



# Status, trends, and patterns of covariation of breeding seabirds at St Lazaria Island, Southeast Alaska, 1994–2006

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## ABSTRACT

**Aim** We examined patterns of covariation among piscivorous and planktivorous seabirds breeding at St Lazaria Island in order to evaluate their responses to interannual changes in sea surface temperature, a variable that affects marine food webs. In addition, we evaluated seabird population trends for responses to decadal-scale changes in the marine ecosystem.

**Location** St Lazaria Island, Sitka Sound, Alaska.

**Methods** Established seabird monitoring protocols for the Alaska Maritime National Wildlife Refuge were followed in estimating population trends, the timing of nesting events and the reproductive success of eight species of seabirds between 1994 and 2006.

**Results** Population increases were noted for storm-petrels (*Oceanodroma furcata* and *O. leucorhoa*), rhinoceros auklets (*Cerorhinca monocerata*) and glaucous-winged gulls (*Larus glaucescens*). We found no population trend for pelagic cormorants (*Phalacrocorax pelagicus*), but it appeared that populations of common (*Uria aalge*) and thick-billed (*U. lomvia*) murrelets and of tufted puffins (*Fratercula cirrhata*) declined. We detected no linear trends in either breeding chronology or reproductive success over the study period for any seabird. All species of piscivorous seabirds apparently responded similarly to environmental cues as there was a positive covariation among species in the timing of nesting. Piscivores tended to nest earlier, and most species had higher rates of reproductive success in years with relatively warm spring sea temperatures. In contrast, planktivorous Leach's storm-petrels (*O. leucorhoa*) tended to nest earlier when spring and summer sea temperatures were relatively cool. Clearly, seabirds at St Lazaria were responding to interannual changes in sea temperatures near the breeding colony, probably as a result of effects on the food webs.

**Main conclusions** Every seabird species we monitored at St Lazaria exhibited significant population trends between 1994 and 2006. For most species there appeared to be a relationship between both the timing of nesting and reproductive rates and spring or summer sea surface temperatures. Responses at both decadal (populations) and interannual (timing and reproductive success) scales make seabirds useful candidates for helping to monitor change in the marine environment.

## Keywords

*Cerorhinca monocerata*, *Fratercula cirrhata*, *Larus glaucescens*, *Oceanodroma*, *Phalacrocorax pelagicus*, population trend, productivity, sea surface temperature, St Lazaria Island, *Uria*.

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## INTRODUCTION

Changes in ocean temperatures can have major impacts on marine food webs (Intergovernmental Panel on Climate Change, 2002; International Arctic Science Committee, 2006), and can particularly affect top-level marine predators such as seabirds (Aebischer *et al.*, 1990; Frederiksen *et al.*, 2004). A long-term monitoring programme for plankton-feeding and fish-feeding seabirds at St Lazaria Island, Alaska (Fig. 1) serves as a data source for describing population trends and other patterns in several vital rates of seabirds relative to variations in sea temperatures in Southeast Alaska. Because seabirds are long-lived, with delayed sexual maturity and relatively low annual reproductive rates (Lack, 1968; Ashmole, 1971; Croxall, 1987; Furness & Monaghan, 1987), seabird population trends integrate food web conditions on multi-year time-scales. In contrast, inter-annual responses of seabirds to environmental conditions through variation in breeding phenology (e.g. hatch dates) and reproductive rates are thought to reflect annual marine food supply availability (see Cairns, 1987; Piatt *et al.*, 2007a,b).

St Lazaria is within an area of relatively high ocean productivity and in most years is free of terrestrial mammalian predators, which can cause additional depredation (their sporadic presence seemed to have little effect at St Lazaria, as these long-lived seabirds can overcome short-term declines by their breeding strategies). These conditions allow the moderately high diversity (11 species) and abundance (c. 450,000 individuals) of nesting seabirds (Nelson *et al.*, 1987). The island has long been recognized as one of the major nesting areas for seabirds in Southeast Alaska (Grinnell, 1897; Willett, 1912), and as part of the Alaska Maritime National Wildlife Refuge is an important link within the network of seabird monitoring sites scattered throughout this far-flung refuge (Byrd, 2007). Monitoring at St Lazaria has been conducted annually between 1994 and 2006, and this data set is the basis for evaluating changes over the 13-year span in a suite of species of seabirds using different niches within the marine food web (e.g. planktivorous and piscivorous species). Specifically, data exist for planktivorous fork-tailed (*Oceanodroma furcata*) and Leach's (*O. leucorhoa*) storm-petrels (c. 200,000 pairs, combining species) and piscivorous pelagic cormorants (*Phalacrocorax pelagicus*;



**Figure 1** Location of St Lazaria Island in Southeast Alaska (western Sitka Sound: 56°59' N, 135°42' W). The rhinoceros auklet colony is located at the most northern point, the murre cliff colony at the south-western-most point.

between 8 and 300 pairs), common (*Uria aalge*) and thick-billed (*U. lomvia*) murre (c. 3000 adults, combining species), rhinoceros auklets (*Cerorhinca monocerata*; c. 2000 pairs), and tufted puffins (*Fratercula cirrhata*; several thousand) as well as opportunistic feeding glaucous-winged gulls (*Larus glaucescens*; roughly 150 breeding pairs) (nomenclature follows American Ornithologists' Union, 2006).

