



# Timing of breeding and reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics

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**ABSTRACT:** Seabirds are thought to time breeding to match the seasonal peak of food availability with peak chick energetic demands, but warming ocean temperatures have altered the timing of spring events, creating the potential for mismatches. The resilience of seabird populations to climate change depends on their ability to anticipate changes in the timing and magnitude of peak food availability and 'fine-tune' efforts to match ('Anticipation Hypothesis'). The degree that inter-annual variation in seabird timing of breeding and reproductive performance represents anticipated food availability versus energetic constraints ('Constraint Hypothesis') is poorly understood. We examined the relative merits of the Constraint and Anticipation Hypotheses by testing 2 predictions of the Constraint Hypothesis: (1) seabird timing of breeding is related to food availability prior to egg laying rather than the date of peak food availability, (2) initial reproductive output (e.g. laying success, clutch size) is related to pre-lay food availability rather than anticipated chick-rearing food availability. We analyzed breeding biology data of common murres *Uria aalge* and black-legged kittiwakes *Rissa tridactyla* and 2 proxies of the seasonal dynamics of their food availability (near-shore forage fish abundance and sea-surface temperature) at 2 colonies in Lower Cook Inlet, Alaska, USA, from 1996 to 1999. Our results support the Constraint Hypothesis: (1) for both species, egg laying was later in years with warmer sea-surface temperature and lower food availability prior to egg laying, but was not related to the date of peak food availability, (2) pre-egg laying food availability explained variation in kittiwake laying success and clutch size. Murre reproductive success was best explained by food availability during chick rearing.

**KEY WORDS:** Phenology · Climate change · Food availability · Forage fish · *Rissa tridactyla* · *Uria aalge*

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## INTRODUCTION

The frequency of warm sea-surface temperature (SST) anomalies has increased across the globe (Mackas et al. 2007), which may be having dramatic consequences for the timing, abundance, and community composition of primary and secondary producers. Through a cascade of complex events, these effects

may be transferred through the food web, resulting in the altered timing and abundance of key prey items for seasonally breeding seabirds or marine mammals (Lit-zow & Ciannelli 2007, Mackas et al. 2007). This may result in mismatches between seabird timing of breeding, reproductive investment, and food availability, ultimately decreasing the fitness of individuals in a population (Visser & Both 2005). The potential for mis-

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matches between predator and prey dynamics are compounded for high-latitude breeding seabirds: the time window during which conditions are suitable for reproduction is short and may limit their ability to adjust timing of breeding to match shifts in timing of seasonal increases in food abundance.

Seabirds are long-lived, and trade-offs between costs of current reproduction versus maintaining residual reproductive value should be tightly regulated (Goodman 1974, Stearns 1992). Timing of reproduction in seabirds and the majority of other high-latitude nesting birds is ultimately timed to coincide with the seasonal peak of food availability (Lack 1968, Perrins 1970): those individuals that feed chicks when food is most abundant produce more offspring (e.g. Perrins 1991, Nager & Van Noordwijk 1995, Svensson & Nilsson 1995, Van Noordwijk et al. 1995) and have higher survival (Golet et al. 1998). Reproductive effort should also match food abundance during the period of peak energetic demand: having a larger brood than resources allow may result in the reduced condition of parents and chicks (Heaney & Monaghan 1995), and reduced survival (Golet et al. 1998).

Extensive effort has gone into monitoring the reproductive performance of seabirds as indicators of these changes and to predict their effects on seabird population dynamics. Across the globe, strong relationships have been found between seabird reproduction, climate, and food availability (e.g. North Atlantic: Wanless et al. 2007, Regular et al. 2009; North Pacific: Bertram et al. 2001, Mackas et al. 2007, Piatt et al. 2007; Central Pacific: Sydeman et al. 2001, Abraham et al. 2004; Antarctic: Le Bohec et al. 2008; tropical Pacific: Erwin & Congdon 2007). In other cases, due to the complex interactions of large and small-scale physical and biological processes, it is often unclear how environmental changes, food availability, and seabird reproductive biology are linked (Springer 2007). In light of efforts to understand these relationships, the need to distinguish between the role of adaptive adjustments in reproductive effort ('Anticipation Hypothesis') versus energetic constraints imposed by current food availability ('Constraint Hypothesis'; Durant et al. 2005, Visser & Both 2005) has become apparent. Species and populations capable of adjusting effort to match changes in the dynamics of their food availability will be more resilient to a changing environment.

Adaptive adjustments may be impossible for high-latitude nesting seabirds with a limited time window to reproduce (Svensson 1995) and potential energetic constraints on egg formation. To do so requires a lack of physiological constraint and the existence of reliable cues prior to egg laying that enable them to predict the timing and abundance of peak food availability,

months or weeks in advance. The onset of reproduction in birds is regulated by a combination of proximate cues that are fixed (e.g. photoperiod) and variable, which interact to modify timing of breeding and reproductive effort (Hahn et al. 1997). Variable proximate cues or 'supplemental cues' may include any environmental features (e.g. ocean temperature, food availability, weather); the only requirement is that they provide reliable information about variation in the timing and/or abundance of food during the period of peak energetic demand on parents (Wingfield et al. 1992). For seabirds, SST may be a useful supplemental cue, as timing of breeding in seabirds has been associated with changes in climate indices partially derived from SST (Rindorf et al. 2000, Durant et al. 2003, Frederiksen et al. 2004), as well as SST itself (Ainley et al. 1996, Bertram et al. 2001, Frederiksen et al. 2004). However, spring SST and food availability may be correlated (Ainley et al. 1996, Bertram et al. 2001) making it difficult to distinguish between its role as a supplemental cue or because it reflects food limitations.

Egg production is costly in terms of energy and nutrients (reviewed by Monaghan & Nager 1997) and is a common phenomenon in birds in general (reviewed by Svensson 1995). These costs increase for larger species (Meijer & Drent 1999). Seabird laying success is related to their physiological condition prior to egg laying (Daunt et al. 2002). Murre reproductive success and survival are related to stress hormone levels and food availability (Kitaysky et al. 2007). Supplemental feeding experiments with seabirds have produced mixed results, possibly because the act of feeding may interfere with a bird's perception of proximate cues: supplementally fed kittiwakes laid eggs earlier (Gill & Hatch 2002, Gill et al. 2002), laid larger clutches (Gill & Hatch 2002, Gill et al. 2002), and had higher laying success (Lancot et al. 2003) than unsupplemented controls. However, they advanced the laying date relatively little compared to natural variation, and laying success was unchanged in 2 yr (Gill et al. 2002). Supplementally fed lesser black-backed gulls *Larus fuscus* did not advance laying (Hiom et al. 1991, Bolton et al. 1993), but increased clutch size (Bolton et al. 1993). Thus, timing of breeding and reproductive performance may reflect a combination of adaptive adjustments and physiological constraints, and the relative importance of these factors is unclear.

