was associated with prey in a few model sets. Murre fledging success was higher when they fed their chicks fewer myctophids (which represented 0.97 of the signal in all offshore prey items), in spite of the relatively high energy content of that prey type (Van Pelt et al., 1997). These results may be spurious, however, because myctophids were rarely found in murre chick diets in the Pribilofs. Myctophids are a deep-water fish occurring beyond the shelf edge; if this is a real result, it suggests that murre fledging success was best when they were able to find food on the shelf, rather than when they had to travel further to the basin for myctophids. None of the shelf-based prey species (pollock, sand lance, or capelin) predicted fledging success, however, indicating that murres may switch readily among prey types and proximity of foraging resources is more important than any one prey type. Kittiwakes had lower fledging success when they fed their chicks more amphipods (which were correlated 0.5 with total invertebrates and -0.6 with total fish). This pattern suggests that fish of any type are preferred to zooplankton for chick feeding, likely due simply to their larger size. Optimal foraging predicts that individuals tend to feed chicks with larger prey than for themselves (Davoren and Burger, 1999).

While we assume that foraging conditions are among the primary drivers of stress and ultimately demographic parameters, we have few data about food availability in most systems. Shultz et al. (2009), who did have a short-term dataset including food availability in the Gulf of Alaska, found that for kittiwakes, pre-laying food availability explained variation in kittiwake laying success and clutch size while murre reproductive success was best explained by food availability during chick-rearing. Although both frequency of occurrence and number of individuals of prey types in seabird diet may somewhat reflect food availability (as described in Renner et al. (2012)), they may need to be paired with foraging studies to determine foraging effort that can be linked to breeding success (Burke and Montevecchi, 2009; Suryan et al., 2002).

Analysis of seabird diet data and breeding success is also biased by collection constraints as well as temporal variation in sampling methods. Most available diet information is obtained during the chick-rearing period, which differs from diet collected at other times of the breeding season (Renner et al., 2012). Murres are more constrained in chick provisioning by their need to deliver single, large prey items they can carry in their bill, while they often use smaller, more abundant crustaceans during incubation when they feed for self-provisioning (Ito et al., 2010). Regurgitated kittiwake chick and adult diet samples often cannot be separated, but are assumed to be more similar (Renner et al., 2012).

5.5. Differences between St. Paul and St. George islands – local-scale implications

Probabilities of success in each stage were correlated between islands, except for murres during the chick-rearing period. Fledging success may relate more to local foraging conditions, as birds are tied to the nest and restricted to make shorter foraging trips to meet chick-feeding rates (Gaston et al., 2007; Orians and Pearson, 1979). Fittingly, tracking data from murres during the chick period in 2008–2010 indicated no overlap in foraging areas between the two islands (Harding et al., 2013), suggesting birds on different islands were subject to different foraging conditions. Laying and hatching success, in contrast, appear set up by conditions earlier in the season (prior to laying or the previous year), when birds can forage widely. Although we have no information on foraging range prior to the chick period, we would predict more foraging overlap earlier in the nesting cycle when adults are not tied as closely to

the nest, resulting in more similar conditions for birds on each island. That fledging success was correlated for kittiwakes (which can fly farther than murres) may be due to occasional overlap in foraging locations between islands (Paredes, pers. comm. data).

Murres had higher reproductive success on St. George Island than on St. Paul Island, mostly coming from strong differences in the egg period. Presumably St. George Island's location closer to the continental shelf break means more regular access to high quality prey (see Renner et al., 2012, indicating strong diet differences between the two islands). In contrast, kittiwake productivity did not differ significantly between islands, during which time the overall population of kittiwakes on St. Paul Island has declined but the population on St. George Island has remained stable (Byrd et al., 2008b). Seabird productivity may have a relatively low contribution to population change (Schmutz and Byrd, 2004), and other factors such as adult survival require further investigation in each locality. A recent tracking study indicated that both kittiwakes and murres at St. Paul Island increased foraging effort to cope with food shortages on the middle shelf, successfully raising chicks but at a cost of higher adult nutritional stress in some years. Birds at St. George Island, in contrast, may have been buffered from the lack of quality prey on the shelf by closer proximity to shelf-edge resources, leading to lower stress levels of piscivorous seabirds on St. George Island compared to St. Paul Island (Benowitz-Fredericks et al., 2008). High stress levels may lead to higher adult mortality or to higher chick mortality after fledging (Goutte et al., 2010; Kitaysky et al., 2010). Preliminary analysis using four years of resighting data suggests adult survival/permanent emigration may be lower at St. Paul Island than at St. George Island for both seabird species (AMNWR, unpubl. data); however larger data sets are required for conclusive results. Further efforts to measure adult survival, and other variables such as colony-age structure ("experience"), recruitment rates, and movements between colonies are needed for a better understanding of causes affecting population processes (Wooller et al., 1992).

