Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*

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ABSTRACT: Variability in ocean climate results in fluctuations in the timing and abundance of zooplankton. In turn, fluctuations in zooplankton as prey may have consequences for reproductive decisions and performance of planktivorous seabirds. We examined interrelationships between mean seasonal oceanographic conditions and prey availability and the timing of breeding, nestling diet, growth and productivity (as number of chicks fledged per breeding pair) of Cassin's auklet *Ptychoramphus aleuticus* in the central California Current System. Substantial inter-annual variability in seasonal ocean climate parameters as well as in auklet reproductive and diet characteristics was evident. Hatching dates and the proportion of all euphausiids in the diet were positively correlated with seasonal sea-surface temperature and negatively correlated with seasonal upwelling values. A significant negative correlation was found between the proportion of *Euphausia pacifica* in the diet and hatch date, while significant positive correlations were found between *Thysanoessa spinifera* in the diet and productivity, and between productivity and growth. Based on the California Cooperative Fisheries Investigations euphausiid data set, significant positive correlations were found between *E. pacifica* abundance and auklet meal mass and productivity and between *T. spinifera* abundance and auklet productivity. As demonstrated by the auklet diet, euphausiids responded to changes in ocean climate on multiple temporal scales. In most years, auklets responded adaptively to variation in oceanographic conditions and prey availability by modifying timing of breeding. However, in years when ocean conditions deteriorated after the initiation of breeding, prey availability was severely reduced beyond the auklet's adaptive response, resulting in diminished nestling growth and productivity.

KEY WORDS: Cassin's auklet · Growth rate · Productivity · Diet composition · *Euphausia pacifica* · *Thysanoessa spinifera* · Sea-surface temperature · Upwelling

INTRODUCTION

Biological evidence suggests that zooplankton abundance and distribution varies significantly both spatially and temporally (Brinton 1981, Brodeur et al. 1996, Sydeman et al. 2001, Marinovic et al. 2002, Brinton & Townsend 2003, Batten & Welch in press), leading some authors to conclude that zooplankton may be reasonable bio-indicators of large-scale and long-term climate change. Ainley et al. (1996), Bertram et al.

(2001) and Sydeman et al. (2001) provided observations from studies of planktivorous seabirds that support this supposition.

In the southern California Current System (CCS), Roemmich & McGowan (1995) reported that zooplankton biomass declined by approximately 70% between 1951 and 1995, although it is unclear which species were affected (Rebstock 2002). Chelton et al. (1982), Hayward (1997) and McGowan et al. (1998) related this observation to ocean warming and changes in

large-scale circulation. Lavaniegos & Ohman (2003) provided evidence that the principal cause of the biomass decline (and reversal in 1999) was related to variations in pelagic tunicates. In addition to basin-scale effects, local processes, such as the timing and intensity of upwelling, may also affect the biomass and community composition of zooplankton.

The euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* (class Crustacea) are the principal prey of the Farallon Islands population of Cassin's auklet *Ptychoramphus aleuticus*, planktivorous marine birds of the California Current ecosystem (Manuwal 1974, Ainley & Boekelheide 1990, Ainley et al. 1990, 1996, Sydeman et al. 1997, 2001). On average, *E. pacifica* and *T. spinifera* together comprise about 80% of the prey items in auklets' diet. In central California, the auklets forage for these euphausiids on the outer continental shelf and shelf-break regions (Briggs et al. 1987, Ainley et al. 1996, Oedekoven et al. 2001, Yen et al. 2004). The abundance and population fluctuations of these species are hypothesized to depend upon seasonal changes in the timing and intensity of upwelling and the corresponding variance in sea temperature and overall ocean productivity (Brinton 1976, Mackas & Sefton 1982, Brinton & Reid 1986, Mackas et al. 1987, Smith & Adams 1988, Tanasichuk 1998a,b, Brinton & Townsend 2003). Inter-annual variability in upwelling in the CCS has been associated with relatively high densities of *T. spinifera*, but information on oceanographic relationships is limited. Euphausiids migrate vertically (Alton & Blackburn 1972), a behavior that is influenced by temperature, salinity and illumination (Banse 1964, Simard & Mackas 1989); it is when euphausiids are near the surface that they are most susceptible to marine bird predation.

At Southeast Farallon Island (SEFI: 37°42' N, 123°00' W), centrally located in the strong upwelling domain of the CCS (US GLOBEC 1992), Cassin's auklet responds to inter-annual variability in ocean climate by alternating its diet between *Euphausia pacifica* and *Thysanoessa spinifera*, although both are consumed in all years (Sydeman et al. 2001). In fact, although *E. pacifica* is substantially more abundant (>100×) than *T. spinifera* in the region (Brinton & Townsend 2003), the 2 species comprise relatively equal proportions of the auklet diet. Additionally, 2 subtropical euphausiid species, *Nyctiphanes simplex* and *Nematocelis difficilis*, are consumed occasionally by Farallon auklets during ocean-warming events such as El Niño (Ainley et al. 1996, Sydeman et al. 1997, 2001). In years when the overall abundance of euphausiids is relatively low in the diet, auklets supplement the nestling diet primarily with amphipods and mysids (class Crustacea). If the euphausiids in coastal central California respond to variability in upwelling intensity and circulation (Chelton et al.

1982, Tanasichuk 1998a,b), it is probable that a connection can be made between euphausiid availability and inter-annual variability in ocean climate (Hayward 1997). Some population data on the auklets suggests that this is the case. For example, the SEFI auklet population has declined by ~85% from 1972 to 2001 (from 105 000 to 17 000 breeding birds: Point Reyes Bird Observatory [PRBO] unpubl. data); this decline has been hypothesized to be linked with the long-term decline in zooplankton biomass in the CCS (Ainley et al. 1996, Sydeman et al. 1997, Pyle et al. 2001). Similarly, decreasing zooplankton abundance in British Columbia is hypothesized to have resulted in a decline in the Cassin's auklet population on Triangle Island (TI: 50°35' N, 127°26' W; Bertram et al. 2000).

In this paper, we investigate the ecological consequences of inter-annual variability in ocean climate in the CCS by examining the timing of breeding, growth, diet composition and parental provisioning of the planktivorous Cassin's auklet from 1973 through 2001. Our specific objectives were as follows: (1) to characterize inter-annual and long-term oceanographic conditions in the Gulf of the Farallones, (2) to examine the association of variable oceanographic conditions with patterns of hatching dates, prey use and provisioning amounts (meal mass) of auklets tending offspring, and (3) to investigate whether variation in ocean climate, prey availability and diet affects nestling growth and productivity. To meet these objectives we examined relationships between mean ocean conditions, timing of breeding and auklet diet; between auklet diet, timing of breeding, growth rate and productivity; and between prey availability and timing of breeding, diet, growth rate and productivity. The relationships between ocean conditions and euphausiid availability and any corresponding implications for nestling growth and productivity to Farallon Cassin's auklets are not well understood; therefore, we have taken an exploratory approach in our examination of these relationships.

MATERIALS AND METHODS

Study area. This study took place at Southeast Farallon Island (SEFI), California (37°42' N, 123°00' W), from 1973 to 2001 (not all years inclusive). SEFI, located approximately 42 km west of San Francisco in the central CCS, is the largest multi-species seabird colony in the United States south of Alaska. The nesting habitat includes an extensive marine terrace, with the remainder of the island consisting of cliffs and rock faces. This granitic island (approximately 44 ha) provides suitable breeding habitat for 12 species of ground-, cliff- and cavity-nesting seabirds (Ainley & Boekelheide 1990, Sydeman et al. 2001).

Oceanographic measurements. We measured the sea-surface temperature (SST) at SEFI each day between 13:00 and 15:00 h for the duration of the study. SST was collected by lowering an empty 5 gallon (18.9 l) bucket a few meters below the sea surface, allowing it to acclimate for a few minutes, and then raising the bucket full of seawater and taking a temperature reading with a glass thermometer. This process was repeated 3 times, and the lowest SST value was recorded. For analysis, we computed seasonal (January–March = winter, April–June = spring, July–September = summer, and October–December = fall) mean values of SST in each year (see Sydeman & Allen 1999 and Botsford & Lawrence 2002 for the use of seasonal mean values of ocean climate variables). To illustrate patterns of change on multiple time-scales, we computed anomaly statistics using Farallon SST climatology from 1929 to 2001.

