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The seasonal cycle revisited: interannual variation and ecosystem consequences

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Abstract

The annual seasonal cycle accounts for much of the total temporal variability of mid- and high-latitude marine ecosystems. Although the general pattern of the seasons repeats each year, climatic variability of the atmosphere and the ocean produce detectable changes in intensity and onset timing. We use a combination of time series data from oceanographic, zooplankton and seabird breeding data to ask if and how these variations in the timing of the spring growing season affect marine populations. For the physical environment, we develop an annual index of spring timing by fitting a non-linear 2-parameter periodic function to the average weekly SST data observed in British Columbia from 1 January to the end of August each year. For each year, the phase parameter describes the timing of seasonal warming (the timing index) and the amplitude parameter describes the magnitude of the temperature increase between the fitted winter minimum and summer maximum. For the zooplankton, which have annual and strongly synchronous cycles of biomass, productivity, and developmental sequence, we use copepodite stage composition to index the timing of the annual maximum. For seabirds, we examine (1975–1999) the timing of hatching, nestling growth performance, and diet for four species of alcids at Triangle Island, British Columbia's largest seabird colony and the world's largest population of the planktivorous Cassin's auklet. Temperature, zooplankton, and seabirds have all shown recent decadal trends toward 'earlier spring', but the magnitudes of the timing perturbations have differed from variable to variable and from year to year. Recent (1996–1999) extreme interannual variation in spring timing and April SST helped to facilitate a mechanistic investigation of oceanographic features that affect the reproductive performance of seabirds. Our results demonstrate a significant negative relationship between the annual spring timing index (and April mean SST) and nestling growth rates for both Cassin's auklet and rhinoceros auklet. Nestling growth rates were significantly lower in early, warm years. We demonstrate that low growth rates of Cassin's auklet occurred when copepod

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composition in nestling diet was low overall and copepods were scarce or absent in samples collected later in the season. We propose that when spring is early and warm, the duration of overlap of seabird breeding and copepod availability in surface waters becomes reduced, effectively creating a seasonal mismatch of prey and predator populations. Such a mismatch could explain the reduced reproductive performance of seabirds compared to years when spring was later and colder. The relationships we develop here can be used as simple predictive models to examine the effects of ocean climate change on seabird reproductive performance within our region. © 2001 Elsevier Science Ltd. All rights reserved.

Contents

1. Introduction	284
2. Methods	287
2.1. Temperature time series and spring timing index (1937–1999)	287
2.2. Zooplankton time series at OSP and coastal Vancouver Island (1975–1999)	288
2.3. Seabird time series (1975–1999)	288
2.3.1. Timing of breeding	289
2.4. Reproductive performance	289
2.5. Diet of Cassin's auklet nestlings	290
2.6. Reproductive consequences for variation in spring timing and April SST	290
3. Results	290
3.1. Physical data	290
3.1.1. SST at Pine Island (1937–1999)	290
3.1.2. Spring timing indexes from the Pine Island time series (1937–1999)	290
3.2. Timing of zooplankton maximum biomass at OSP and coastal Vancouver Island (1975–1999)	292
3.3. Timing of seabird breeding on Triangle Island (1975–1999)	292
3.4. Seabird reproductive performance	294
3.4.1. Interdecadal and interannual patterns	294
3.4.2. Within season variation in nestling growth rate (1996–1999)	294
3.5. Variation in Cassin's auklet nestling diet (1996–1999)	296
3.6. Reproductive consequences for variation in spring timing and April SST	298
3.6.1. Within season effects	298
3.6.2. Annual effects	298
4. Discussion	301
Acknowledgements	304
References	305

1. Introduction

Climate change is affecting marine ecosystems worldwide. In the Atlantic, Aebisher, Coulson, and Colebrook (1990) reported parallel long-term (1955–1987) trends across four marine trophic levels (gauged by the abundance of phytoplankton, zooplankton, herring and the reproductive

timing and performance of seabirds) and weather. These authors demonstrated that the signal of weather was so strong that it was evident at all levels of the marine ecosystem. In a recent review of climate–ocean variability and ecosystem responses in the Northeast Pacific, McGowan, Cayan, and Dorman (1998) concur with Aebischer, Coulson, and Colebrook (1990) and also Hayward (1997) and argue that “there are large-scale biological responses in the ocean to low-frequency climatic variations in the atmosphere acting through changes in the horizontal and vertical movements of water”. Further, McGowan, Cayan, and Dorman (1998) posit that there is no doubt that interannual and interdecadal variations strongly affect the structure and function of marine ecosystems.

Top predators such as seabirds have shown population declines from California to Alaska in response to climate driven changes in either the abundance, or the timing of zooplankton availability in surface waters. For example, in the California Current ecosystem a 65% population decline of the planktivorous Cassin’s auklet on the Farallon Islands from 1972 to 1997 (Nur, Sydeman, Hester, & Pyle, 1998) has been linked (Ainley, Spear, & Allen, 1996) to a significant long-term decline in zooplankton production in the California Current system (Roemmich & McGowan, 1995). Significant declines in populations of seabirds wintering in the California Current were also reported (Veit, Pyle, & McGowan, 1996). A decline in the world’s largest population of Cassin’s auklet on Triangle Island, British Columbia, may similarly be related to the long-term zooplankton decline in the California Current (Bertram, Jones, Cooch, Knechtel, & Cooke, 2000). In the Gulf of Alaska (GOA) ecosystem, declines in marine bird populations appear to be related to changes in forage fish abundance (Agler, Kendall, Irons, & Klosiewski, 1999; Anderson & Piatt, 1998) that occurred because of extensive reorganization of the marine ecosystem following the shift in 1977 to a warm regime (Anderson & Piatt, 1998; Francis, Hare, Hollowed, & Wooster, 1998; Hare, Minobe, & Wooster, 2000).

To explain the decline of numerous taxa in the GOA during the recent warm regime, Anderson and Piatt (1998) invoked the match–mismatch hypothesis. The match–mismatch hypothesis suggests that recruitment strongly depends on a temporal match in timing of larval emergence and availability of zooplankton prey (Cushing, 1995). In the subarctic Pacific, a single copepod species, *Neocalanus plumchrus*, is dominant in the mesozooplankton biomass (Mackas, Goldblatt, & Lewis, 1998). The vertical distribution and developmental sequence are both strongly seasonal and together they produce a strong but short-lived (<60 d) annual peak in upper ocean zooplankton biomass in spring and early summer. At Ocean Station P (50° N 145° W) seasonal phasing of this annual maximum has shifted dramatically between 1956 and 1996. Population development was very late in the 1970s (biomass maximum in mid to late July), early in the 1950s (late May–early June) and very early in the 1990s (early to mid May). These changes in timing were strongly correlated with large scale interannual and interdecadal ocean climate fluctuations as reflected by spring temperature anomalies in the surface mixed layer where the juvenile copepods feed and grow. Development is about 60 d earlier in warm, than in cold years. The change in developmental timing is too large to be explained solely by the physiological acceleration of individual development rates. Mackas et al. (1998), therefore, argued that variation in timing of the zooplankton peak was also influenced by interannual differences in survival among early versus late components of the annual copepodite cohort, with significantly higher survival of the early cohorts in warm years. Anderson and Piatt (1998) reasoned that such variability in the timing of zooplankton production could have a profound effect on recruitment of fish and

decapods of the GOA. Seasonal biomass peaks of zooplankton were 1–2 months later during the cold regime than during the warm regime. Organisms such as the majority of shrimp, crabs and capelin, which spawn or release their larvae in late spring or early summer are expected to be negatively affected by a shift towards earlier zooplankton biomass peaks (Anderson & Piatt, 1998). Following the regime shift, capelin (*Mallotus villosus*) disappeared from the diets of seabirds and marine mammals and was replaced largely by juvenile pollock (*Theragra chalcogramma*), a species which spawns early and has likely to have benefited from the shift towards earlier zooplankton peaks. Declines in GOA seabird populations may be attributable to changes in diet composition (Anderson & Piatt, 1998) because juvenile pollock have low energy densities compared to fatty forage species such as capelin (Van Pelt, Piatt, Lance, & Roby, 1997).