5.6. Implications for seabird monitoring

We expected to find that each sequential stage of reproductive success was reflective of different climate conditions in the marine environment. Instead, we found that climate effects were strongly trumped by success in the previous year or previous stage and, for kittiwakes, timing of breeding. This suggests adult condition (going into the breeding season or going into each successive stage) plays a strong role in success for kittiwakes and murres at the Pribilof Islands. Given that both species, particularly murres, appear to work hard to raise their chicks at the cost of high nutritional stress in poor years (Benowitz-Fredericks et al., 2008; Satterthwaite et al., 2010) fledging rates may not reflect adult condition unless local food conditions are above or below certain thresholds. We currently have no consistent time series on body condition or stress during any part of the year in the Pribilof Islands. Data on body condition of banded birds at the beginning and end of the breeding season in successive years would be valuable for relating breeding performance to condition at the individual level and understanding differences at the population level.

Although prey availability earlier in the season or at the end of the prior season appear important drivers of breeding success, we lack much data on fall, winter, and early spring foraging conditions for seabirds. Diet data from seabirds are important as a proxy of prey quality and amount (biomass) that can be used to explain differences in breeding success (e.g., Suryan et al., 2002 for kittiwakes). Data on foraging behavior, available from an increasing number of GPS tracking studies, can be used in conjunction with diet data for a better picture of foraging effort (e.g., Paredes et al., 2014) and possible predictor of body condition or physiological

stress. However, most diet and tracking data are collected during the chick period (e.g., Barrett et al., 2007; Burger and Shaffer, 2008) and we have little understanding of food resources the rest of the year. Given the period prior to the breeding season seems to play an important role in determining reproductive output, some index of winter food availability seems critical.

Winter foraging conditions may also be critical for the transition between good years (high breeding success) and bad years (low breeding success). Food availability regardless of the mechanisms behind its variability is ultimately the driving force affecting foraging effort, adult condition, nutritional stress and at in many circumstances reproductive success. Given that hatching or laying success along with previous year breeding success were good predictors of breeding success within a year suggest food conditions prior to chick-rearing are critical. If previous year's success determines the following year's laying and/or hatching success (which is in turn a predictor of fledging success), then success would presumably continue to be always good or always bad until something breaks the cycle. We know that overall success of kittiwakes and murre fluctuates among years (see Figs. 1–4) so foraging conditions might override the influence of previous year's success. Unfortunately, the lack of enough data in seabird diets (proxy of prey quality/amount) at early stages of the reproduction precluded us to determine its influence in laying or hatching success. Likewise, foraging conditions during the non-breeding season may be also an important missing link to understanding what drives reproductive success at the Pribilof Islands.

5.7. Conclusions

Using a 36-year dataset of reproductive success for black-legged kittiwakes and thick-billed murre at the Pribilof Islands, we modeled sequential stages of success using reproductive, climatic, and diet variables. We found: (1) Success in previous stages and the previous year were more important predictors of overall success than any environmental variables. Timing was also an important predictor of laying success for kittiwakes. These relationships suggest a cascade effect, in which adult condition carrying over from the previous year plays a large role in reproductive success. (2) An increase of oceanic prey (mediated by distance traveled) and small invertebrates in diets negatively affects fledging success, which may indicate low availability of high quality prey near the colonies. (3) Differences in reproductive variables at St. Paul and St. George islands do not completely match population trends between the two islands, suggesting adult survival and condition may be important contributors to population dynamics. (4) Adult condition and foraging conditions during the non-breeding season may be important datasets for understanding drivers of kittiwake and murre reproductive success at the Pribilofs.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2014.03.006>.

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