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.

Contents

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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 Aebisher, Coulson, and Colebrook (1990) and also Hayward (1997) and argue that "there are large-scale biological responses in the ocean to low-frequency

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 timingint21.esthe vernal warming may have a si1 ficant effect on the ecosystems. To explore relationships between biology and physics more fully, we developed annual indices of spring timing ( ) and warming ( ) by fitting a simple sine function to a zero-centered (annual mean removed) daily SST series as

$$ {}_{i,j} = \sin({}_{ij} + {}_{i}) \times {}_{i} $$

where i=year, j=day of year, =predicted temperature, =((day of year−1)/365.25)×2π, =timing (phase) parameter, =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

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 information was available for the common murres. Mass at fledging was also available for Cassin’

Table 1
Annual spring timing anomaly ( ) in days estimated from daily sea surface temperatures at Pine Island, BC

Year		Year		Year	
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, ^{2}=7.0, df=1, P=0.008; TUPU: Mann–Whitney U=22.5, ^{2}=5.0, df=1, P=0.03; COMU: Mann–Whitney U=12, ^{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

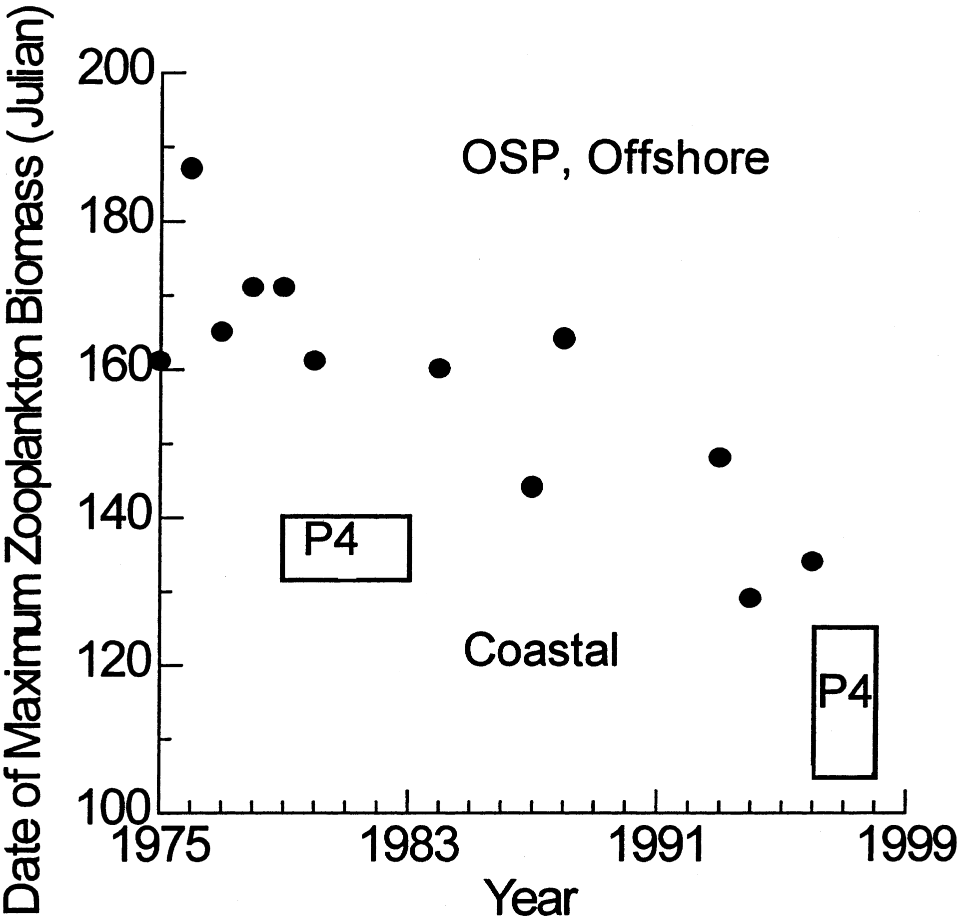

Fig. 3. Estimated dates of annual biomass peak for *Neocalanus plumchrus* at Ocean Station P (OSP: ●; data from Mackas et al., 1998) and at a coastal station off Vancouver Island, P4. The boxes represent the range of estimated peak biomass dates for 1979–1983, and for 1996–1998 at station P4.