To estimate the extent to which seabird timing of breeding and reproductive performance reflect current food limitations versus anticipated food, it is necessary to simultaneously measure the seasonal dynamics of prey availability and seabird reproductive performance. We quantified the seasonal dynamics of seabird food availability using 2 proxies (SST and near-shore fish abundance) while simultaneously mea-

surging timing of breeding and reproductive performance of 2 colonial seabird species, the common murre and black-legged kittiwake. The goals of this analysis were: (1) to assess the degree to which inter-annual variation in the seasonal dynamics of food availability accounted for variation in seabird timing and breeding and reproductive performance, (2) evaluate the strength of evidence in support for the 'Anticipation' versus 'Constraint' Hypotheses. For the second goal, we specifically addressed 2 predictions of the 'Constraint Hypothesis': (1) seabird timing of breeding is related to food availability prior to egg laying rather than to the date of peak food availability, (2) initial reproductive output (e.g. laying success, clutch size) is related to pre-lay food availability rather than to anticipated chick-rearing food availability.

## MATERIALS AND METHODS

**Study area.** Our work was conducted at and around 2 seabird colonies in Lower Cook Inlet, Gulf of Alaska, from May to September in 1996 to 1999. The colonies, Gull Island (east side of Cook Inlet; 59° 35' N, 151° 19' W) and the Barren Islands at the mouth of Cook Inlet (58° 55' N, 152° 10' W), are separated by about 100 km. The data presented here were collected as part of a larger study and have been published elsewhere (see Piatt & Harding 2007 for references and references herein).

**Proxies of food availability.** To assess the seasonal dynamics of food availability for murre and kittiwakes, we used 2 proxies: SST and near-shore fish abundance. To examine the effects of small-scale, regional differences in oceanographic conditions (Abookire & Piatt 2005, Speckman et al. 2005), we measured SST and near-shore fish abundance immediately adjacent to each study colony.

SST may be a reliable reflection of food availability in Cook Inlet (for both birds and scientists): (1) colder spring SST reflects stronger winter upwelling, more nutrient-rich surface water, a prolonged phytoplankton bloom, greater zooplankton abundance, and potentially higher survival and recruitment of forage fish (Cooney 2007); (2) the distribution and abundance of principle prey species of murre and kittiwakes are closely tied to surface temperatures in Cook Inlet (Robards et al. 2002, Abookire & Piatt 2005, Speckman et al. 2005); and (3) approximately 80% of the principle prey species for murre and kittiwakes in Cook Inlet feed in the top 30 m of the water column (Abookire & Piatt 2005, Speckman et al. 2005, Piatt & Harding 2007).

SSTs were obtained by deploying temperature loggers (StowAway and TidbiT models, Onset Electron-

ics) 3 to 10 m below the low tide line. They recorded temperatures every 10 min during June to August. Data were unavailable until August in 1996 at the Barrens. Average daily temperatures were used in the analyses.

We used beach seines to sample near-shore fish abundance in surface waters adjacent to breeding colonies where birds were known to actively forage (Speckman 2004). We used small-meshed nets designed to capture small schooling fish that are the appropriate size for seabird prey (80 to 150 mm). For detailed methods see Robards et al. (1999). Sites were sampled every 2 wk, weather permitting, near Gull Island from late May to early September and at the Barren Islands during June through August, 1996 to 1999. Seines were also conducted year round at Gull Island in 1996. Nets were deployed from a small boat and set parallel to shore, about 25 m from the beach. Two sites were sampled at the Barrens and 12 sites at Gull Island (except at Gull Island in 1996 where an additional 26 sites were sampled). Beach seine trawling was conducted within a 1.5 h window on either side of low tides. A single set was carried out on each site visit as this provided adequate representation of species richness and dominant species rank (Allen et al. 1992, Robards et al. 1999).

Catch per unit effort (CPUE) was calculated as the total catch of all forage fish taxa (80 to 150 mm) per seine (Litzow et al. 2000). Forage species included in the analyses were sand lance *Ammodytes hexapterus*, herring *Clupea pallasii*, and all species of salmonids (*Oncorhynchus* spp.), *Osmeridae*, and *Gadidae*. These fish species and size classes comprised >90% of the diet (frequency of occurrence in stomach samples) of kittiwake and murre adults in this study (Shultz et al. 2002, Van Pelt et al. 2002). CPUE data were  $\log(x+1)$  transformed to meet assumptions of homoscedasticity for parametric statistical procedures (Zar 1999), then averaged by site and day (Litzow et al. 2000).

**Timing of clutch initiation and reproductive performance.** Egg-lay dates and reproductive performance were measured at both colonies during 1996 to 1999, using sample plots and standardized methods (Birkhead & Nettleship 1980, 1982, Hatch & Hatch 1988, 1989, 1990). We monitored 10 to 11 kittiwake plots, containing 25 to 30 nests. Kittiwake plots were checked every 3 d.

We monitored 5 to 10 murre plots with an average of 20 and 22 nest sites with eggs. Murre plots were checked every 1 to 2 d at Gull Island and every 3 d at the Barren Islands from observation points on the island using binoculars and telescopes.

Murre chicks were considered 'fledged' if they disappeared from the nest site  $\geq 15$  d after hatching—the minimum nest departure age (Swennen 1977). Kittiwake chicks were considered fledged if they were

observed at the nest until 32 d old (fledging age is typically 42 d; Baird 1994).

For kittiwakes, laying success (LS) was defined as the percentage of nest structures in which 1 or more eggs were laid. We could not estimate this for murre, as many eggs are laid and lost and it is nearly impossible for us to keep track of these failed attempts. **Clutch size (CS)** is the mean number of eggs per nest in which eggs were laid. **Hatching success (HS)** is the percentage of eggs laid that hatched. **Total reproductive success (RS)** is the number of chicks fledged per nest built for kittiwakes, and chicks fledged per egg for murre.