Here we report on the consequences of climate induced variation in the timing of the seasonal cycle on seabird reproductive timing and performance. We couple ocean temperature data and estimates of spring timing derived from SST measurements at Pine Island, BC from 1937 to 1999, the timing of *N. plumchrus* peak biomass estimates from Ocean Station P and coastal Vancouver Island, and information on seabird reproduction for four species of alcids (one planktivorous, three piscivorous) from Triangle Island, BC (Fig. 1). Copepods of three *Neocalanus* species (*N. plumchrus*, *N. flemingeri* and *N. cristatus*) dominate the spring and early summer mesozooplankton biomass in most deep water regions of the subarctic North Pacific (Mackas & Tsuda, 1999). Although life history characteristics vary between the three species, all three have large body

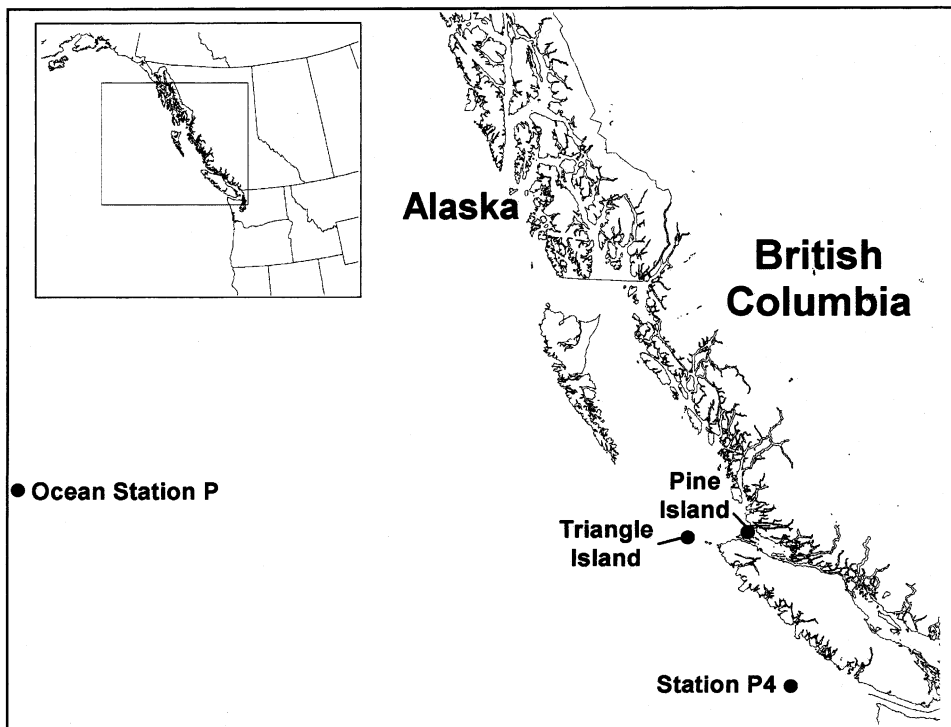


Fig. 1. Study region showing Ocean Station P and station P4 where the zooplankton was sampled, Pine Island, where the SST data were collected, and Triangle Island where the seabird data were obtained.

sizes and strongly-seasonal life cycles involving a relatively brief spring and early summer growth season spent in the upper 100 m, accumulate substantial lipid reserves by the end of the growing season, undertake ontogenetic vertical migrations, with prolonged periods of dormancy, and delayed maturation and spawning at depths ranging between 400 and 2000 m (Miller, Frost, Batchelder, Clemons, & Conway, 1984; Kobari & Ikeda, 1999). Because of these life history strategies, the seasonal peak in total upper ocean zooplankton biomass is pronounced and relatively brief. At both Ocean Station P (where the annual biomass peak is dominated by *N. plumchrus* and *N. cristatus*) and in the Strait of Georgia (dominated by *N. plumchrus*), the timing of the annual maximum has been observed to fluctuate by several weeks, and covaries with the spring season mixed layer temperature (Mackas et al., 1998). These copepods are important forage items for the British Columbian colonial alcids, either directly as prey for Cassin's auklets, or indirectly as the primary prey of small fishes such as the Pacific sand lance (*Ammodytes hexapterus*), which are among the main diet of rhinoceros auklets and tufted puffins (Vermeer, Cullen, & Porter, 1979; Bertram, Kaiser, & Ydenberg, 1991; Field, 1988). Fifth copepodite stage of the largest-bodied species (*N. cristatus*) is especially important in the diet of Cassin's auklets (Vermeer 1981, 1985 and Hedd, Ryder, Cowen, & Bertram, pers.comm.). Although this species has a more prolonged growing season than *N. plumchrus* (Miller, Frost, Batchelder, Clemons, & Conway, 1984; Kobari & Ikeda, 1999; Saito & Tsuda, 2000) its developmental cycle is also strongly seasonal. Interannual variability of its developmental timing has not yet been described in detail, but it also appears to have been 'early' along Line P in the mid-late 1990s (Goldblatt, Mackas, & Lewis, 1999). We propose a mechanism based on the duration of the seasonal match and mismatch of predators and prey to explain some of the observed changes in seabird reproductive performance between years. Further, our analyses have identified several simple relationships, which can be used to make predictions about seabird reproductive performance based on a knowledge of ocean temperatures in April or estimates of spring timing.

2. Methods

2.1. Temperature time series and spring timing index (1937–1999)

Interannual variation in the phase and amplitude of the dominant cycle may affect marine ecosystems more than sources of variation at other frequencies. Temperature is important to the structure and function of biological systems because of its pervasive effects on behaviour, physiology, distribution and migration. Seasonal temperatures may warm more or less rapidly in spring to a variable summer peak, and then fall more or less rapidly to a variable winter minimum. The progression from winter to summer is a time of dramatic change in biological activity, so the timing and magnitude of the vernal warming may have a significant effect on the ecosystems. To explore relationships between biology and physics more fully, we developed annual indices of spring timing (τ) and warming (ψ) by fitting a simple sine function to a zero-centered (annual mean removed) daily SST series as

$$\xi_{i,j} = \sin(\delta_{ij} + \tau_i) \times \psi_i$$

where i =year, j =day of year, ξ =predicted temperature, $\delta=((\text{day of year} - 1)/365.25) \times 2\pi$, τ =timing

(phase) parameter, ψ =warming (amplitude) parameter, using daily SST observations from Pine Island (50°35'N, 127°26'W) between 1 January through 31 August. (Note that at Pine Island SST is an indicator of water column temperature because of deep tidal mixing.) These dates span both the timing of the winter minimum (late January) and summer maximum, but avoid influencing the estimation of a springtime phenomenon with autumnal data. Least squares was used to estimate the model parameters from the data using the SYSTAT NONLIN module. Although τ was estimated in units of radians in the model, it was transformed to an anomaly measure in units of days. By subtracting the annual mean from each year, the variation in spring timing and warming can be examined independently of regime shifts (Hare et al., 2000), long-term trends, or low frequency cycles (Ware, 1995). We examined the spring timing index as well as a simpler measure of ecosystem state (mean April SST) in relation to seabird reproductive timing and performance. As there was a positive association between the spring timing index and April mean SST, it was possible to quantify the amount of variation in the spring timing index that could be accounted for by variation in the estimates of April mean SST.

2.2. Zooplankton time series at OSP and coastal Vancouver Island (1975–1999)

The copepod *N. plumchrus* is a deep water migrant. The copepodites hatch from eggs laid at depth, and migrate to surface waters to complete their development in spring, they then return to depth to overwinter, reproduce and die. Data reported here from Ocean Station P (50°N, 145°W) are from Mackas et al. (1998) which contains a full description of the methods. Samples collected at Station P4 (48°39'N, 126°40'W) along Line P were vertically integrated tows from 150 m to the surface. Estimates of the annual timing of the peak *N. plumchrus* biomass were based upon stage ratios.

2.3. Seabird time series (1975–1999)

We studied four species of alcids on Triangle Island (50°52'N, 129°05'W), the largest and most diverse seabird colony in British Columbia, Canada. All of the species we examined have a single egg clutch. Cassin's auklet (CAAU: *Ptychoramphus aleuticus*) is a small (190 g) planktivorous, burrow nesting seabird, which visits the breeding colony only at night. Nestlings leave the burrow (fledge) when they are between 40 and 60 d old. In 1989, the breeding population of Cassin's auklet at Triangle Island was estimated to be 548,000 pairs (Rodway, 1991), making it the largest known colony of this species in the world. The rhinoceros auklet (RHAU: *Cerorhinca monocerata*) is a 550 g piscivorous, burrow nesting species which only visits the colony at night. Nestlings are cared for from 45 to 60 d until fledging. In 1989, the breeding population of rhinoceros auklet was estimated to be 41,682 pairs (Rodway, 1991), making Triangle Island the third largest colony of this species in British Columbia. The tufted puffin (TUPU: *Fratercula cirrhata*) is a 750 g, piscivorous, burrow nester which visits the colony repeatedly throughout the day. Its nestlings fledge at 40–50 d. The breeding population for Triangle Island was estimated to be 26,000 pairs (Rodway, 1991). The common murre (COMU: *Uria aalge*) is a large (950 g), piscivorous, cliff nesting, diurnal species. Nestling development is semi-precocial and the chicks leave the colony with their fathers at age 20–25 d and complete the majority of their development at sea. The breeding population on Triangle Island was estimated to be 4100 pairs (Rodway,

1991). Readers are referred to Gaston and Jones (1998) for additional details on the natural history of these species.

2.3.1. *Timing of breeding*

To gauge timing of breeding we estimated hatch dates from 1975 to 1999 with a combination of historical data, literature values (where original data were unavailable) and current information. For Cassin's and rhinoceros auklets in the 1990s we inspected burrows at 3–5 d intervals to determine if an egg had been laid. Following the discovery of a Cassin's or rhinoceros auklet egg, the burrows were left undisturbed for 30–38 d. These burrows were then inspected at 3–5 d intervals to look for nestlings, and estimate the hatch dates based upon a wing length/age relationship of those nestlings whose exact ages were known. Hatch date estimates for rhinoceros auklets in the 1980s were back-calculated from the first available measurements of nestlings using a wing length/age relationship. In the 1990s we also back calculated hatch dates of tufted puffins based upon the first available measurements of nestlings, again using a wing length/age relationship established from known aged chicks. For the common murre, the sole sources of historical data were the estimates of the first date on which chicks were observed by Vallée and Carter (1987). To make comparisons legitimate we also report the date that the nestlings were first seen in the 1990s, in addition to providing estimates of the mean hatching dates. Data sources for annual estimates of the timing of breeding follow:

Cassin's auklet: 1978 (Vermeer, 1987); 1981 (K. Vermeer, Canadian Wildlife Service, unpubl.); 1982 (hatch date was estimated from fledging date in 1982 [cited in Vermeer, 1987] by subtracting the average fledging age of 45 d); 1994 (Y. Morbey, Simon Fraser University, unpubl.).