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.

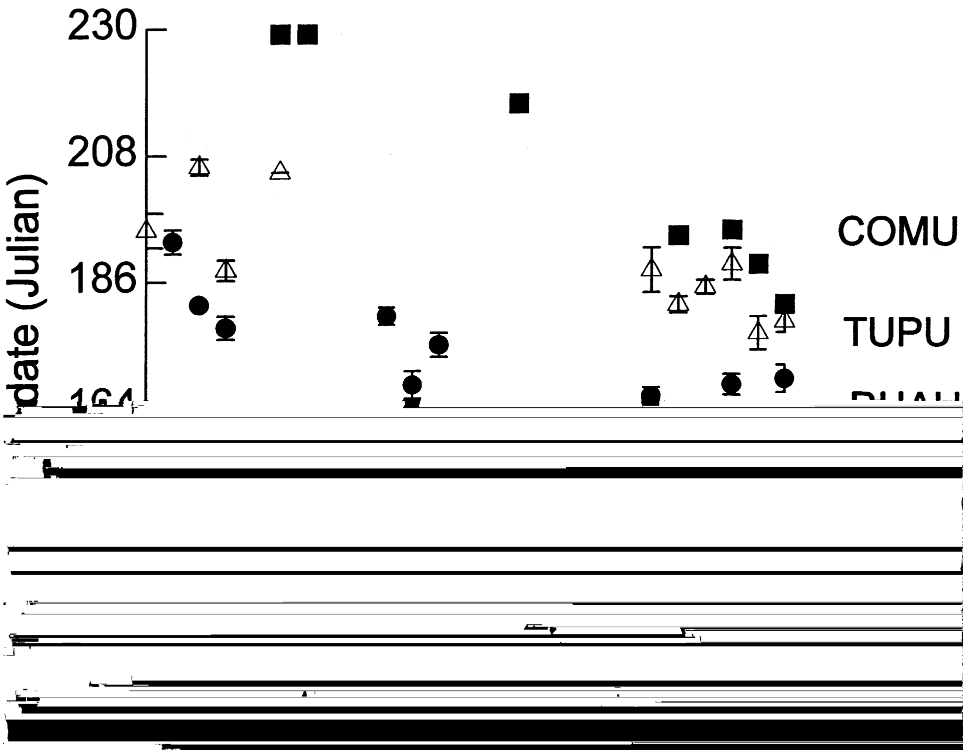

Fig. 4. Estimates of seabird breeding dates on Triangle Island, BC, 1975–1999. Error bars are 95% confidence intervals around mean values. Absence of error bars indicates that estimates of variation are not available. Values for Cassin's auklet (CAAU: ▽), rhinoceros auklet (RHAU: ○), and tufted puffins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