**Data analysis. Proxies for food availability:** We estimated 'lay SST' by calculating the average SST for the first half of June for kittiwakes and the first half of July for murre, as average lay date differed between species: the first half of June for kittiwakes and the first half of July for murre.

We estimated near-shore fish abundance for the exact dates of interest by fitting non-linear regressions and interpolation. We determined the best fitting non-linear function by averaging all from all years at each colony, including year round data from 1996 at Gull Island. The data followed a uni-modal distribution, and we compared the fit of a quadratic function to a Gaussian distribution. The Gaussian function provided the best fit to the data (Table 1, Fig. 1) and was defined by the equation:

$$y = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(-\frac{1}{2}\left[\frac{x-\mu}{\sigma}\right]^2\right)} \quad (1)$$

We used the fitted curves to estimate several parameters of near-shore abundance: 'lay CPUE', 'chick CPUE', and **peak CPUE date**. Lay CPUE was defined as fish abundance at the onset of egg formation, or the average lay date minus the egg formation duration (14 d for kittiwakes; 15 d for murre; Baird 1994, Ainley et al. 2002). We defined 'chick CPUE' as near-shore fish abundance from average hatch date through the peak demand date (PDD). We defined PDD as the average

date when chicks reach maximum energetic demands (kittiwakes: 26 d, Gabrielsen et al. 1992; murre: 20 d). Murre growth rates increase roughly linearly through fledging (Benowitz-Fredericks et al. 2006), and we defined murre PDD as the average fledging age of murre in this study. **Peak CPUE date was the date when near-shore fish abundance reached its highest level.**

**Timing of clutch initiation and reproductive performance:** In order to pool data from both colonies, between which geographic differences in water temperature, food supply and breeding biology persisted among years (Robards et al. 1999, Abookire & Piatt 2005; Speckman et al. 2005, Piatt et al. 2007), **data were converted into colony-specific annual residuals by subtracting the average of all years from the value of a given parameter for each year.** Each colony-year was treated as a sample unit. Before pooling data from different colonies for analyses, we first used analysis of covariance (ANCOVA) on annual residuals to test for colony effects. All ANCOVA tests for colony-effects were non-significant.

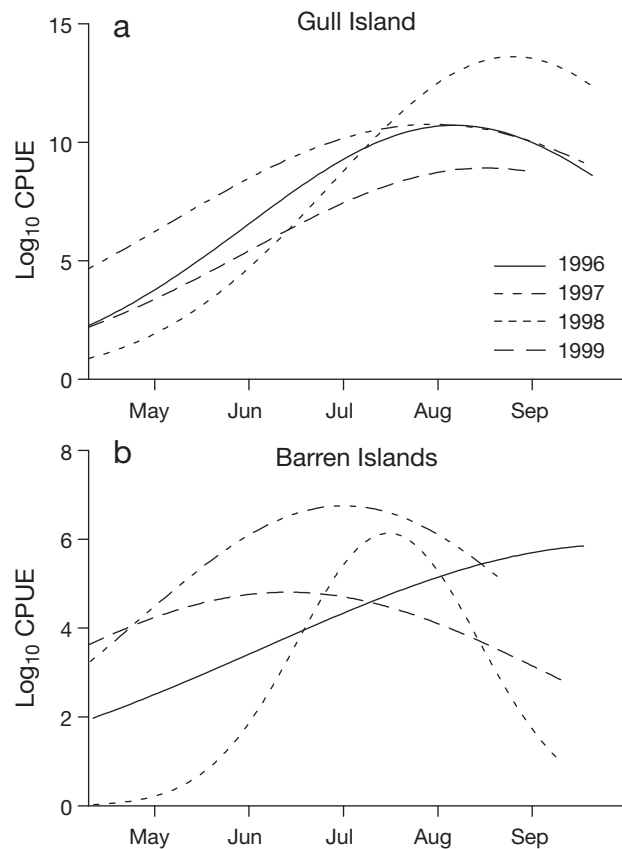


Fig. 1. Seasonal dynamics of forage fish abundance among years (1996–1999) at (a) Gull Island and (b) Barren Islands. Curves represent data fitted with a Gaussian function. Goodness of fit statistics are presented in Table 1. Curves were used to estimate forage fish abundance at the onset of egg laying, forage fish abundance at the period of peak energetic demand, and **the date of peak food abundance.** CPUE: catch per unit effort

Table 1. Summary of goodness of fit statistics for the seasonal dynamics of forage fish abundance (catch per unit effort, CPUE) around Gull and the Barren Islands, 1996–1999, fitted using Gaussian functions

Island	Year	R <sup>2</sup>	SD of residuals	df (n – 3)
Gull	1996	0.95	0.64	4
	1997	0.91	0.32	3
	1998	0.86	1.36	5
	1999	0.74	0.60	4
Barren	1996	0.93	0.25	2
	1997	0.90	0.32	2
	1998	0.83	1.22	2
	1999	0.91	0.31	3

**Environment:** Pearson's correlation was used to examine the relationship between lay SST and lay CPUE. Non-linear regressions were performed with Graphpad Prism version 4.00 for Windows. All other statistical analyses were performed with SAS (ver 91, 2003).

### Beach seine catch composition

### Seasonal dynamics of near-shore fish and peak demand date

Table 2. Catch per unit effort (CPUE) of the major taxonomic groups caught in beach seine sets in June to August 1996–1999 at Gull and Barren Islands

[illegible]



May to early June (Robards et al. 1999). Peak near-shore fish abundance (peak CPUE date) was 22 August (26 June to 21 August) at Gull Island, and 26 July (4 July to 22 August) at the Barren Islands (Fig. 1). Lay date and PDD were not correlated with peak CPUE date. PDD was calculated by adding the peak demand age for each species to mean lay date, so the correlation statistics are identical (kittiwake:  $r = 0.10$ ,  $p = 0.81$ ,  $n = 8$ ; murre:  $r = 0.26$ ,  $p = 0.53$ ,  $n = 8$ ).

### SST and near-shore fish abundance

Lay SST and lay CPUE were negatively correlated for both species (murre:  $r^2 = 0.63$ ,  $p = 0.03$ ,  $n = 7$ ; kittiwake:  $r^2 = 0.98$ ,  $p = 0.0001$ ,  $n = 7$ ) and was similar between colonies (ANCOVA;  $SST \times Colony$ :  $F_{2,4} = 0.68$ ,  $p = 0.43$ ).