The objectives of this paper are to document the status of these seabird populations at the beginning of the 21st century in this oceanographically interesting region, and to examine covariation among species and between various species and spring and summer sea temperatures. We predicted that species within the same foraging guilds (Table 1) would respond similarly to differences in interannual spring and summer temperatures mediated through changes in marine food webs. The data presented here constitute a baseline from which future change may be evaluated.

## MATERIALS AND METHODS

### Population trends

#### Burrow counts

Storm-petrels, rhinoceros auklets and tufted puffins nest in burrows, which they dig in the deep soils of the island. Counting burrow entrances is the accepted method of assessing the density and population trends of birds with this nesting strategy (see Gaston *et al.*, 1988; Terrestrial Ecosystems Task Force Resources Inventory Committee, 1997; Byrd, 2000a). At St Lazaria, for every year between 1994 and 2006 we counted the number of storm-petrel and rhinoceros auklet burrow entrances in permanent study plots located within three density strata based on information from random transects over the entire island (Nishimoto *et al.*, 1985; Slater *et al.*, 1996; Slater & Loy, 2000). Because tufted puffins were confined mostly to the island's perimeter, where human access is more difficult, we established 3-m-wide transects that ran perpendicularly from the coastline to the inland edge of puffin habitat and counted the puffin burrow entrances found within

**Table 1** Foraging guilds and habitats used by seabirds of St Lazaria Island, Alaska.

Species	Foraging guild	Foraging habitat*
Fork-tailed storm-petrel	Planktivore	Slope
Leach's storm-petrel	Planktivore	Oceanic
Pelagic cormorant	Piscivore	Coastal
Glaucous-winged gull	Piscivore	Coastal
Common murre	Piscivore	Coastal/shelf
Thick-billed murre	Piscivore	Coastal/shelf
Tufted puffin	Piscivore	Shelf
Rhinoceros auklet	Piscivore	Coastal

\*Coastal: < 100 m deep; shelf: 100–200 m deep; slope: 200–1500 m deep; oceanic: > 1500 m deep (see Piatt & Drago, 2005).

each transect. Some plots contained multiple species of burrow-nesters, and we separated storm-petrels, rhinoceros auklets and tufted puffins by burrow entrance size (Fischer & Griffin, 1999). There is no difference in burrow-size entrance for the two species of storm-petrels, so we determined the species' relative abundances in a subset of plots, within which we extracted storm-petrels to identify their species.

#### Counts of birds and nests on ledges

Pelagic cormorant nests were counted by surveying all the nesting cliffs from land-based observation points, or from a skiff in cases where cliff ledges could not be seen from land (see Hobson, 1997, for nesting habitat preferences). We censused glaucous-winged gull nests on the discrete rocky and grass-covered spires and outcrops where they nested at St Lazaria. We marked each nest with flagging to avoid duplication.

Like cormorants, murre nest on ledges of sea cliffs, but, unlike cormorants, they do not construct nests; instead they lay eggs on flat, bare ledges (Gaston & Hipfner, 2000). Therefore, the standard method for assessing murre populations at breeding colonies is to count individuals (Wanless *et al.*, 1982). At St Lazaria, we counted murre present at nesting ledges in segments identified by hand-drawn boundaries on photographs of the murre nesting colony at Southwest Cliff. We replicated counts of clusters of nesting murre on 4–11 days each year at times of day (11:00–18:00 h) and of season (incubation and early chick-rearing) when the number of adults attending colonies is least variable (Swartz, 1966; Hatch & Hatch, 1989; Byrd, 2000b; Williams *et al.*, 2002). Plots were too far from the observation point to allow us reliably to separate the two species of murre, so we derived annual indices for the genus by averaging daily counts.

#### Timing of nesting and reproductive rates

To estimate the timing of nesting and reproductive rates of storm-petrels, we used a subset of plots for which the contents of nests were determined by physically reaching into burrows. For burrows with tunnels too long for the nest chamber to be reached from the entrance, we cut small earthen plugs to access chambers. We then closed the access holes with a small board and sod to maintain the burrow's integrity. We considered a burrow to be 'occupied' if an egg or chick was present during at least one check. We checked burrow status every 5 days throughout the breeding season to determine reproductive rates and the timing of nesting events. We calculated hatch dates by determining the nearest even Julian date of the mid-point between status checks.

We checked the status of pelagic cormorant nests at intervals of 10–14 days throughout the breeding season to evaluate productivity. Photographs of cliff areas containing nests were annotated with unique nest codes. The presence of adults and ultimately the number of chicks were noted for each nest. We counted large chicks in each study area just prior to their fledging as a measure of productivity.

