

# Combined influence of intrinsic and environmental factors in shaping productivity in a small pelagic gull, the black-legged kittiwake *Rissa tridactyla*

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**ABSTRACT:** While we have a good understanding in many systems of the effects of single variable changes on organisms, we understand far less about how variables act in concert to affect living systems, where interactions among variables can lead to unanticipated results. We used mixed-effect models to evaluate the effects of multiple variables that we expected to play a role in the early reproductive stages of a North Pacific seabird, the black-legged kittiwake *Rissa tridactyla*, during 1992–2008 using data collected on known-aged individuals. Our work revealed the potential for contrasting stressor effects across successive stages of reproduction. Bird age, timing of egg laying, and winter ENSO conditions best explained individual laying success, such that laying success was greater when parents were older, the average winter ENSO index was positive (as occurs during El Niño episodes), and the median laying date for the colony was earlier. Age and salmon run timing (a proxy for predator presence at the colony) best explained hatching success, such that hatching success was greater when parents were older and when salmon runs were early. Identifying such differential effects of multiple stressors across consecutive reproductive stages can greatly enhance our ability to interpret trends and manage populations in the face of changes currently occurring in living systems.

**KEY WORDS:** *Rissa tridactyla* · Black-legged kittiwake · Seabird · Productivity · Age · Multiple stressors

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## 1. INTRODUCTION

The ecological literature is replete with experiments documenting the effects of biotic and abiotic factors acting singly on a vast assortment of ecological levels, taxa, and morphological, physiological, and genetic expressions of individual organisms. However, we increasingly recognize that in nature, organisms, populations, and communities do not experience such influential forces in a vacuum; instead, multiple stressors (i.e. factors that can cause adverse

effects) act simultaneously on a system, either additively, antagonistically (i.e. combined effects are less severe than the sum of individual effects), or synergistically (i.e. combined effects are more severe than the sum of individual effects; Folt et al. 1999, but see Piggott et al. 2015) to affect the system in complex ways. These interactions can be further complicated by the pathway of each stressor's effect; some may affect an organism directly, while others may act indirectly by altering the effects of another stressor (e.g. coral reef system, Ban et al. 2014). Stressors that

have little influence on their own can have substantial effects in combination (e.g. tree swallows, Gentes et al. 2006, Hallinger & Cristol 2011), and non-additive interactions may lead to unexpected outcomes (e.g. freshwater systems, Ormerod et al. 2010, Jackson et al. 2016). Several reviews of controlled experiments across a wide range of taxa and environments suggest that interacting stressors often do have non-additive effects (e.g. Darling & Cote 2008), especially in marine systems (e.g. Crain et al. 2008).

As part-time denizens of 2 systems (marine and terrestrial), breeding seabirds provide ideal case studies for investigating how multiple factors may act in concert to influence population vital rates. All seabirds are tied to terrestrial nesting sites during the breeding season but must acquire food for themselves and their offspring from the marine environment. Seabirds are currently undergoing dramatic global declines (Palczyński et al. 2015); their downward population trends combined with their potential role as marine indicators (e.g. Einoder 2009, Le Bohec et al. 2013) provide powerful incentives for us to understand how environmental and biological factors from both systems combine to affect seabird population parameters.

Seabird species are generally long-lived; evidence suggests that adult survival is well-buffered against environmental perturbation (e.g. Brandt's cormorants, Schmidt et al. 2015). In contrast, seabird reproductive parameters (e.g. hatching success, provisioning trip duration, fledgling mass) are more sensitive; stressor effects are likely more detectable in breeding metrics than in other aspects of seabird biology. Many studies have focused on the effects of food supply on seabird reproductive success (i.e. fledgling production per breeding attempt; e.g. Cury et al. 2011), a widely used (e.g. Dragoo et al. 2012) and relatively cost-effective metric that can be estimated from 1 or 2 visits to a breeding colony. However, seabird reproductive success involves a sequence of events from nest site establishment and mate acquisition through egg production and incubation, culminating in successful chick rearing. Reproductive success therefore integrates the effects of a variety of factors that differentially affect each stage of the process (Etterson et al. 2011) and may therefore be largely buffered by competing forces at different stages, obscuring relationships between stressors and seabird breeding parameters.

At the colony level, events affecting early stages of reproduction could be masked by later events with opposing effects on reproductive success. For example, negative effects associated with high breeder

mortality prior to the breeding season can be partially compensated by increased recruitment of pre-breeders (e.g. black-legged kittiwakes, Porter & Coulson 1987). Likewise, when populations exist under density-dependent controls (e.g. northern gannets, Lewis et al. 2001), heavy mortality of eggs or young nestlings may release survivors from the effects of prey limitation. Such confounding effects may hinder our attempts to understand and interpret patterns in seabird reproductive success.

Although many studies have investigated reproductive success at the level of a colony or regional population (e.g. Alaskan seabird species, Dragoo et al. 2012), comparatively few have done so at the level of individual breeders, which is necessary to identify contrasts in stressor effects among reproductive stages. Further, individual characteristics (e.g. physical condition, age, phenotype) can lead to correlations in the probabilities of success across reproductive stages and breeding attempts in long-lived seabirds. Inherent quality (i.e. individual variation in performance that persists over a lifetime) can affect both survival and reproductive success, where better-quality individuals may secure more resources seemingly without incurring extra costs (e.g. black-legged kittiwakes, Cam et al. 2002), allowing them to both survive and reproduce better than lesser-quality counterparts (van Noordwijk & deJong 1986). In particular, reproductive success can vary with age, where success is relatively poor in young birds (e.g. short-tailed shearwaters, Wooller et al. 1990; wandering albatross, Weimerskirch 1992) and gradually improves with age (e.g. northern fulmars, Ollason & Dunnet 1978; western gulls, Sydeman et al. 1991; brown thornbills, Green 2001). This age-based pattern may result at least in part from improvements in breeding performance associated with a combination of proximate factors that may correlate with age. These include breeding experience (e.g. short-tailed shearwaters, Wooller et al. 1990; but see Pyle et al. 2001 for Cassin's auklets), particularly when comparing initial attempts to later attempts (black-legged kittiwakes, Naves et al. 2007), and mate retention (e.g. Australasian gannets, Ismar et al. 2010), which can in turn be reduced following a skipped breeding season (Pyle et al. 2001).

How do multiple intrinsic and environmental factors combine to affect sequential breeding stages in individual seabirds? While we know that food quality and availability are crucial during the chick-rearing period (e.g. black-legged kittiwakes, Jodice et al. 2006), other biological and environmental conditions prior to hatching may also be important to seabird

productivity. Our objective was to evaluate contributions of multiple environmental, biological, and individual variables and their potential for interaction across reproductive stages, including laying and incubation in a long-lived colonial seabird. We tested hypotheses describing laying success as a function of breeder age, winter conditions, spring conditions, early breeding season conditions, population size, carryover effects, and combinations of the above (Table 1). We also tested hypotheses describing hatching success as a function of these same factors as well as incubation weather and predation (Table 2).