### Lay date, SST, and food availability

The model that best explained variation in timing of breeding for murre and kittiwakes contained the single variable of lay SST; however, there was nearly equal support for the model containing lay CPUE for kittiwakes (ER = 1.45; Fig. 2, Table 3). There was no evidence in support of other models for either species (ER > 77 for the next competing model; Table 4).

As lay SST increased, lay CPUE decreased, and both species laid eggs

later. This relationship was similar among colonies (ANCOVA;  $SST \times Colony$ , murre:  $F_{2,4} = 0.0$ ,  $p = 0.99$ ; kittiwake:  $F_{2,4} = 0.27$ ,  $p = 0.64$ ; lay CPUE  $\times$  Colony, kittiwake:  $F_{2,4} = 0.28$ ,  $p = 0.66$ , murre:  $F_{2,4} = 0.11$ ,  $p = 0.76$ ).

### IRO and food availability

The best model contained only the variable lay CPUE: it explained over 66 % of variation in kittiwake clutch size (Table 4). The best model for kittiwake LS contained only lay date, with weak support for the

Table 3. *Rissa tridactyla* and *Uria aalge*. Models of egg-laying date for kittiwakes and murre nesting at Gull and the Barren Islands, Cook Inlet, Alaska, 1996–1999, using Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>). K: number of model parameters + 1, R<sup>2</sup>: coefficient of determination

Variable	K	R <sup>2</sup>	SSE	$\Delta AIC_c$	$w_i$	Evidence Ratio
<b>Kittiwake</b>						
Lay SST	3	0.95	5.53	0.00	0.59	1.0
Lay CPUE	3	0.96	6.17	0.76	0.40	1.5
Peak CPUE date	3	0.93	19.19	8.70	0.01	77.6
Lay CPUE + peak CPUE date	4	0.92	3.87	11.50	0.00	314.8
Lay SST + peak CPUE date	4	0.93	5.30	13.70	0.00	945.4
Lay SST + lay CPUE	4	0.93	5.31	13.70	0.00	946.0
Lay SST + lay CPUE + peak CPUE date	5	0.75	3.16	52.07	0.00	$2.0 \times 10^{11}$
<b>Murre</b>						
Lay SST	3	0.96	3.08	0.00	0.98	1.0
Lay SST + lay CPUE	4	0.96	1.46	8.77	0.01	80.2
Lay SST + peak CPUE date	4	0.94	2.27	11.87	0.00	377.8
Lay CPUE	3	0.91	30.36	16.01	0.00	2998.2
Peak CPUE date	3	0.16	32.55	16.50	0.00	3826.4
Lay CPUE + peak CPUE date	4	0.10	29.93	29.91	0.00	$3.1 \times 10^6$
Lay SST + lay CPUE + peak CPUE date	5	0.17	1.27	49.82	0.00	$6.6 \times 10^{10}$

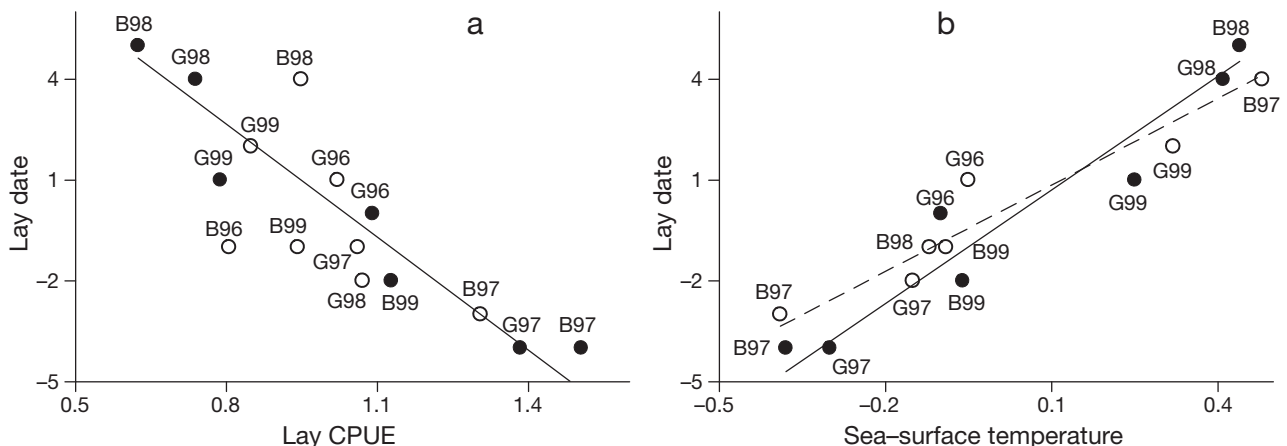


Fig. 2. *Uria aalge* and *Rissa tridactyla*. Relationships between (a) the residuals of average forage fish abundance during egg laying (lay catch per unit effort, CPUE) and (b) sea-surface temperature (SST) during egg laying, and egg lay date for murre (O) and kittiwakes (●) nesting at Gull (G) and the Barren (B) Islands, 1996–1999. Lines are Deming Model II regression lines shown for significant correlations

Table 4. *Rissa tridactyla* and *Uria aalge*. Models examining the relative importance of average lay date, average forage fish abundance during egg laying (lay catch per unit effort, CPUE) and during chick-rearing (chick CPUE) for explaining variation in reproductive output of kittiwakes and murre nesting at Gull and the Barren Islands, Cook Inlet, Alaska, 1996–1999. K: number of model parameters + 1,  $R^2$ : coefficient of determination

