



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 (Lanctot 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 ≥ 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 murres, 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 murres.

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 murres, as average lay date differed between species: the first half of June for kittiwakes and the first half of July for murres.

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 murres; 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; murres: 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 murres 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.

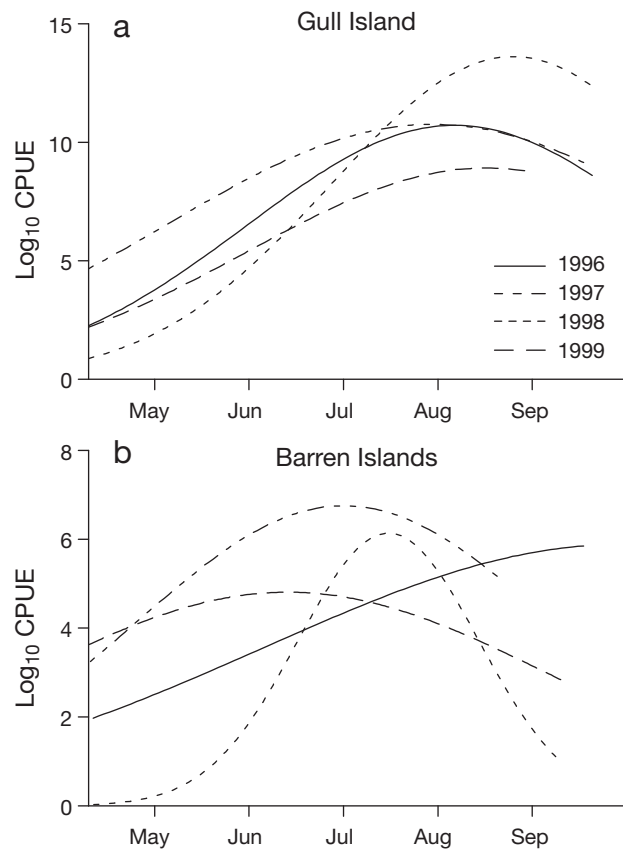


Fig. 1. Seasonal dynamics of forage fish abundance among years (1996–1999) at (a) Gull Island and (b) Barren Islands. Curves represent data fitted with a Gaussian function. Goodness of fit statistics are presented in Table 1. Curves were used to estimate forage fish abundance at the onset of egg laying, 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 ²	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

We used the Akaike Information Criterion adjusted for small sample size (AIC_c) to evaluate models of the data for lay date and reproductive performance. The model with the lowest AIC_c was the best model (Burnham & Anderson 2002). We calculated AIC_c weight (w_i) to evaluate the relative probability of each model representing the true model. The ratios of Akaike weights (Evidence Ratio, ER: w_{min}/w_j) were compared to assess the strength of evidence for a particular model compared to others in the model set (Burnham & Anderson 2002).

Models of timing of laying and reproductive performance: We modeled lay date using all combinations of the variables lay CPUE, lay SST, and peak CPUE date. We modeled reproductive performance parameters that potentially reflect decisions made at egg laying, using the explanatory variables lay date, lay CPUE, and chick CPUE. For kittiwakes, these parameters included LS and CS. For murres, because we were unable to measure LS, and CS is 1, we modeled HS, the parameter most likely to reflect pre-lay conditions. We refer to these parameters as 'initial reproductive output' (IRO). We modeled total RS for both species (combination of LS, CS, HS, and FS for kittiwakes; HS and FS for murres) to evaluate the relative importance of lay date itself versus food abundance (lay CPUE and chick CPUE) for explaining variability in total RS.

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).

RESULTS

Beach seine catch composition

In total, 815 398 fish representing at least 70 species were captured in 717 seine nets deployed from June to August, 1996 to 1999 (Table 2). Pacific sand lance dominated the near-shore community, and herring was the second most important taxon at Gull Island, while gadids (primarily walleye pollock) were second at the Barrens. As reported elsewhere (Shultz et al. 2002, Van Pelt 2002), fish species and size classes caught in seines comprised >90% of the diet of kittiwake and murre adults (Shultz et al. 2002, Van Pelt et al. 2002).