We obtained indices of the timing and strength of upwelling (Bakun's upwelling index) from the National Oceanic and Atmospheric Administration (NOAA) Pacific Fisheries Environmental Laboratory (available at: www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html) (Bakun 1973, Schwing et al. 1996). Calculation of these coastal upwelling indices is based on Ekman's theory of mass transport due to wind stress (Bakun 1973). Ekman transports are resolved into components oriented parallel and normal to the local coastline. The magnitude of the offshore component is considered to be an index of the amount of water upwelled from the Ekman layer. Positive upwelling index (UI) values result from equatorward wind stress and result in transport of nutrients from deep water to surface layers, whereas negative values imply downwelling. We used the average UI values at 36 and 39° N. The Farallones are located at 37.42° N (approximately halfway between 36 and 39° N), and therefore, the upwelling indices at these latitudes encompass the range of foraging auklets. Again, using the average UI values at 36 and 39° N, we computed seasonal (January–March = winter, April–June = spring, July–September = summer, and October–December = fall) mean values of the UI. To illustrate patterns of change on multiple timescales, we computed anomaly statistics using upwelling index climatology from 1946 to 2001.

Euphausiid abundance. We obtained *Euphausia pacifica* and *Thysanoessa spinifera* abundance data from individual stations sampled in both southern (1975 to 2002) and central (1975 to 1998, not all years inclusive) California from the 'Pelagic Invertebrates Collection', Scripps Institution of Oceanography, University of California, San Diego, which houses the CalCOFI samples. Abundance data collected during both day and night surveys from March to May were used in summarizing annual data. We log-transfomed all raw arithmetic euphausiid abundance data (natural log of [abundance +1]) to normalize the data and de-emphasize infrequent extreme euphausiid densities (Brinton & Townsend 2003), and then calculated annual geometric means. We derived regression equations (weighted by the square root of the number of CalCOFI stations sampled in each year) for each species in order to estimate values of euphausiid abundance in central California (for years where data was not collected) from those observed in southern California. We examined the relationships between euphausiid abundance values in central California (1975 to 2001, all years now inclusive) and auklet timing of breeding, diet, growth and productivity.

Use of euphausiids. The availability of euphausiids in the marine ecosystem was indexed by examining the prey brought to the colony by adult auklets provisioning their dependent offspring. Prey-use was determined by collecting regurgitations from parents as they returned to the island to feed young at night (see Sydeman et al. 1997, 2001). We captured adults by hand as they attempted to enter their nesting burrows. Partially digested prey are brought back to the colony the by parent auklets in a 'gular pouch' (Speich & Manuwal 1974), and each collection from 1 pouch was considered a sample. We attempted to obtain 10 regurgitations each week throughout the chick-rearing period (May to August) each year (1977 to 2001). Auklet diet samples were not collected from 1973 to 1976, in 1978, from 1982 to 1984 or in 1992. Each regurgitation sample was stored in a plastic Whirlpac specimen bag, weighed and frozen for later analysis. During analysis, the contents of each sample were identified, separated by species and/or order, enumerated and weighed. Analysis of diet composition for the years 1977 to 1993 was performed by L. Spear (PRBO). Analysis of diet composition for the years 1994 to 2001 was performed by M. Galbraith at the Institute of Ocean Sciences (Sidney, British Columbia). For statistical analyses, we used the annual percent prey composition (by number) of each of the 2 primary euphausiid species and of all euphausiid species combined found in samples. On average, *Euphausia pacifica* and *Thysanoessa spinifera* together comprise about 80% (by number) of the prey items in the diet. Although percent diet composition by mass is commonly used to report trophic relationships in marine birds and other top predators, we did not have these data available for the years prior to 1994. However, the percent diet composition of *E. pacifica* and *T. spinifera* by mass and by number were highly correlated from 1994 to 2001 (*E. pacifica*: $y = 1.0442x - 0.0244$, $R^2 = 0.9805$; *T. spinifera*: $y = 0.7259x + 0.0655$, $R^2 = 0.8991$), indicating that measurements for prey contribution by mass and number would be similar for the entire data set.

Parental provisioning amount (meal mass) was determined by examining the total mass of each regurgitation/gular pouch sample as described above. We used the mass (g) of all diet samples obtained between 1985 and 2001 (data not available prior to 1985) for analysis.

Timing of breeding, growth rate and productivity. We studied timing of breeding, nestling development and productivity of Cassin's auklets breeding in artificial burrows (i.e. nest boxes). Growth data was not collected from 1979 to 1989, or in 1992. After 30 d incubation, boxes were checked every 1 to 5 d to determine hatching date (collected in all years, 1973 to 2001). Offspring were then weighed every 1 to 5 d between 13:00 and 17:00 h until they became well-feathered (~30 d of age), after which they were weighed daily until they departed the nest at independence (~42 d of age; Ainley et al. 1990). We used mass collected within the linear portion of the growth curve (age 15 to 30 d; see Ainley at al. 1990, Hedd et al. 2002) to obtain a mean growth rate (g d^{-1}) for each chick each year. For analyses we used growth rate and hatch-date data for first breeding attempts only; data from second breeding attempts was not included. Statistical analyses were performed only on those chicks for which hatch date was known. Auklet productivity was calculated as the number of chicks fledged per breeding pair in each year.

Statistical analysis. Quadratic equations are commonly used to describe trends in physical or biological data over time. It is widely accepted that ecosystem regime shifts transpired in the North Pacific Ocean in 1976 to 1977 and 1989 to 1990 (Hare & Mantua 2000). Preliminary evidence also suggests that a regime shift occurred in 1998 to 1999 (Bograd et al. 2000, Minobe 2000, Schwing & Moore 2000, Durazo et al. 2001). Therefore, it is reasonable to expect quadratic trends in ocean climate data through time, since these regimes have been characterized as cold (pre-1977)➝warm (1978 to 1989)➝warmer (1990 to 1998)➝cold (1999 to 2001).

We were also interested in determining how seasonal variability in ocean climate may influence biological parameters such as the abundance of euphausiids in the auklet diet. Although they do consume juveniles, SEFI auklets feed primarily on adult euphausiids (by number, average of 87% adults for *Euphausia pacifica* and 70% adults for *Thysanoessa spinifera* from 1994 to 2001, PRBO unpubl. data). These euphausiids are estimated to attain adulthood at about 1 yr (17 mm in length) in Oregon (W. T. Peterson pers. comm.) and 1 yr in British Columbia (D. Mackas pers. comm.). Therefore, the survival, development and recruitment of adult euphausiids (and their use by auklets) is likely to depend on ocean conditions in the previous year (Year $x-1$), and in the current year (Year x). Therefore, we lagged the seasonal climate data such that the euphausiid diet data in the current year (Year x) was compared with the ocean climate data from the previous year's seasons (Year $x-1$) as well as the current year's seasons (Year x). Thus, because our diet data begins in 1973, our seasonal ocean climate time series begins in 1972. In addition, we were interested in examining potential consequences related to the direction and strength of the spring transition. We used the difference between mean spring (April to June) and mean winter

Table 1. Numbers of samples analyzed each year for auklet *Ptychoramphus aleuticus* diet samples, prey items, meal mass, growth rate and hatch date, and for the number of CalCOFI stations sampled for euphausiid abundance in central and southern California. In some years, this data was not available (na)

Year	Diet samples	Prey items	Meal masses	Growth rates	Hatch dates	Stations sampled in CA: Central	Southern
1973	na	na	na	14	17	na	na
1974	na	na	na	20	22	na	na
1975	na	na	na	23	31	27	65
1976	na	na	na	na	14	na	21
1977	na	966	na	5	8	24	49
1978	na	na	na	13	24	22	54
1979	na	10907	na	na	69	15	40
1980	na	7031	na	na	65	17	75
1981	na	6005	na	na	73	25	50
1982	na	na	na	na	67	18	38
1983	na	na	na	na	12	25	44
1984	na	na	na	na	59	22	45
1985	107	6371	107	na	63	16	46
1986	48	2792	48	na	32	na	42
1987	84	5246	84	na	33	8	44
1988	62	5384	62	na	29	7	39
1989	48	3797	48	na	27	na	42
1990	47	4657	47	25	38	na	48
1991	92	6233	92	24	26	23	48
1992	na	na	na	na	16	na	45
1993	64	3487	64	21	40	na	46
1994	81	11322	81	33	47	na	44
1995	80	15603	80	38	57	na	39
1996	108	12254	108	34	55	na	41
1997	81	9011	81	40	56	na	41
1998	85	6252	85	45	60	19	48
1999	113	12983	113	33	73	na	46
2000	93	11118	93	48	75	na	47
2001	115	10534	115	29	64	na	47
2002	na	na	na	na	na	na	38
Mean	77	7236	82	28	43	19	45

(January to March) values of UI and SST (in Year x) as an index of the spring transition. Because the diet composition data was expressed as a proportion, we transformed these values (arcsine-transform) prior to analyses.