Variable	K	$R^2$	SSE	$\Delta AIC_c$	$w_i$	Evidence Ratio
<b>Kittiwake clutch size</b>						
Lay CPUE	3	0.66	0.02	0.00	0.97	1.0
Chick CPUE	3	0.00	0.07	7.52	0.02	43.0
Lay CPUE + chick CPUE	4	0.67	0.02	13.00	0.00	664.2
Lay date + lay CPUE	4	0.70	0.02	13.02	0.00	673.0
Lay date + chick CPUE	4	0.67	0.02	13.69	0.00	939.4
Lay date	3	0.65	0.25	16.19	0.00	3285.9
Lay date + lay CPUE + chick CPUE	5	0.71	0.02	54.89	0.00	$8.3 \times 10^{10}$
<b>Kittiwake laying success</b>						
Lay date	3	0.78	0.04	0.00	0.94	1.0
Lay CPUE	3	0.47	0.09	6.15	0.04	21.7
Chick CPUE	3	0.17	0.13	9.28	0.01	103.7
Lay date + chick CPUE	4	0.85	0.02	11.13	0.00	260.5
Lay date + lay CPUE	4	0.81	0.03	13.12	0.00	705.9
Lay CPUE + chick CPUE	4	0.84	0.25	27.77	0.00	$1.1 \times 10^6$
Lay date + lay CPUE + chick CPUE	5	0.87	0.02	52.60	0.00	$2.6 \times 10^{11}$
<b>Kittiwake reproductive success</b>						
Lay date	3	0.94	0.06	0.00	0.43	1.0
Lay CPUE + chick CPUE	4	0.94	0.01	0.74	0.30	1.4
Chick CPUE	3	0.91	0.08	2.11	0.15	2.9
Lay date + chick CPUE	4	0.73	0.01	3.36	0.08	5.4
Lay CPUE	3	0.60	0.11	4.47	0.05	9.3
Lay date + lay CPUE	4	0.46	0.04	11.34	0.00	289.9
Lay date + lay CPUE + chick CPUE	5	0.25	0.01	42.56	0.00	$1.7 \times 10^9$
<b>Murre hatching success</b>						
Chick CPUE	3	0.64	0.03	0.00	0.96	1.0
Lay CPUE	3	0.05	0.09	6.81	0.03	30.1
Lay CPUE + chick CPUE	4	0.77	0.02	10.85	0.00	227.0
Lay date + chick CPUE	4	0.72	0.03	12.39	0.00	489.3
Lay date	3	0.51	0.44	18.27	0.00	9289.5
Lay date + lay CPUE	4	0.56	0.40	31.52	0.00	$7.0 \times 10^6$
Lay date + lay CPUE + chick CPUE	5	0.93	0.01	44.90	0.00	$5.6 \times 10^9$
<b>Murre reproductive success</b>						
Chick CPUE	3	0.99	0.03	0.00	0.90	1.0
Lay date	3	0.87	0.06	4.88	0.08	11.5
Lay CPUE	3	0.82	0.11	9.50	0.01	115.3
Lay CPUE + chick CPUE	4	0.77	0.02	9.76	0.01	131.3
Lay date + chick CPUE	4	0.53	0.02	12.25	0.00	457.5
Lay date + lay CPUE	4	0.55	0.06	18.57	0.00	10 776.1
Lay date + lay CPUE + chick CPUE	5	0.09	0.00	36.31	0.00	$7.7 \times 10^7$

model containing lay CPUE (ER = 21.66; Fig. 3, Table 4). CS increased with increasing lay CPUE. LS increased with earlier lay date. Murre HS was best explained by the model containing only chick CPUE, with weak evidence that lay CPUE might be important (ER = 30.06). HS increased with increasing chick

CPUE. Relationships were similar among colonies (ANCOVA; LS  $\times$  Colony:  $F_{2,4} = 0.35$ ,  $p = 0.59$ ; CS  $\times$  Colony:  $F_{2,4} = 0.05$ ,  $p = 0.84$ ; HS  $\times$  Colony:  $F_{2,4} = 1.05$ ,  $p = 0.39$ ).

#### Near-shore fish abundance, lay date, and RS

The model that best explained variation in total RS of kittiwakes contained only the variable lay date ( $R^2 = 0.94$ ); however, there was strong support for the model containing the combination of lay CPUE and chick CPUE (ER = 1.45; Table 4). For murre, the best model of total RS contained only the variable chick CPUE ( $R^2 = 0.99$ ). There was also some support for the model containing lay date only (ER > 11,  $R^2 = 0.87$ ).

## DISCUSSION

### Breeding biology and proxies of food availability

Colder spring SST was associated with higher near-shore fish abundance prior to egg laying, earlier mean lay date, and higher average reproductive performance. Global SST has increased 1 to 2°C in the last 50 yr (Mackas et al. 2007), and evidence indicates that these changes have decreased the availability of key prey items for seabirds and marine mammals in the Gulf of Alaska (Litzow 2006, Litzow & Ciannelli 2007) and elsewhere (e.g. North Sea: Edwards & Richardson 2004; Antarctic: Le Bohec et al. 2008). The mechanisms linking colder spring SST and higher forage fish abundance in our study area (Gulf of Alaska) are unclear, although it is likely that colder spring temperatures reflect stronger winter upwelling (Lit-

zow 2006), resulting in cold, nutrient-rich water being brought to the surface. In spring, this cold, nutrient-rich water promotes the growth of sub-arctic zooplankton communities (Mackas et al. 2007), possibly by promoting the production of slow-growing, large diatoms that are high in nutrient content and are a valuable