Gull nests, identified by numbered flags, were checked every 5 days to determine the clutch size and date of hatch of first egg, and large chicks were counted to evaluate reproductive success. Hatch dates were calculated as described above for storm-petrels. Chick counts were possible because of the unique characteristics of the gull nesting areas at St Lazaria (i.e. isolated rocky spires where chicks remained until they were flight-capable and departed the nesting areas).

For murres, we checked the status of nest sites (i.e. locations on ledges where eggs were laid) in systematically selected plots at regular intervals (approximately every 3 days) to calculate the timing of nesting events and reproductive success. By using photographs of plots on which nest sites were numbered, we could then identify and view each site through a spotting scope to record its status on each visit (see Birkhead & Nettleship, 1980; Gaston & Nettleship, 1981).

**Data analysis**

*Population trends*

Abundance indices comprising counts of burrow entrances for storm-petrels, tufted puffins and rhinoceros auklets, counts of murres on ledges, and counts of gull nests were plotted over time to evaluate trends. We conducted simple linear regressions on natural log-transformed data to test the null hypothesis of no trend in populations throughout the study period.

*Breeding chronology and reproductive success*

We looked for temporal trends in hatch dates, reproductive rates, and spring and summer sea temperatures independently. We then used Spearman’s correlations to compare inter-annual response variables (i.e. mean annual hatch dates and reproductive rates) and to test correlations between these variables and environmental covariates (i.e. average monthly sea temperature in May, June, July and August).

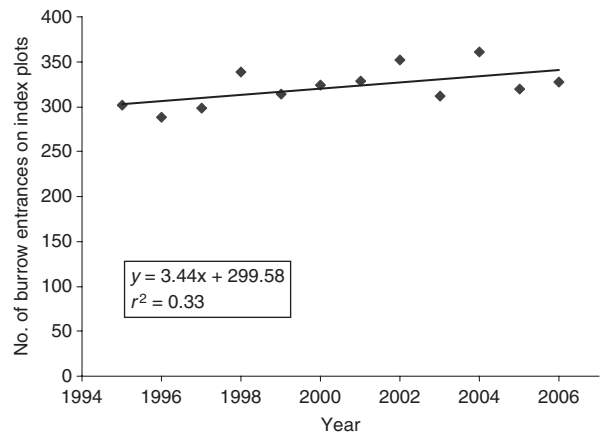
We obtained monthly average anomalies of sea surface temperatures during the primary breeding period of seabirds (May–August primarily, until October for storm-petrels: Huntington *et al.*, 1996; Boersma & Silva, 2001) from 1994 to 2006. Isobar charts showing deviations from long-term temperature means on a monthly basis (Fisheries and Oceans Canada, 2006) were examined to derive values for the area covering the summer foraging range of St Lazaria seabirds (i.e. a 40-km radius from the island; Piatt & Dragoo, 2005).

**RESULTS**

**Population trends**

*Planktivores*

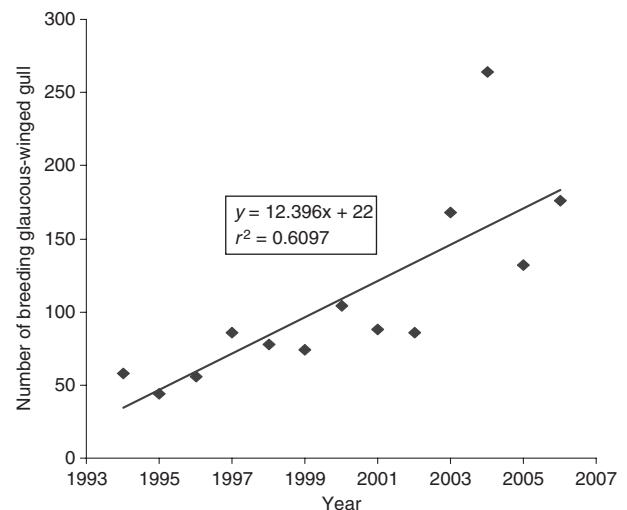
Between 1995 and 2006 there was a significant increase in the number of storm-petrel burrow entrances on index plots ( $t = 1.920$ ,  $P = 0.084$ , d.f. = 11; Fig. 2).



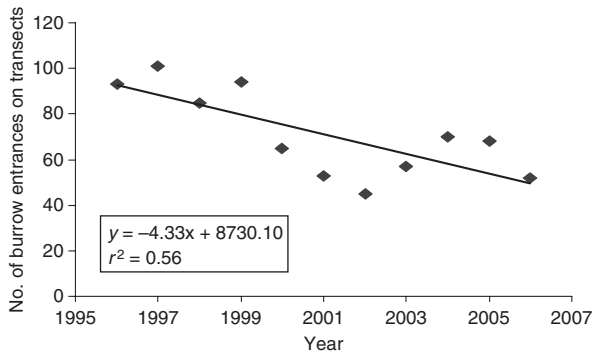
**Figure 2** Population trend, based on counts of burrow entrances on index plots, of fork-tailed and Leach’s storm-petrels at St Lazaria Island, Alaska, between 1995 and 2006.