## 2. MATERIALS AND METHODS

### 2.1. Focal species

Black-legged kittiwakes (hereafter 'kittiwakes') are small, long-lived (mean life expectancy at a North Pacific colony = 13 yr; Hatch et al. 1993) gulls with a circumpolar distribution throughout the northern hemisphere and a global population size estimated to be from 17 to 18 million individuals (Delany & Scott 2006). These birds are largely piscivorous, foraging in both nearshore and pelagic habitats. Many questions remain about their winter distribution; kittiwakes from Prince William Sound, Alaska, USA, can disperse widely throughout the North Pacific during the non-breeding season but may not always do so (McKnight et al. 2011), a behavior that may depend upon the severity of weather in the northern Gulf of Alaska. Kittiwakes are colonial cliff-nesters, rearing 1, 2, or rarely 3 young per breeding season. As in many seabird species, both parents share incubation and chick-rearing duties equally (Coulson & Wooller 1984). Both mate- and nest-site fidelity are high (Coulson & Thomas 1985).

### 2.2. Site description

The Shoup Bay kittiwake colony is located in northeastern Prince William Sound (PWS), Alaska, USA (61° 10' N, 146° 35' W; Fig. 1). Shoup Bay is a fjord that adjoins Port Valdez with a tidewater glacier that terminates at the fjord's western end. The fjord connects to PWS via a reversing tidal river 0.7 km in total length. Through the early 2000s, the fjord was frequently filled with large icebergs calved from the glacial face. By the late 2000s, the

glacier had retreated mostly onto land and the fjord became mostly iceberg-free. The kittiwake colony is located primarily on the south-facing side of a rocky island ~0.4 km in length and ~100 m from the mainland. Based on annual nest counts starting in 1985, colony size peaked in 2002, with 19 000 actively breeding birds, but declined to 14 100 active breeders by 2008, the final year of this study. Predators at the colony are predominantly avian and include bald eagles *Haliaeetus leucocephalus*, peregrine falcons *Falco peregrinus*, common 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*. Eagle-driven mortality can be substantial in some years due to the eagles' 'sit-and-wait' strategy that allows opportunistic corvids to take advantage of nests vacated by flushing adult kittiwakes (Robbins 2009). We noted anecdotally in several years that eagle attendance at the colony seemed to decrease substantially after salmon began spawning in nearby Valdez Arm, where large numbers (50+) of eagles were observed congregating on several visits.

### 2.3. Field data collection

#### 2.3.1. Laying/hatching success and histories of known-aged individuals

Annually during 1979 and 1988–2008, we banded up to 600 (95% confidence interval =  $369 \pm 74$ ) 12–32 day-old kittiwake chicks at the Shoup colony. We individually marked chicks with either a 3-band cohort-specific mark or a unique color band combination. Four to 8 observers resighted (with binoculars and 60× spotting scopes) color-banded birds during 1992–2010 in mornings and evenings in May when breeders were actively building nests. We divided the colony into 10 major nesting sections, delineated by easily discerned cliff features, and sections were resighted  $9.8 \pm 0.7$  (mean  $\pm$  95% CI) times on average each year between 1998 and 2010; resighting effort in earlier years was not recorded but was comparable. We evaluated each individual's breeding status based on the number of times it was recorded at a particular nest site, as holding a nest site is the essential condition that affects kittiwake survival irrespective of reproductive success (Aubry et al. 2011) and is a good indicator of an individual's intent to breed. Birds seen at a particular nest site 3 or more times were considered to be probable breeders ('breeders'

Table 1. Single variable hypotheses and variables explaining laying success in known-aged black-legged kittiwakes *Rissa tridactyla* from the Shoup Bay colony in Prince William Sound (PWS), Alaska, USA. 'Winter' refers to November–February, prior to the breeding season; 'spring' refers to March–April, prior to the breeding. PDO: Pacific Decadal Oscillation; GOA: Gulf of Alaska; US FWS: US Fish and Wildlife Service

Hypothesis	Variable	Source
<b>Laying success is a function of individual characteristics.</b>		
	Individual kittiwake age	US FWS Monitoring data
	Number of years individual bred previously	US FWS Monitoring data
	First or second breeding attempt vs. later	US FWS Monitoring data
	Breeding status in previous year	US FWS Monitoring data
<b>Laying success is a function of winter conditions.</b>		
	Mean winter PDO index values	JISAO (2016)
	Mean winter Niño 3.4 index values	ESRL (2016a)
	Mean monthly modeled winter winds in northern GOA	ESRL (2016b)
	N–S vector component	
	Absolute value N–S vector component	
	E–W vector component	
	Absolute value E–W vector component	
	Absolute value combined vectors	
	Mean monthly winter sea surface temperature	ESRL (2016c)
	PWS (60° N, 147° W)	
	Northern GOA (58° N, 147° W)	
	Maximum monthly winter sea surface temperature	ESRL (2016c)
	PWS (60° N, 147° W)	
	Northern GOA (58° N, 147° W)	
<b>Laying success is a function of pre-breeding conditions.</b>		
	Median laying date	US FWS Monitoring data
	Mean monthly modeled spring winds in northern GOA	ESRL (2016b)
	N–S vector component	
	Absolute value N–S vector component	
	E–W vector component	
	Absolute value E–W vector component	
	Absolute value combined vectors	
	Mean monthly spring sea surface temperature	ESRL (2016c)
	PWS (60° N, 147° W)	
	Northern GOA (58° N, 147° W)	
<b>Laying success is a function of population size.</b>		
	Number of nesting pairs at the Shoup colony	US FWS Monitoring data
<b>Laying success is a function of carryover effects from previous season.</b>		
	Colony productivity in previous season	US FWS Monitoring data

hereafter). Birds seen fewer than 3 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 (and was the proximate cause of nearly all breeding failures), the majority of predation occurred following the period when we resighted marked individuals at the colony, and thus did not appreciably influence breeding status assignments by removing banded breeders prior to their third sighting.