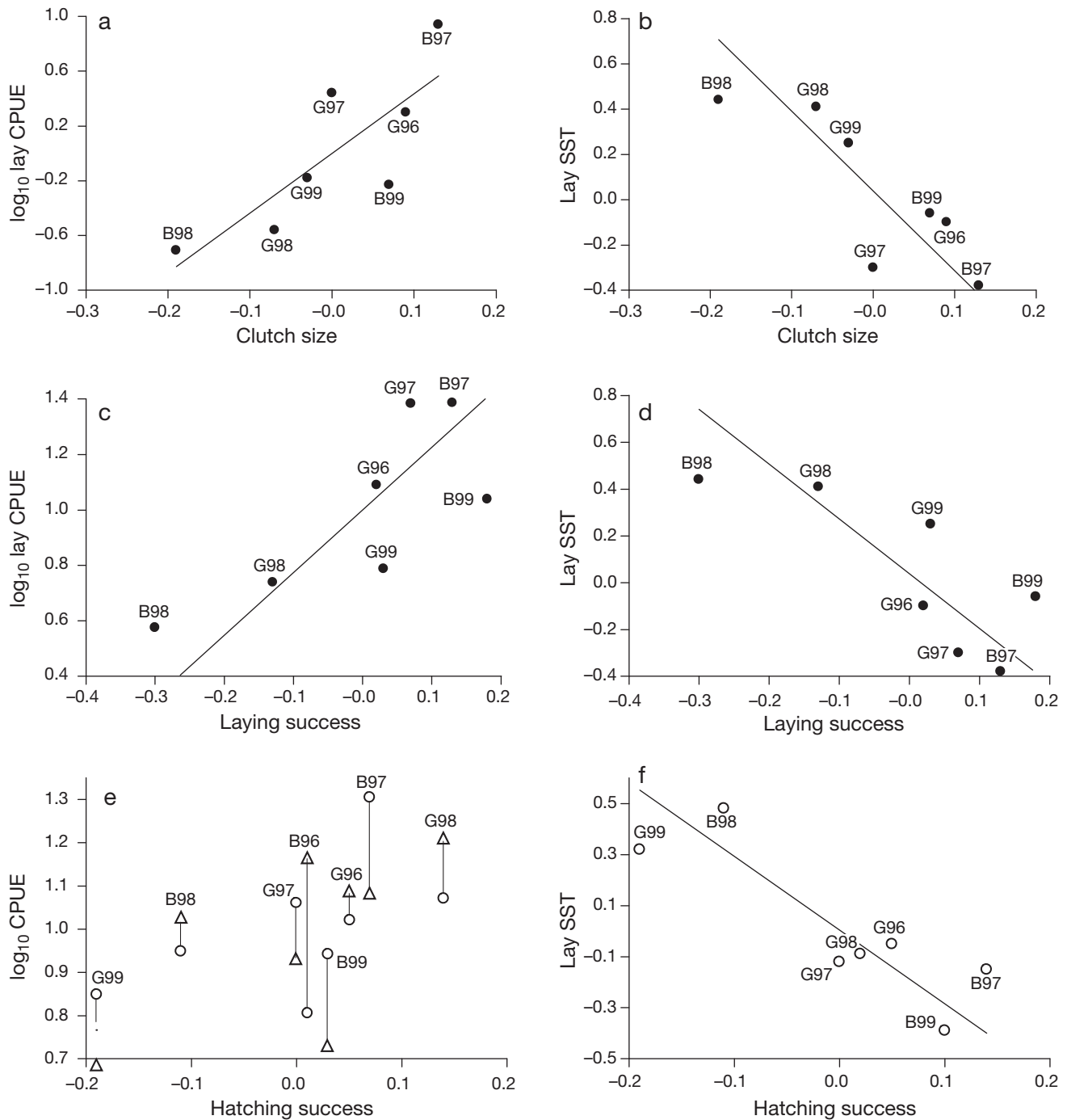


Fig. 3. *Uria aalge* and *Rissa tridactyla*. Relationships between the residuals of average forage fish abundance during egg laying (lay catch per unit effort, CPUE), sea-surface temperature (SST) during egg laying, and components of reproductive performance for (a,b,c,d) kittiwakes (clutch size, laying success) and (e,f) murre (hatching success) breeding at Gull (G) and the Barren (B) Islands, 1996–1999. (e) Murre is plotted versus lay CPUE and chick CPUE (forage fish abundance during chick rearing). (●) Lay period kittiwake, (○) lay period murre, (Δ) chick period murre. Lines are Deming Model II regression lines shown for significant correlations

food source for grazing zooplankton (Cooney 2007). The benefits associated with colder spring temperatures for forage fish may be related to the timing of their peak biomass—large, lipid-rich copepods (*Neocalanus plumchrus*) peak in abundance later during

colder springs (Mackas et al. 2007), and this is correlated with higher seabird reproductive performance. Our study encompassed the end of a relatively warm 'regime shift' in the Gulf of Alaska (Litzow & Ciannelli 2007) that resulted in seabird and marine mammal



population declines (Anderson & Piatt 1999). Years with colder spring SST may more closely resemble those prior to this regime shift, which were more productive for seabirds and marine mammals. Capelin are high quality forage fish (Van Pelt et al. 1997) that are important in the diet of murres and kittiwakes in our study area (Van Pelt et al. 2002), and warmer ocean temperatures have been linked to fewer capelin in the Gulf of Alaska (Anderson & Piatt 1999, Litzow & Cianelli 2007). Capelin were more abundant in colder years of our study and were found primarily in cold water (Abookire & Piatt 2005).

Similar relationships between cold spring SST, higher food availability for seabirds, and higher RS have been found elsewhere (Ainley et al. 1996, Abraham & Sydeman 2004, Mackas et al. 2007). However, the relationships between physical oceanographic processes and the transfer of energy through the food web are complex, and we do not expect to see the same relationships everywhere. In the Sea of Okhotsk, the reproductive performance of planktivorous and piscivorous seabirds responded in opposite ways to the same changes in SST: piscivorous species were more successful in warm years (Kitaysky et al. 2000). In the North Atlantic, warmer ocean temperatures (e.g. positive North Atlantic Oscillation and SST anomalies) were associated with advanced timing of seabird breeding (Durant et al. 2004, Frederiksen et al. 2004, Regular et al. 2009). In British Columbia, Canada, rhinoceros auklets *Cerorhinca monocerata*, Cassin's auklet *Ptychoramphus aleuticus*, and tufted puffin *Fratercula cirrhata* breed earlier in warmer years, but in contrast to results presented here, this was associated with reduced reproductive performance and greater mismatch with macrozooplankton prey abundance (Bertram et al. 2001, Gjerdrum et al. 2003).

#### 'Anticipation' or 'Constraint'?

Forage fish abundance increased after the onset of egg laying in all years and usually peaked during chick rearing. Inter-annual variation in food availability (near-shore fish abundance and SST) prior to egg laying accounted for nearly all of the observed variation in timing of egg laying for both species and the majority of kittiwake reproductive performance; when near-shore fish abundance was low, reproduction was delayed and birds produced fewer young. This delay in the onset of egg laying was apparently not an attempt to better match peak energetic demands of chicks with peak food availability, as the date of peak forage fish abundance was not related to timing of breeding. These results support the Constraint Hypothesis; the ability of birds to initiate reproduction was

likely constrained by current food availability. Lay SST was apparently not a cue allowing birds to predict the timing of peak food abundance, but simply reflected current near-shore fish abundance and the degree of food limitation. Thus, in concordance with life-history theory, birds appeared to prioritize their own condition over their current RS.

Although food availability prior to egg laying was not important for explaining variation in murre RS, several lines of evidence suggest that its importance may be underestimated here: (1) lay date explained 87% of variability in RS and was the second best model, (2) lay date was related to pre-lay food availability, but not timing of peak food, (3) our estimate of murre RS does not include LS. Taken together, these results suggest that murre RS may have been limited by food availability prior to egg laying. This is supported by results from a concurrent study showing that murres with high peak stress hormone levels during incubation (indicative of prior nutritional stress) had reduced hatching success (Kitaysky et al. 2007).