*Piscivores*

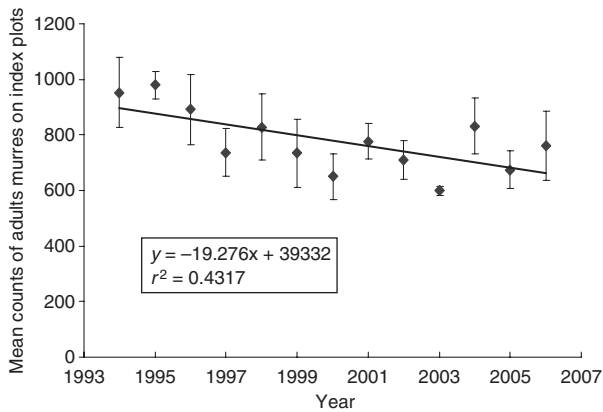
No population trend emerged for pelagic cormorants; however, other species of fish-feeding seabirds that foraged primarily in near-shore coastal habitats (Table 1) experienced population increases during the study. Those piscivores whose breeding populations increased on index plots during our study were surface-feeding glaucous-winged gulls ( $t = 5.971$ ,  $P < 0.001$ , d.f. = 12; Fig. 3) and diving rhinoceros auklets ( $t = 5.619$ ,  $P < 0.001$ , d.f. = 12; Fig. 4). In contrast, species feeding in deeper-slope and oceanic waters, such as murres ( $t = -2.743$ ,  $P = 0.019$ , d.f. = 12; Fig. 5) and tufted puffins ( $t = -3.032$ ,  $P = 0.014$ , d.f. = 10; Fig. 6), apparently declined between 1994 and 2006.



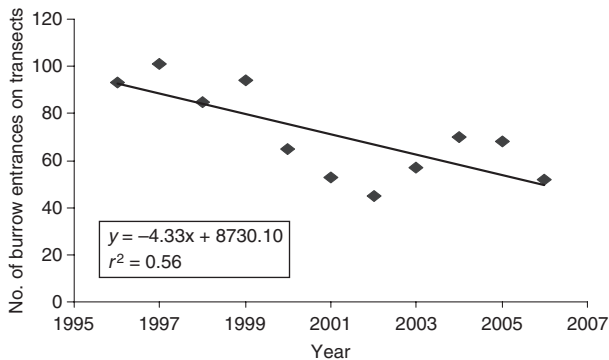
**Figure 3** Population trend, based on counts of active nests (X2) on index plots, of glaucous-winged gulls at St Lazaria Island, Alaska, between 1994 and 2006.



**Figure 4** Population trend, based on counts of burrow entrances on index plots, of rhinoceros auklets at St Lázaria Island, Alaska, between 1994 and 2006.



**Figure 5** Mean counts of adult murre (common and thick-billed combined) at the Southwest Cliff colony, St Lázaria Island, Alaska, between 1994 and 2006. Error bars reflect the standard deviation of replicate counts performed in each year.



**Figure 6** Population trend, based on counts of burrow entrances on permanent transects, of tufted puffins at St Lázaria Island, Alaska, between 1995 and 2006.

**Breeding chronology and reproductive success**

No linear trends were detected in either breeding chronology or reproductive success over the study period for any species of piscivore or planktivore, but correlations were detected as indicated below.

*Planktivores*

*Hatch dates.* Mean hatch dates were significantly different between the two storm-petrel species ( $t = 4.9410, P = 0.0004, d.f. = 11$ ). Mean hatch dates for fork-tailed storm-petrels ranged from 23 June to 2 August, with an overall mean of 14 July (see Appendix S1). In all years, Leach’s storm-petrels nested later than their congener; the earliest mean hatch date was 21 July and the latest was 10 August, with a mean of 31 July.

*Productivity.* Mean annual productivity for fork-tailed storm-petrels varied from 0.36 to 0.80 fledglings per egg laid, with an overall mean of 0.61 (Appendix S1). Results for Leach’s storm-petrels were statistically indistinguishable from those for their congener, with 0.24 to 0.70 fledglings per egg and a mean productivity for all years of 0.58.

*Covariation among species.* Hatch dates for fork-tailed and Leach’s storm-petrels covaried positively ( $r_s = 0.671, P \leq 0.05, n = 12$ ; Appendix S2), as did rates of productivity ( $r_s = 0.492, P \leq 0.10, n = 11$ ; Appendix S2). Furthermore, there appeared to be a relationship between timing of nesting and productivity for fork-tailed storm-petrels (i.e., productivity tended to be higher when nesting was earlier;  $r_s = -0.664, P \leq 0.05, n = 11$ ; Appendix S2), but no such relationship was detected for Leach’s storm-petrels.