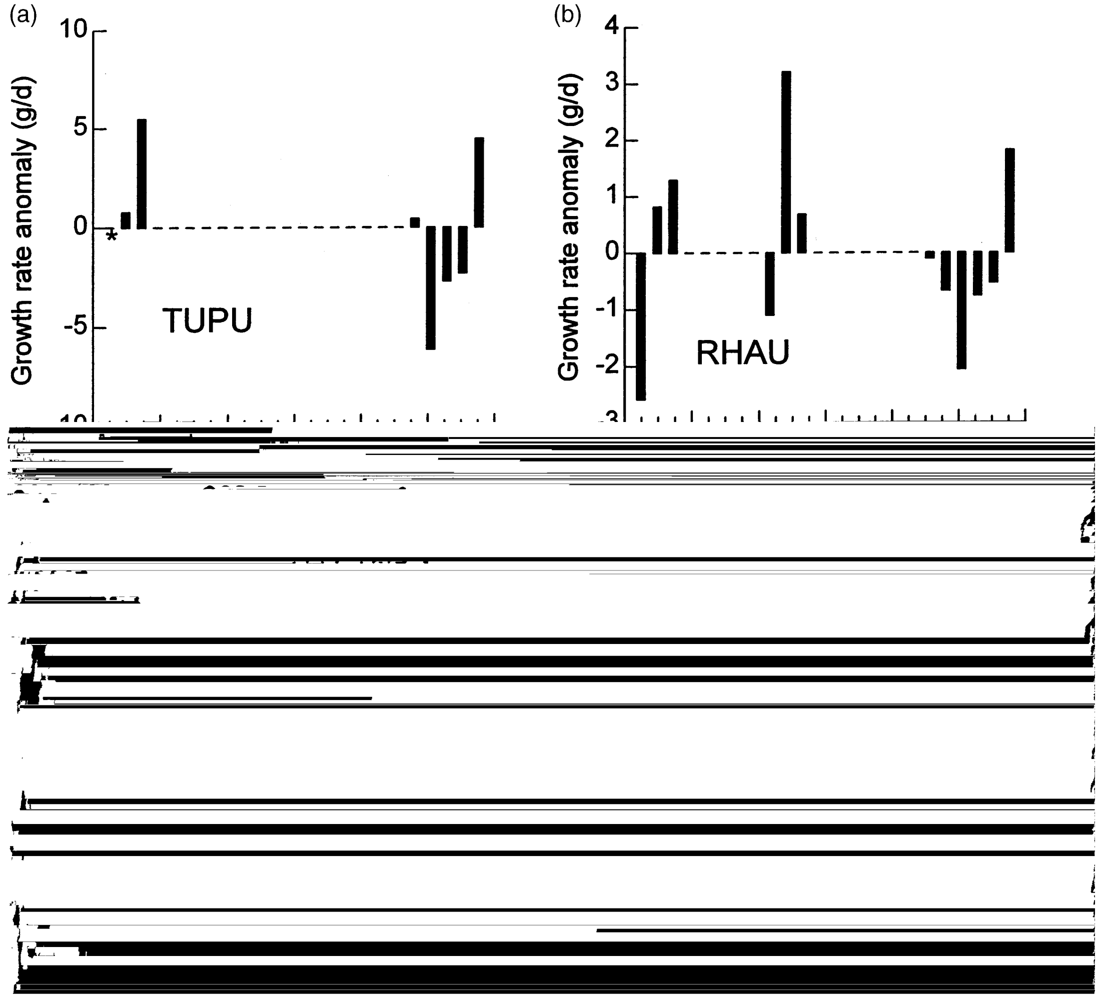

Fig. 5. Anomalies in annual nestling growth rates for populations of tufted puffin (TUPU), rhinoceros auklet (RHAU) and Cassin's auklet (CAAU) on Triangle Island, BC, 1976–1999. The asterisk for tufted puffin in 1976 indicates that hatching success was exceedingly low and no chick growth rates were reported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

