

Tufted puffin reproduction reveals ocean climate variability

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Anomalously warm sea-surface temperatures (SSTs) are associated with interannual and decadal variability as well as with long-term climate changes indicative of global warming. Such oscillations could precipitate changes in a variety of oceanic processes to affect marine species worldwide. As global temperatures continue to rise, it will be critically important to be able to predict the effects of such changes on species' abundance, distribution, and ecological relationships so as to identify vulnerable populations. Off the coast of British Columbia, warm SSTs have persisted through the last two decades. Based on 16 years of reproductive data collected between 1975 and 2002, we show that the extreme variation in reproductive performance exhibited by tufted puffins (*Fratercula cirrhata*) was related to changes in SST both within and among seasons. Especially warm SSTs corresponded with drastically decreased growth rates and fledging success of puffin nestlings. Puffins may partially compensate for within-season changes associated with SST by adjusting their breeding phenology, yet our data also suggest that they are highly vulnerable to the effects of climate change at this site and may serve as a valuable indicator of biological change in the North Pacific. Further and prolonged increases in ocean temperature could make Triangle Island, which contains the largest tufted puffin colony in Canada, unsuitable as a breeding site for this species.

Ocean climate varies considerably between years and over decades along the Pacific coast of North America (1, 2). Nutrient-poor, warm surface waters characterize both the El Niño southern oscillation, which occurs every 2–7 years, and the positive phase of the Pacific decadal oscillation, which alternates with the negative phase on a 20- to 30-year cycle (3). The biological response to such large-scale fluctuations in ocean climate are best known in the California current and in the Gulf of Alaska, where studies have documented associated changes in zooplankton biomass (4) and community composition (5, 6), fish population declines (5), geographical range changes in fish and invertebrate species (6, 7), poor reproductive success, range expansions, and contractions, and population declines in a number of breeding marine birds (8–10). Because of the sensitivity of marine food webs to the physical changes associated with these oscillations, predicted future changes in global climate (11) are likely to have dramatic effects on marine ecosystems throughout the Pacific.

Such a combined effect of climate and regime changes may already be apparent off the coast of British Columbia, where the northern edge of the up-welling California current meets the southern edge of the down-welling Alaska current (12). In this transitional region, the relative influence of these two domains on local conditions fluctuates seasonally and from year to year, as do oceanic patterns driven by the Aleutian low and North Pacific high atmospheric pressure centers (6). The ecological consequence of ocean climate variability is generally not well understood in this region, but the breeding responses of seabirds may serve as useful indicators of changes to other trophic levels (13–16). For example, warm sea-surface temperatures (SSTs)

were associated with low masses of ancient murrelet (*Synthliboramphus antiquus*) chicks fledging in the Queen Charlotte Islands (52.9°N, 131.5°W), presumably via effects on their planktivorous and piscivorous prey (17). Farther south, on Triangle Island (50°52'N, 129°05'W), the world's largest Cassin's auklet (*Ptychoramphus aleuticus*) population has exhibited poor reproductive performance and a decline in breeding numbers as a result of climate-driven changes in zooplankton availability (18–20). With this article we show that local oceanographic conditions are strongly associated with colony-wide reproductive failures of tufted puffins on Triangle Island. Although these failures afflict the largest tufted puffin breeding colony (~50,000) in Canada (21) and they seem to be increasing in frequency, their causes have been elusive (22–25). By investigating the effects on puffins of short-term fluctuations in SSTs, we also hope to identify target guilds for mechanistic work so as to inform predictions about the ecosystem effects of future changes in global climate.

Methods

The tufted puffin is a long-lived, upper-trophic-level predator that occurs only in the North Pacific, with the center of its breeding distribution in the eastern Aleutians, Alaska. Although they occur as far south as California, Triangle Island supports the only large breeding colony south of Alaska (21).