Every 3 d from the beginning of the incubation period until the research crew departed in early August each year, we monitored contents of nests (mean  $\pm$  95% CI = 120  $\pm$  40 nests) belonging to known-aged breeders. The youngest birds included in this study were 3 yr old. The spread of ages gradually increased over time as the number of banded cohorts increased. In 1996, the earliest year included in our analysis, most individuals monitored (N = 133) were between 3 and 8 yr old, with a small group (N = 10) of 17 yr old birds. In contrast, nests monitored in

Table 2. Single variable hypotheses and variables explaining hatching success in known-aged black-legged kittiwakes *Rissa tridactyla* from the Shoup Bay colony in Prince William Sound (PWS), Alaska, USA. Details as in Table 1

Hypothesis	Variable	Source
<b>Hatching success is a function of individual characteristics.</b>		
	Individual kittiwake age	US FWS Monitoring data
	Number of years individual bred previously	US FWS Monitoring data
	First or second breeding attempt vs. later	US FWS Monitoring data
	Breeding status in previous year	US FWS Monitoring data
<b>Hatching success is a function of winter conditions.</b>		
	Mean winter PDO index values	JISAO (2016)
	Mean winter Niño 3.4 index values	ESRL (2016a)
	Mean monthly modeled winter winds in northern GOA	ESRL (2016b)
	N-S vector component	
	Absolute value N-S vector component	
	E-W vector component	
	Absolute value E-W vector component	
	Absolute value combined vectors	
	Mean monthly winter sea surface temperature	ESRL (2016c)
	PWS (60° N, 147° W)	
	Northern GOA (58° N, 147° W)	
	Maximum monthly winter sea surface temperature	ESRL (2016c)
	PWS (60° N, 147° W)	
	Northern GOA (58° N, 147° W)	
<b>Hatching success is a function of pre-breeding conditions.</b>		
	Median laying date	US FWS Monitoring data
	Mean monthly modeled spring winds in northern GOA	ESRL (2016b)
	N-S vector component	
	Absolute value N-S vector component	
	E-W vector component	
	Absolute value E-W vector component	
	Absolute value combined vectors	
	Mean monthly spring sea surface temperature	ESRL (2016c)
	PWS (60° N, 147° W)	
	Northern GOA (58° N, 147° W)	
<b>Hatching success is a function of incubation conditions.</b>		
	Precipitation	NCEI (2016)
	Number of days in June with precipitation >2.54 mm	
	Mean daily maximum precipitation in June	
	Mean precipitation in June	
	Temperature	NCEI (2016)
	Mean daily maximum temperature in June	
	Mean temperature in June	
<b>Hatching success is a function of feeding conditions.</b>		
	Mean incubation body condition	US FWS Monitoring data
	Pacific herring spawn detections within 45 km	Moffitt (2016)
	Modeled age-1 herring abundance in PWS	Estimated from HRMT (2014)
<b>Hatching success is a function of eagle predation.</b>		
	Salmon run timing (alternate eagle prey)	S. Moffitt pers. comm.
	Day of year when salmon landings surpass 30000 fish	
	Day of year when salmon landings surpass 1 million fish	
	Salmon run magnitude	S. Moffitt pers. comm.
	Total salmon landings for the season	
<b>Hatching success is a function of population size.</b>		
	Number of nesting pairs at the Shoup colony	US FWS Monitoring data
<b>Hatching success is a function of carryover effects from previous season.</b>		
	Colony productivity in previous season	US FWS Monitoring data

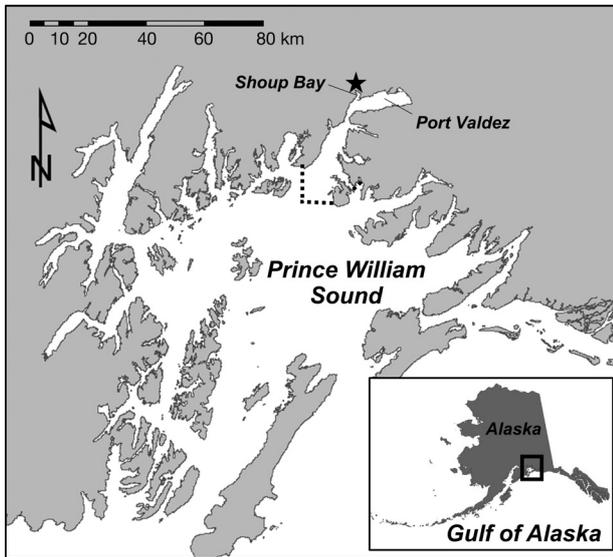


Fig. 1. Location (star) of the Shoup Bay kittiwake colony in Prince William Sound, Alaska, USA. Dotted line represents the approximate outer boundaries of the Valdez fisheries subdistricts providing salmon timing data. Inset map shows the location of Prince William Sound within Alaska

2008 belonged to individuals ranging in age from 4 to 20 yr ( $N = 151$ ) (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m633p207\\_supp.pdf](http://www.int-res.com/articles/suppl/m633p207_supp.pdf)). We improved sample sizes of older ( $>16$  yr) birds by monitoring nests of individuals banded as adults (minimum age = 2 yr) that were at least 16 yr old (i.e. banded in 1991 and observed in the 2006–2008 samples). While the bulk of breeders had either failed or fledged chicks by the time we ceased monitoring each year, we were sometimes unable to document the final fate of late-hatching chicks that had not yet fledged by the end of the monitoring season; we therefore restricted our investigation to laying success (i.e. whether 1 or more eggs were laid in the nest of a probable breeder) and hatching success (i.e. whether 1 or more eggs hatched in nests where 1 or more eggs were laid).

In addition to gathering these data on reproductive success, we also constructed a breeding history for each individual using the breeding state criterion described above. We were thus able to compute the following individual metrics for each bird: (1) the number of seasons in which the individual previously bred, (2) whether the current breeding season represented the individual's first or second attempt at breeding vs. a later attempt, and (3) whether the individual bred in the previous season. For a limited number of cases in which the individual's mate was also banded, we were able to deter-

mine whether the individual was breeding with the same mate vs. a different mate compared to the previous season.

### 2.3.2. Median laying date

We calculated breeding phenology annually for the colony using nests located in ~15 permanent 'productivity plots' that included both edge and central nesting habitat patches. We captured Polaroid photos of each productivity plot section as seen from above and numbered all of the nests ( $N \approx 30$  per photo) visible from the photo vantage point. We recorded the contents of each nest every 3 d beginning prior to egg laying. Because we were interested only in calculating a median lay date from these data, we combined plots into a simple random sample representing the entire colony. We used these data to calculate the median date on which the first egg was laid in each nest (Table S2 in the Supplement), and used this metric to represent breeding season phenology, which reflects local foraging conditions immediately prior to the kittiwake breeding season in Alaska (Moe et al. 2009, Shultz et al. 2009), as seabirds likely must attain a minimal body condition threshold before commencing breeding (e.g. Sorensen et al. 2009). We also calculated the median date on which the first chick hatched in each nest as an alternative phenology metric, although hatch timing potentially can be uncoupled from breeding commencement if clutches are replaced or the onset of incubation is delayed after clutch completion.