Statistical analyses were performed using STATA (Version 7.0 for Windows, Stata Corporation). We used ANOVA to examine variability in oceanographic parameters, hatch date, meal mass and growth. We used Spearman's rank correlations to examine relationships between oceanographic variables (UI and SST) and euphausiid abundance in central California and timing of breeding, diet composition, meal mass, productivity and nestling growth rates. Because these analyses are largely exploratory in nature, we have not accounted for the problem of multiple tests (e.g. Botsford & Lawrence 2002). In addition, because of the potential effects of temporal autocorrelation on significance levels, we tested (Cochrane-Orcutt transformation) for first-order effects in our data sets of timing of breeding, growth rate, meal mass and productivity. In all cases, the autocorrelation coefficient ranged from -0.164 to 0.2; none of these values were significant (all $p > 0.3$). Sample sizes included in all analyses are shown in Table 1.

RESULTS

Inter-annual variability

Ocean climate. There was significant variation in the mean seasonal values of the upwelling index by season and year (2-way ANOVA: $F[\text{year}]_{29,87} = 1.80$, $p = 0.0193$; $F[\text{season}]_{3,87} = 265.62$, $p < 0.001$, $R^2 = 0.9071$). When considering each season separately (Fig. 1), we found quadratic trends for all seasons, indicating a sequential decrease and increase in upwelling through time, but these were significant only for spring ($\beta_1 = -1355.59 \pm 513.84$, $t_1 = -2.64$, $p_1 = 0.014$, $\beta_2 = 0.341 \pm 0.13$, $t_2 = 2.64$, $p_2 = 0.014$, $R^2 = 0.2422$, where β is the regression coefficient and t is the t-statistic) and summer ($\beta_1 = -902.765 \pm 347.163$, $t_1 = -2.60$, $p_1 = 0.015$, $\beta_2 = 0.227 \pm 0.087$, $t_2 = 2.60$, $p_2 = 0.015$, $R^2 = 0.2045$).

There was also significant variation in mean seasonal sea-surface temperature values by month and year (2-way ANOVA: $F[\text{year}]_{29,87} = 3.43$, $p < 0.001$; $F[\text{season}]_{3,87} = 53.11$, $p < 0.001$; $R^2 = 0.7484$). When considering each season separately (Fig. 2), we found quadratic trends, indicating a sequential increase and decrease in sea-

surface temperature through time; however, none of these were significant.

Auklet timing of breeding. There was significant inter-annual variability in hatching date (1-way ANOVA: $F[\text{year}]_{28,1223} = 131.69$, $p < 0.001$, $R^2 = 0.7509$). However, there was no evidence of a significant temporal trend in the data (Fig. 3A). Note that during the El Niño Southern Oscillation (ENSO) events of 1983, 1992 and 1998, hatch dates were the latest reported in the series.

Auklet diet composition. The relative importance of the 2 major components of auklet diet varied through time. The harvest of *Euphausia pacifica* and *Thysanoessa spinifera* by auklets showed significant opposite quadratic trends through time (*E. pacifica*: $\beta_1 = 10.97 \pm 3.07$, $t_1 = 3.57$, $p_1 = 0.002$, $\beta_2 = -0.003 \pm 0.0008$, $t_2 = -3.57$, $p_2 = 0.002$, $R^2 = 0.4485$; *T. spinifera*: $\beta_1 = -10.14 \pm 4.35$, $t_1 = -2.33$, $p_1 = 0.032$, $\beta_2 = 0.003 \pm 0.001$, $t_2 = 2.33$, $p_2 = 0.032$, $R^2 = 0.2486$; Fig. 3B). *E. pacifica*
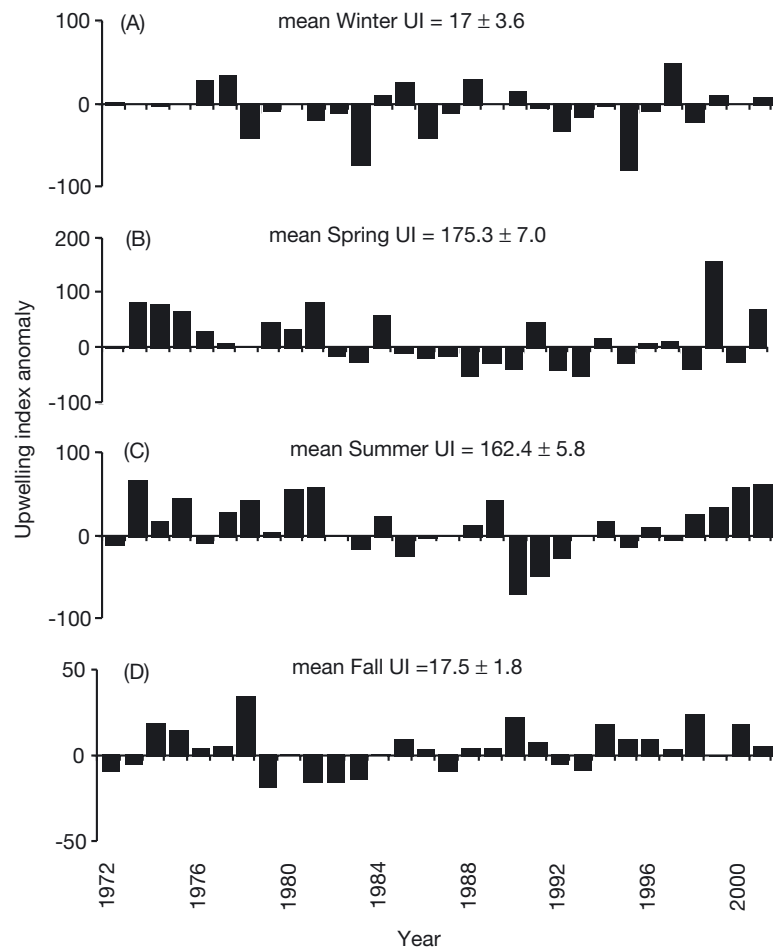

Fig. 1. Annual anomalies in mean seasonal upwelling index (UI) values in (A) winter, (B) spring, (C) summer and (D) fall. Note different scales on y-axes. Seasonal anomalies calculated were based on upwelling index climatology from 1946 to 2001
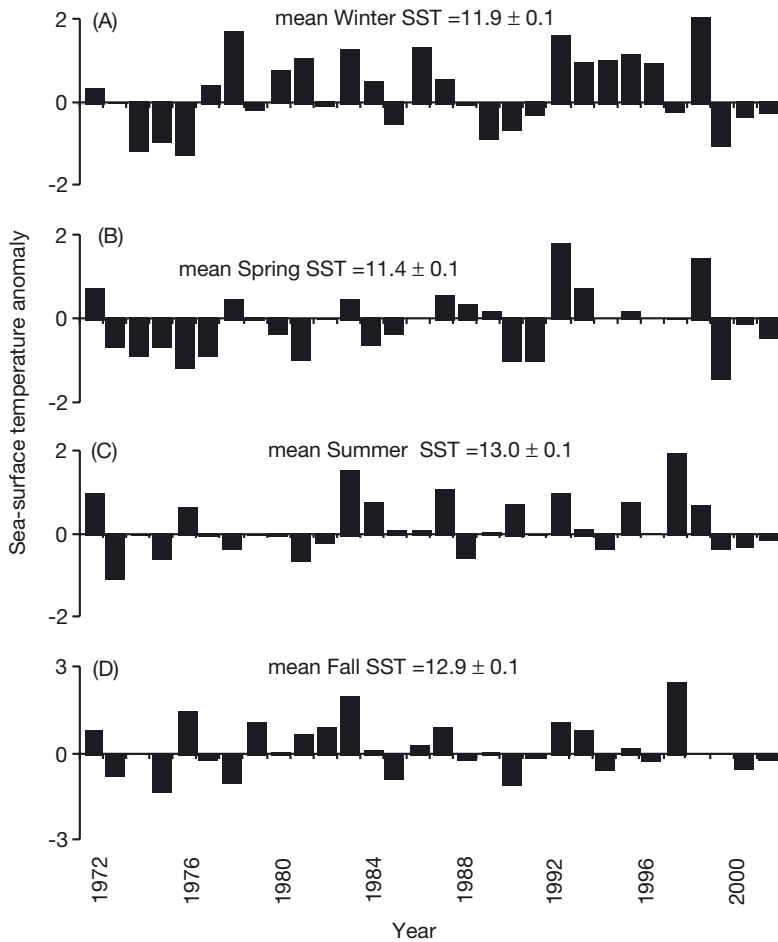
Fig. 2. Annual anomalies in mean seasonal Southeast Farallon Island (SEFI) sea-surface temperatures (SST) in (A) winter, (B) spring, (C) summer and (D) fall. Note different scales on *y*-axes. Anomalies calculated were based on sea-surface temperature climatology from 1929 to 2001

increased in the late 1970s and decreased by the late 1990s, with *T. spinifera* showing the opposite trend. The proportion of all euphausiid prey in the diet did not show any significant quadratic trends through time (Fig. 3C).