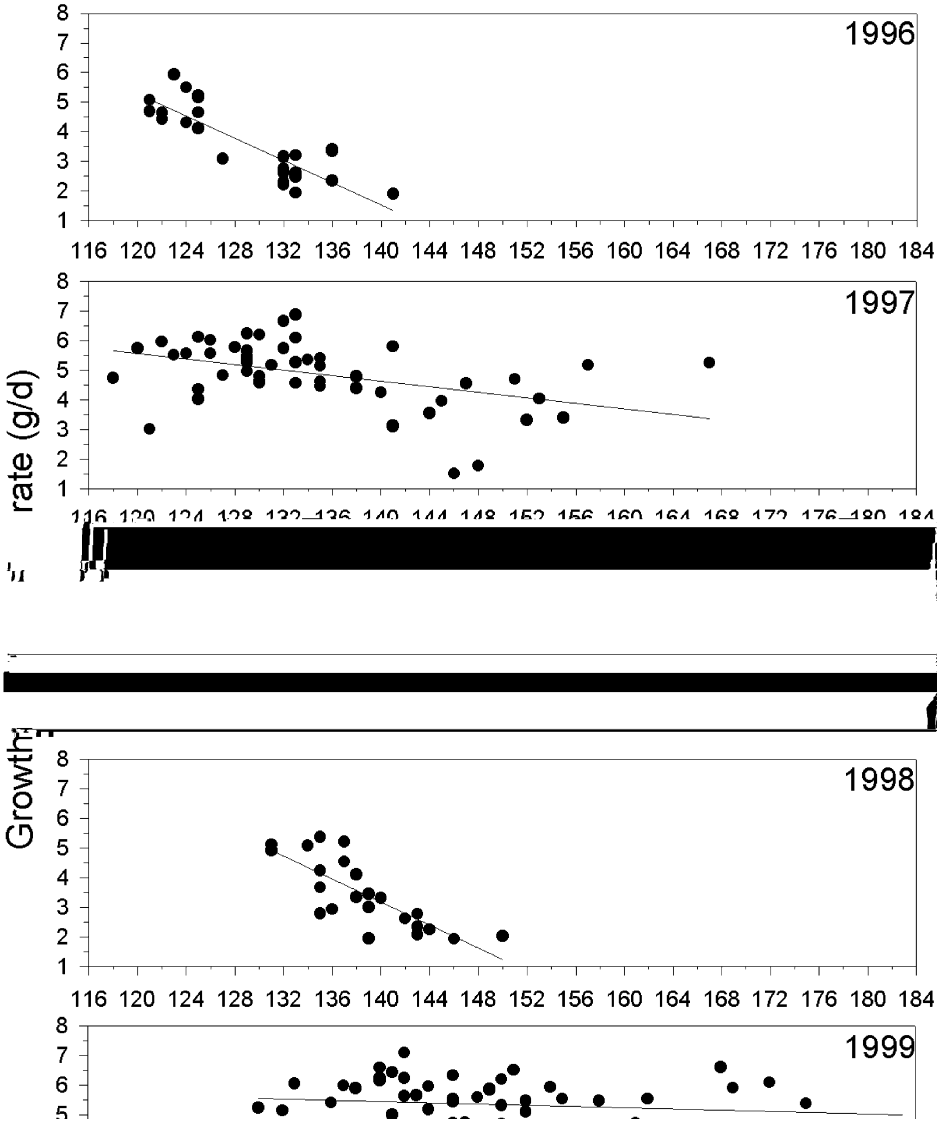

Fig. 6. Within season variation in nestling growth rates for Cassin's auklet. Individual nestling growth rates are plotted against hatch date contrasting two early spring years (1996 and 1998) and two late spring years (1997 and 1999).