Rhinoceros auklet: 1976 (calculated from Vermeer, 1980); 1977 [hatch date was estimated from fledging date in 1977 (calculated from Vermeer, 1980) by subtracting the fledging age of 53 d (based on estimates for 1976 and 1978 cited in Vermeer & Cullen, 1979); 1978 (calculated from Vermeer, 1980), 1984–1986 (DFB unpubl.)].

Tufted puffin: 1975 (calculated from Vermeer et al., 1979); 1977 (calculated from Vermeer et al., 1979); 1978 (K. Vermeer, Canadian Wildlife Service, unpubl.); 1981 (A. Vallée, University of British Columbia, unpubl.).

Common murre: 1981, 1982 (Vallée & Carter, 1987); 1995 (J. Parrish, University of Washington, unpubl.); 1989 (Rodway, Lemon, & Summers, 1990).

The time series for the seabirds are fragmented, but are most complete for the 1990s. For the statistical tests concerning changes in the timing of breeding we combined the available information from the 1970s and 1980s to contrast them with the 1990s. For each species we compared the two time periods using a Mann–Whitney U-test.

2.4. *Reproductive performance*

We report annual anomalies from the grand mean of nestling growth rates as our main measure of reproductive performance. For Cassin's auklet, the annual means of growth rates were based on mass change for each individual nestling between 5 and 25 d, the period of linear growth (Vermeer, 1981; Morbey & Ydenberg, 2000). Similarly, for rhinoceros auklets and tufted puffins, growth rates were calculated for each individual nestling between 9 and 41 d during the linear growth phase (when repeated measures separated by at least 10 d were available). No growth

information was available for the common murre. Mass at fledging was also available for Cassin's auklet and rhinoceros auklet. The data sources for values prior to the 1990s are reported in the Pacific Seabird database with the exception of the value for Cassin's auklet in 1981, which was calculated from raw unpublished data (K. Vermeer unpubl.). Within-season variation in nestling growth rate was examined by plotting individual growth estimates against the date of hatching. Annual population-level estimates for seasonal change in nestling growth were estimated as the slopes of the linear regressions of individual growth rates on hatch date within each year.

2.5. *Diet of Cassin's auklet nestlings*

Diet of nestlings of the planktivorous, Cassin's auklet is reported for 1996–1999. At ten day intervals from 18 May to 28 June, 10 food samples intended for nestlings were collected from incoming adults by encouraging the birds to regurgitate into a plastic funnel connected to a container. Samples were preserved in 15% formalin for subsequent identification and enumeration. Data are reported as percent composition by wet mass for the major prey classes. Differences between years in the percent composition of copepods in the diet were assessed using ANOVA followed by post hoc contrasts as appropriate. Data were arcsin transformed prior to analysis.

2.6. *Reproductive consequences for variation in spring timing and April SST*

Regression analyses were used to examine the relationships between the physical variables (spring timing index and mean April SST) and hatch date, nestling growth rates, and fledging masses. The analyses were necessarily confined to the period when seabird information was available.

3. Results

3.1. *Physical data*

3.1.1. *SST at Pine Island (1937–1999)*

Pine Island light station data from 1937–1999 indicate variation in April SST on interannual and decadal scales [Fig. 2(a)]. Water temperatures have increased from the lowest temperatures on record in 1971 to some of the highest values ever observed in the 1980s and particularly in the 1990s. Note that the temperature in 1999 dropped to the lowest value observed in over 10 yr, to values in line with the long-term average.

3.1.2. *Spring timing indexes from the Pine Island time series (1937–1999)*

The spring timing index based on SST from Pine Island (Table 1) spans a range of 40 d with the latest value observed in 1954 and the earliest value observed in 1993 [Fig. 2(b)]. Note that within the 4-yr period from 1996 to 1999 almost the entire range of values was observed; spring timing was very early in 1996 and 1998 but late in 1997 and 1999. The spring timing index and

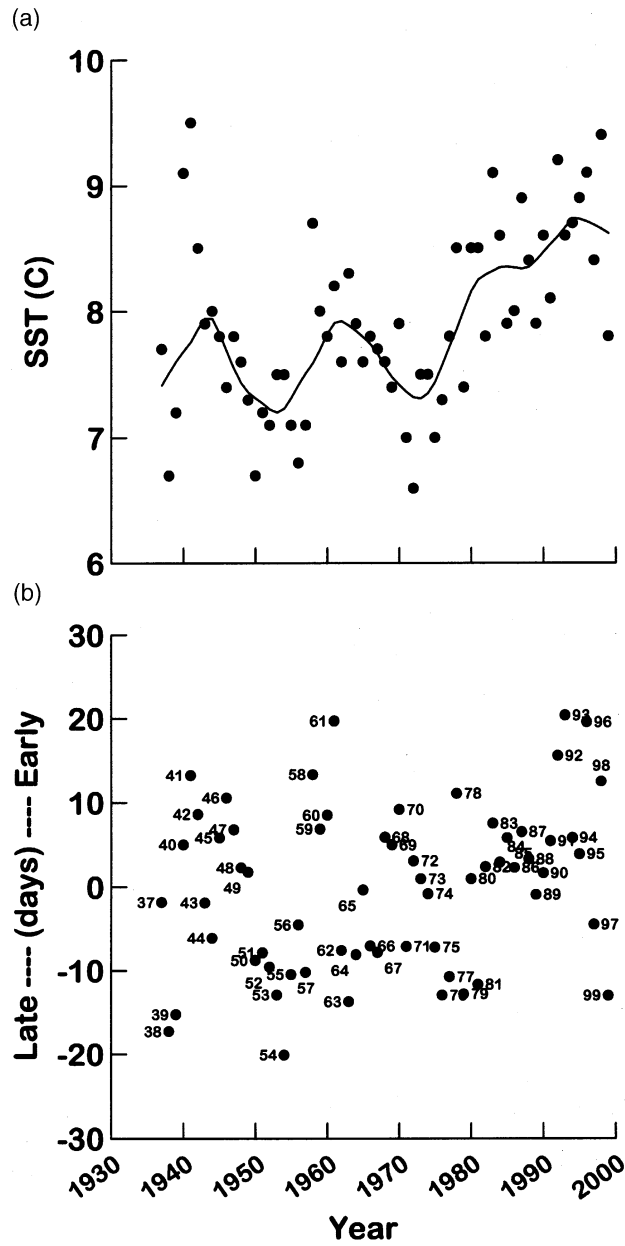


Fig. 2. Average April sea surface temperatures with lowess trend line, tension = 0.2 (a) and spring timing anomalies (b, see Methods) for Pine Island BC from 1937 to 1999.

the April SST were positively correlated ($r=0.60$, $n=50$, $P<0.00001$) with April SST accounting for 37% of the variation in the spring timing index.

Table 1

Annual spring timing anomaly (τ) in days estimated from daily sea surface temperatures at Pine Island, BC

Year	τ	Year	τ	Year	τ
1937	-1.9	1958	13.3	1979	-12.8
1938	-17.3	1959	6.9	1980	1.0
1939	-15.3	1960	8.5	1981	-11.7
1940	5.0	1961	19.7	1982	2.4
1941	13.2	1962	-7.6	1983	7.5
1942	8.6	1963	-13.7	1984	2.9
1943	-1.9	1964	-8.1	1985	5.8
1944	-6.2	1965	-0.4	1986	2.3
1945	5.8	1966	-7.1	1987	6.5
1946	10.5	1967	-7.9	1988	3.3
1947	6.8	1968	5.9	1989	-0.9
1948	2.3	1969	5.0	1990	1.7
1949	1.7	1970	9.2	1991	5.4
1950	-8.8	1971	-7.2	1992	15.6
1951	-7.9	1972	3.1	1993	20.4
1952	-9.6	1973	0.9	1994	5.8
1953	-12.9	1974	-0.8	1995	3.9
1954	-20.1	1975	-7.2	1996	19.6
1955	-10.5	1976	-13.0	1997	-4.5
1956	-4.6	1977	-10.8	1998	12.5
1957	-10.2	1978	11.1	1999	-13.0

3.2. Timing of zooplankton maximum biomass at OSP and coastal Vancouver Island (1975–1999)

The date of maximum biomass of *N. plumchrus* advanced by 6–8 weeks at OSP between 1975 and 1996 (Fig. 3). Consequently, the peak availability of zooplankton in surface waters has tended to end progressively earlier in more recent years of that time series. At coastal locations, the timing of zooplankton maximum biomass is earlier than at the oceanic locations. More importantly, samples from a station on coastal Vancouver Island (P4) also indicate that the date of maximum zooplankton biomass has been advancing and so confirm that the phenomenon is not confined to the offshore copepod populations at OSP (Fig. 3).