Auklet meal mass. We examined mass of gular pouch samples (meal mass) obtained in the field between 1985 and 2001 (Fig. 3D). Meal mass varied significantly on an inter-annual basis ($F_{15,1292} = 7.15$, $p < 0.001$, $R^2 = 0.0766$). Meal mass decreased, although not significantly, through time (Fig. 3D), with no curvature detected in the data. Note that the smallest annual mean meal mass was obtained during the ENSO year of 1998.

Auklet growth rate and productivity. There was significant inter-annual variability in auklet growth rate ($F_{15,428} = 15.29$, $p < 0.001$, $R^2 = 0.3649$; Fig. 3E). Growth was highly variable in the 1990s, with the lowest

recorded growth rates occurring in 1990 and 1997 and the highest in 1996. However, there was no evidence of a temporal trend in growth rate.

Annual productivity showed a significant quadratic trend through time ($\beta_1 = -5.28 \pm 2.09$, $t_1 = -2.53$, $p_1 = 0.018$, $\beta_2 = 0.0013 \pm 0.0005$, $t_2 = 2.53$, $p_2 = 0.018$, $R^2 = 0.2028$; Fig. 3E). Productivity was particularly low in 1983, 1990, 1992 and 1997.

Relationships between ocean climate and timing of breeding and diet

The results of all Spearman's rank correlations between seasonal ocean climate variables, timing of breeding and diet characteristics are presented in Table 2 and Figs. 4 & 5. Hatch date was positively correlated with both winter and spring SST in Year *x*, negatively correlated with the spring SST transition in Year *x*, and positively correlated with fall SST in Year *x*–1. In other words, when SST is warm in the fall of the previous year, and warm in both winter (e.g. Fig. 4A) and spring in the current year, timing of breeding is delayed. When SST in spring is much colder than in winter (strong spring SST transition in the current year), timing of breeding is advanced. Similarly, hatch date was negatively correlated with both the winter and spring UI in Year *x* and with the summer UI in Year *x*–1. In other words, when upwelling is high in summer of the previous year, and high in both winter (e.g. Fig. 4B) and spring in the current year, timing of breeding is advanced.

The proportions of both *Euphausia pacifica* and *Thysanoessa spinifera* in the nestling diet were not significantly related to any seasonal value of SST or UI (Table 2). The proportion of all euphausiids in nestling diet was positively correlated with fall SST in Year *x*–1 (Table 2). In other words, when SST was high in fall of the previous year, the proportion of euphausiids in the diet is high in the following year (Fig. 5A). The proportion of all euphausiids in the nestling diet was also negatively correlated with spring UI in Year *x* and with the spring UI transition in Year *x*. In other words, when UI is high in spring of the current year, and when UI in spring is much higher than in winter (strong spring UI transition in the current year), the proportion of euphausiids in the diet is low (Fig. 5B,C). Nestling meal mass was not significantly related to any seasonal value of SST or UI (Table 2).

Relationships between auklet timing of breeding, diet, growth and productivity

The results of all Spearman's rank correlations between timing of breeding, diet, growth rate and productivity are presented in Table 3 and Fig. 6. Hatch date was negatively correlated with the proportion of *Euphausia pacifica* in the nestling diet (Fig. 6A). In other words, when hatch date was delayed, the proportion of *E. pacifica* in the diet was low. Meal mass did not show any significant associations. Nestling growth rate was positively correlated with productivity (Fig. 6B). Although insignificant, growth rate was positively related to the proportion of *Thysanoessa spinifera* in the diet and negatively correlated with the proportion of *E. pacifica* in the diet. Also insignificant, nestling meal mass was positively correlated with both the proportion of *E. pacifica* in the diet and nestling growth rate. Productivity was positively related to the proportion of *T. spinifera* in the diet (Fig. 6C).

Euphausiid abundance

In southern California, the abundance of both *Euphausia pacifica* and *Thysanoessa spinifera* increased through time (1975 to 2002), although this was significant only for *T. spinifera* ($\beta = 0.055 \pm 0.026$, $t = 2.13$, $p = 0.043$, $R^2 = 0.1484$). The central California abundance of *E. pacifica* increased and *T. spinifera* decreased through time (1975 to 1998, not all years inclusive), although these trends were not significant.

The abundance of *Euphausia pacifica* in central California was significantly related to the abundance in southern California ($F_{1,12} = 7.78$, $p = 0.0163$, $R^2 = 0.3934$, $y = 0.5462x + 3.5212$; Fig. 7A). The abundance of *Thysanoessa spinifera* in central California was also significantly related to the abundance in southern California ($F_{1,12} = 8.25$, $p = 0.014$, $R^2 = 0.4075$; $y = 1.1191x + 1.1925$; Fig. 7B). We used these regression equations to estimate the abundance of each euphausiid species in central California in years where CalCOFI surveys were not conducted in that region (see Table 1, Fig. 7C). Using a com-
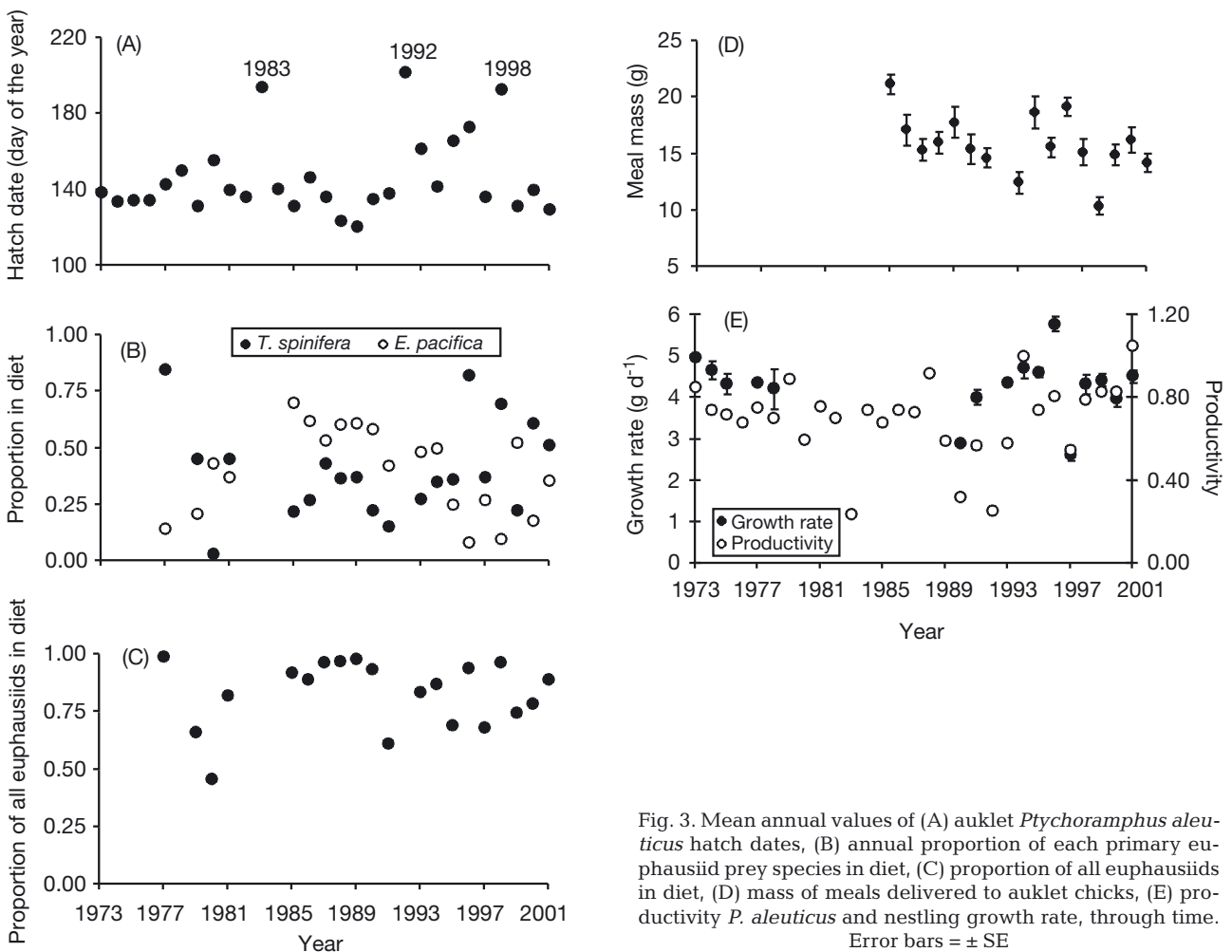