3.5. Variation in Cassin'

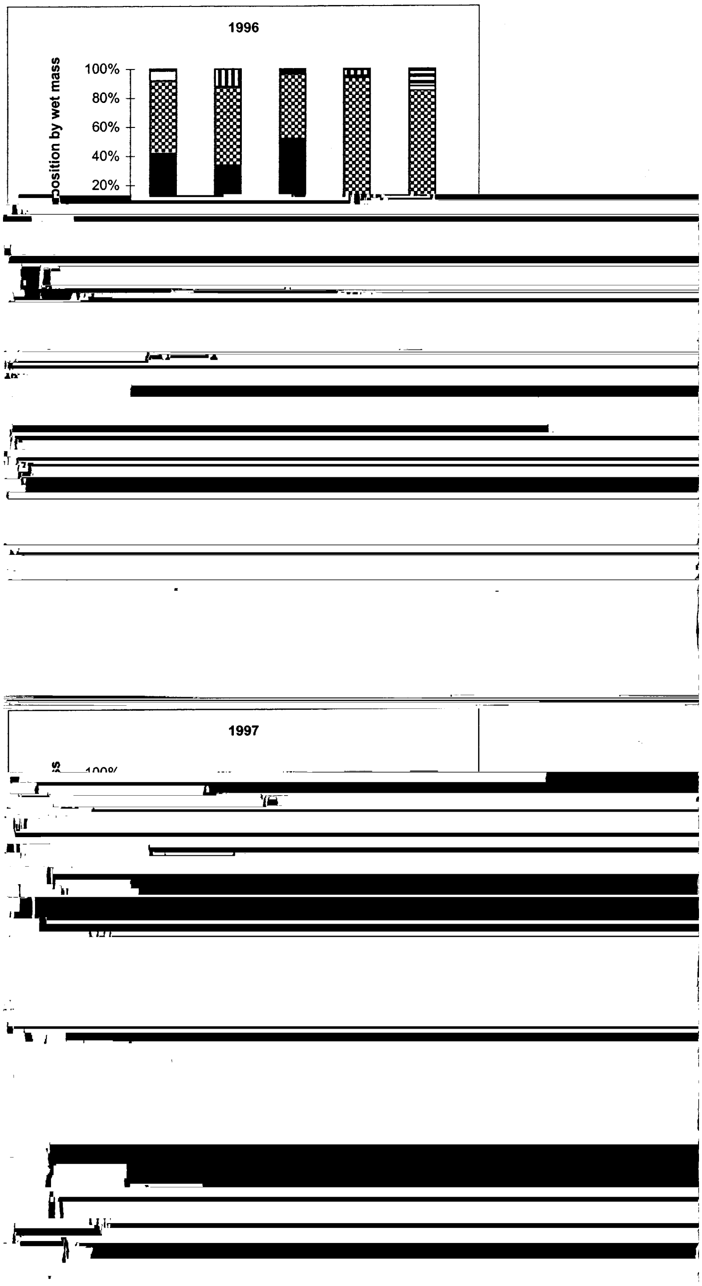

Fig. 7. General composition of the Cassin's auklet nestling diet on Triangle Island. Copepods were more abundant in 1997 and 1999 than in 1996 and 1998 during May and June. Note the low levels or absence of copepods from 18 June onwards in 1996 and 1998.

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): $y=265.6-11.1x$;

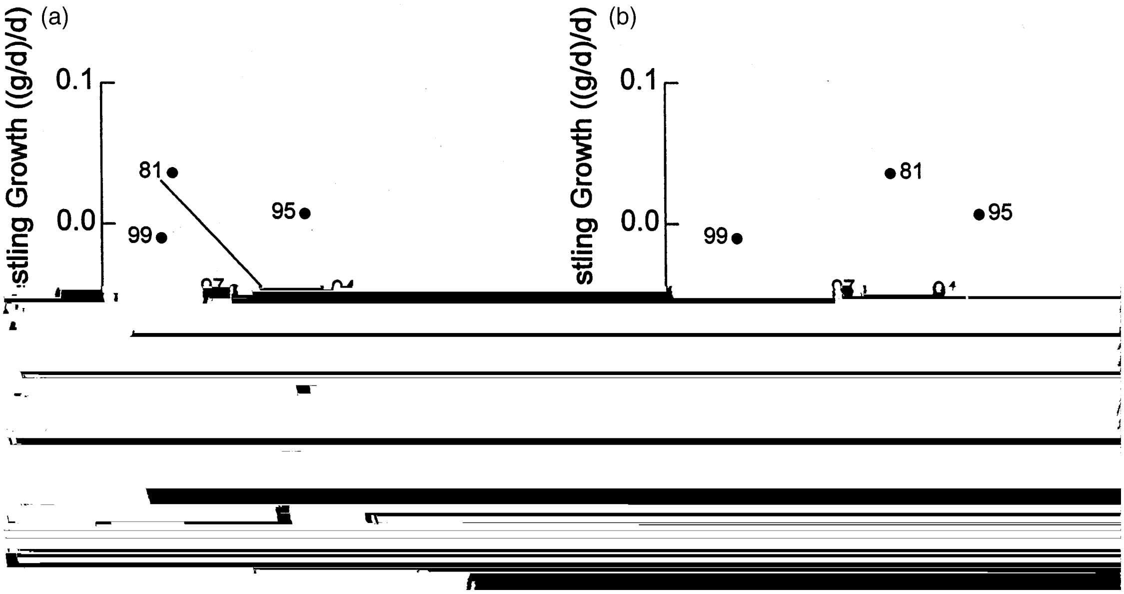

Fig. 8. Within season change in nestling growth rate of Cassin's auklet in relation to the spring timing index (a) and April SST from Pine Island Light Station (b). Regression lines are shown for significant relationships.