SSTs. Data on SSTs were obtained from the Institute of Ocean Sciences Lighthouse Data web site (www-sci.pac.dfo-mpo.gc.ca/osap/data/SearchTools/Searchlighthouse.e.htm). For comparison with tufted puffin reproductive data (below), we used SST values reported from Pine Island (50°35'N, 127°26'W) during the tufted puffin breeding season (average SST from April to August). We used this station in preference to two others in the vicinity because it is a site of deep tidal mixing (19, 26) where SSTs are more likely to be reflective of ocean temperatures over the range of conditions in which puffins forage. Because such comparisons necessarily involve serial autocorrelation, we used a conservative approach (by reducing the degrees of freedom in significance testing) to identify the warming trend in the history of these temperature data (1937–2002) (27). Thus, the total number of observations was reduced from 66 to 18.7 (the effective number of independent observations). We used this same approach to determine the significance of the linear change in SST during the nestling period within each year. Nestling period was defined as the dates between the first-hatched egg

Abbreviation: SST, sea-surface temperature.

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and the last nestling to reach 31 days old, which is the end of the linear growth period (28). The nestling period varied from year to year in duration ($27 \pm \text{SE of } 2.4 \text{ days}$), start date ($26 \text{ June} \pm \text{SE of } 2.5 \text{ days}$), and end date ($22 \text{ July} \pm \text{SE of } 2.7 \text{ days}$). Deriving these dates made it possible to calculate the average SST during the linear growth period for each nestling as the mean SST between 9 and 31 days after its hatch date. Hatch dates for each chick were back-calculated from early nestling measurements (below).

Reproductive Data. We collected data on timing of breeding, nestling growth, and fledging success in 16 seasons spanning 28 years (1975–2002). Hatch dates were estimated by using a wing-length/age relationship established from a group of known aged nestlings (C.G., unpublished data) except for 1975, when we took values from the literature (25). No hatch-date estimate is available for 1976, when most puffins deserted their burrows during incubation (25). Sample sizes for hatch-date estimates ranged from 11 in 1994 to 112 in 1999. Nestlings were measured daily in 1977 (mass only, $n = 43$), every other day in 1978 (mass only, $n = 37$), every 3 days in 1980 and 1981 (mass and wing length, $n = 59$ and 67 , respectively), and every 5–10 days between 1995 and 2001 (mass and wing length, $n = 73, 11, 37, 28, 103, 102$, and 37 , respectively) from hatch to fledge. Measurements were not taken throughout the nestling period in 1982 or 1994. The annual means of growth rates were based on the change in mass and wing length for each individual nestling between 9 and 31 days, the period of linear growth (28). Nestlings were considered fledged if they were missing from their burrow after the age of 40 days with a wing length ≥ 130 mm when they were last measured. We used the number of fledged nestlings per egg hatched (as opposed to per egg laid) as our measure of success, because the number of eggs laid cannot not be determined accurately without disturbing the incubating adults and causing abandonment (29). In 1976, only 3 of 70 eggs hatched, and only one of those produced a fledgling, leading to an inflated estimate of success for that year. Original data were unavailable for 1975 and 1976 to calculate growth rates, and fledging-success estimates for these years were obtained from the literature (25, 28). Comparable data for growth and fledging success do not exist for 2002 because a change in protocol at Triangle Island apparently increased rates of nest abandonment, thus influencing these measures of reproductive performance.

Results

Data collected at Pine Island Light Station from 1937 to 2002 indicated substantial interannual fluctuations in SST (Fig. 1A) and decadal-scale shifts to colder temperatures during the 1950s and 1970s (Fig. 1B). In addition to these two ongoing and short-term forms of variation, records show a significant ($P = 0.0006$) warming trend, with an increase of 0.9°C over the last 66 years (1937–2002). The 1990s have been the warmest decade on record with 8 of the 10 warmest years occurring between 1990 and 1998 (Fig. 1B). Temperature anomalies from this station were strongly correlated with SSTs from Kains Island ($50^\circ 27' \text{N}$, $128^\circ 03' \text{W}$; $r = 0.85$, $n = 66$, $P < 0.0001$) and Egg Island ($51^\circ 15' \text{N}$, $127^\circ 51' \text{W}$; $r = 0.47$, $n = 28$, $P = 0.01$) and are therefore representative of oceanographic changes throughout the region.