Fig. 3. Mean annual values of (A) auklet *Ptychoramphus aleuticus* hatch dates, (B) annual proportion of each primary euphausiid prey species in diet, (C) proportion of all euphausiids in diet, (D) mass of meals delivered to auklet chicks, (E) productivity *P. aleuticus* and nestling growth rate, through time. Error bars = ± SE

Table 2. *Ptychoramphus aleuticus.* Results of Spearman's rank correlations (r_s values) between seasonal mean values of sea-surface temperature (SST) and upwelling index (UI) (average from 36 and 39° N) in Year x (current year) and Year x–1 (previous year) and auklet diet composition, meal mass and hatch date (1973 to 2001, not all years inclusive for some parameters: see Table 1). Significant values are shaded in light gray ($p \le 0.05$) and in dark gray ($p \le 0.1$)

Factor	Year	Winter (Jan–Mar)	Spring (Apr–Jun)	Summer (Jul–Sep)	Fall (Oct–Dec)	Spring transition (Spring minus Winter)
Hatch date (n = 29)						
SST	Year x	0.83	0.46	–	–	−0.57
	Year x–1	−0.03	−0.11	0.25	0.37	–
UI	Year x	−0.62	−0.35	–	–	−0.05
	Year x–1	−0.03	0.03	−0.55	−0.22	–
***Euphausia pacifica* in nestling diet (n = 20)**						
SST	Year x	−0.30	−0.05	–	–	0.21
	Year x–1	0.03	0.17	0.08	−0.08	–
UI	Year x	0.15	−0.17	–	–	−0.31
	Year x–1	0.07	−0.17	0.02	−0.25	–
***Thysanoessa spinifera* in nestling diet (n = 20)**						
SST	Year x	0.22	0.27	–	–	0.05
	Year x–1	−0.05	−0.15	0.16	0.16	–
UI	Year x	−0.07	−0.02	–	–	0.05
	Year x–1	0.03	0.19	0.08	0.09	–
All euphausiids in nestling diet (n = 20)						
SST	Year x	0.02	0.30	–	–	0.15
	Year x–1	−0.24	0.03	0.28	0.48	–
UI	Year x	0.14	−0.49	–	–	−0.50
	Year x–1	0.28	−0.16	−0.18	−0.26	–
Meal mass (n = 16)						
SST	Year x	−0.09	−0.11	–	–	−0.01
	Year x–1	−0.04	−0.08	−0.26	−0.06	–
UI	Year x	0.14	0.06	–	–	−0.16
	Year x–1	−0.03	0.06	0.11	−0.29	–

bination of measured and derived (to complete the time series) abundance values, both species showed an increase in abundance over time, but this was significant only for *T. spinifera* ($\beta = 0.173 \pm 0.05$, $t = 3.73$, $p = 0.001$). The values in Fig. 7C for *E. pacifica* and *T. spinifera* abundance (combination of measured values and derived values for years of missing data) for central California were used for the remainder of the analyses.

Relationships between euphausiid abundance and auklet timing of breeding, diet, growth and productivity

The results of Spearman's rank correlations between euphausiid abundance in central California and the timing of Cassin's auklet breeding, diet, nestling growth and productivity are presented in Table 4 and Fig. 8. *Euphausia pacifica* abundance in central California was positively related to both meal mass and auklet productivity (Table 4, Fig. 8A,B). *Thysanoessa spinifera* abundance in central California was also positively related to productivity (Table 4, Fig. 8C). Although insignificant, the abundance of both species showed positive correlations with auklet growth rate.

DISCUSSION

Euphausiid response to variable oceanographic climate

There was significant inter-annual variability in seasonal values of the upwelling index and sea-surface temperature throughout the duration of this study (Figs. 1 & 2). Generally, there was moderate-to-strong spring and summer upwelling at the beginning and end of the time series and weak-to-moderate spring and summer upwelling during much of the 1980s and 1990s (prior to 1998). There were cooler winter, spring and summer sea temperatures at the beginning and end of the time series and warmer temperatures through much of the 1980s and 1990s. Spring sea temperature showed strings of cold years: low from 1973 to 1977, 1990 to 1991, and 1999 to 2000 and much higher in ENSO years of 1992 and 1998. The highest summer sea temperatures occurred in the ENSO years of 1983 and 1997.

Few studies have examined the effects of interannual variability in oceanographic conditions on the biology of euphausiids in the CCS, and among those that have, few have successfully demonstrated func-
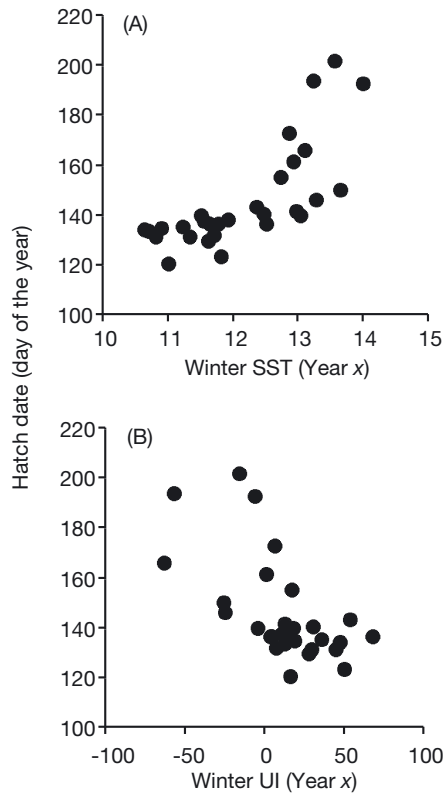
Fig. 4. *Ptychoramphus aleuticus.* Relationship between auklet hatch date and (A) winter SST in Year *x* and (B) winter upwelling index (UI) in Year *x*

tional relationships between ocean conditions and euphausiid abundance. Although some investigators have suggested differences in the responses of *Euphausia pacifica* and *Thysanoessa spinifera* to variable ocean conditions, assessing the relative influence of individual ocean climate parameters on euphausiid abundance remains extremely challenging. Several studies have suggested that some euphausiid species may be adversely affected by anomalously warm sea temperatures (Brinton 1981, Tanasichuk 1998b, Marinovic et al. 2002, Brinton & Townsend 2003), while others have suggested that upwelling plays a significant
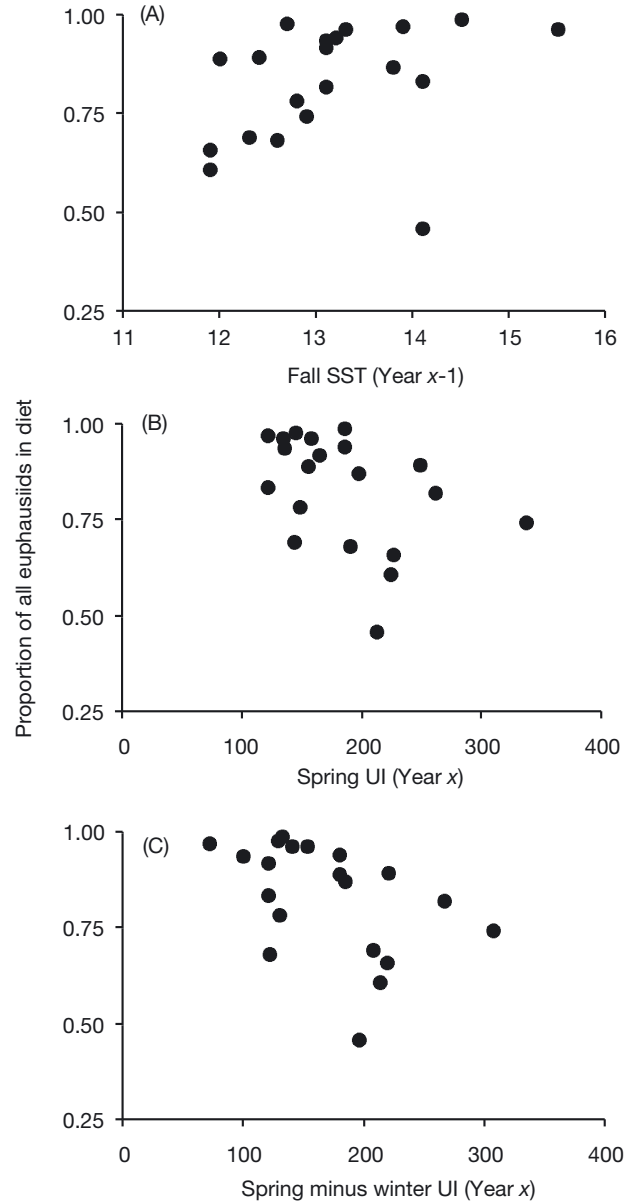
Fig. 5. *Ptychoramphus aleuticus.* Relationship between proportion of euphausiids in auklet nestling diet and (A) fall SST in Year *x*–1, (B) spring UI in Year *x*, (C) spring minus winter UI in Year *x*