### 2.3.3. Food availability

We represented prey availability using archived Pacific herring *Clupea pallasii* (hereafter 'herring') datasets, as herring of age classes 0 and 1 are important components of the kittiwake diet during the breeding season (Suryan et al. 2000). From aerial surveys of spring herring spawning activity (Moffitt 2016), we extracted the number of geographic cells ( $100 \text{ m}^2$ ) representing herring spawning activity within foraging range of the Shoup Bay colony. We designated foraging range as the area within 45 km overwater distance from the colony (the maximum average annual forage range documented by Ainley et al. 2003). We related this metric to the current year's kittiwake productivity as an index of age-0 herring availability. We used the modeled number of age-3 herring from a PWS age-structure-analysis

(HRMT 2014) as an index of age-1 herring availability for kittiwake productivity 2 yr prior to the estimate.

We also randomly selected and captured adult kittiwakes during different stages of the breeding season each year between 1995 and 2008 for body condition assessment. Capture devices included snare traps set on the nest or roosting rock, telescoping noose poles, and dipnets. Trapping locations were chosen from regions of the colony cliffs accessible from above or below by scrambling, by boat, or by extension ladder. We recorded the nest contents of each bird, then measured the bird's mass, head-bill length (head), diagonal right tarsometatarsus length (tarsus), and flattened right wing length (wing). We noted any existing leg band combinations and banded any previously unmarked birds with unique color band combinations.

#### 2.3.4. Breeding population size and productivity

Beginning in 1985 and continuing to the present, we visited the Shoup Bay kittiwake colony in PWS annually as part of a larger effort to document breeding effort and productivity at all kittiwake colonies in PWS. In late May/early June, when birds had begun incubation, we counted all active nests (attended by at least 1 bird) on all faces of the colony with binoculars from a boat. We then counted all chicks present at the end of the chick-rearing period (late July/early August), when the vast majority of chicks were either close to fledging or recently fledged but still sporadically attending the colony, and divided the total number of chicks by the total number of nests each year to calculate colony productivity. Although some recently fledged individuals were undoubtedly missing from each count, we assume that the percentage of recently fledged chicks present at the colony was similar among years and that this index provides a reasonable annual index of productivity.

## 2.4. Data analysis

### 2.4.1. Body condition index

We used average body condition across the colony each year to represent annual mean forage conditions during the laying and incubation stages. To this end, we developed a body condition index for all adults measured during 1996–2008 ( $N = 1154$  observations) using the difference between predicted and observed standardized mass as predicted by standardized structural body size, with positive residual values indicating that a bird had more mass than predicted based on its size ('good' condition) (Table 3). We created the structural body size index from the first principal component (PC) of a principal components analysis (PCA) of the body size measurements for all bird observations with complete measurements (head, tarsus, and wing;  $N = 1034$ ) conducted using the 'prcomp' function from the stats library in Program R (R Core Team 2016). Next, we calculated the body size index value for all birds and regressed mass on body size index value using the 'lm' function (R Core Team 2016). We then interpolated missing tarsus measurements from 1996 and 2000 ( $N = 49$ ) using a linear regression of tarsus predicted by head and wing size for all birds and calculated their body size index values using interpolated tarsus values. As kittiwake mass changes over the course of the breeding season (Bech et al. 2002), we averaged within-year body condition index values for birds measured throughout the incubation period (May) only each year, thus generating a single average incubation body condition value per year to use in reproductive success modeling. Coulson (2011) found a gradual increase in adult mass over the course of the incubation period at a British colony; if Pacific kittiwakes follow the same pattern, this trend would be averaged out in a similar fashion within each year of our study by the dispersed timing of our captures within the incubation season. These values thus represent the relative differences in average incubation condition from year to

Table 3. Equations describing body condition of black-legged kittiwakes captured at the Shoup Bay colony in Prince William Sound, Alaska, USA, during 1996–2008. PC: principal component

Equation	Formula
Structural size PC1	$PC1 = -0.613head - 0.553tarsus - 0.564wing$
Tarsus prediction	$tarsus = 0.188 head + 0.025 wing + 9.641$
Mass prediction	$\ln(mass) = -0.098 \times \ln(body\ size\ index + 3.6) - 6.14$
Body condition index	$body\ condition\ index\ value = 100 \cdot \frac{(observed\ mass - predicted\ mass)}{predicted\ mass}$

year. Because the average body condition variable was available only for 1996 on, we restricted our analysis to laying and hatching success between 1996 and 2008. Sex was unknown for most birds; however, while size is known to differ by sex in kittiwakes (Jodice et al. 2000), the relationship between body size and mass does not (Golet & Irons 1999).

#### 2.4.2. Relationships between age and experience

We investigated the relationships between age and experience by computing correlation coefficients between age and (1) the number of previous years' breeding experience, (2) whether the current breeding attempt was the first or second of the individual's life vs. a later attempt, and (3) whether the individual bred in the previous season. We also used the 'glm' function from the stats library in R to perform a logistic regression of age on mate retention from the previous year using a subset of data from individuals with known mates in the current and previous seasons. We then compared the results to the null model and used Akaike's information criterion (AIC) model selection criteria to assess the relationship between age and the probability of mate retention.

#### 2.4.3. Reproductive effects modeling

In addition to kittiwake metrics and food availability described above, we also modeled individual reproductive success as a function of a number of annual environmental factors we hypothesized could affect kittiwake reproduction via carryover effects (Tables 1 & 2). First, we calculated the mean winter (November through February) Pacific Decadal Oscillation (PDO) index value prior to the breeding season using index values representing the first PC of North Pacific (>20° N latitude) monthly sea surface temperature (SST) anomalies (JISAO 2016). We computed a similar mean winter El Niño–Southern Oscillation (ENSO) index value from a 5 mo running mean SST anomaly in the region between 5° N–5° S and 170°–120° W (ESRL 2016a). We suspected that migratory decisions may be made based on local conditions affecting foraging efficiency, specifically wind and SST. For an index of winter and spring (March through April) weather conditions in the northern coastal shelf of the Gulf of Alaska, we extracted and averaged mean monthly modeled wind magnitudes for 59° N, 147° W (ESRL 2016b). We similarly averaged monthly optimally interpolated SSTs (ESRL 2016c) for

2 representative locations that may be used by non-migrating individuals in the winter (McKnight et al. 2011): PWS (60° N, 147° W) and the northern coastal shelf of the Gulf of Alaska (59° N, 147° W) for both winter and April, the month prior to commencement of breeding activity. We characterized temperature and precipitation patterns experienced during incubation each year with June temperature and precipitation metrics documented by the Valdez Weather Service Office (61.13° N, 146.35° W), including mean temperature, mean maximum daily temperature, mean daily precipitation, mean maximum daily precipitation, and the number of June days with precipitation >2.54 mm (NCEI 2016).