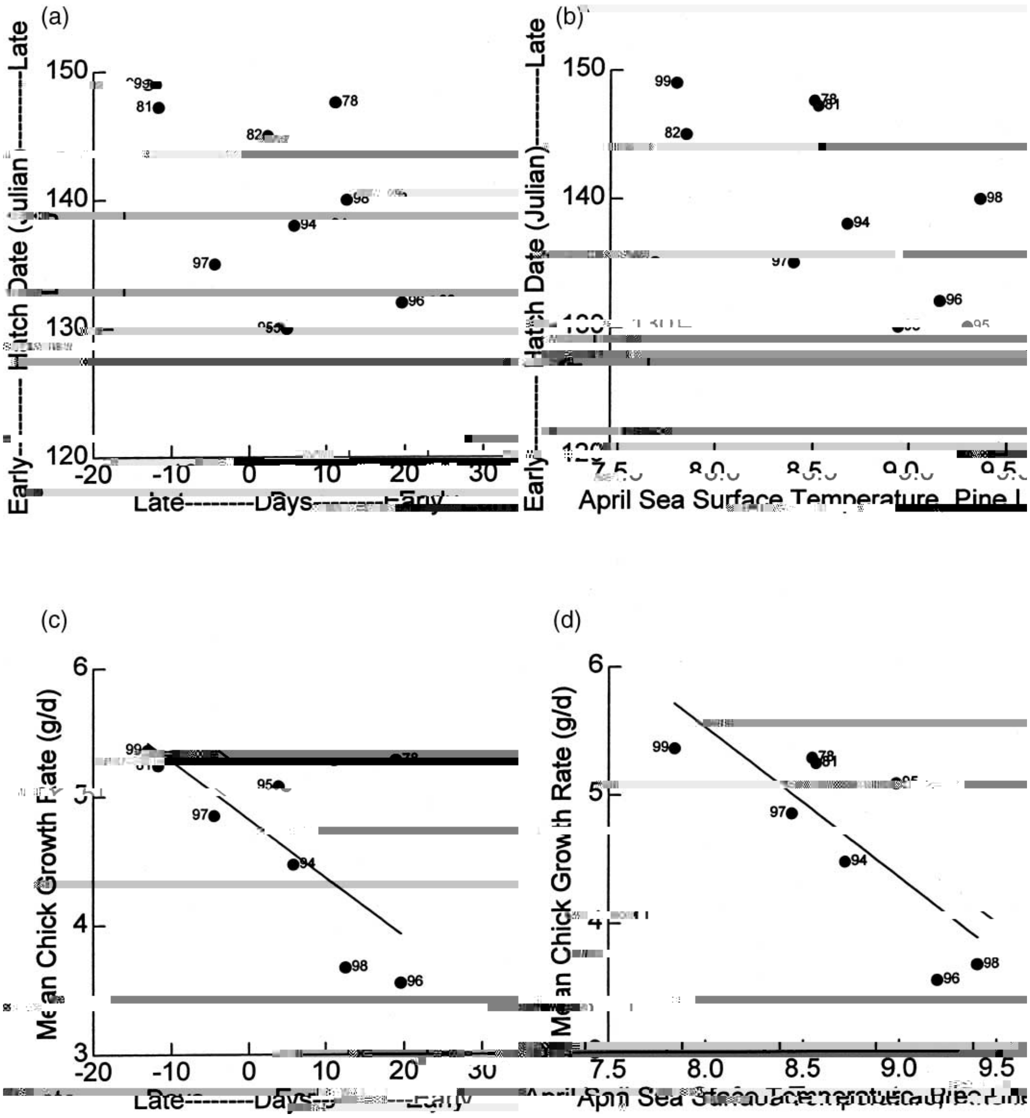

Fig. 9. Consequences of interannual variation in the spring timing index and Pine Island April SST for Cassin's auklet reproduction on Triangle Island, BC. Shown are mean annual population estimates of hatch date and nestling growth rate in relation to the spring timing index (a,c) and the average SST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