Table 3. *Ptychoramphus aleuticus.* Results of Spearman's rank correlations (r_s values) between mean auklet hatch date, meal mass, growth rate, productivity and diet composition (1973 to 2001, not all years inclusive for some parameters: see Table 1). Significant values are shaded in light gray ($p \le 0.05$). Values in parentheses: sample sizes

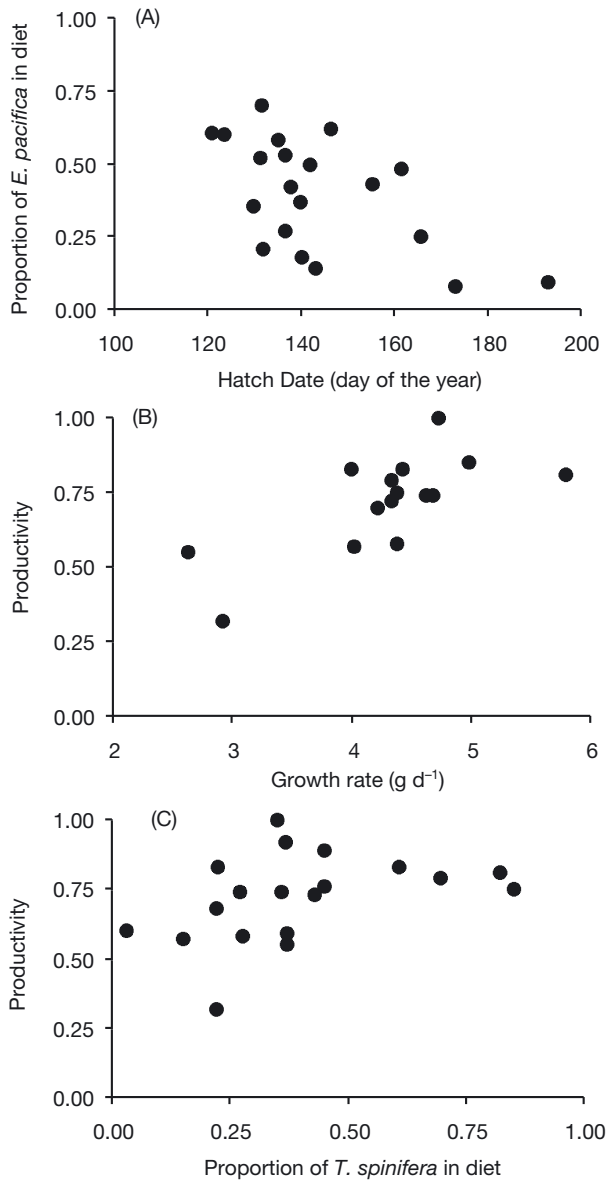|	Hatch date	Meal mass	Growth rate	Productivity	*Euphausia pacifica*	*Thysanoessa spinifera*	All euphausiids
Hatch date	–	–0.09 (16)	0.16 (16)	–0.22 (29)	–0.52 (20)	0.16 (20)	–0.12 (20)
Meal mass	–	–	0.33 (11)	0.13 (16)	0.35 (16)	–0.05 (16)	0.25 (16)
Growth rate	–	–	–	0.65 (16)	–0.13 (12)	0.20 (12)	–0.22 (12)
Productivity	–	–	–	–	–0.28 (20)	0.48 (20)	0.13 (20)

Fig. 6. Relationship between (A) hatch date and proportion of *E. pacifica* in diet, (B) nestling growth rate and productivity and (C) proportion of *T. spinifera* in diet and productivity

role in determining peaks in abundance of some euphausiids (Tanasichuk 1998a, Brinton 1981). The results of Brinton & Townsend (2003) show that although the abundance of *E. pacifica* and *T. spinifera* in southern California declined in response to ENSO warming events, both species were relatively resilient, displaying rapid post-event recoveries. In Barkley Sound, Canada, Tanasichuk (1998a) hypothesized that increases in adult abundance in the warm-water years of 1992 to 1993 were due to strong recruitment in 1992, with strong upwelling that year being an important causal mechanism. This conclusion is supported by

previous studies in the southern California Current reporting that enhanced recruitment of *E. pacifica* also coincides with significant increases in seasonal upwelling (Brinton 1976). The results of Tanasichuk (1998a) indicated that the increased sea temperature during the 1992 to 1993 El Niño had no direct effects on either larval or adult abundance of *E. pacifica*. However, Tanasichuk (1998b) described dissimilar trends in *T. spinifera* abundance over the same time period. In this case, larval abundance was relatively low in 1992 to 1993 (warm-water years) while adult biomass declined throughout the study period. This steady decline was probably due to a series of recruitment failures in terms of poor survival from larvae to adult (Tanasichuk 1998b). Therefore, because the
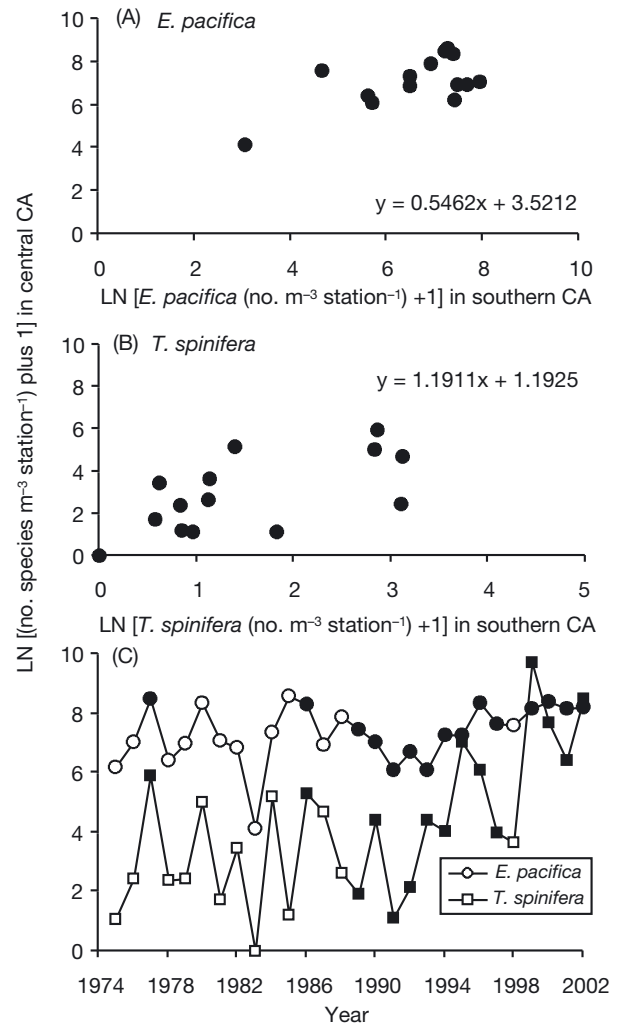

Fig. 7. *Euphausia pacifica* and *Thysanoessa spinifera.* Relationship between (A) abundance of *E. pacifica* in southern and central California, (B) abundance of *T. spinifera* in southern and central California, (C) measured (□, ○) and derived (■, ●) euphausiid abundance in central California over time

Table 4. *Ptychoramphus aleuticus.* Results of Spearman's rank correlations (r_s values) between *Euphausia pacifica* and *Thysanoessa spinifera* abundance in central California (March to May) and auklet hatch date, diet composition, meal mass, growth rate and productivity (1973 to 2001, not all years inclusive for some parameters: see Table 1). Significant values are shaded in light gray (p ≤ 0.05) and in dark gray (p ≤ 0.1)

Factor	Abundance in central CA	
	E. pacifica	*T. spinifera*
Hatch date (n = 27)	−0.16	0.10
E. pacifica (n = 20)	0.10	–
T. spinifera (n = 20)	–	0.22
All euphausiids (n = 20)	0.23	−0.04
Meal mass (n = 16)	0.47	−0.07
Growth rate (n = 14)	0.22	0.35
Productivity (n = 27)	0.47	0.48

results of several of these studies are open to interpretation, it seems that characterizing and predicting these causal/functional relationships may be more difficult than previously thought.

As indexed by SEFI auklet diet composition, there is some indication that euphausiids responded to changes in the ocean climate. Although these specific oceanographic–diet relationships were not significant, coincident with the long-term trend in upwelling, the proportion of *Thysanoessa spinifera* decreased in the late 1970s, remained relatively low in the 1980s and began to increase again after 1995, while *Euphausia pacifica* showed the opposite trend, coincident with the long-term trend in SSR (Fig. 3B).