3.3. Timing of seabird breeding on Triangle Island (1975–1999)

Within all years the planktivorous Cassin's auklet are the first species to breed, followed in succession by the piscivores, rhinoceros auklet, tufted puffin and common murre (Fig. 4). For the piscivores, breeding was significantly earlier in the 1990s than in the previous decades pooled (RHAU: Mann–Whitney $U=34.5$, $\chi^2=7.0$, $df=1$, $P=0.008$; TUPU: Mann–Whitney $U=22.5$, $\chi^2=5.0$, $df=1$, $P=0.03$; COMU: Mann–Whitney $U=12$, $\chi^2=4.6$, $df=1$, $P=0.03$). For the piscivores the earliest breeding dates on record were all in the 1990s. Note that to allow for comparison with the common murre data from 1980 and 1981, breeding dates in the 1990s are reported as

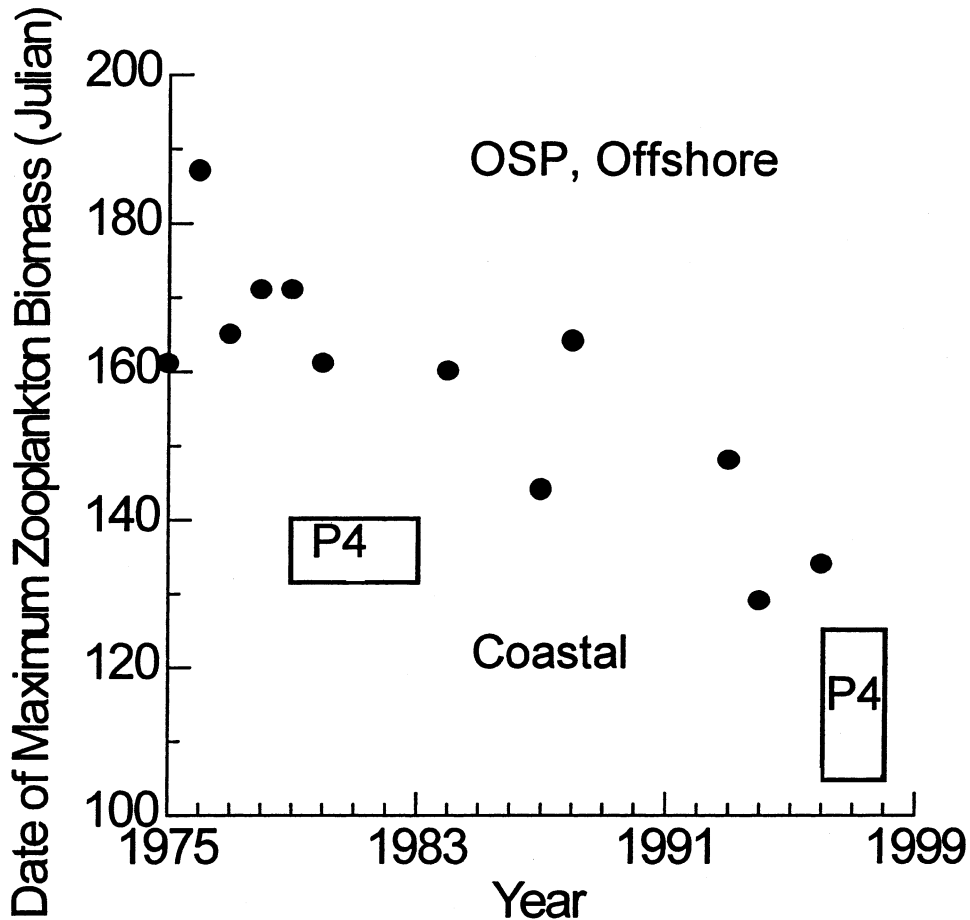


Fig. 3. Estimated dates of annual biomass peak for *Neocalanus plumchrus* at Ocean Station P (OSP: ●; data from Mackas et al., 1998) and at a coastal station off Vancouver Island, P4. The boxes represent the range of estimated peak biomass dates for 1979–1983, and for 1996–1998 at station P4.

dates when the first nestlings were seen. Observations of common murre mean Julian hatch dates within the 1990s also indicate an advance from 1995 to 1999 (1995: day 211; 1997: day 204; 1998: day 195; and 1999: day 189).

In contrast to the piscivores, we could not detect a significant advance in the timing of breeding for Cassin's auklet. Instead, we observed extreme variation in the timing of hatching during the 1990s and a tendency for breeding dates to become later since 1994. Values for hatch date in Cassin's auklet ranged from the earliest record of 18 May in 1994 to the latest date ever observed on 29 May 1999.

It is interesting to note that because of the interspecific difference in hatch dates over time, the breeding season of these species has converged since the 1970 and 1980s, creating a shorter period of breeding activity at the seabird colony in the 1990s. For example, in 1981 there was an 82 d lag between the hatch date of Cassin's auklet and the first sighting of murre nestlings.

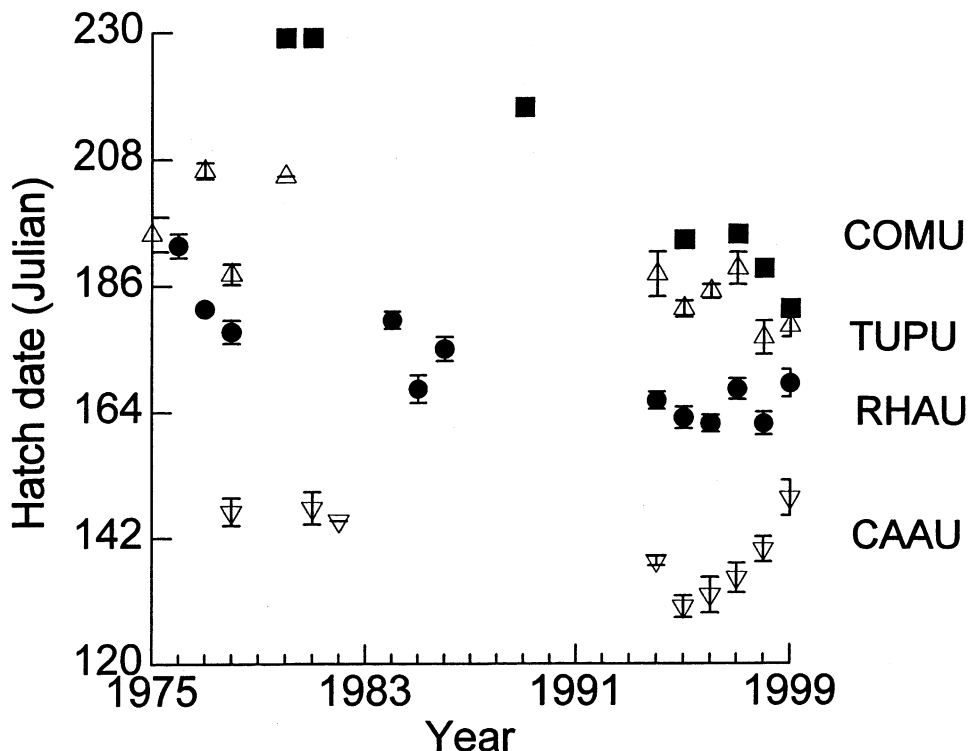


Fig. 4. Estimates of seabird breeding dates on Triangle Island, BC, 1975–1999. Error bars are 95% confidence intervals around mean values. Absence of error bars indicates that estimates of variation are not available. Values for Cassin's auklet (CAAU: ∇), rhinoceros auklet (RHAU: \circ), and tufted puffins (TUPU: \triangle) are mean hatching dates (sample sizes range from 12 to 174). Values for common murre (COMU: \square) are dates when nestlings were first observed.

In 1999, however, this lag period had shortened to 33 d, resulting in increased overlap in the timing of seabird breeding on Triangle Island in that year.

3.4. Seabird reproductive performance

3.4.1. Interdecadal and interannual patterns

Nestling growth rate anomalies for tufted puffin, rhinoceros auklet, and Cassin's auklet indicate that there were frequent years of poor growth for all species in the 1990s [Fig. 5: note that for the tufted puffin, no growth rate estimates were available for 1976 when only 4% of eggs hatched (Vermeer & Cullen, 1979)]. Nevertheless, the 1990s were also a decade when extreme interannual variation was observed for all species. Within the decade the worst year for all species was 1996, whereas nestling growth rates were most rapid in 1999. In contrast to the piscivorous in general, Cassin's auklet showed positive growth anomalies in 1995 and 1997.