Seasonal dynamics of near-shore fish and peak demand date

As reported elsewhere, near-shore fish abundance around Gull Island was low from October through April (<2% of total catch), but increased rapidly in

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

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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_c). K: number of model parameters + 1, R²: coefficient of determination

Variable	K	R ²	SSE	ΔAIC_c	w_i	Evidence Ratio
Kittiwake						
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	2.0×10^{11}
Murre						
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	3.1×10^6
Lay SST + lay CPUE + peak CPUE date	5	0.17	1.27	49.82	0.00	6.6×10^{10}

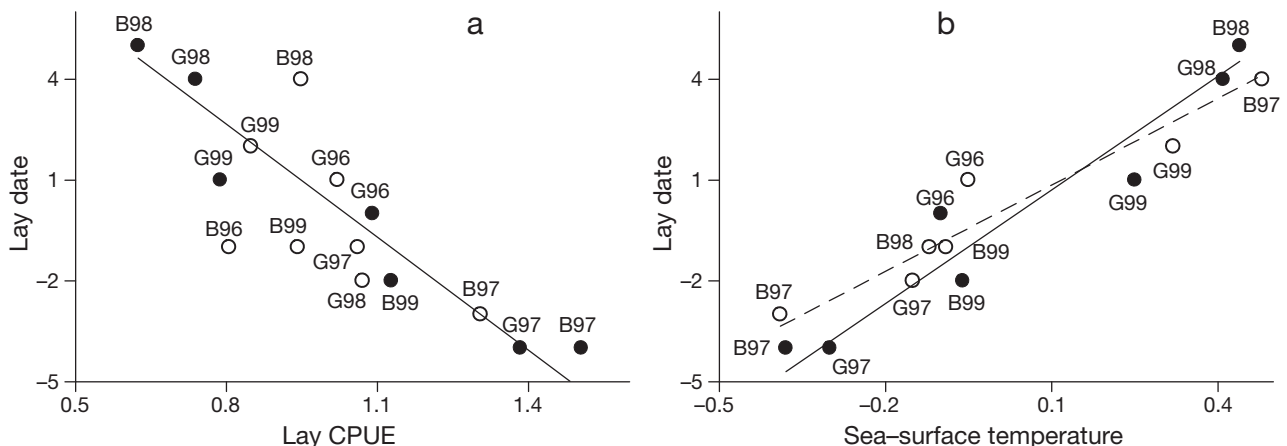


Fig. 2. *Uria aalge* and *Rissa tridactyla*. Relationships between (a) the residuals of average forage fish abundance during egg laying (lay catch per unit effort, CPUE) and (b) sea-surface temperature (SST) during egg laying, and egg lay date for murre (O) and kittiwakes (●) nesting at Gull (G) and 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	ΔAIC_c	w_i	Evidence Ratio
Kittiwake clutch size						
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	8.3×10^{10}
Kittiwake laying success						
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	1.1×10^6
Lay date + lay CPUE + chick CPUE	5	0.87	0.02	52.60	0.00	2.6×10^{11}
Kittiwake reproductive success						
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	1.7×10^9
Murre hatching success						
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	7.0×10^6
Lay date + lay CPUE + chick CPUE	5	0.93	0.01	44.90	0.00	5.6×10^9
Murre reproductive success						
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	7.7×10^7