We characterized annual predation pressure from the largest predation risk (eagles), with pink salmon harvest data for Valdez Arm and Port Valdez from Steve Moffitt of the Alaska Department of Fish and Game (S. Moffitt pers. comm.). From these, we calculated 2 phenology metrics (calendar dates, adjusted for leap years, when the annual harvest surpassed 30 000 and 1 million fish, respectively). Anecdotal observations over the breadth of our study of the colony suggest that eagles switch from preying on kittiwakes to preying on salmon when the spawning migration begins in earnest. Our initial metric was designed to predict this prey switch (i.e. the duration of pre-salmon-run eagle attendance at the colony), and the latter metric was designed to represent the degree of switching (i.e. the total seasonal harvest, or availability of salmon as a prey source for eagles. We centered and scaled all continuous covariates prior to modeling.

We used the 'glmer' function from the 'lme4' library (Bates et al. 2014) in Program R (R Core Team 2016) to build mixed effects models that predict either laying or hatching success of individually identifiable birds and as a function of individual age, colony size, colony breeding phenology, mean colony body condition, food availability, salmon phenology, colony productivity in the previous year, winter (prior to breeding) and spring winds, winter SST, April SST, regional climate indices, and local weather during the breeding season. We designated individual bird identity and colony section (southern islands, south end, central face, north end, and back side) within year as random effects to account for variation in section quality over time as the colony expanded and contracted. We modeled the probability of success as a binomial variable with a logit link and used the 'bobyqa' optimizer as the numerical optimization algorithm. During each analysis set, we evaluated the top model's residual distribution, normality, and dispersion to assess whether model assumptions

were met. If residuals were sufficiently homoscedastic and either normally distributed or not overdispersed, we accepted the model fit as sufficient.

Prior to multi-variable modeling, we identified the best representative metric within each hypothesis group by building and comparing single variable models with AIC model selection. Variable groups included individual characteristics (individual age, number of years of previous breeding experience held by the individual, whether the current season represented the individual's first or second breeding season, and breeding status in the previous year), breeding phenology (median lay date for alpha eggs, median hatch date for alpha chicks), food conditions (average incubation body condition, age-0 herring index, age-1 herring index), winter wind (north-south wind magnitude, directional north-south wind, east-west wind magnitude, directional east-west wind, and overall wind magnitude), spring wind (same variables as winter wind), winter SST (PWS winter maximum monthly SST, PWS winter monthly mean SST, Gulf of Alaska winter maximum monthly SST, Gulf of Alaska winter monthly mean SST), April SST (PWS April SST, Gulf of Alaska April SST), incubation precipitation (maximum daily July precipitation, number of July days with precipitation >2.54 mm, total July precipitation), temperature (July mean maximum daily air temperature, July mean daily air temperature, predator pressure (date salmon landings exceeded 30 000 fish, date salmon landings exceeded 1 million fish, total salmon landings), and climate (mean winter Niño 3.4 index value, mean winter PDO index value). The remaining candidate predictive variables (colony size, colony productivity in the previous season) were represented by only a single index. The single variable within each set that outperformed the others in the set as well as the null model and that was not correlated ( $r \leq 0.65$ ) with a higher ranked representative variable was used in subsequent modeling.

We tested our intrinsic and extrinsic hypotheses by first combining all of these best-performing metrics with the variables for hypotheses represented by only a single metric (if the metric outperformed the null model in a single variable model) into a global model. We then tested each hypothesis by determining whether the individual removal of each variable decreased model performance by 2.0 AIC.

We constructed a final model for both laying success and hatching success using the set of variables whose omission increased the AIC score. Variables whose omission improved model performance were dropped from the final metric set (and the associated hypothesis was considered not supported). For bor-

derline variables that worsened the global model's AIC score by fewer than 2 AIC units upon omission, we assessed their relative contribution by comparing them to the same model with the variable removed.

#### 2.4.4. Model validation

Although our primary purpose was hypothesis testing, we also tested the predictive power of the 2 top models (for laying and hatching success) with metrics from all supported hypotheses by using them to predict success for observations of known-aged birds that were not individually identifiable and thus not used in the training dataset, substituting 0 for the random effect coefficient associated with individual identity for each record. Starting with probability >0.50 = success and iteratively adding/subtracting to the success threshold to maximize the proportions of correctly predicted successes and failures, we determined the probability threshold value (to the nearest 0.01) that optimized these proportions.

### 3. RESULTS

#### 3.1. Colony-level metrics

Colony size during the study period ranged from 6128 nests in 1999 to 9545 nests in 2002 (mean  $\pm$  95% CI = 7711  $\pm$  578 nests). Likewise, mean colony productivity (i.e. chicks produced per nest built) ranged 0.002 in 2005 to 0.62 in 1996 (mean  $\pm$  95% CI = 0.29  $\pm$  0.12 chicks nest<sup>-1</sup>).

#### 3.2. Body condition index

We captured 86  $\pm$  26 (mean  $\pm$  95% CI) randomly selected birds each year for body condition assessment (N = 1034 individuals captured in total during 1995–2008). Of these, 41  $\pm$  10 were captured each June while incubating eggs. The first PC of the PCA explained 64% of the variance in the structural body measurements. The linear regression of tarsus on head and wing measurements (used to interpolate the body size index for 49 individuals across all years) produced homoscedastic, normally distributed residuals and an R<sup>2</sup> value of 0.26. The regression of the natural logarithm of mass on the natural logarithm of body size produced homoscedastic, normally distributed residuals and an R<sup>2</sup> value of 0.25 (Table 3).

### 3.3. Relationships between age and experience

We calculated the correlation coefficients with the full dataset for the relationships between age and the number of years of breeding experience (0.79), whether the individual was breeding for the first or second time (0.67), and whether the individual had bred in the previous season (0.02). For the subset of records with known mates in the current and previous season ( $N = 56$ ), logistic regression revealed the 95% CI for the slope coefficient to be  $0.21 \pm 0.19$  for the effect of age on mate retention, suggesting a significant positive relationship, as '0' was not included in the confidence interval. The model including age outperformed the intercept-only model for mate retention (AIC = 88.17 and 92.53, respectively). The correlation coefficient between age and mate retention in this dataset was 0.29.

### 3.4. Laying success

#### 3.4.1. Model results

We modeled laying success using 1595 observations of 877 known-aged individuals during 1996–2004 and 2006–2008, representing 1245 successes and 350 failures; 42% ( $N = 372$ ) of the individuals were observed in more than 1 year, representing 68% of the observations.