Our results support the idea that both upwelling and sea temperature, to some degree, influence euphausiid availability during the auklet chick-rearing period in the Gulf of the Farallones, at least as measured by auklet diet composition. Either independently, or more probably acting in concert, upwelling and sea temperature may both be important factors influencing the abundance and/or availability of both euphausiids in the region surrounding the Farallones. Perhaps each of these ocean climate parameters exerts varying levels of positive or negative effects, depending not only on their relative frequency and intensity, but the timing of each. Fall sea temperature in the previous year (Year *x*–1) seems to play an important role in overall euphausiid abundance in auklet diet in the current year (Year *x*) (Table 2, Fig. 5A). The higher the fall SST in the previous year, the greater the overall proportion of euphausiids in the diet. This suggests that nestling growth may be influenced, as the auklets prefer larger prey items. Conversely, as spring UI in the current year increases, the overall proportion of euphausiids in the diet decreases (Table 2, Fig. 5B). Similarly, if the spring upwelling transition is very strong (spring UI

much higher than in winter), then the proportion of euphausiids in the diet will be reduced (Table 2, Fig. 5C).

The positive relationship between fall SST in the previous year and euphausiid abundance in the diet suggests that perhaps fall sea temperatures may play an important role in euphausiid growth and development. Lindley (1978) found that the timing of euphausiid reproduction in spring was correlated with
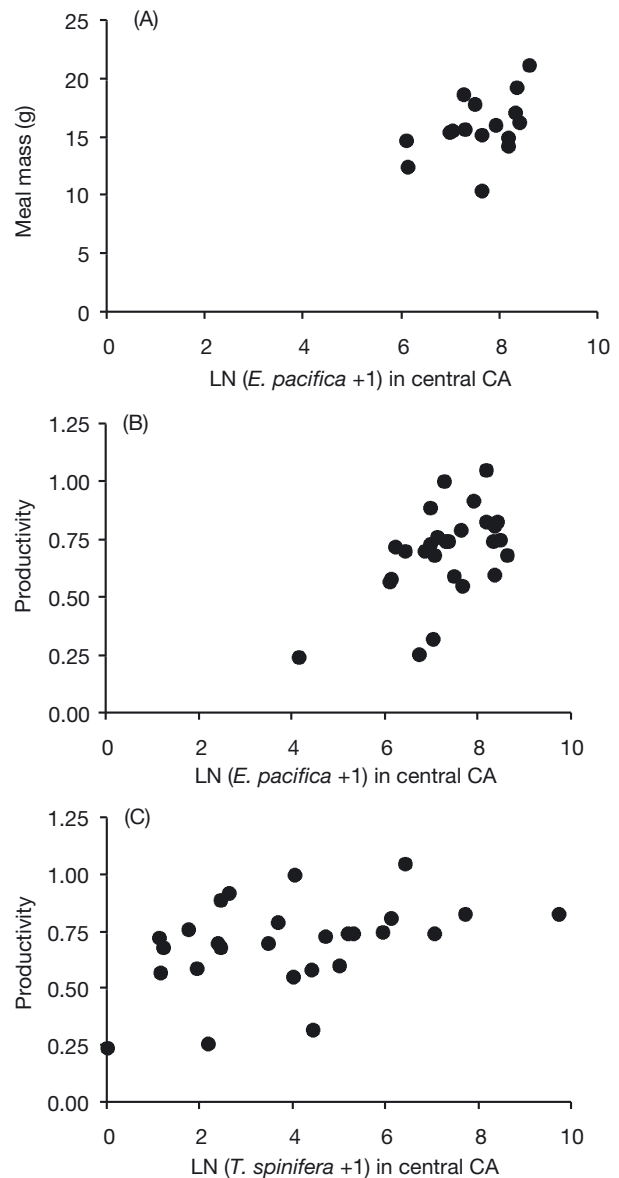

Fig. 8. *Ptychoramphus aleuticus.* Relationship between (A) abundance of *Euphausia pacifica* in central California and auklet meal mass, (B) abundance of *E. pacifica* in central California and auklet productivity, (C) abundance of *Thysanoessa spinifera* in central California and auklet productivity, 1975 to 2001

sea temperature and suggested that adults may take advantage of brief periods of warming between upwelling events to accelerate gonadal development in warm surface layers. Similarly, Smith & Adams (1988) suggested that one of the functions of daytime surface swarming is to prolong exposure of reproductive individuals to the warmer surface layers where maturation of sexual characteristics will be accelerated.

The relationships observed between upwelling in spring (as well as the relative strength of the spring upwelling transition) and all euphausiids in auklet diet support the idea that a threshold of tolerance to upwelling exists, such that upwelling values above a certain range (excess turbulence and/or advection) are unfavorable for euphausiids. For example, during years of extremely high upwelling in spring, conditions may be less favorable for surface swarms of euphausiids (Smith & Adams 1988), and juveniles may be advected out to the open ocean (Lu et al. 2003), reducing recruitment in that season.

Auklet response to variable oceanographic conditions

Variable ocean climate results in changes in the marine food-web structure and dynamics. Several investigators have reported an association between seabird reproductive parameters (breeding phenology, nestling growth, reproductive performance) and prey availability and/or diet composition (e.g. Ainley et al. 1996, Monaghan et al. 1996, Kitaysky et al. 2000, Bertram et al. 2001, Sydeman et al. 2001, Hedd et al. 2002). Seabird parents may compensate for interannual variation in prey availability through (1) an increase in foraging effort to provide for offspring (Burger & Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994), (2) a delay in timing of reproduction such that breeding matches the peak in resource availability (Lack 1968, Cushing 1995, Sydeman 1999, Bertram et al. 2001), and/or (3) the cessation of breeding efforts entirely in years of severely depleted prey availability (Ainley et al. 1995, Nur & Sydeman 1999a,b, Sydeman et al. 2001).

For the northern CCS, Bertram et al. (2001) suggested that the timing of the spring transition and sea-surface temperature influences the timing of peak abundance of copepods, and thereby limits the amount of time that preferred prey is available for adult auklets to provision their offspring. Bertram et al. (2001) reported that when spring sea temperature is warm on Triangle Island (TI), British Columbia, the duration of overlap between breeding of Cassin's auklet and copepod availability is reduced, creating a seasonal mismatch between the period of peak copepod availability and nestling development.

The diet of auklets provisioning chicks on TI is composed primarily of the copepod *Neocalanus cristatus*, with diet composition closely related to chick growth (Bertram et al. 2001, Hedd et al. 2002). *N. cristatus* develop approximately 60 d earlier in warm years than in cold years. Warm-water years are not characterized consistently by advanced breeding of the birds; therefore, the match between the chick-rearing period and peak food availability is poor, resulting in reduced offspring growth. Although overall nestling growth is poor in warm years, those individuals that bred earliest in the season display higher growth rates (Bertram et al. 2001). On TI, substantial within- and between-year variation in the growth of Cassin's auklet nestlings corresponded to variation in diet composition and parental provisioning (Hedd et al. 2002). In addition, Hedd et al. (2002) suggest that parents may have a greater capacity to respond in some years than others.

This concept is supported by the results of other field studies that have shown that, in some pelagic seabird species, parents are able to effectively compensate for variation in food availability through an increase in foraging effort (Burger & Piatt 1990, Uttley et al. 1994). In other species, parents maintain constant foraging effort despite high variation in food supply (Obst et al. 1995). Therefore, some seabird species may be capable of behavioral changes that effectively buffer certain aspects of their breeding biology (Monaghan et al. 1996, Kitaysky et al. 2000). A further consideration is the quality of breeding parents. Several studies have supported the view that body condition is the most plausible proximate determinant of breeding decisions of birds (e.g. Perrins 1970, Hamer et al. 1991). Pyle et al. (2001) suggested, for Cassin's auklets, that a reduction or delay in food supply may prevent all but the 'highest quality' breeding adults from reproducing. Therefore, in poor food years, if a large proportion of the breeding population is comprised of the highest-quality parents, they may be capable of adjusting their foraging effort to ensure high nestling growth rates. Following the 1997–1998 ENSO event, the annual survival of female Cassin's auklet on SEFI was also severely reduced (PRBO unpubl. data), with the probability of breeding also very low in 1997 and 1998. However, the population has increased following the 1997–1998 ENSO and the 1999 regime shift to cooler conditions, but is not yet near pre-ENSO levels. On SEFI, fewer birds attempt to breed in 'warm' years, and those that do may indeed be of higher 'quality' (see Pyle et al. 2001). Therefore, it seems as though these higher-quality adults adjust their timing of breeding to match adequate prey availability, but also that in years when the ENSO signal is very strong, prey availability may be so severely reduced that growth and productivity (which are strongly related: Table 3) are compromised.