Inter-annual variation in murre lay dates was half that of kittiwakes, suggesting that murres may have been less food limited prior to egg laying. Food abundance during egg formation was always higher for murres than kittiwakes, which laid eggs 3 to 4 wk earlier. However, our interpretation is confounded by a number of factors, including differential costs of egg production, about which we know little. Also, there is strong selection pressure for murres to lay eggs and fledge chicks synchronously with neighbors (Benowitz-Fredericks & Kitaysky 2005), and social cues may play an important role in reducing variability in murre egg laying.

#### Implications for climate change

The results of this study provide insight into how seabird populations may respond to long-term changes in climate. Here we demonstrate that seabird reproductive performance is sensitive to ocean temperature and food availability; small increases in spring SST ( $<1^{\circ}\text{C}$ ) accounted for over 94% of variability in seabird timing of breeding and near-shore fish abundance, which in turn, accounted for over 94% of variability in seabird RS. The rate of seabird population declines in response to climate change will largely depend on adult survival rates, and to a lesser degree, RS, and recruitment. However, when food availability is low, adult seabirds increase energy expenditure (Kitaysky et al. 2000, Harding et al. 2007) and stress hormone levels (Kitaysky et al. 2007, Shultz & Kitaysky 2008, Benowitz-Fredericks et al. 2008) which are asso-

ciated with reduced RS and survival (Golet et al. 2004, Kitaysky et al. 2007). Also, chicks reared during periods of low food availability may have reduced chances of survival (Kitaysky et al. 2006). Thus, warmer spring ocean temperatures are likely to result in population declines of seabirds in the Gulf of Alaska, due to decreased RS, recruitment, and adult survival.

The results presented here highlight the importance of a multi-species approach to monitoring environmental changes; kittiwake lay date may best reflect spring near-shore forage fish abundance and SST, while murre RS may be most indicative of near-shore fish abundance during August.

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#### LITERATURE CITED

- Abookire AA, Piatt JF (2005) Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. *Mar Ecol Prog Ser* 287:229–240
- Abraham CL, Sydeman WJ (2004) Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*. *Mar Ecol Prog Ser* 274:235–250
- Ainley DG, Spear LB, Allen SG (1996) Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. *Mar Ecol Prog Ser* 137:1–10
- Ainley DG, Nettleship DN, Carter HR, Storey AE (2002) Common murre (*Uria aalge*). In: Poole A, Gill F (eds) *The birds of North America*, No. 666, The Birds of North America, Philadelphia, PA
- Allen DM, Service SK, Ogburn-Matthews MV, Service SK (1992) Factors influencing the collection efficiency of estuarine fishes. *Trans Am Fish Soc* 121:234–244
- Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189:117–123
- Baird PH (1994) Black-legged kittiwake (*Rissa tridactyla*). In: *The birds of North America*, No. 92. Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC
- Benowitz-Fredericks ZM, Kitaysky AS (2005) Benefits and costs of rapid growth in common murre (*Uria aalge*) chicks. *J Avian Biol* 36:287–294
- Benowitz-Fredericks ZM, Kitaysky AS, Thompson CW (2006) Growth and resource allocation by common murre (*Uria aalge*) chicks in response to experimentally restricted diets. *Auk* 123:722–734
- Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in two years. *Deep-Sea Res II* 55:1868–1876.
- Bertram DF, Mackas DL, McKinnell SM (2001) The seasonal cycle revisited: interannual variation and ecosystem consequences. *Prog Oceanogr* 49:283–307
- Birkhead TR, Nettleship DN (1980) Census methods for murre, *Uria* species: a unified approach. *Can Wildl Serv Occas Pap* 43:1–25
- Birkhead TR, Nettleship DN (1982) The adaptive significance of egg size and laying date in thick-billed murre *Uria lomvia*. *Ecology* 63:300–306
- Bolton M, Monaghan P, Houston DC (1993) Proximate determination of clutch size in lesser black-backed gulls—the roles of food-supply and body condition. *Can J Zool* 71: 273–279
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, NY
- Cooney T (2007) The marine production cycle. In: Spies RB (ed) *Long-term ecological change in the Gulf of Alaska*. Elsevier, Amsterdam, p 47–60
- Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Esilton DA, Wanless S (2002) Foraging strategies of black-legged kittiwakes *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245: 239–247
- Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic Puffin as an example. *Proc R Soc Lond B Biol Sci* 270: 1461–1466
- Durant JM, Anker-Nilssen T, Hjermann DO, Stenseth NC (2004) Regime shifts in the breeding of an Atlantic puffin population. *Ecol Lett* 7:388–394
- Durant JM, Hjermann DO, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelly N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol Lett* 8:952–958
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884
- Erwin CA, Congdon BC (2007) Day-to-day variation in sea-surface temperature reduces sooty tern *Sterna fuscata* foraging success on the Great Barrier Reef, Australia. *Mar Ecol Prog Ser* 331:255–266
- Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob Change Biol* 10: 1214–1221
- Gabrielsen GW, Klaassen M, Mehlum F (1992) Energetics of black-legged kittiwake *Rissa tridactyla* chicks. *Ardea* 80: 29–40
- Gill VA, Hatch SA (2002) Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *J Avian Biol* 33:113–126