*Single variable models.* The top-performing variables from each category were age (individual char-

acteristics), median first egg lay date (phenology), average incubation body condition (food), winter N–S wind magnitude (winter wind), spring wind magnitude (spring wind), PWS winter maximum monthly SST (winter SST), PWS April SST (April SST), and the mean winter Niño 3.4 index value (climate) (Table S3 in the Supplement). The April SST models failed to outperform the null model and were not incorporated in further modeling. While the winter wind and winter SST models did outperform the null model, each top-ranked variable correlated with a better performing variable from another category (winter wind/colony size:  $r = 0.84$ , winter SST/median first lay date:  $r = 0.67$ ) and were also not used in further modeling in order to avoid violating the assumption of independence among predictor variables. The top-ranked single-variable model explaining laying success included only age as a fixed effect (Akaike weight  $w_i > 0.99$ ). Median first lay date was the second-best predictor of laying success ( $\Delta\text{AIC} = 47.57$ , Akaike weight  $w_i < 0.01$ ).

*Multiple variable models.* While AIC selection favored the retention of colony size in the final multi-variable model, ANOVA results favored its elimination ( $p = 0.06$ ), and the reduced model performed equivalently during validation. Our final multivariable model of laying success therefore included only additive effects of age, median first lay date, and winter ENSO index ( $w_i = 0.32$ ; Tables 4 & 5), such that laying success was greater when an individual was older (slope estimate  $\pm$  SE =  $0.25 \pm 0.03$ ), the average winter ENSO index was positive (as occurs during El

Table 4. Performance of multiple variable generalized linear mixed effects models explaining the probability of laying success at a black-legged kittiwake colony in Prince William Sound, AK, from 1996–2008, with individual ID and nested year and colony section as random effects. 'Spring' refers to monthly values from March–April prior to the breeding season. The global model was of the form  $\text{Pr}(\text{eggs}) \sim \text{age} + \text{phenology} + \text{climate} + \text{colony size} + \text{condition} + \text{spring wind}$ . Models in the 'global minus one' set tested the ability of each variable to improve the model by comparing model performance of the global model versus the model with each individual variable removed. **Bold** type indicates models that performed worse than the global model due to the omission of influential variables. Models in the 'key variables' set explored the relative contribution of variables whose omission worsened the global model's performance by  $< 2.0 \Delta\text{AIC}$  units. Asterisk denotes the best-supported model based on a combination of AIC score, parsimony, and validation using non-individually identifiable data. Akaike weights are denoted by  $w_i$ , and  $k$  represents the number of model parameters

Set	Model	AIC	$\Delta\text{AIC}$ (from global)	$w_i$	Deviance	$k$
Global minus one	Global – spring wind	1381.72	–1.77	0.27	1366	8
	Global – condition	1383.46	–0.03	0.11	1367	8
	Global	1383.49	0.00	0.11	1365	9
	<b>Global – colony size</b>	1385.02	1.53	0.05	1369	8
	<b>Global – climate</b>	1390.91	7.41	0.00	1375	8
	<b>Global – phenology</b>	1391.50	8.00	0.00	1375	8
	<b>Global – age</b>	1467.18	83.69	0.00	1451	8
Key variables	Age + phenology + climate + colony size	1381.50	–1.99	0.30	1368	7
	*Age + phenology + climate	1383.00	–0.49	0.14	1371	6

Table 5. Fixed effect coefficients and random effect variance and standard error from the best-performing model of black-legged kittiwake laying success at the Shoup Bay colony in Prince William Sound, AK, from 1996–2008

FIXED EFFECTS				
Coefficient	Estimate	SE	z	p
Intercept	−0.35	0.22	−1.57	0.12
Age	0.25	0.03	8.02	<0.001
Phenology	−0.83	0.12	−6.67	<0.001
Climate	0.42	0.12	3.43	<0.001
RANDOM EFFECTS				
Intercept	Variance		SE	
Individual bird ID	0.22		0.47	
Colony section nested within year	0.30		0.55	

Niño episodes; slope estimate  $\pm$  SE =  $0.42 \pm 0.12$ ) and median laying date for the colony was earlier (slope estimate  $\pm$  SE =  $-0.83 \pm 0.12$ ). This model far outperformed the ‘age only’ model ( $\Delta$ AIC = 45.72) and was competitive with both the global model (AIC = 1383.49) as well as the top-scoring ‘global minus one’ model (‘global – spring wind’; AIC = 1381.72).

### 3.4.2. Validation

The laying success validation dataset included 617 records; of these, 537 represented successes and 80 represented failures. The top model for laying success described above (constructed from individually identified individuals) significantly predicted laying success for known-aged but individually unidentifiable individuals over the same range of years. Prediction using the final model was best using a cutoff of 0.86 (predicted laying success of 0.86 or higher = ‘success,’ less than 0.86 = ‘failure’). Using this cutoff value, 64 % of successes, 65 % of failures, and 64 % of overall outcomes were correctly predicted by the top model. Including colony size in the model did not substantially change its predictive ability; prediction in this case was best using a cutoff value of 0.85, with 65 % of successes, 63 % of failures, and 64 % overall outcomes correctly predicted.

## 3.5. Hatching success

### 3.5.1. Model results

We modeled hatching success using 1246 observations of 733 known-aged individuals during 1996–

2004 and 2006–2008, representing 562 successes and 684 failures; 42 % (N = 308) of the individuals were observed in more than 1 year, representing 66 % of the observations.

*Single variable models.* The top-performing variables from each category were age (individual characteristics), median first egg lay date (phenology), average incubation body condition (food), winter E–W wind magnitude (winter wind), spring directional N–S wind (spring wind), PWS winter maximum monthly SST (winter SST), PWS April SST (April SST), maximum daily July precipitation (precipitation), July mean maximum daily air temperature (temperature), the mean winter PDO index value (climate), and the date salmon landings exceeded 30 000 fish (salmon timing) (Table S4 in the Supplement). The April SST, precipitation, temperature, and climate models failed to outperform the null model and were not incorporated in further modeling. While the winter SST models did outperform the null, the top-ranked variable correlated with a better performing variable from another category (winter SST/median first lay date:  $r = 0.70$ ) and was not used in further modeling in order to avoid violating the assumption of independence among predictor variables. The top-ranked single-variable model explaining hatching success included only salmon timing ( $w_i = 0.27$ ; Table S4). Colony size was the second-best predictor of hatching success ( $\Delta$ AIC = 0.61,  $w_i = 0.20$ ).

*Multiple variable models.* Multivariable modeling identified only age and salmon timing as influential when all variables were considered simultaneously (‘global minus one’ model  $\Delta$ AIC = 2.92 and 4.28, respectively). The final multiple-variable model of hatching success included additive effects of age and the calendar date when the pink salmon harvest exceeded 30 000 fish ( $w_i = 0.14$  when included with all ‘global minus one’ models; Tables 6 & 7), such that hatching success was greater when birds were older (slope estimate  $\pm$  SE =  $0.07 \pm 0.02$ ) and when salmon runs were early ( $-0.84 \pm 0.25$ ).