In contrast to TI, the SEFI auklet population delays breeding substantially in strong ENSO years (Fig. 3A). Auklet timing of breeding was positively related to fall SST in the previous year and winter and spring SST in the current year (Table 2, Fig. 4). SEFI auklets breed earlier in years when SST in fall through spring is relatively cool, and later when SST in fall through spring is relatively warm. Timing of breeding was also negatively related to the strength of the spring SST transition (Table 2). In other words, when SST in spring is much cooler than in winter, auklets advance their breeding effort. Timing of breeding was negatively related to the summer UI in the previous year and the winter and spring UI in the current year (Table 2, Fig. 4). In general, SEFI auklets breed earlier in years when summer through spring upwelling is relatively high, and later when summer through spring upwelling is relatively weak.

The proportion of *Euphausia pacifica* in the diet of nestling auklets is negatively correlated with timing of breeding in response to variable ocean climate (Table 3, Fig. 6A). Also, although these trends are not significant, growth rates are higher and reproductive success is lower when breeding is delayed (Table 3). However, the trend of lower productivity with delayed breeding is driven primarily by the very poor reproductive success in the strong ENSO years of 1983 and 1992; Fig. 3A,E). In fact, when we remove the very strong ENSO years of 1983 and 1992 from the time series, this relationship breaks down completely. Growth rate was correlated with productivity (Table 3, Fig. 6B), and productivity was strongly correlated with the proportion of *Thysanoessa spinifera* in the diet (Table 3, Fig. 6C). Therefore, of the 2 primary prey species in the diet, *T. spinifera* seems to be most important in terms of growth and productivity, while *E. pacifica* may be more important in terms of timing of breeding.

The overall decline in parental meal mass over time (Fig. 3D), although not significant, is consistent with the observation that along with ocean-warming and changes in large-scale circulation patterns, zooplankton biomass in the southern CCS declined appreciably between 1951 and 1995 (Roemmich & McGowan 1995, Hayward 1997, McGowan et al. 1998). However, declining meal mass is inconsistent with the relatively stable (if not increasing) euphausiid abundance trends in central California, at least since 1975 (Fig. 7C). Brinton & Townsend (2003) did not demonstrate a substantive decline in the abundance of either euphausiid species in the southern and central CCS, leading some investigators to conclude that other zooplankton species are primarily responsible for the overall decline (Rebstock 2002, Lavaniegos & Ohman 2003). For the last 3 yr of our study, meal mass was very close to the long-term average, perhaps suggesting a rever-

sal in the declining trend and consistent with the regime shift in 1999 to cooler conditions.

The abundance of *Euphausia pacifica* in central California was positively correlated with meal mass, growth rate (although insignificantly) and productivity (Table 4, Fig. 8A,B). The abundance of *Thysanoessa spinifera* in central California was also positively correlated with growth rate (although insignificantly) and productivity (Table 4, Fig. 8C). Rather surprisingly, the spring abundance of both species showed only weak relationships with timing of breeding and with the proportions of both species in the diet (Table 4). However, we used euphausiid abundance data that was collected between March and May, and auklet diet samples were generally collected between May and September (abundance data not available for these months); therefore, it is possible that the abundance of euphausiids in central California in summer (during the period of chick-rearing) may have been substantially different than earlier in the year.

It may be no coincidence that, in addition to having the highest growth rates observed, 1996 was a year in which abundances of both *Euphausia pacifica* and *Thysanoessa spinifera* were equal to some of the highest recorded in the central California CalCOFI time series (Fig. 7C; see also Brinton & Townsend 2003). Interestingly, these high-density years in southern California were consistently followed by a 90% decrease in *E. pacifica* abundance and a decline, although less substantial, in *T. spinifera* abundance within 1 to 2 yr. These trends were less pronounced for *E. pacifica* and more pronounced for *T. spinifera* in central California (Fig. 7C). This projected decline may also help to explain the poor nestling growth observed in 1997.

On SEFI, the availability of *Thysanoessa spinifera* has been hypothesized to explain variation in the breeding phenology of the auklet population (Ainley et al. 1990, 1996). However, it seems more likely that the availability of both *Euphausia pacifica* and *T. spinifera* are relevant to auklet reproductive activities and success. In contrast to TI, when the ocean is warm in spring in the Gulf of the Farallon, the initiation of effectual upwelling is delayed, presumably resulting in a delay in euphausiid abundance. In general, the Farallon population of Cassin's auklets appears to respond adaptively to changes in ocean climate by delaying the initiation of breeding in warm years such that the critical period of growth coincides with adequate prey availability (Figs. 3A & 4A,B).

Nestling growth rate varied significantly on an annual basis (Fig. 3E): in 1996, growth rates were the highest reported for the series, while in 1990 and 1997, growth rates were the lowest reported for the series. In ENSO years, winter, spring and summer SST is typically warm (Fig. 2), and auklets presumably use this as

a cue to delay breeding until such time as conditions become more favorable. This was the case in 1998, and growth rates were relatively high (Fig. 3E). However, 1998 may not represent a typical ENSO year: several lines of evidence suggest that there was a dramatic recovery in ocean climate by May in the tropics (Chavez et al. 1999) and by July in Monterey Bay (Marinovic et al. 2002) to cold, La Niña-like conditions, which would facilitate auklet chick growth and development. Therefore, the relatively high growth rates observed in 1998 may not only be attributable to a delay in breeding but also to dramatically increased ocean productivity during the critical chick-rearing period. The years of 1990 and 1997 were relatively unique in our time series in that they were the only years (for which we have auklet growth data) in which SST was substantially warmer in summer (period of chick-rearing) than in spring (Fig. 2). In 1997, this change probably reflected the start of the 1997–1998 ENSO event (Chavez et al. 1999). Because both winter and spring sea temperatures were low in 1990 and 1997, auklets did not delay breeding efforts in those years (Fig. 3A). The subsequent increase in sea temperature by summer may have resulted in reduced prey availability during the period of chick-rearing. Consequently, there was a mismatch between the timing of breeding and prey availability, resulting in the very low growth rates observed. Our results suggest that when the breeding season becomes progressively warmer, the availability of euphausiids, and *Thysanoessa spinifera* in particular, may be delayed and/or reduced, resulting in lower overall nestling growth rates.

It may not be surprising that we did not observe any significant relationships between auklet diet composition and nestling growth. The 2 primary euphausiid species are similar in energy density (4900 cal g^{-1} for *Euphausia pacifica* and 4700 to 5200 cal g^{-1} for *Thysanoessa spinifera*: Mooney 1999), and therefore are equally valuable prey items in terms of energy content. It is also likely that growth rate may also be influenced by some other component of diet (or a combination of diet characteristics) that we have not yet investigated. Our interpretation of the relationships (or lack thereof) observed between nestling meal mass and growth rate should be viewed with caution: although we examined the average mass of prey delivered to nestlings, we do not know how each individual parent responds to the nutritional needs of offspring under variable conditions. While we believe that each parent makes a single nightly visit to the nestling (Manuwal 1974), we do not know whether and under what conditions individual parents deliver food each night. For example, estimates of the number of food loads delivered to rhinoceros auklet nestlings (each rhinoceros auklet parent also makes only 1 nightly visit to the nest site) range between 1 and 2 bill-loads per night, depending on year (Takahashi et al. 2001). Perhaps in years of extremely poor nestling growth (e.g. 1990 and 1997), although meal mass is relatively high, ocean conditions are so poor and prey availability so low that individual Cassin's auklet parents are unable to increase their foraging effort and maintain adequate growth rates. In such years, although the mean meal mass is relatively high, parents may be, on average, delivering a smaller number of bill-loads to chicks throughout the nestling period, thereby reducing growth rate. In 1990 and 1997, meal masses were relatively high, while nestling growth rates were low. In these years, if the mismatch between timing of breeding and prey availability was too pronounced, perhaps the total parental foraging effort (total mass of prey delivered throughout the nestling period) was not sufficient to maintain adequate growth.

In any attempt to link characteristics such as growth rates on seabird colonies to oceanographic conditions, questions concerning prey distribution and abundance must be considered. We, and others, have shown that these relationships are both complex and difficult to quantify. In addition, the strategy utilized by seabirds and the magnitude in which seabirds respond to ocean and ecosystem fluctuations is complicated, and may vary differently within and between years and decades. We are in the process of developing fine-scale hydroacoustic surveys of the Farallon Cassin's auklet prey base to further elucidate these relationships. In addition, further studies on the foraging effort of individuals under variable oceanographic conditions will help to explain oceanic predator–prey relationships.

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