*Covariation with sea surface temperature anomalies.* For fork-tailed storm-petrels, hatch dates had only weak, non-significant relationships with sea temperatures (Table 2, Appendix S2), but Leach’s storm-petrel mean hatch dates were significantly negatively correlated with sea surface temperature anomalies. These correlations were significant

**Table 2** Correlations of seabird response variables and sea surface temperature anomalies (i.e. positive or negative) at St Lázaria Island, Alaska.

Species	Response variables	Spring SST	Summer SST
Fork-tailed storm-petrel	Hatch date	n.s.	n.s.
	Productivity	+	+
Leach’s storm-petrel	Hatch date	-	-
	Productivity	n.s.	n.s.
Pelagic cormorant	Productivity	-	-
Glaucous-winged gull	Hatch date	n.s.	-
	Productivity	n.s.	n.s.
Common murre	Hatch date	n.s.	-
	Productivity	n.s.	+
Thick-billed murre	Hatch date	n.s.	-
	Productivity	n.s.	+
Tufted puffin	Productivity	n.s.	n.s.
Rhinoceros auklet	Hatch date	-	n.s.
	Productivity	n.s.	n.s.

SST, sea surface temperature anomaly. n.s., no significance; +, significantly positive; -, significantly negative.

for all spring and summer months, with the strongest correlations in June and July ( $r_s$  values between May and August ranged from  $-0.50$  to  $-0.67$ ; Table 2, Appendix S2).

We found a positive correlation between the annual productivity of fork-tailed storm-petrels and sea temperature anomalies in spring (May) and summer (August) ( $r_s = 0.532$  and  $0.474$ , respectively,  $P \leq 0.10$ ,  $n = 11$ ; Appendix S2). However, no significant correlations were detected between productivity and sea temperatures for Leach's storm-petrels.

*Piscivores*

*Hatch dates.* Coastal-feeding glaucous-winged gulls (average annual hatch dates ranged from 26 June to 22 July with an overall mean of 7 July) and rhinoceros auklets (average annual hatch dates ranged from 12 June to 7 July with an overall mean of 25 June) were the earliest to breed among the piscivores at St Lazaria (Appendix S1). Murres, which tended to feed in deeper water, nested later. Common murre annual hatch dates ranged from 4 August to 20 August with an overall mean of 12 August, and thick-billed murres ranged from 31 July to 16 August with an overall mean of 10 August (Appendix S1). We were unable to determine hatch dates for pelagic cormorants and tufted puffins.

*Productivity.* Productivity for pelagic cormorants at St Lazaria was highly variable, ranging from 0.10 to 1.70 large chicks per nest with an overall average of 0.62 (Appendix S1). Mean annual productivity for glaucous-winged gulls varied from 0.38 to 1.04 fledglings per nest with an overall mean of 0.61 (Appendix S1). Common murre productivity at St Lazaria ranged from 0.35 to 0.76 fledglings per egg, and thick-billed murre productivity ranged from 0.28 to 0.75 fledglings per egg. Overall productivity for common and thick-billed murres was 0.53 and 0.45 fledglings per egg, respectively (Appendix S1). We found a highly significant difference in mean annual productivity between common and thick-billed murres ( $t = 3.1962$ ,  $P = 0.0077$ , d.f. = 12). Rhinoceros auklet productivity ranged from 0.16 to 0.89 fledglings per egg, and tufted puffin productivity ranged from 0.07 to 0.72 fledglings per egg (Appendix S1). Overall productivity for rhinoceros auklets (a misnomer for this puffin) and tufted puffins was almost identical, at 0.47 and 0.46 fledglings per egg, respectively (Appendix S1).

*Covariation among species.* For all species of piscivorous seabirds for which we monitored hatch dates (glaucous-winged gull, common murre, thick-billed murre and rhinoceros auklet), inter-annual nesting chronology covaried positively (Table 3).

Annual reproductive rates of the two species of murres were positively correlated with each other (Table 3), and, for thick-billed murres, reproduction tended to be better in years when nesting was initiated relatively early ( $r_s = -0.539$ ,  $P \leq 0.10$ ,  $n = 13$ ; Appendix S2). Similarly, reproductive rates for the two

**Table 3** Correlations among mean hatch dates and annual productivity (i.e. positive or negative) of seabirds breeding at St Lazaria Island, Alaska.