### 3.5.2. Validation

The hatching success validation dataset included 537 observations of non-individually identifiable birds; of these, 279 represented successes and 258 represented failures. The top model for hatching success constructed with birds of known identity significantly predicted success in unidentified but known-aged individuals over the same range of years. Prediction was best using a cutoff of 0.52 (predicted

Table 6. Performance of multiple variable generalized linear mixed effects models explaining the probability of hatching success at a black-legged kittiwake colony in Prince William Sound, AK, from 1996–2008, with individual ID and nested year and colony section as random effects. The global model was of the form  $\text{Pr}(\text{chicks}) \sim \text{age} + \text{salmon timing} + \text{condition} + \text{phenology} + \text{winter wind} + \text{previous productivity} + \text{spring wind} + \text{colony size}$ . Asterisk denotes the final model formulation containing only those fixed effects whose omission significantly increased the AIC score of the global model. 'Winter' refers to monthly values from November–February prior to the breeding season. Other details as in Table 4

Set	Model	AIC	$\Delta\text{AIC}$ (from global)	$w_i$	Deviance	$k$
Global minus one	Global – colony size	1481.50	–1.92	0.15	1462	10
	Global – spring wind	1481.54	–1.88	0.15	1462	10
	Global – previous productivity	1481.85	–1.57	0.13	1462	10
	Global – winter wind	1481.90	–1.52	0.13	1462	10
	Global – phenology	1482.13	–1.30	0.11	1462	10
	Global – condition	1482.19	–1.23	0.11	1462	10
	Global	1483.42	0.00	0.06	1461	11
	<b>Global – salmon timing</b>	1486.34	2.92	0.01	1466	10
	<b>Global – age</b>	1487.71	4.28	0.01	1468	10
Final model	*Age + salmon timing	1481.66	–1.76	0.14	1472	5

Table 7. Fixed effect coefficients and random effect variance and standard error from top model of black-legged kittiwake hatching success at the Shoup Bay colony in Prince William Sound, AK, from 1996–2008

FIXED EFFECTS				
Coefficient	Estimate	SE	$z$	$p$
Intercept	–1.29	0.29	–4.48	<0.001
Age	0.07	0.02	2.91	0.004
Salmon timing	–0.84	0.25	–3.36	<0.001
RANDOM EFFECTS				
Intercept	Variance		SE	
Individual bird ID	0.13		0.37	
Colony section nested within year	1.84		1.36	

laying success of 0.52 or higher = 'success,' less than 0.52 = 'failure'). Using this cutoff value, 75 % of successes, 73 % of failures, and 74 % of overall outcomes were correctly predicted by the final model.

#### 4. DISCUSSION

Successful seabird reproduction at the Shoup Bay colony is driven by factors that differ with reproductive stage. Laying success reflected a combination of seasonal carryover effects and age (or individual factors correlating with age), while hatching success correlated best with within-season effects, namely age and the salmon timing variable that we associate with predation pressure. The majority of defended nests in our study produced at least 1 egg, suggesting that individuals with the resources necessary to

establish and defend a nest site are also reasonably assured of laying success.

##### 4.1. Patterns in laying and hatching success

Median laying date was a strong predictor of laying success in PWS kittiwakes. Renner et al. (2014) and Shultz et al. (2009) also found a strong relationship between phenology and population-level laying success in kittiwakes breeding in the Bering Sea and the northern Gulf of Alaska, respectively. The Gulf of Alaska study, along with a similar study in the high Arctic north of Norway, further revealed that phenology was coupled with SST (Moe et al. 2009, Shultz et al. 2009) and corresponding patterns of fish availability, where years with colder SST had greater fish availability, allowing for earlier egg laying in kittiwakes (Shultz et al. 2009). While we found a similar link between phenology and laying success in Shoup kittiwakes, we found no comparable relationship between spring SST and laying success in our work, which may reflect our use of a coarser SST metric or, alternatively, a different prey/oceanography dynamic in PWS kittiwakes. The fact that phenology had such a strong relationship with laying success in 3 Alaskan populations with very different diet compositions (Dragoo et al. 2012) suggests that phenology drives laying success via some overarching process (e.g. spring bloom) that transcends specific diet composition.

We also found, somewhat counterintuitively, that winter El Niño conditions were associated with greater laying success the following spring. Orben et

al. (2015) noted that wintering kittiwakes in the North Pacific migrate less extensively during El Niño episodes, presumably due to a northward shift in favorable wintering conditions. Greater laying success in such years could therefore reflect some degree of migratory cost savings or changes in overwinter foraging success that lead to increased condition at breeding onset.

Bird age and salmon run timing had the strongest relationship with hatching success in Shoup Bay kittiwakes. Many studies report a trend toward greater reproductive success with age in seabird populations. This phenomenon in part reflects selective elimination of poorer quality individuals (black-legged kittiwakes, Cam et al. 2002, Aubry et al. 2009; Adelie penguins, Lescroël et al. 2009), which can cause an apparent increase in quality of a cohort through time (black-legged kittiwakes, Cam & Monnat 2000). Learning, including greater foraging experience in the marine environment (e.g. north Pacific seabirds, Porter & Sealy 1982; Manx shearwaters, Fayet et al. 2015), breeding experience (short-tailed shearwaters, Wooller et al. 1990), mate familiarity (Australasian gannets, Ismar et al. 2010), and the mate's own breeding experience (black-legged kittiwakes, Coulson 2011) also increase with age and improve breeding success.

Improvements in reproductive success with age may also reflect changing hormonal strategies and changes in individual phenology. Elliott et al. (2014) found that middle-aged kittiwakes from a colony in the Gulf of Alaska showed a lower stress response than young and old birds, suggesting a strategy of greater investment in reproduction during ages and years with high potential for success. This non-linear relationship between stress and age may mean that environmental factors may also interact with age. According to the reproductive success vs. age curves derived for this Gulf of Alaska kittiwake colony, however, the decline in reproductive performance may become most apparent after individuals reach an age of 15 yr or more, an age group not represented well in our study. Reproductive improvement with age and breeding experience may also occur via phenological pathways; Coulson (2011) reported that female kittiwakes at a well-studied British colony tended to lay earlier when they had more breeding experience, with less experienced females tending to lay later in the season. Earlier breeders generally had larger clutch sizes, larger eggs within those clutches, and higher breeding success than later breeders (Coulson 2011).