Concomitant with this trend for increasing temperatures, reproductive timing advanced significantly within the study period (Fig. 2A). Between 1975 and 1982, mean annual hatch date ranged from July 8 to July 25 (average July 16). Hatch dates between 1994 and 2002 ranged from June 22 to July 10 (average June 30), 16 days earlier than the average for the previous decades [$t(13) = 4.7$, $P = 0.0004$]. The relationship between mean annual hatch date and breeding-season SST was strongly negative for the years between 1975 and 1998 [$F(1,9) = 10.68$, $P = 0.01$; Fig. 2B]. However, the relationship between SST and

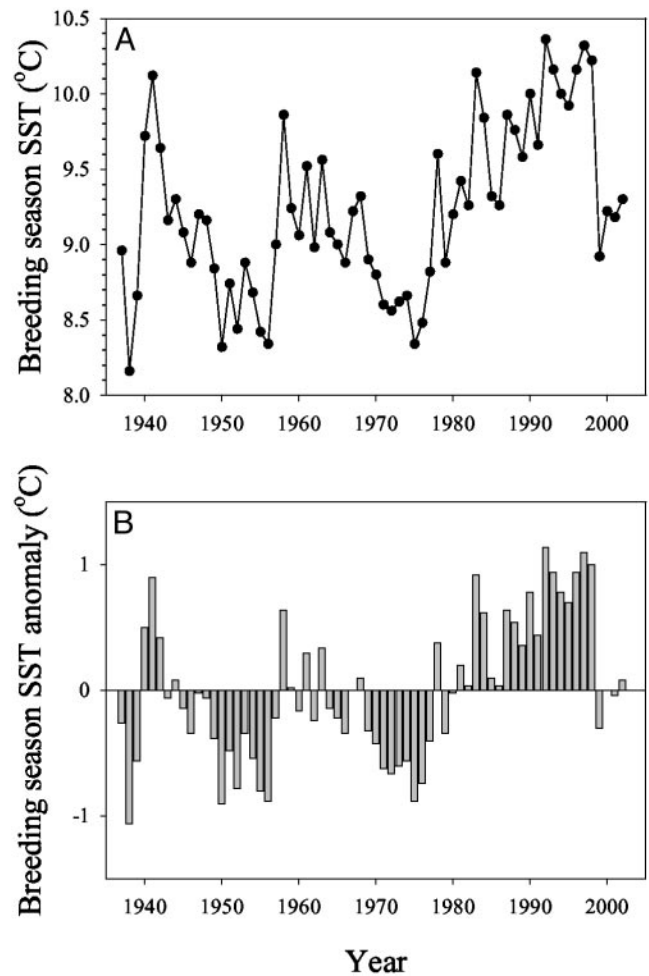


Fig. 1. (A) Annual mean SST ($^\circ\text{C}$) during the tufted puffin breeding season (April to August) recorded at Pine Island Lighthouse Station from 1937 to 2002. (B) Breeding-season SST anomalies from the long-term mean (9.2°C between 1937 and 2002) indicating decadal-scale shifts to colder temperatures during the 1950s and 1970s and persistent warm waters through the 1980s and 1990s.

hatch date lacked statistical significance when we included data from 1999–2002 [$F(1,13) = 2.55$, $P = 0.13$], when a substantial drop in temperature occurred. This difference suggests that hatch dates reflect changes to ocean climate over a longer time period than would be produced by interannual variation. Consistent with this interpretation we found no significant relationship between hatch date and SST [$F(1,13) = 0.06$, $P = 0.81$] after detrending both variables with respect to time (using the residuals from both after being regressed against year). Moreover, without detrending relationships with year, the strongest relationship between SST and hatch date was apparent when temperatures were lagged by 4 years [$F(1,13) = 27.47$, $P = 0.0002$, $r^2 = 0.68$].