3.4.2. Within season variation in nestling growth rate (1996–1999)

For Cassin's auklet 1996 and 1998 were years of exceptionally poor nestling growth at the population level. Moreover, in 1996 and 1998, the individual parents breeding early in the season

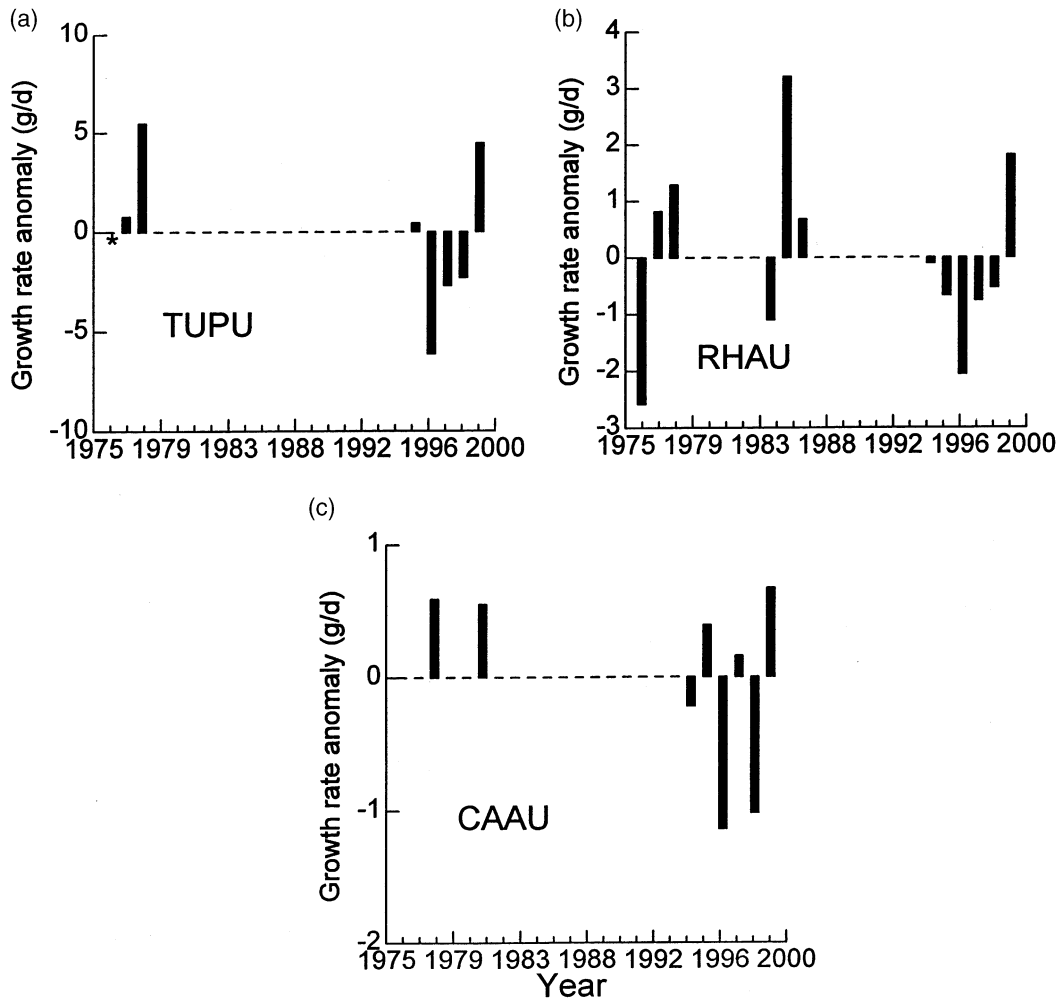


Fig. 5. Anomalies in annual nestling growth rates for populations of tufted puffin (TUPU), rhinoceros auklet (RHAU) and Cassin's auklet (CAAU) on Triangle Island, BC, 1976–1999. The asterisk for tufted puffin in 1976 indicates that hatching success was exceedingly low and no chick growth rates were reported in that year.

produced nestlings with a significantly higher growth rate than those breeding later (Fig. 6: 1996: $y=27.6-0.19x$, $F_{1,27}=67.5$, $P=0.0001$; 1998: $y=30.4-0.19x$; $F_{1,22}=35.3$, $P=0.0001$). In contrast, 1997 and 1999 were good years for nestling growth at the population level, and hatch date had a limited effect on growth rate of individuals (Fig. 6: 1997: $y=11.1-0.04x$; $F_{1,53}=12.4$, $P=0.0009$; 1999: slope not significantly different than zero). In general, we did not observe strong seasonal changes in nestling growth rates for either rhinoceros auklets or tufted puffins during 1996–1999.

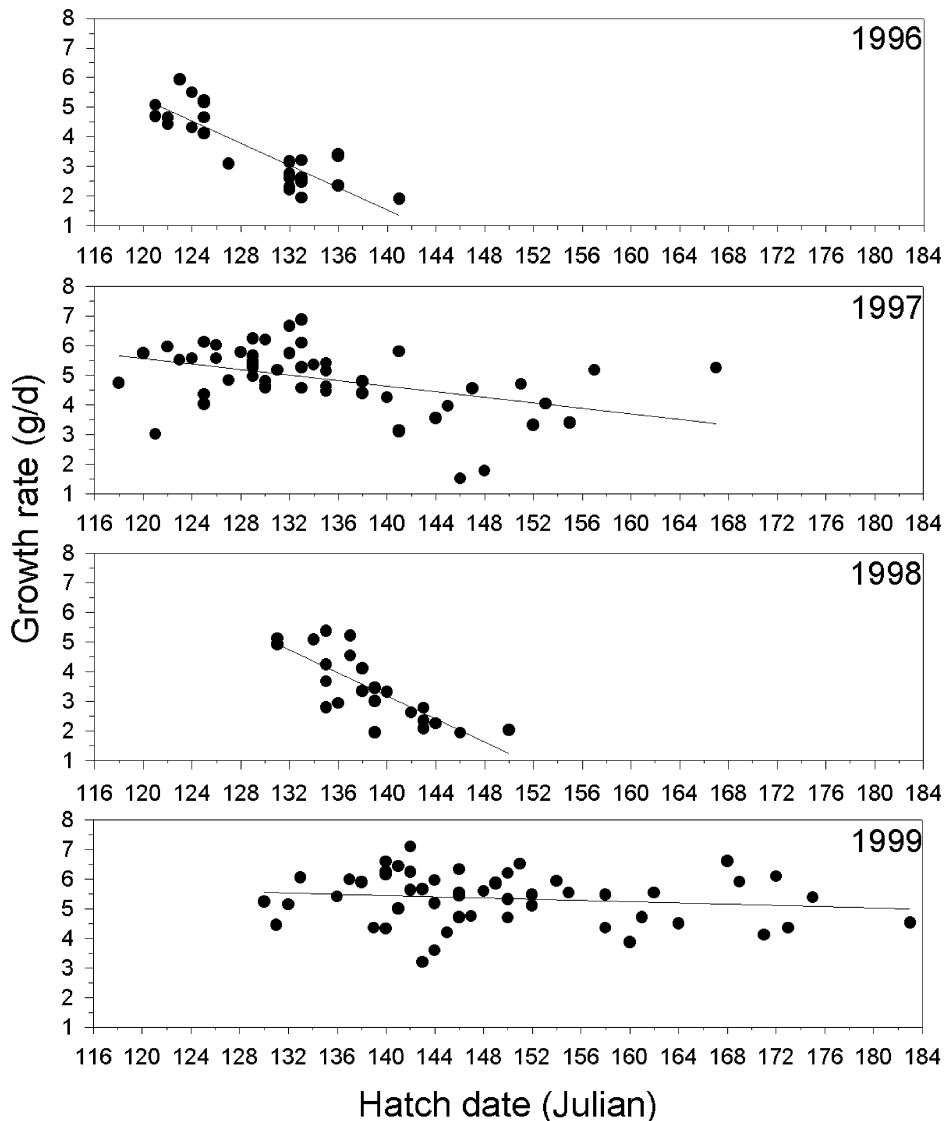


Fig. 6. Within season variation in nestling growth rates for Cassin's auklet. Individual nestling growth rates are plotted against hatch date contrasting two early spring years (1996 and 1998) and two late spring years (1997 and 1999).

3.5. Variation in Cassin's auklet nestling diet (1996–1999)

The nestling diet of Cassin's auklet on Triangle Island includes copepods, euphausiids, fish, carideans, amphipods, and crab larvae (Fig. 7). Copepods were the primary prey and were dominated (>99% by mass) by a single species, *N. cristatus*, all of which were in their final copepodite stage, C5. However, the importance of copepods in the diet varied significantly between years ($F_{3,194}=14.1$, $P<0.000001$). In 1996 and 1998, when nestling growth was poor, copepods contributed 25% (based on the mean of 55 food loads) and 30% ($n=50$) respectively of the nestling diet