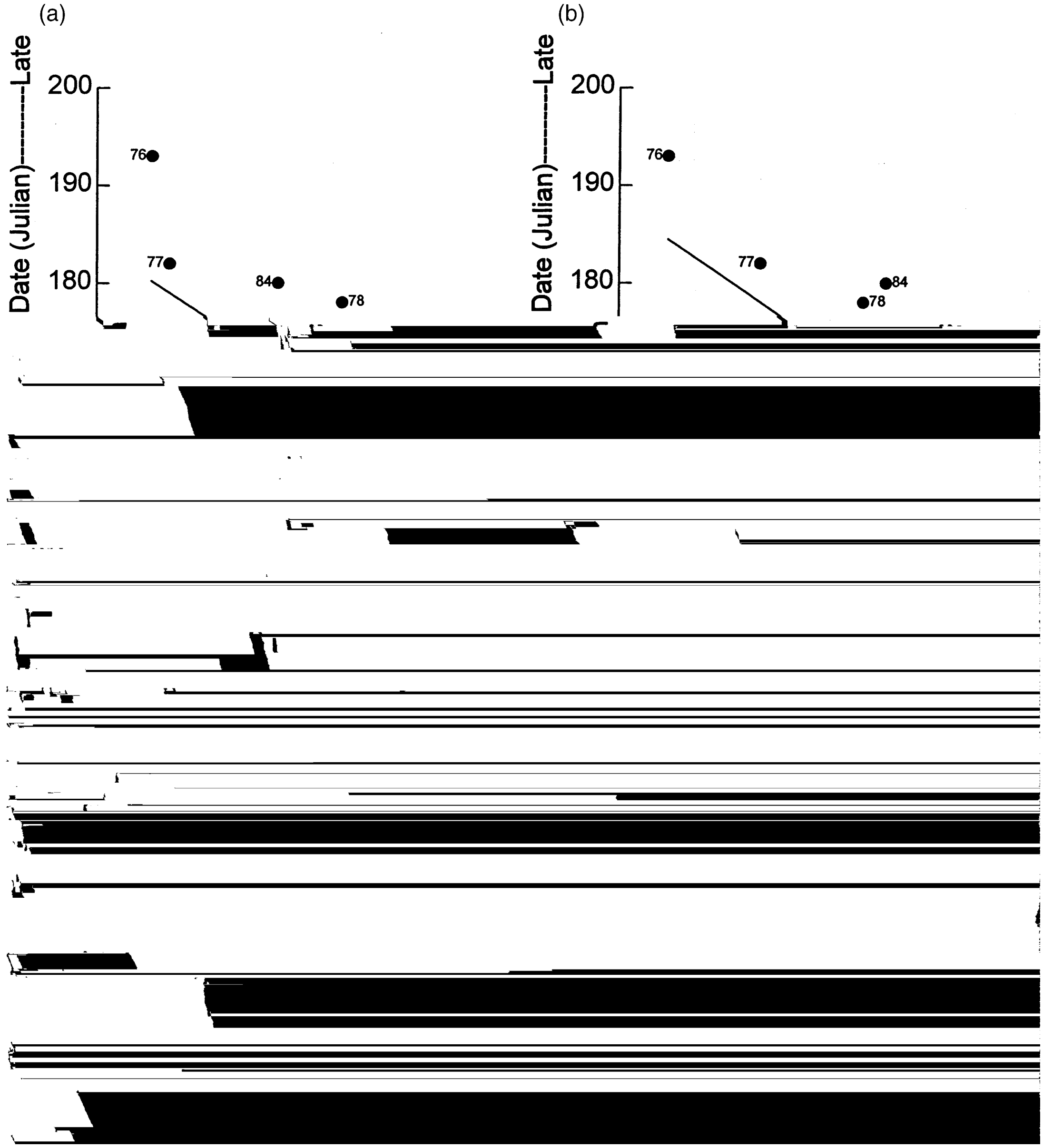

Fig. 10. Consequences of interannual variation in the spring timing index and Pine Island April SST for rhinoceros auklet on Triangle Island, BC. Shown are mean annual population estimates of hatch date and nestling growth rate in relation to the spring timing index (a,c) and the average SST in April 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],

led by W. J. Sydeman. Additional financial support to DFB and DLM was provided by the Nestucca Trust Fund. DFB also received funds from the Canadian Climate Change Action Fund, and the Canadian Nature Federation.

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