Relative to its variable effect on hatch dates, changes in SST were associated with dramatic changes in nestling growth rates both among and within years. Among years, breeding-season SST explained 56% of the variation in nestling mass growth rate [$F(2,8) = 5.01$, $P = 0.04$; Fig. 3A]. A quadratic relationship indicated that the highest rates of mass gain occurred in years with intermediate temperatures in the range of 8.9 and 9.9°C . We did not have wing growth data for the 1970s, when temperatures were coolest; however, our data between 1980 and 2001 indi-

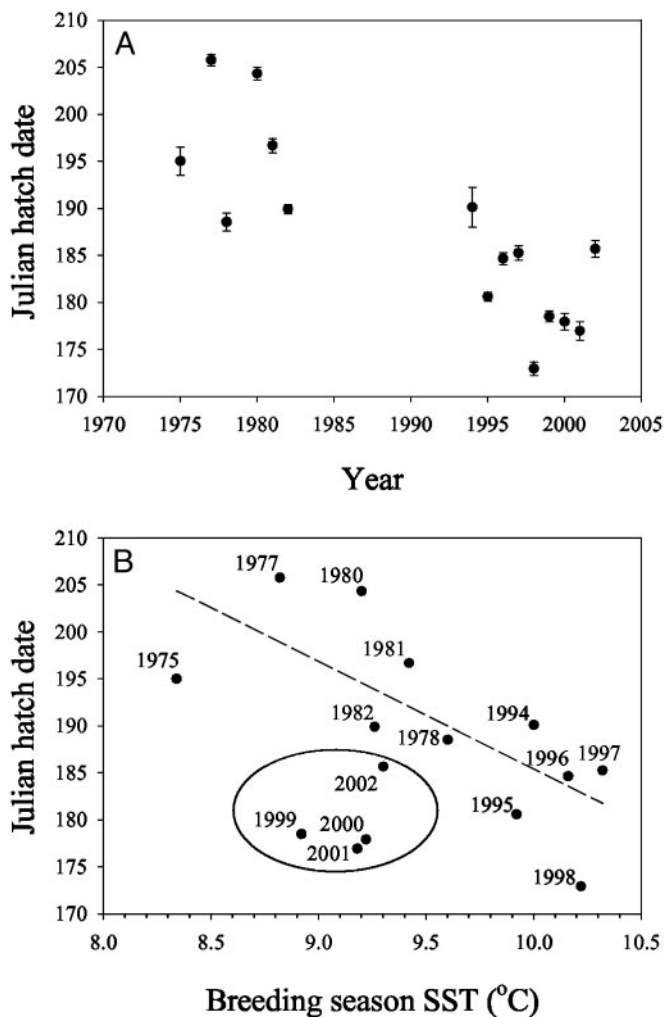


Fig. 2. (A) Mean annual hatch date advanced significantly ($P = 0.0004$) within the study period (between 1975 and 2002). Error bars indicate ± 1 SE. (B) Mean annual hatch date advanced significantly ($P = 0.01$) with increasing breeding-season SST (dashed regression line) without the inclusion of data from 1999 to 2002 (encircled), the period following an abrupt change to cooler SSTs.

cated that wing growth rate was lowest during seasons with the highest water temperatures [$F(1,7) = 7.50, P = 0.03, r^2 = 0.52$].

Warm SSTs were associated with poor mass growth rates not only among but also within seasons and are particularly well illustrated with data from 1981 (Fig. 3B). In this year, SST increased until late July, whereas nestling growth rates declined. Late in this year, SST declined and growth rates increased. Similar and significant seasonal declines in nestling mass growth rate occurred in all five seasons (1977, 1998, 1999, 2000, and 2001; $P < 0.01$ in all comparisons) for which there was a significant within-season linear increase in SST (Fig. 3C). No seasonal change in growth rate ($P > 0.10$) was found in four of the remaining years when SST either declined over the nestling period (1980 and 1997) or did not change (1978 and 1996). The general relationship for within-season increases in SST to be associated with declines in growth rates was countered in just 1 year (1995) when SST declined through the season and chick growth rates also declined [significant positive relationship: $F(1,71) = 40.30, P < 0.0001, r^2 = 0.36$].