Our results likely reflect the combined effects of these factors on both laying success and hatching success in Shoup kittiwakes. The age effect was most apparent in our laying success modeling, where age was by far the best single predictor of success. Age was a less influential predictor of hatching success, likely owing in part to the conditional nature of our analysis, as individuals without eggs were not included in hatch success modeling. Although age outperformed indices for breeding experience, there were strong correlations among all of these variables. As such, 'age' here should be interpreted as a composite variable of sorts, integrating the effects of many other factors that improve an individual's breeding success over time. While predation is generally acknowledged to affect seabird reproductive success (e.g. roseate terns, Wittam & Leonard 1999), it is difficult and labor-intensive to quantify. Effects of predation vary among kittiwake colonies; nest predation is minimal in the oceanic Pribilof Islands (Byrd et al. 2008), but it can be substantial at coastal colonies accessible by mainland predators. Robbins (2009) found that bald eagles in particular posed a triple threat to Shoup kittiwakes; not only did they take an occasional adult, but their presence at the colony while hunting kept kittiwakes off their nests, exposing eggs to both opportunistic scavengers and the elements. According to our top models, hatching success at the Shoup colony was reduced in years with later salmon runs. We hypothesize that this pattern is the result of prolonged eagle presence at the colony when salmon runs are late, although additional study would be required to definitively establish this linkage.

Because predation may vary annually, identifying a proxy metric for predation effects can improve predictions of seabird productivity; including salmon timing in our analysis resulted in much more variation explained than individual age alone. Other drivers of kittiwake hatching success have been noted elsewhere. Population-level hatching success in kittiwakes from the Pribilof Islands in the Bering Sea, more than 300 km from the mainland and its predator populations, was associated with both laying success as well as the previous year's colony-wide reproductive success (Renner et al. 2014). This suggests that these remote colonies are driven largely by ecological factors internal to the population. In contrast, we found no relationship with the previous year's colony success, which suggests that factors external to the population, such as predation, may dampen or disrupt temporal correlation in annual productivity for Shoup Bay kittiwakes.

#### 4.2. Multiple stressors

Laboratory work on smaller organisms shows that in contrast to freshwater systems, where the majority of stressor interactions are antagonistic (Jackson et al. 2016), marine populations are more apt to experience synergistic interactions (Crain et al. 2008). Testing for such interactions in highly mobile macrofauna is somewhat more challenging, however, as it is virtually impossible to establish controlled experimental conditions in the field. Despite this limitation, researchers have identified synergistic interactions between food shortage and predation on seabird reproductive success (black-legged kittiwakes, Regehr & Montevecchi 1997) by modeling data collected in the field.

Our work revealed the potential for contrasting stressor effects across successive stages of reproduction. For example, the positive influence of an early salmon run on hatching success may partially compensate for negative effects of negative ENSO conditions on laying success in years when both occur. Likewise, negative winter ENSO conditions coupled with a late salmon run could be a sequential blow on laying and hatching success. Identifying the potential for differential effects of multiple stressors across consecutive reproductive stages, including stages not addressed here, can greatly enhance our ability to interpret trends and manage populations. The results of this study make the potential for interaction clear, but further work would be necessary to determine whether such interactions are likely to be additive or non-linear.

Regardless of the nature of these interactions, they are likely dynamic. We report 2 phenological events (the onset of egg laying and the timing of salmon migration) that are tightly tied to kittiwake reproductive success, although the timing of these events is not closely coupled ( $r = -0.08$ ), and phenological interactions that reflect discordant timing could profoundly alter the ultimate effects on reproductive success. Kittiwake reproduction would appear to be maximized if laying occurred significantly prior to salmon migration, but there were years where timing was different and lower reproduction occurred.

Dynamic interactions in phenology also may reflect other stressors. Shultz et al. (2009) found that kittiwake phenology in Lower Cook Inlet, Alaska (400 km from our study site), is determined by early season food availability ('constraint' hypothesis) rather than by anticipation of peak forage availability for chick rearing ('anticipation' hypothesis) (Shultz et

al. 2009). This linkage between early season conditions and the nesting schedule may allow mismatches to occur between kittiwake phenology and the timing of optimal prey availability for growing chicks, if the timing of optimal foraging resources for chicks is not tightly coupled to early season conditions (e.g. rhinoceros auklets, Watanuki et al. 2009; common guillemots, Burthe et al. 2012). We found evidence for a third phenological element, predator phenology, that could interact in complex ways with cues for laying onset and the availability of offspring food resources. With more timing components influencing reproductive success, the potential for mismatches increases dramatically.

Such patterns offer a glimpse into the potential resilience of seabirds to changes in parameters affecting breeding success. Phenology, in particular, is changing for many kittiwake populations, with a trend toward later timing in the North Sea (Frederiksen et al. 2004a, Burthe et al. 2012) and earlier timing in the Bering Sea (Byrd et al. 2008), but no significant trend for kittiwakes in a European high Arctic colony (Moe et al. 2009). Our work, along with that of Renner et al. (2014) and Shultz et al. (2009), highlights the important association between phenology and kittiwake laying success. However, the buffering potential of early salmon run timing suggests that poor food availability during the early breeding season may not have consistent effects on reproductive success. Conversely, reduced food availability early in the breeding cycle attributable to overfishing (e.g. Frederiksen et al. 2004b) or climate shifts (e.g. Hunt et al. 2002) may impair the ability of seabird colonies to produce chicks during years with prolonged predation periods, such as altered salmon migration with changing climates (e.g. Taylor 2008).

#### 4.3. Management implications

The International Panel on Climate Change predicts major transformations in the world's oceans in response to the rising concentration of greenhouse gases in the atmosphere (IPCC 2007). These changes will potentially shift species distributions, disrupt predator-prey interactions, impose new physiological constraints on organisms, and alter primary production levels (Sverdup et al. 1942, Mann 1993, Cox et al. 2000, Etherington et al. 2004, Sarmiento et al. 2004). In response, natural resource conservation and management strategies are shifting from species-specific approaches to ecosystem-based ap-

proaches and marine spatial planning (e.g. United Nations Educational, Scientific, and Cultural Organization Marine Spatial Planning Initiative, Executive Order No. 13547, Magnuson-Stevens Reauthorization Act 16.U.S.C. § 1801(3)(3), NOAA Next-Generation Science Plan, U.S. Fish and Wildlife Service National Wildlife Refuge System), yet the relationships among organisms and between organisms and their physical environment remain poorly understood (Weimerskirch et al. 2003, Arkema et al. 2006, Leslie & McLeod 2007). Our limited understanding of complex ecological interactions hinders our assessment of biological dynamics of marine ecosystems and potential effects of large-scale environmental disturbances such as climate change (Griffies 2004).

Seabirds in the early stages of their breeding cycle have the potential to react differently to stressors acting in concert. Exposure to one stressor can degrade an organism's ability to deal with a second, and alleviating pressure from that stressor could improve the organism's resilience to another stressor. Identifying and addressing such interactions may enhance the success of ecosystem management efforts. As climate change alters multiple aspects of marine systems simultaneously, our predictive abilities will rely upon our ability to understand effects of complex interactions on individuals, populations, and communities.

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