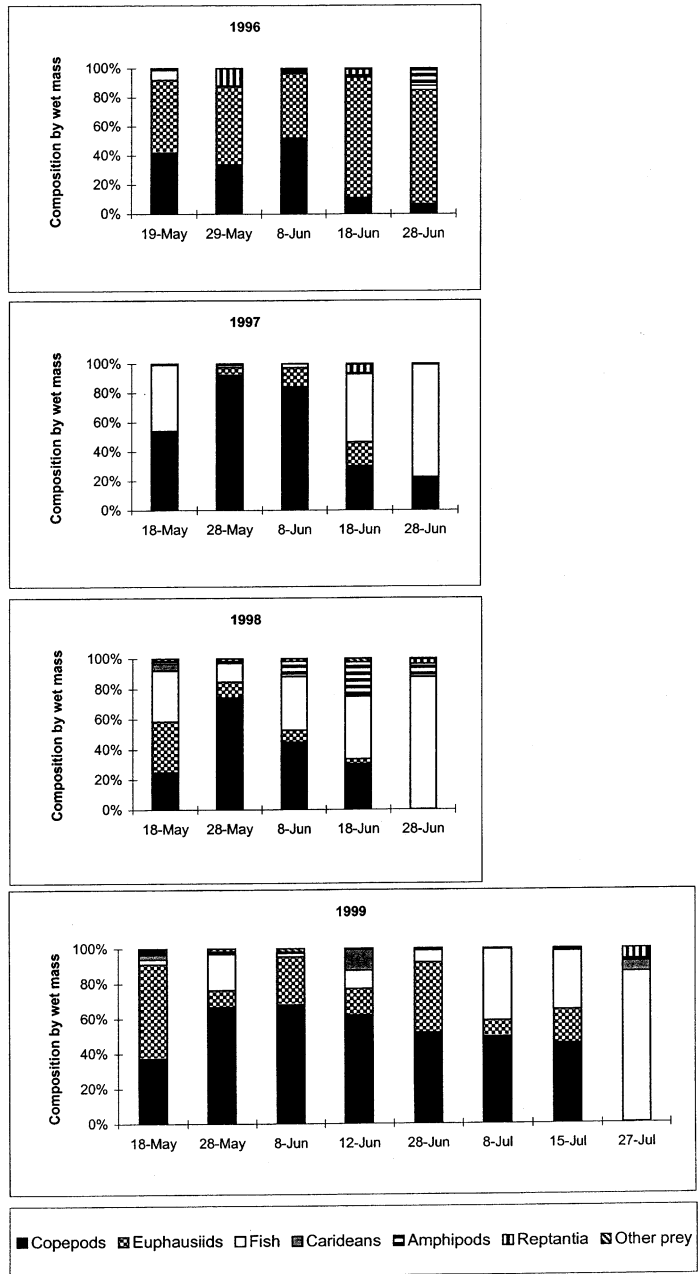


Fig. 7. General composition of the Cassin's auklet nestling diet on Triangle Island. Copepods were more abundant in 1997 and 1999 than in 1996 and 1998 during May and June. Note the low levels or absence of copepods from 18 June onwards in 1996 and 1998.

between 18 May and 28 June. In contrast, copepods contributed significantly more to the diet in 1997 (63%, $n=47$) and 1999 (56%, $n=46$) when nestling growth was more rapid (Tukey's HSD $P<0.01$ for all comparisons). Note too, that copepod content tended to fall to very low levels or even disappear from the diet samples from 18 June onwards in 1996 and 1998 (Fig. 7), both years when significant within season declines in nestling growth rates were observed.

3.6. Reproductive consequences for variation in spring timing and April SST

3.6.1. Within season effects

We observed a significant negative relationship between the timing of spring warming and the magnitude of seasonal change in nestling growth rates [Fig. 8(a); $y=-0.05-0.0063x$; $F_{1,5}=11.6$, $P=0.019$]. In those years when spring was early, 1996 and 1998, nestling growth rates declined strongly later in the breeding season. For years when spring was late, such as 1997 and 1999, nestling growth rates showed little or no decline and even increased within the season in 1981 ($F_{1,26}=5.8$, $P=0.023$), a late spring year [Fig. 8(a)]. We did not detect a significant relationship between April SST at Pine Island and seasonal change in nestling growth rate [Fig. 8(b); $F_{1,5}=4.4$, $P=0.09$] although the trend is in the same direction as the relationship with spring timing.

3.6.2. Annual effects

We could not detect significant relationships between hatch dates and spring timing [Fig. 9(a); $F_{1,7}=2.1$, $P=0.19$] or hatch date and April SST [Fig. 9(b); $F_{1,7}=4.6$, $P=0.068$] for Cassin's auklets. In contrast, for rhinoceros auklets hatch dates were earlier when spring was early [Fig. 10(a); $y=173.2-0.54x$; $F_{1,10}=5.3$; $P=0.04$] and April SST were warmer [Fig. 10(b); $y=265.6-11.1x$;

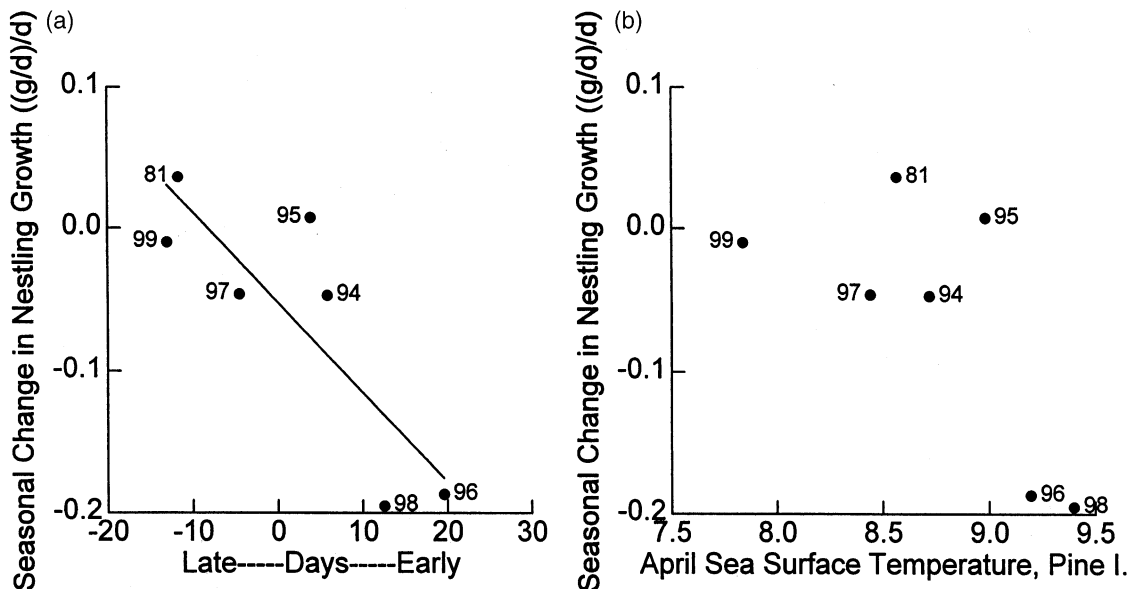


Fig. 8. Within season change in nestling growth rate of Cassin's auklet in relation to the spring timing index (a) and April SST from Pine Island Light Station (b). Regression lines are shown for significant relationships.

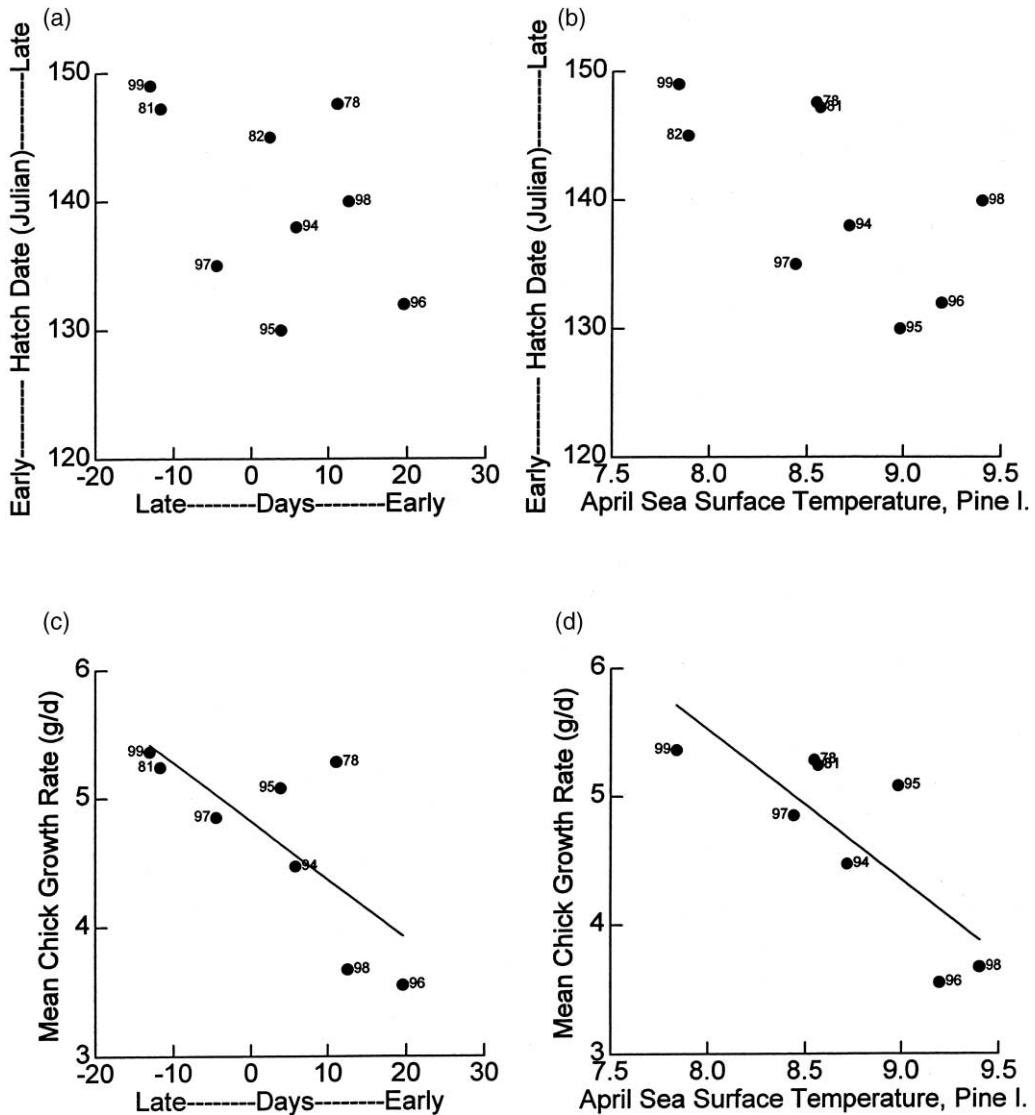


Fig. 9. Consequences of interannual variation in the spring timing index and Pine Island April SST for Cassin’s auklet reproduction on Triangle Island, BC. Shown are mean annual population estimates of hatch date and nestling growth rate in relation to the spring timing index (a,c) and the average SST in April at Pine Island Light Station (b,d).