Beyond their striking correlations with SST, seasonal averages of linear growth rates were highly correlated with seasonal

fledging success ($r = 0.88, n = 11, P = 0.0003$). In 6 of the 14 years studied (1976, 1977, 1994, 1996, 1997, and 1998), this colony experienced almost complete reproductive failure, and average growth rates in those years were well below 5 g/day. Although there was no significant correlation between fledging success and mean annual hatch date ($r = 0.05, n = 13, P = 0.87$), 55% of the observed variation in annual fledging success was explained by breeding-season SST [$F(2,11) = 6.67, P = 0.01$; Fig. 3D]. As would be predicted by growth rates, significantly more nestlings survived to fledge at intermediate temperatures (between 8.9 and 9.9°C). We found lower-than-expected fledging success in 2001 (Fig. 3D) given the relatively high growth rates and intermediate breeding-season SST (Fig. 3A). However, in this year, 75% of nestlings that did not fledge ($n = 22$) died or went missing after August 8 (Julian date 220), when SST dramatically increased (Fig. 3C). Finally, fledging success was near zero in years when breeding-season temperature exceeded 9.9°C.

Discussion

The significant warming that occurred in the 66-year period over which SST has been measured at Pine Island reflects an average increase of 0.013°C/year and a total increase of 0.9°C that is consistent with global climate trends (11). This suggests that SST is increasing in this area of the Pacific, independent of variation caused by both interannual events and decadal shifts. Nonetheless, the variability throughout this period and the relative decline in temperatures since 1999 suggest that short-term variability continues to be superimposed on longer-term climate change.

Before 1999, when SST decreased abruptly (Fig. 1B), puffins consistently responded to increasing average temperatures by breeding earlier. The significant association we found between SST and hatch dates explains the advancement in the timing of breeding for puffins that has occurred on Triangle Island since the 1970s (19). A similar association between SST and hatch dates has been documented for the rhinoceros auklet (*Cerorhinca monocerata*), another piscivore breeding at this site (19). Zooplankton biomass also peaked progressively earlier over this same period (19), a temporal shift that may influence the availability of sand lance (*Ammodytes hexapterus*), a predator of copepods (30) and the main prey species of puffin nesting at this colony (31). In the Atlantic, such parallel trends were reported across four marine trophic levels (32). Because puffins are predicted to initiate reproduction to align the period of maximum food demands (i.e., chick rearing) with the period when food is most available (33), their breeding phenology may be advancing in response to climate-induced changes in the availability of their prey species (34). At present, it is unclear the extent to which the early-season ocean environment (when birds initiate breeding) reflects the later environment (during chick rearing), what cues puffins use to initiate breeding, and whether their responses reflect short-term averages or a lagged response to specific phenomena. Interestingly, the adjustment to later hatch dates in 2002 (Fig. 2A) occurred 4 years after a precipitous drop in SST, consistent with the strongest response we observed between hatch dates and SSTs throughout the span of our data set. However, the absence of a relationship between hatch date and SST independent of year and with or without a lag suggests that puffins are breeding earlier in response to long-term oceanographic changes associated with increasing temperatures.

In addition to advancing hatch dates, our results show that puffins respond to increases in SST with decreased growth rates both among and within seasons. Among-season variation clearly shows that average puffin growth rates vary substantially over a narrow temperature range, again suggestive of temperature-based changes in prey availability. The immediacy with which