- Gill V, Hatch S, Lancot R (2002) Sensitivity of breeding parameters to food supply in black-legged kittiwakes *Rissa tridactyla*. *Ibis* 144:268–283
- Gjerdrum C, Vallee AM, Clair CCS, Bertram DF, Ryder JL, Blackburn GS (2003) Tufted puffin reproduction reveals ocean climate variability. *Proc Natl Acad Sci USA* 100:9377–9382
- Golet GH, Irons DB, Estes JA (1998) Survival costs of chick rearing in black-legged kittiwakes. *J Anim Ecol* 67:827–841
- Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multiyear experiment. *Ecol Monogr* 74:353–372
- Goodman D (1974) Natural selection and a cost ceiling on reproductive effort. *Am Nat* 108:247–268
- Hahn TP, Boswell T, Wingfield JC, Ball GF (1997) Temporal flexibility in avian reproduction: patterns and mechanisms. In: Nolan V Jr (ed) *Current ornithology*, Vol 14. Plenum Press, New York, NY, p 39–80
- Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Speckman SG (2007) Behavioural plasticity and the functional response of a marine predator: the common guillemot (*Uria aalge*). *Ecology* 88:2024–2033
- Hatch SA, Hatch MA (1988) Colony attendance and population monitoring of black-legged kittiwakes on the Semidi Islands, Alaska. *Condor* 90:613–620
- Hatch SA, Hatch MA (1989) Attendance patterns of murres at breeding sites: implications for monitoring. *J Wildl Manag* 53:483–493
- Hatch SA, Hatch MA (1990) Breeding seasons of oceanic birds in a subarctic colony. *Can J Zool* 68:1664–1679
- Heaney V, Monaghan P (1995) A within-clutch trade-off between egg-production and rearing in birds. *Proc R Soc Lond B Biol Sci* 261:361–365
- Hiom L, Bolton M, Monaghan P, Worrall D (1991) Experimental evidence for food limitation of egg-production in gulls. *Ornis Scand* 22:94–97
- Kitaysky A, Hunt GL, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser* 206:283–296
- Kitaysky AS, Kitaikaia EV, Piatt JF, Wingfield JC (2006) A mechanistic link between chick diet and decline in seabirds. *Proc R Soc Lond B Biol Sci* 273:445–450
- Kitaysky AS, Piatt JF, Wingfield JC (2007) Stress hormones link food availability and population processes in seabirds. *Mar Ecol Prog Ser* 352:245–258
- Lack D (1968) *Ecological adaptations for breeding in birds*. Methuen, London
- Lancot RB, Hatch SA, Gill VA, Eens M (2003) Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? *Horm Behav* 43:489–502
- Le Bohec C, Durant JM, Gauthier-Clerc M, Stenseth NC and others (2008) King penguin population threatened by Southern Ocean warming. *Proc Natl Acad Sci USA* 105:2493–2497
- Litzow MA (2006) Climate regime shifts and community reorganization in the Gulf of Alaska: How do recent shifts compare with 1976/1977? *ICES J Mar Sci* 63:1386–1396
- Litzow MA, Ciannelli L (2007) Oscillating trophic control induces community reorganization in a marine ecosystem. *Ecol Lett* 10:1124–1134
- Litzow MA, Piatt JF, Abookire AA, Prichard AK, Robards MD (2000) Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with pigeon guillemot (*Cepphus columba*) diets. *ICES J Mar Sci* 57:976–986
- Mackas DL, Batton S, Trudel M (2007) Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. *Prog Oceanogr* 75:223–252
- Meijer T, Drent R (1999) Re-examination of the capital and income dichotomy in breeding birds. *Ibis* 141:399–414
- Monaghan P, Nager RG (1997) Why don't birds lay more eggs? *Trends Ecol Evol* 12:270–274
- Nager RG, Van Noordwijk AJ (1995) Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *Am Nat* 146:454–474
- Perrins CM (1970) The timing of birds' breeding seasons. *Ibis* 112:242–255
- Perrins CM (1991) Tits and their caterpillar food supply. *Ibis* 133:49–54
- Piatt JF, Harding AMA (2007) Population ecology of seabirds in Cook Inlet. In: Spies RB (ed) *Long-term ecological change in the Gulf of Alaska*. Elsevier, Amsterdam, p 335–351
- Piatt JF, Harding AMA, Shultz MT, Speckman SG, van Pelt TI, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supply: Cairns revisited. *Mar Ecol Prog Ser* 352:221–234
- Regular PM, Shuhod F, Power T, Montevecchi WA and others (2009) Murres, capelin and ocean climate: inter-annual associations across a decadal shift. *Environ Monit Assess* 156:293–302
- Rindorf A, Wanless S, Harris MP (2000) Effects of changes in sandeel availability on the reproductive output of seabirds. *Mar Ecol Prog Ser* 202:241–252
- Robards MD, Piatt JF, Kettle AB, Abookire AA (1999) Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. *Fish Bull (Wash DC)* 97:962–977
- Robards MD, Rose GA, Piatt JF (2002) Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes. *Environ Biol Fishes* 64:429–441
- Shultz MT, Kitaysky AS (2008) Spatial and temporal dynamics of corticosterone and corticosterone binding globulin are driven by environmental heterogeneity. *Gen Comp Endocrinol* 155:717–728
- Shultz MT, Harding AMA, Kettle AB (2002) Response of seabirds to fluctuations in forage fish density: black-legged kittiwakes. In: Piatt JF (ed) *Final report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region)*. Alaska Science Center, U.S. Geological Survey, Anchorage, AK, p 86–99
- Speckman SG (2004) *Characterizing fish schools in relation to the marine environment and their use by seabirds in Lower Cook Inlet, Alaska*. PhD dissertation, University of Washington, Seattle, WA
- Speckman SG, Piatt JF, Minte-Vera CV, Parrish JK (2005) Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. *Prog Oceanogr* 66:25–65
- Springer AM (2007) Seabirds in the Gulf of Alaska. In: Spies RB (ed) *Long-term ecological change in the Gulf of Alaska*. Elsevier, Amsterdam, p 311–334
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Svensson E (1995) Avian reproductive timing: When should parents be prudent? *Anim Behav* 49:1569–1575
- Svensson E, Nilsson JA (1995) Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). *Ecology* 76:1804–1812

- Swennen C (1977) Report on a practical investigation into the possibility of keeping sea-birds for research purposes. Netherlands Inst Sea Res, Texel
- Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Prog Oceanogr* 49:309–329
- Van Noordwijk AJ, McCleery RH, Perrins CM (1995) Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J Anim Ecol* 64:451–458
- Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. *Comp Biochem Physiol A* 118:1393–1398
- Van Pelt TI, Shultz MT, Kettle AB (2002) Response of seabirds to fluctuations in forage fish density: common murre. In: Piatt JF (ed) Final report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region). Alaska Science Center, U.S. Geological Survey, Anchorage, AK, p 70–85
- Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc R Soc Lond B Biol Sci* 272:2561–2569
- Wanless S, Frederiksen M, Daunt F, Scott BE, Harris MP (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Prog Oceanogr* 72:30–38
- Wingfield JC, Hahn TP, Levin R, Pulmu H (1992) Environmental predictability and control of gonadal cycles in birds. *J Exp Zool* 261:214–231
- Zar JH (1999) Biostatistical analysis. Prentice-Hall, Upper Saddle River, NJ

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