	FTSP hatch	GWGU hatch	COMU hatch	TBMU hatch	FTSP productivity	LHSP productivity	PECO productivity	GWGU productivity	COMU productivity	TBMU productivity	TUPU productivity	<i>n</i> (no. years included in analysis)
FTSP hatch	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	12
LHSP hatch	+	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	12
GWGU hatch	+	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	8
COMU hatch	n.s.	+	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	-	n.s.	13
TBMU hatch	n.s.	+	+	n.s.	-	n.s.	n.s.	n.s.	n.s.	-	n.s.	13
RHAU hatch	n.s.	+	+	+	-	n.s.	+	n.s.	n.s.	n.s.	+	8
LHSP productivity	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	11
TBMU productivity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	11
TUPU productivity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	11
RHAU productivity	n.s.	n.s.	n.s.	n.s.	+	n.s.	-	n.s.	n.s.	n.s.	+	8

Species: FTSP, fork-tailed storm-petrel; LHSP, Leach's storm-petrel; PECO, pelagic cormorant; GWGU, glaucous-winged gull; COMU, common murre; TBMU, thick-billed murre; TUPU, tufted puffin; RHAU, rhinoceros auklet. Productivity was defined as the number of fledglings produced per egg laid. n.s., no significance; +, significantly positive; -, significantly negative. Results derived from Spearman's pair-wise frequency test,  $P < 0.10$ .

species of puffins (rhinoceros auklet and tufted puffin) were positively correlated with each other ( $r_s = 0.589$ ,  $P \leq 0.05$ ,  $n = 11$ ; Appendix S2), and there was a significant positive correlation between hatch date and productivity between these species ( $r_s = 0.535$ ,  $P \leq 0.10$ ,  $n = 10$ ; Appendix S2). Besides these correlations among species-pairs, we found that the reproductive success of surface-feeding glaucous-winged gulls was negatively related to annual productivity rates for the two species of deep-diving puffins (rhinoceros auklet:  $r_s = -0.559$ ,  $P \leq 0.10$ ,  $n = 13$ ; tufted puffin:  $r_s = -0.600$ ,  $P \leq 0.05$ ,  $n = 11$ ; Appendix S2).

*Covariation with sea surface temperature anomalies.* Gulls, murrets and rhinoceros auklets seemed to time their nesting events in response to common cues in the environment (see above and Table 2). We found a significant negative relationship between mean hatch dates and sea temperatures for rhinoceros auklets in May ( $r_s = -0.457$ ,  $P \leq 0.10$ ,  $n = 12$ ; Appendix S2). For the other piscivores we detected a negative correlation between mean hatch dates and August sea temperatures (glaucous winged-gulls,  $r_s = -0.568$ ,  $P \leq 0.10$ ,  $n = 8$ ; common murrets,  $r_s = -0.483$ ,  $P \leq 0.10$ ,  $n = 13$ ; thick-billed murrets,  $r_s = -0.448$ ,  $P \leq 0.10$ ,  $n = 13$ ; Appendix S2).

Significant correlations between annual productivity and sea surface temperature anomalies were detected for three species of fish-eating seabirds. For pelagic cormorants, annual productivity was negatively correlated with spring and summer sea surface temperatures ( $r_s$  values ranged from  $-0.479$  to  $-0.572$ ;  $P \leq 0.10$ ,  $n = 13$ ; Appendix S2). In contrast, positive correlations between productivity and summer sea temperatures (July and August) were found for common and thick-billed murrets (Table 2, Appendix S2).

## DISCUSSION

### Population trends

Although a general warming of the eastern North Pacific Ocean has taken place as a result of the effects of the Pacific Decadal Oscillation (Mantua *et al.*, 1997), we found no overall trend in spring and summer sea surface temperatures in the vicinity of St Lazaria (in an area of downwelling of the Alaska Current; Ware & McFarlane, 1989) over the 13-year study period. However, the seabirds breeding there appeared to respond to changes in their environment because every species we monitored exhibited significant population trends over the span of our study. Because we saw little evidence of changes in seabird mortality as a direct result of predation or disease at the breeding colony (L. Slater, unpublished data), populations probably responded to conditions in the marine food web, integrated over a decadal time-scale. For example, storm-petrel population increases suggest good productivity in the planktivorous portion of the marine food web, and similar increases in coastal piscivorous seabirds indicate that the near-shore forage fish portion of the food web also was adequate over the past decade. Declines in species feeding in

deeper water near St Lazaria are a little more difficult to explain. Possibly, piscivore foraging conditions for murrets and tufted puffins were inadequate to sustain populations, but factors associated with distant, and largely unknown, wintering areas also could have influenced survival or breeding condition.

We were unable to evaluate concordance among population trends in seabirds at St Lazaria in a regional context because there are no comparable monitoring data elsewhere in south-east Alaska for the species we studied. However, other colonies within the Alaska Current that allowed comparisons include those at Triangle Island, British Columbia (c. 800 km south-east of St Lazaria and near the northern reach of the upwelling California Current ecosystem; Ware & McFarlane, 1989), and Middleton and East Amatuli islands, Alaska (c. 680 km north-west and 1000 km west-north-west of St Lazaria, respectively), which lie within the downwelling Alaska Current.

Storm-petrel populations apparently have increased or remained stable at most colonies within the Alaska Current, as they have at St Lazaria (Dragoo *et al.*, 2008), over the past 15–20 years, suggesting adequate prey resources for these surface-feeding planktivores over a broad geographical area.