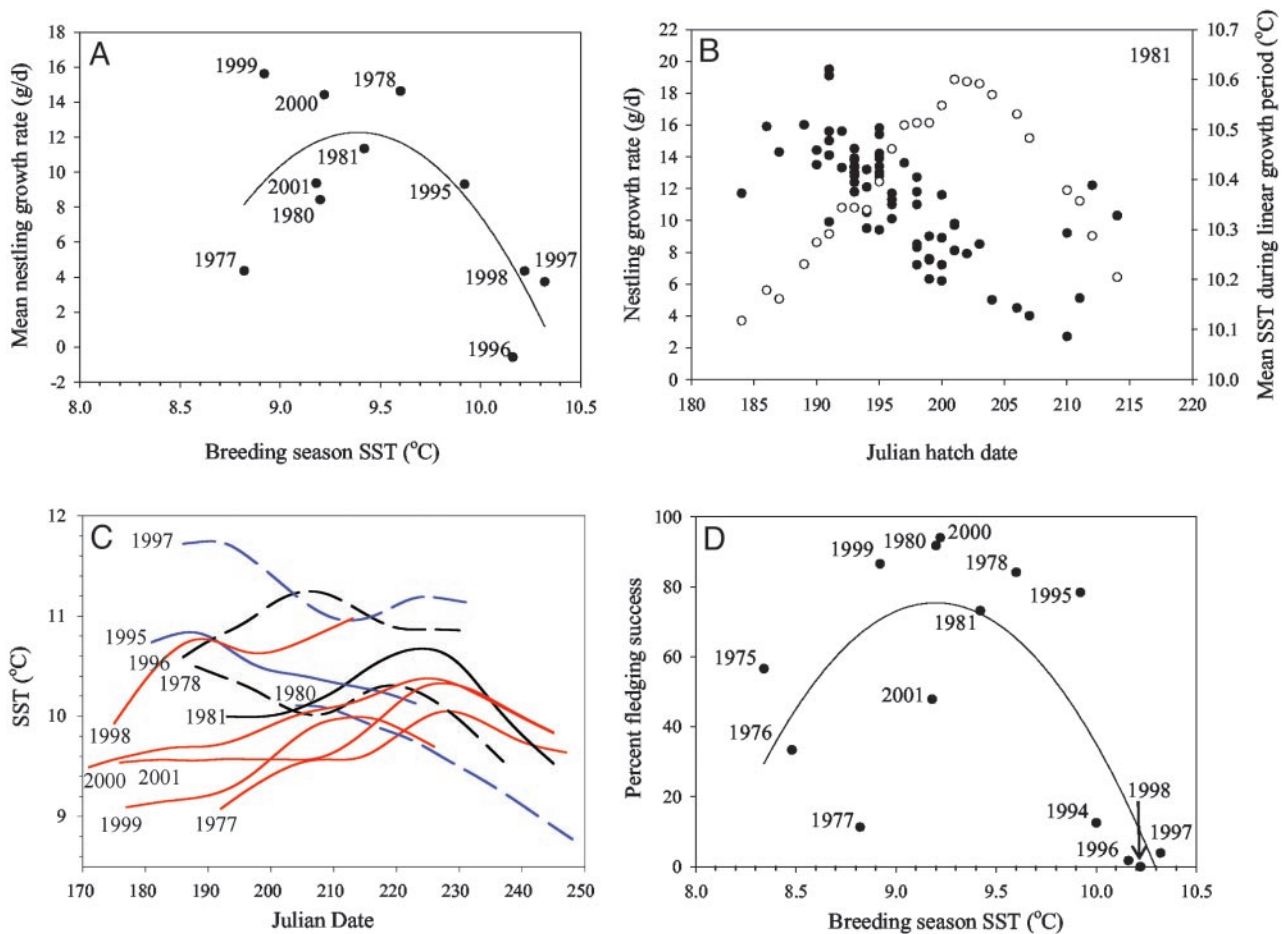


Fig. 3. (A) Interannual changes in nestling mass growth rate as a function of breeding-season SST. (B) The negative correlation between SST and nestling mass growth rate in 1981 [$F(1,65) = 34.50, P < 0.0001$]. Nestling mass growth rate (filled circles) declined over the season with an associated increase in SST during that same period (open circles). A late-season decline in SST coincided with a late-season increase in nestling growth rates. (C) The pattern of changing SST during the nestling period across all years in which we have nestling growth data (11 years). A spline function ($\lambda = 1,000$) was fit to the data for each year. Red indicates years in which we detected a significant seasonal linear increase in SST (see *Methods*), blue indicates a significant seasonal decrease in SST, and black indicates no linear change in SST over the nestling period. Solid lines indicate the years in which mass growth rate correlated significantly with SST during the linear growth period, and dashed lines indicate no significant relationship between mass growth rate and SST. (D) Interannual changes in fledging success as a function of breeding-season SST.