$F_{1,10}=10.9, P=0.008$). For tufted puffin we could not detect a significant relationship between hatch date and spring timing ($F_{1,7}=0.9, P=0.37$) or hatch date and April SST ($F_{1,7}=1.8, P=0.22$).

There was a significant negative relationship between mean nestling growth rate and the spring timing index for Cassin’s auklet [Fig. 9(c): $y=4.8-0.046x; F_{1,6}=7.3, P=0.036$]. In early years such as 1996 and 1998 the nestling population grew slowly, in contrast to late years such as 1981, 1997 and 1999 when nestling growth was more rapid. We could not detect an effect of spring timing on the mean population nestling growth rate for either rhinoceros auklet [Fig. 10(c):

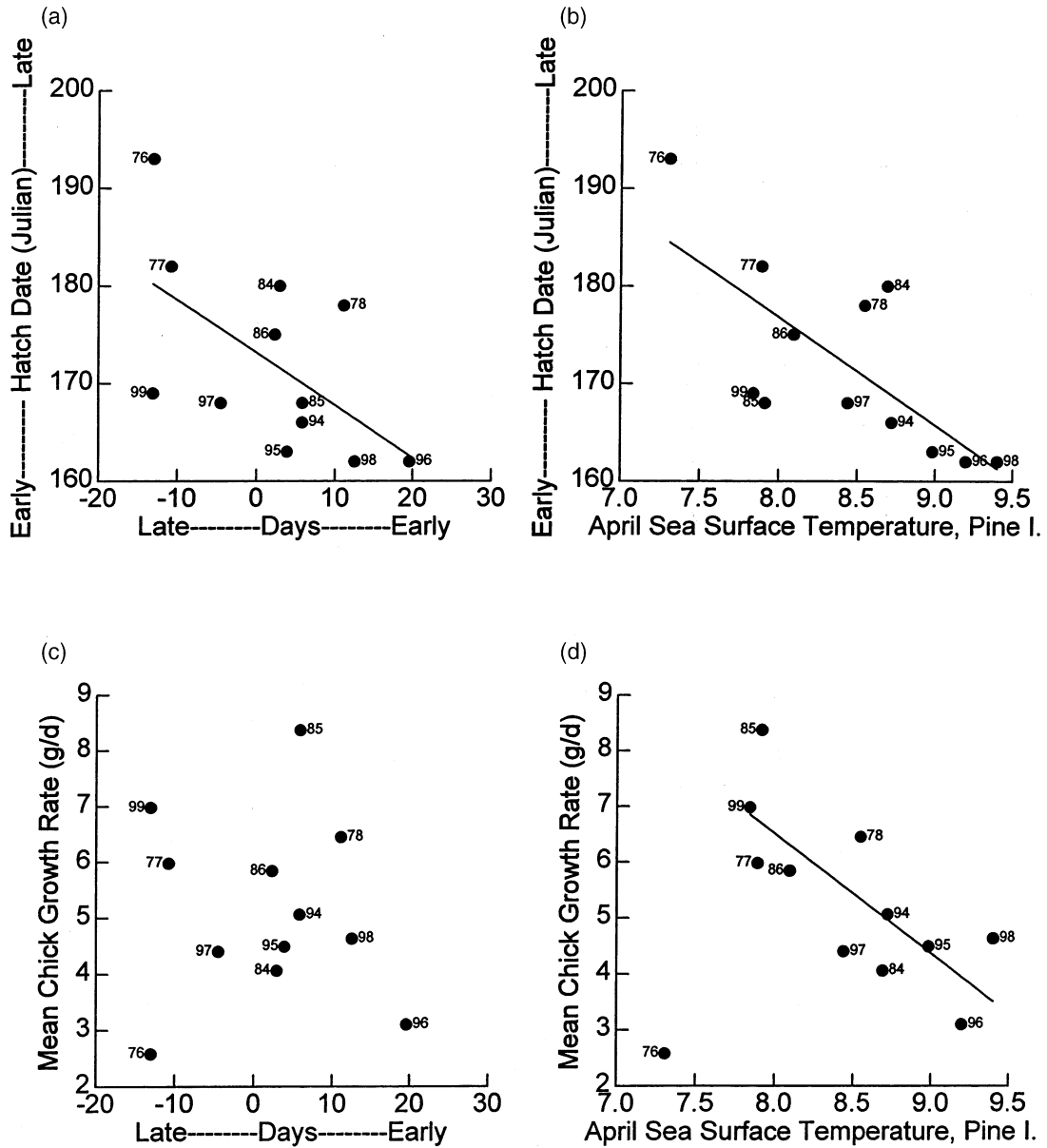


Fig. 10. Consequences of interannual variation in the spring timing index and Pine Island April SST for rhinoceros auklet on Triangle Island, BC. Shown are mean annual population estimates of hatch date and nestling growth rate in relation to the spring timing index (a,c) and the average SST in April at Pine Island Light Station (b,d). Note that the regression line in panel 'd' does not include 1976, the coldest year in the series.

$F_{1,10}=0.84, P=0.38]$ or tufted puffin ($F_{1,5}=3.5, P=0.12$). For Cassin's auklet [Fig. 9(d); $y=14.9-1.18x, F_{1,6}=10.087, P=0.019$] nestling growth rates were negatively related to April SST. In cool years, they grew more rapidly than in warm years. For rhinoceros auklet we could not detect a relationship between growth rate and SST using the full data set [Fig. 10(d); $F_{1,10}=0.84 P=0.38$],

but this lack of significance was caused entirely by a single extreme outlier in 1976, which was by far the coldest year recorded (it was also a very rainy and stormy year at Triangle Island, see below). When 1976 was excluded from the analysis, we observed a highly significant negative relationship between nestling growth and SST [Fig. 10(d); $y=23.6-2.1x$; $F_{1,9}=13.2$, $P=0.005$] as was observed for Cassin's auklet. We could not detect a relationship between April SST and the growth rates of nestling tufted puffins ($F_{1,5}=2.9$, $P=0.15$).

The fledging masses of Cassin's auklet were also significantly related to the spring timing index ($y=162.1-1.25x$; $F_{1,7}=10.6$, $P=0.014$) and April SST ($y=376.1-25.3x$; $F_{1,7}=9.4$, $P=0.018$). We could not detect significant relationships between fledging mass and the spring timing index or April SST for rhinoceros auklet and the data were too limited for such an investigation for the tufted puffin because nestlings are abandoned by their parents well before fledging in poor years.

4. Discussion

Our results show how variation in the local physical marine environment can translate into reproductive consequences for seabirds on Triangle Island, BC. In general, for years when ocean temperatures were cold or spring was late, nestling growth rates were more rapid for the planktivorous Cassin's auklet and the piscivorous rhinoceros auklet than in warmer years with earlier springs. For the planktivore, we argue that the mechanism relating spring timing to nestling performance operates through effects on the timing of zooplankton availability relative to seabird breeding. We propose that when spring is early and warm, the zooplankton biomass peaks early and ends early, reducing the duration of the overlap between copepod availability in surface waters and the seabird's breeding; this effectively creates a seasonal mismatch between the prey and predator populations. In those ecosystems in which the breeding seabirds prey heavily on a single species of *Neocalanus* copepod, such a mismatch could explain the reduced reproductive performance of Cassin's auklet compared to years when spring was later and colder.