Coastal-foraging glaucous-winged gulls probably reflect very local conditions, being opportunistic feeders exploiting offal and other human-created foraging opportunities (Hayward & Verbeek, 2008). Fish processing and municipal waste disposal sites, as well as commercial and sport fishing activities, are within the foraging range of St Lazaria gulls and have probably enhanced population growth. In contrast, gull numbers at Middleton Island declined steadily between 1996 and 2004 (Ramey & Hatch, 2005) and are now at roughly half the number counted since monitoring began in 1993. Because Middleton is isolated, gulls have fewer foraging options compared with colonies near concentrations of anthropogenic food resources such as St Lazaria. The distribution and numbers of gulls in the Queen Charlotte Islands (also to the south of St Lazaria) have seen little change over a longer period of time, from the mid-1980s to the present (M. Hipfner, unpublished data).

The rhinoceros auklet, another coastal-foraging piscivore that increased at St Lazaria, has also experienced broad-scale increases over much of its breeding range in the North Pacific in recent decades (Gaston & Dechesne, 1996).

For murrets and tufted puffins, species that feed in deeper waters, population trends varied at seabird colonies throughout the Alaska Current. Between 1994 and 2006, murre numbers declined at St Lazaria and Middleton islands (this study; S. Hatch, unpublished data, respectively), as well as at Triangle Island between 1989 and 2004 (Hipfner, 2005). Changes in nesting habitat at Middleton and an increase in the number of avian predators at all three colonies are thought to have contributed to the downward trend in murrets (S. Hatch, unpublished data; Bertram, 1999), although evidence for this at St Lazaria is less clear (L. Slater, unpublished data). At East Amatuli Island, there was a decline following the *Exxon Valdez* oil spill in 1989, but populations have since increased and

have recently been considered fairly stable (Roseneau *et al.*, 2000; A. Kettle, unpublished data).

Murres winter along both inner and outer coastal areas and prefer the protected marine areas off straits, inlets, bays and channels (Ainley *et al.*, 2002), where, at least in some locations on the Pacific coast, they are inadvertently taken as by-catch in gill nets (Thompson *et al.*, 1998). Although the winter distribution of St Lazaria's murres has not been studied, it is possible that they join birds from other colonies in the north-eastern Pacific in coastal areas where congregated flocks experience similar conditions.

Similarly to the case in St Lazaria, tufted puffin colonies at East Amatuli Island (Dragoo *et al.*, 2008) and along the United States west coast are declining (Piatt & Kitaysky, 2002), but, in contrast, the large colony at Triangle Island is stable (D. Bertram, unpublished data; Gjerdrum *et al.*, 2003). However, recent repeated breeding failures there (Gjerdrum *et al.*, 2003) may result in future population declines owing to reduced recruitment.

At St Lazaria, small, discrete areas of peripheral nesting habitat have sloughed or deteriorated, thereby minimizing the amount of available habitat. However, < 5% of formerly used nesting habitat has sloughed, which does not account for the scale of the puffin population decline (L. Slater, unpublished data). The winter distribution of St Lazaria's tufted puffins is not known precisely, but in general puffins disperse widely in sub-tropical waters (Piatt & Kitaysky, 2002), where environmental perturbations, such as changes in prey availability, at-sea oil spills or chronic exposure to oil, and to a lesser degree incidental mortality as by-catch in high-seas drift nets, may be affecting the survival of puffins from many of the west coast colonies.

### Timing of nesting and reproductive rates

All the species we monitored at St Lazaria appeared to respond similarly with respect to cues in the environment in initiating nesting (i.e. all correlations among species for hatch dates were negative). Temperature alone did not explain these responses because we did not find significant relationships between hatch dates and spring or summer temperatures for several species. However, in the significant relationships found (Leach's storm-petrel, glaucous-winged gull, common murre and rhinoceros auklet), where species represented each foraging guild, all relationships were negative, indicating later nesting in years with relatively cool temperatures.

St Lazaria is the only site in the Alaska Current for which storm-petrel hatch dates were reported. The slight advancement in mean annual hatch date there may indicate that conditions enhanced the physiological state of adults, enabling them to initiate nesting earlier, as demonstrated in other species (Parker, 2002; Arnold *et al.*, 2006; Barea & Watson, 2007).

For piscivorous seabirds monitored throughout the Alaska Current, we found that hatch dates for murres were earlier at St Lazaria and Triangle islands when spring water temperatures were higher (Hipfner, 2005; Fisheries and Oceans Canada,

2006), but not at East Amatuli Island (Dragoo *et al.*, 2008). This may support the supposition that birds from the two colonies located near the southern part of the Alaska Current may winter in common areas and respond similarly to conditions there.

Mean hatch dates for rhinoceros auklets at St Lazaria did not show a trend during the study, but advanced for auklets breeding at Triangle Island (Hipfner, 2005).