declines in nestling growth rates followed increasing SST within seasons more strongly implicates a prey-based mechanism for this association. In particular, changes in SST must limit the ability of the puffin to catch prey not only by effects on prey abundance (19, 35, 36) but also, or perhaps mainly, via their distribution (37, 38). Sand lance and other key prey species may leave areas with SSTs over a certain threshold with horizontal or vertical migrations, causing immediate declines in foraging success and potentially reducing chick growth rates only a few days later (Fig. 3B). The northern sand lance (*Ammodytes dubius*) found on the Newfoundland Grand Bank, for example, move to deeper water during the summer as temperatures increase (39). Such geographic shifts in prey distribution are particularly likely to affect puffins, relative to the three other species of Alcidae that breed on Triangle Island (19), because they forage diurnally close to their breeding colonies (40) and have semiprecocial nestlings that are provisioned multiple times a day (21). This hypothesis, that sand lance and other prey species change distribution with rising SST both within and among seasons, is readily testable and may have substantial implications for the variety of commercial fish stocks that rely on these species (30) and which have also exhibited poor recruitment in warm-water

years (41). More generally, increasing temperatures may be part of the reason that breeding performance often declines over time but within seasons for diverse seabird species (42).

The likely consequences of SST effects on prey, and hence puffin provisioning, are made dramatically clear with fledging success. When average breeding-season SSTs exceeded 9.9°C, growth rates dropped below 5 g/day, and fledging success was virtually zero. Such a precipitous decline in fledging success suggests that this temperature depicts an upper threshold to some essential biological process on which successful puffin reproduction depends. The sharpness of this boundary also emphasizes the potential magnitude of ecological responses to seemingly slight additional changes in global climate. Poor reproductive success occurred during periods of very low temperatures as well, producing quadratic relationships between SST and both growth rates and fledging success. These relationships identify an optimal temperature range of 8.9–9.9°C for puffin reproduction at this site (Fig. 3A and D). Both dome-shaped relationships may exist because sand lance and other fish prey also exhibit nonlinear changes in response to oceanic conditions at this (19) and other locations (43–45). Within the temperature range we documented, the seabird responses to

these effects are more pronounced at higher temperatures than at lower ones. At Triangle Island, both rhinoceros and Cassin's auklets have also exhibited poor performance in the warmest years, suggesting that there are underlying climate-induced trophic impacts for both piscivorous and planktivorous seabirds (19, 46). However, only the tufted puffin exhibited near-zero values for fledging success at these warm temperatures, which suggests that they (or more likely their prey) are particularly sensitive to high SSTs. If puffins depend disproportionately on particular fish species such as sand lance and these species change distribution and abundance rapidly with changes in SST, the severity of these failures may support a previous suggestion that tufted puffins lack the flexibility to switch to alternative prey species when their primary prey disappear (25). This hypothesis could be tested with better information about puffin diets and prey species' responses to SST and may recommend puffins as valuable indicators of marine ecosystem in this relatively unknown region of the Pacific.

Together, our analyses of a long-term data set show that SST exerts clear effects on puffin hatch dates, chick growth, and fledging success that are mediated by complex and poorly understood ecological relationships. A mechanistic understanding of these relationships would make it possible to predict the probable effects of future climate change on this and potentially other species well before they are detectable with conventional monitoring protocols. At our study colony, there has been no apparent change in population size (no change in the number of occupied nesting burrows surveyed at 5-year intervals from 1984 to 1999; Canadian Wildlife Service, unpublished data) despite the recent increase in reproductive failures. However, the population impacts of climate change on long-lived species are likely to be lagged by several years (47), which may be particularly true of puffins. In Røst, Lofoten Islands, Norway, the fisheries-induced collapse of the Norwegian herring stock in the late 1960s caused successive breeding failures of the Atlantic puffin, *Frater-*

cula arctica, that resulted in a 64% decline in population size by the late 1980s (48). Our data show that tufted puffins cannot reproduce successfully at high SSTs, and the frequency of both warm SSTs and reproductive failure has increased at this colony. Projected further increases in global temperatures (11) and a lack of any islands north of Triangle Island that are free of introduced predators, treeless, and otherwise suitable for puffin colonization (49) may dramatically reduce numbers on Triangle Island, the stronghold of the species in Canada, within a few decades. Indeed, significant population declines have been reported already for the most southerly colonies in Washington, Oregon, and California (50), suggesting that range contraction may be occurring already. Future changes in ocean climate will likely be the major factor determining the viability of existing populations of tufted puffins and perhaps many other marine species.

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