Our inferences on these trophic connections are strongest for the planktivorous Cassin's auklet, simply because there are fewer trophic steps between new production and seabird consumption, also there are relevant independent data on timing of peak availability for *Neocalanus* prey in addition to data on nestling diet. It is noteworthy, however, that in 1999 when spring was cold and late, nestlings of both the piscivorous rhinoceros auklet and tufted puffin exhibited rapid growth rates, in marked contrast to other years within the 1990s. In addition, 1999 was different from the other years in the decade, because young-of-year Pacific sand lance dominated the nestling diet for both the rhinoceros auklet (DFB unpubl.) and tufted puffin (C. Gjerdrum, Simon Fraser University, unpubl.). It seems plausible that the cool ocean conditions of 1999 also favoured the development of a strong year class of sand lance, which themselves feed primarily on copepods (Field, 1988). In 1999, 98% of the sand lance delivered to nestlings were 0+ fish. Moreover, the number of 0+ sand lance delivered in 1999 was at least three times greater than in any other year (note the sampling effort was always the same) within the decade (DFB, unpubl.). Further, on Triangle Island from 1984 to 1986 Bertram and Kaiser (1993) (see also Bertram et al., 1991) reported that rhinoceros auklet nestlings grew most rapidly in the coolest year when sand lance recruitment was argued to be strong and again young-of-year fish dominated the nestling diet (see also McFarlane & Beamish, 1992, for evidence of climate influence linking strong year-classes

of sable fish, *Anoplopoma fimbria*, to exceptional copepod production). There is no information on temporal changes of the diet of sand lance in the vicinity of Triangle Island (or elsewhere) but it seems plausible that during cool years the temporal overlap between copepod availability and growing populations of sand lance is longer. Our data suggest that in contrast to 1996, 1997 and 1998, in 1999 *N. cristatus* was present in the surface waters until mid July, well into the peak chick rearing period for both rhinoceros auklets and tufted puffins. Consequently in 1999, there was a period of at least one month, from 15 June when rhinoceros auklet food sample collection was initiated, to 15 July when diet samples of nestling Cassin's auklet contained significant levels of *N. cristatus* (Fig. 7), when young-of-year sand lance and their potential prey, *N. cristatus*, were both present in the surface waters around Triangle Island. Clearly, data on the temporal (and spatial) availability of sand lance and their prey populations in surface waters would strengthen our understanding of the trophic connections between piscivorous seabirds and the physical parameters.

We found that when we excluded data for the coldest year in our time series, 1976, there was a highly significant negative relationship between rhinoceros auklet nestling growth rate and April SST. Indeed, 1976 proved to be an exceptional year in many respects: the hatch date for rhinoceros auklet was the latest ever observed; diet being fed to the rhinoceros auklet nestlings was dominated (>80% biomass) by Pacific Saury (*Cololabis saira*), many of which appeared too large for chicks to swallow and may well have caused lethal choking in some nestlings (Vermeer, 1980); moreover tufted puffin parents abandoned breeding during incubation resulting in a hatch success of only 4% (Vermeer & Cullen, 1979), the lowest record for Triangle Island (DFB unpubl.). The paucity of sand lance in the rhinoceros auklet nestling diet in 1976 prompted Vermeer (1980) to suggest that recruitment was poor in that year because of the low SST temperatures. It is plausible that sand lance recruitment has a dome-shaped response in relation to ocean temperatures, with poor recruitment at very low and very high temperatures and most successful recruitment at intermediate temperatures [see Fargo & McKinnell, 1989, for an example of such a dome-shaped recruitment function for rock sole (*Lepidopsetta bilineata*) in British Columbian waters]. In addition, rapid growth of rhinoceros auklet nestlings has been associated with strong recruitment to sand lance populations within British Columbia (Bertram & Kaiser, 1993). If a dome-shaped recruitment/temperature relationship exists for sand lance, and the cold year of 1976 lies at the lower tail end, it could partially explain the pattern of growth rate variation (particularly the low values for 1976) observed in our study. Importantly, Vermeer (1980) noted that bad weather ("rainfall ...twice the average for the same months over the preceding ten years" and "rough water conditions") may also have contributed to the poor reproductive performance in 1976. He hypothesized that "the mortality of rhinoceros auklets and desertion by tufted puffins on Triangle Island in 1976 may be closely related, and both perhaps resulted from adverse weather and/or prey unavailability brought about by oceanic changes" (Vermeer, 1980). The addition of data on winds and precipitation could contribute meaningfully to the further development of predictive models for seabird reproductive performance in British Columbia.

When April SSTs were warm (>7.5°C), nestling growth was significantly poorer for both the planktivorous Cassin's auklet and the piscivorous rhinoceros auklet, than when April SSTs were cooler. For both auklets low nestling growth rates were generally associated with poor nestling pre-fledging survival and low fledging masses (DFB unpubl.). Survival during the first year at sea is also widely believed to be positively related to fledging mass in alcids (see Gaston, 1997,

for supporting data for the ancient murrelet, *Synthliboramphus antiquum*) such that recruitment to populations on Triangle Island is expected to be diminished during early, warm years.

We could not detect any significant relationships between the timing of spring warming or SST and the timing of breeding for Cassin's auklet on Triangle Island. For birds in general, the timing of breeding is thought to be related to the health and vigour of the female and fulfillment of the nutrition requirements of breeding females determines clutch initiation dates (Perrins, 1970). Butler (1993), for example, reported that egg laying began 9 d after a female's daily food intake exceeded an energy threshold estimated to be 1715 kJ/d in the great blue heron (*Ardea herodias*). More recent studies have generally supported the view that body condition is the most plausible proximate determinant of breeding decisions in birds (e.g. Moreno, de León, Fargallo, & Moreno, 1998). Condition may be effected by body size, age, experience, and foraging skills, effects which may be mediated through more proximate factors such as health status and immune function (e.g. Moreno et al., 1998). In the early and warm spring of 1996, the Cassin's auklet bred earlier than in 1999, when spring was late and cold. In the summer of 1998, following the large El Niño event, despite the spring being early and warm, not only did the Cassin's auklets breed comparatively late, but also the number of burrows occupied by breeders decreased dramatically (DFB unpubl.). The delayed in breeding and the reduction in burrow occupancy in 1998 was also observed in Cassin's auklets both on Frederick Island in northern British Columbia (DFB unpubl.) and on the Farrallon Islands (W. Sydeman, Point Reyes Bird Observatory, pers. comm.) in California. Their breeding on the Farallon Islands was similarly delayed after the 1982/83 El Niño, when the occupancy of burrows also dropped precipitously compared with the previous 13 years (Ainley, Boekelheide, Morrell, & Strong, 1990). Perhaps, during El Niño years, Cassin's auklet take longer to attain breeding condition and hence laying and hatching dates are later than in non El Niño years. In El Niño years many birds may either opt out of breeding altogether or perish, thus accounting for the reduced numbers attempting breeding in those years. A comparative study of adult survival on Triangle and Frederick Island is currently underway to examine whether the Cassin's auklets either chose not to breed in 1998 or failed to attend the colony because they had died or had emigrated.

In contrast to our results, Ainley et al. (1990) reported that egg laying dates for Cassin's auklet on the Farallon Islands are strongly related to ocean temperatures in the month immediately prior to egg laying. When the mean SST rose, egg laying dates were significantly later during 1970–1983. In the Farallon Islands, the Cassin's auklet feed primarily on euphausiids (Ainley et al., 1996) rather than on copepods. Moreover, the birds on the Farallon Island are often able to raise two broods within a season, a phenomenon that never occurs on Triangle Island. The differences in the timing of breeding/ocean warming relationship between the populations at Triangle Island and the Farallon Islands demonstrate that even within the same species, responses to environmental variation can be very different and presumably reflect regional ecosystem differences in prey species composition and dynamics.

Our study also demonstrates that within a colony, different seabird species may respond in different ways to the same environmental change (see also Kitaysky & Golubova, 2000). For example, in contrast to the behavior of Cassin's auklet, we found that the rhinoceros auklets on Triangle Island bred significantly earlier when spring was early and water temperatures were warm. In addition, the piscivorous seabirds on Triangle were all breeding significantly earlier in the 1990s than indicated by the available data for the 1970s and 1980s, as in many species of

land birds (e.g. Crick, Dudley, Glue, & Thomson, 1997; McCleery & Perrins, 1998) a tendency that we could not detect for the planktivorous Cassin's auklet.

While some of the interannual variation in the timing of spring warming of the coastal ocean can be attributed to phenomena such as El Niño, the source of the general pattern has yet to be explored fully. Interdecadal variation in wind patterns can account for some of the variation. During the 1990s, there was a significant change in upper atmospheric wind patterns in the northeast Pacific (Beamish, McFarlane, & Thomson, 1999) and in local surface winds in Queen Charlotte Sound (McKinnell, Wood, Rutherford, Hyatt, & Welch, 2001). A greater influence of southeasterly winds in spring during the 1990s may have delayed the transition from downwelling to upwelling conditions at Triangle Island, increased the northward advection of more southerly ocean water, and changed the species composition of prey and predators during spring (Mackas, Thomson, & Galbraith, 2001).

The relationships we develop here can be used to predict the effects of climate change on seabird reproductive performance for Cassin's auklet and rhinoceros auklet on Triangle Island. In a review of climate change in the NE Pacific, Ware (1995) speculated that the most recent warm regime would soon end, and that cold regime conditions should return in the early 2000s. The observation that 1999 was by far the coldest year of the decade is a tantalizing suggestion that such a regime shift reversal may indeed have begun. In a recent analysis of the zooplankton community of the British Columbia continental margin 1985–1999, Mackas et al. (2001) reported an abrupt change in 1999, and concluded that the community composition responds strongly to ocean climate fluctuations. Our results predict that (within the major range of our data set, April SST >7.5°C) nestlings of both Cassin's and rhinoceros auklets will exhibit high rates of growth in any future years when the spring is cool and late. Alternatively, if ocean temperatures continue to rise and spring timing advances, we will observe a deterioration in nestling performance and reduced production of nestlings among future cohorts.

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