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

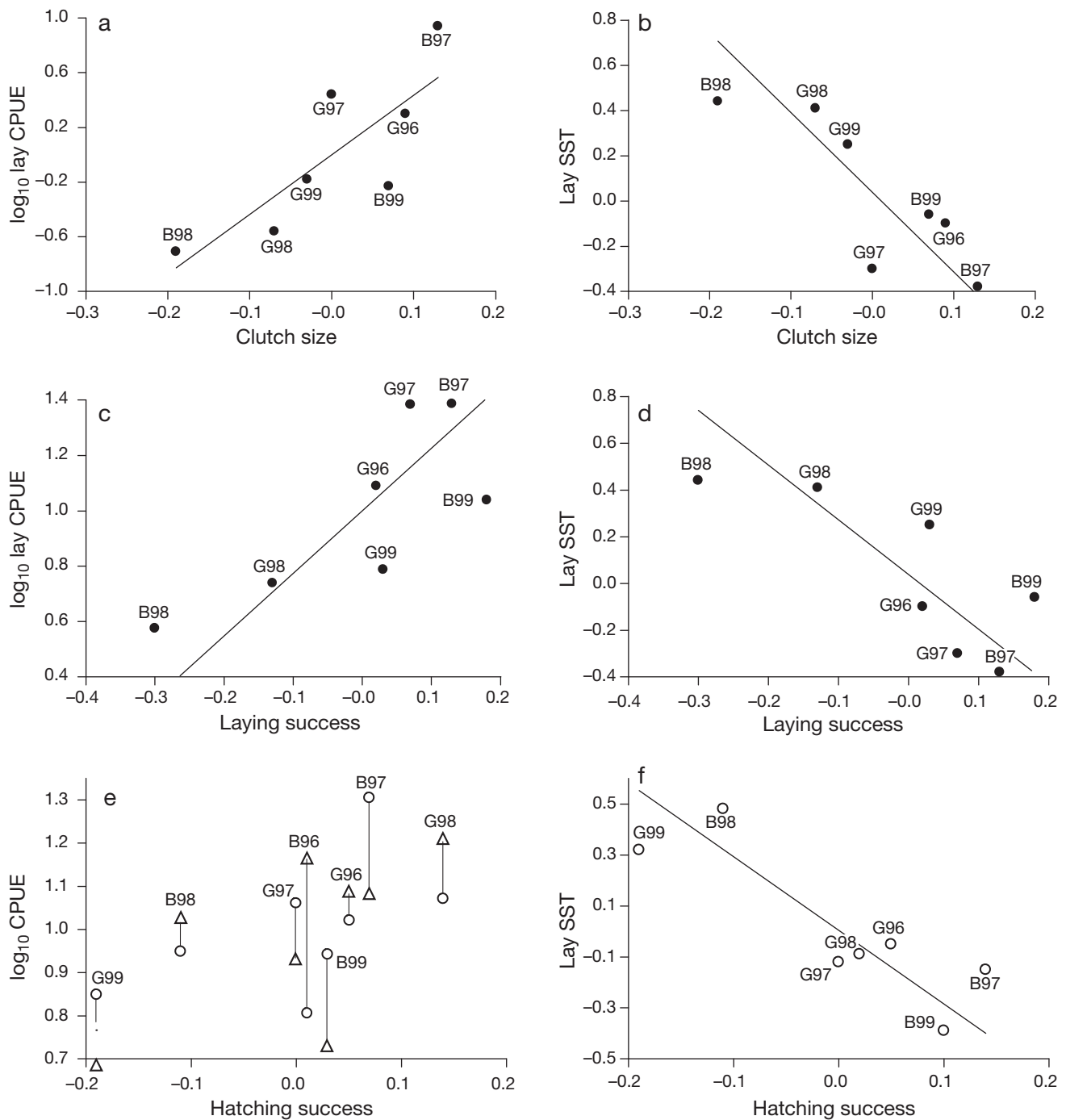


Fig. 3. *Uria aalge* and *Rissa tridactyla*. Relationships between the residuals of average forage fish abundance during egg laying (lay catch per unit effort, CPUE), sea-surface temperature (SST) during egg laying, and components of reproductive performance for (a,b,c,d) kittiwakes (clutch size, laying 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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