The few significant correlations between seabird productivity and sea temperatures at St Lazaria (e.g. for the fork-tailed storm-petrel, common murre, thick-billed murre) were mostly positive, indicating higher reproductive rates in years with warmer sea temperatures. The only exception was for very near-shore-feeding pelagic cormorants, for which cold temperatures were related to higher productivity. Mantua *et al.* (1997) found that, within the context of the Pacific Decadal Oscillation (PDO), warm eras have seen enhanced coastal ocean biological productivity in Alaska and inhibited productivity off the west coast of the contiguous United States, whereas cold PDO eras have seen the opposite north-south pattern of marine ecosystem productivity.

Positive correlations for mean annual productivity within taxonomic groups of seabirds indicated that the two species within each group (i.e. storm-petrels, murres and puffins – tufted puffin and rhinoceros auklet) responded similarly to breeding season food web conditions near St Lazaria. This suggests that fluctuations in the food web were at a broad enough scale that species within pairs, which typically have slightly different foraging strategies, were not affected differently.

Although reproductive rates were similar for the two species of storm-petrels, it is interesting to note that fork-tailed storm-petrels have experienced consistently higher productivity since 2001 than have Leach's storm-petrels; the opposite condition existed between 1996 and 2000. We were unable to discern temperature differences between the areas where the two species of storm-petrels forage separately, but the slight difference in reproductive success may indicate a recent reduction in foraging quality for Leach's storm-petrels (oceanic waters beyond the continental slope) but not for fork-tailed storm-petrels (continental slope).

There was no trend in reproductive rates for common murres at St Lazaria Island, the only colony for which data were available. This may be an artefact of stable conditions within the marine environment near the colony.

Hedd *et al.* (2006) found that rhinoceros auklet breeding performance at Triangle Island was higher when cooler spring sea surface temperatures prevailed. Reproductive rates for auklets at St Lazaria varied more widely than those recorded at Triangle Island (this study; Hipfner, 2005).

In the California Current System, strong upwelling brings cooler water to the surface, generally creating better conditions for seabirds, particularly planktivores (Mantua *et al.*, 1997; for distribution of colonies, see SOWLS *et al.*, 1980). Just north of the California Current, at Triangle Island, alcids other than murres showed negative reproductive success responses



to warm sea surface temperatures in spring. Triangle Island lies close to the zone of divergence of the California and Alaska currents (upwelling and downwelling currents, respectively). It also lies closer to cyclic events such as El Niños, which originate much farther south. The current divergence and El Niños extend in varying degrees into Southeast Alaska, but may have relatively more influence on southern colonies (Triangle) than on those more distant (St Lázaria).

It is not surprising that the responses of seabirds to sea temperatures vary among systems. The relationships between sea temperatures and the timing of seabird breeding activities and productivity are probably mediated through the food web. That is, forage availability and quality, as influenced by sea temperatures, can affect seabird fitness. Other studies have shown that the timing of breeding activities often coincides with optimum availability of forage (Ainley & Boekelheide, 1990), which can also be a function of sea temperatures. Although sea temperatures can influence marine food webs in a number of ways (i.e. ocean productivity, distribution and abundance of prey), other ecosystem processes can also influence seabird breeding. For example, near St Lázaria the formation of broad coastal eddies that move offshore while carrying prey and nutrients (Melsom *et al.*, 1999; Fisheries and Oceans Canada, 2000) may have an important influence on the distribution of prey independent of temperature anomalies. Clearly, the relationships between temperature and seabird response variables need to be viewed in a regional context, because, as indicated, warm temperatures may enhance conditions for seabirds in one area, and cold temperatures may enhance them in another.

## CONCLUSIONS

Significant population trends were exhibited by all the species of seabirds we monitored at St Lázaria over the period of the study: plantivores and coastal-foraging piscivores increased whereas piscivores feeding in deeper water declined. Comparable data sets from St Lázaria and Triangle islands indicated that piscivorous seabirds adjusted the timing of breeding in similar fashion – specifically that cooler sea surface temperatures resulted in later hatching. Reproductive success was less consistent between the two sites: common murrelets at St Lázaria experienced higher productivity when sea temperatures were warmer, whereas the productivity of both species of puffins at Triangle Island improved when sea temperatures were cooler. All the species we monitored appeared to respond to environmental cues by adjusting the timing of nesting interannually, nesting earlier in warmer years. Reproductive rates of related species (i.e. the two species of storm-petrels; the two species of murrelets; tufted puffin and rhinoceros auklet) covaried positively; most species for which we found significant relationships tended to have higher productivity in warmer years.

Seabirds at St Lázaria, as they reflected conditions across marine habitats and across years, responded to changes in the marine environment on interannual and decadal scales. As

such, they become useful samples to help to understand and ultimately predict relationships between ocean temperature and marine food webs (Frederiksen, 2006), a topic of considerable interest in view of predictions of unprecedented ocean warming in the future.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Annual summaries of hatch dates and productivity for seabirds monitored at St Lázaria Island, Alaska, 1994–2006.

**Appendix S2** *R* values of Spearman's pair-wise rank correlation tests for data sets at St Lázaria Island, Alaska, 1994–2006.

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