UC San Diego
UC San Diego Previously Published Works

Title

Linking nitrogen dynamics to climate variability off central California: a 51 year record based on 15N/14N in CalCOFI zooplankton

Permalink

Journal

ISSN

Authors

Rau, Greg H
Ohman, Mark D
Pierrot-Bults, Annelies

Publication Date

DOI

Peer reviewed

Linking nitrogen dynamics to climate variability off central California: a 51 year record based on $^{15}N/^{14}N$ in CalCOFI zooplankton

Greg H. Rau[a],*, Mark D. Ohman[b], Annelies Pierrot-Bults[c]

[a] *Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA*
[b] *Integrative Oceanography Division, Scripps Institution of Oceanography, UCSD, La Jolla, CA 92093-0218, USA*
[c] *Institute for Biodiversity and Ecosystem Dynamics, Zoological Museum, University of Amsterdam, Netherlands*

Abstract

Long-term variability in zooplankton $^{15}N/^{14}N$ was investigated in two species of calanoid copepods (*Calanus pacificus* and *Eucalanus californicus*) and two chaetognaths (*Sagitta bierii* and *Sagitta euneritica*) sampled in the spring of selected years from 1951 to 2001 off the central California coast. No statistically significant trend in $^{15}N/^{14}N$ was detected for any of the four species, with isotopic ratios in 2001 resembling those in copepods and chaetognaths sampled five decades earlier. Zooplankton body lengths also showed no long-term trends. With respect to proposed regime shifts in this region, heterogeneity in $^{15}N/^{14}N$ was detected only for *S. bierii* when comparing the periods 1951–1975, 1978–1998, and 1999–2001. In this species the $^{15}N/^{14}N$ in the most recent, brief period (1999–2001) averaged slightly lower than in the previous period. Three of the four species (*C. pacificus*, *S. bierii*, and *S. euneritica*) showed significant increases in $^{15}N/^{14}N$ during major El Niños. El Niño-related enrichment in ^{15}N could arise as a consequence of increased nitrate demand:supply at the base of the food web or advection of ^{15}N-enriched nitrate from more southerly waters. While a range of physical and climate indices were evaluated, anomalies of $^{15}N/^{14}N$ from the long-term mean were found to be significantly related only to: (i) the Southern Oscillation Index in the case of both chaetognath species, (ii) a regional surface water temperature record (*S. bierii* only), (iii) an index of wind-driven coastal upwelling for the surface-dwelling *C. pacificus*, and (iv) variability in the Pacific Decadal Oscillation for the somewhat deeper-dwelling *E. californicus*. The relationships among each species' $^{15}N/^{14}N$ averaged over the total sampling period was: *E. californicus* ≈ *C. pacificus* ≪ *S. euneritica* < *S. bierii*, consistent with trophic ^{15}N biomagnification and the predatory nature of *Sagitta*.

1. Introduction

Temporal changes in at least some North Pacific pelagic populations may be linked to climate variations (e.g., Roemmich and McGowan, 1995a, b; Brodeur et al., 1996; Lavaniegos and Ohman, 1999; Hare and Mantua, 2000; Hollowed et al., 2001). The possible physical forcing mechanisms causing such variations include changes in circulation, upwelling intensity, altered stratification, and mixed-layer dynamics, which in turn affect biological production, dispersal, and

*Corresponding author.

E-mail addresses: rau4@llnl.gov (G.H. Rau), mohman@ucsd.edu (M.D. Ohman), pierrot@bio.uva.nl (A. Pierrot-Bults).

survival. The major source of interannual ocean variability in this region is the El Niño/Southern Oscillation (ENSO) cycle with periodicity ranging from 3–7 years. During such events primary production generally decreases and significant changes in zooplankton species composition and abundance have been documented (Chelton et al., 1982; Smith and Eppley, 1982; Fiedler, 1984; Brodeur et al., 1996; Kahru and Mitchell, 2000; Rebstock, 2001; Lavaniegos and Ohman, 2003). Changes in the abundance, recruitment, and distribution of many fish species are also evident (e.g., Hollowed et al., 2001).

In addition to ENSO-scale ecosystem temporal variability, lower-frequency changes in atmospheric, oceanic, and biological conditions have been widely discussed (e.g., Ebbesmeyer et al., 1991; Mantua et al., 1997; McGowan et al., 1998; Conversi and Hameed, 1998; Hare and Mantua, 2000). Although the mechanisms leading to such changes as well as the rapidity of the transitions are under debate, empirical evidence indicates that some characteristics of the NE Pacific physical environment and biotic assemblages undergo appreciable changes on multi-decadal scales. Sometimes such changes appear to occur relatively quickly and at other times a slower, multi-year transition can be identified (e.g., Anderson and Piatt, 1999). Climate-forced "regime shifts" in the biomass of zooplankton, fish, and other taxa have been suggested in the NE Pacific in 1977 and 1989 (Hare and Mantua, 2000; Hollowed et al., 2001; Rebstock, 2002), and considerable anecdotal evidence is accumulating that a cooling that began in late 1998 has persisted much longer than a typical La Niña episode (Schwing and Moore, 2000; Greene, 2002; Lavaniegos and Ohman, 2003).

If climate changes affect marine ecosystems as the preceding observations indicate, how do variations in climate and physical ocean processes actually impact marine biota? One often-cited possibility is that physical processes control the vertical advection of nutrients to surface waters and, in turn, primary and secondary production (Polovina et al., 1995; Roemmich and McGowan, 1995a, b; Gargett, 1997; Goes et al., 2001). However, advection alone may be insufficient to

impact biological production if the source of the advected water is itself depleted in nutrients (e.g., nitrate, silicate and/or iron) that limit photosynthesis in this region (White and Dugdale, 1997; Kudela and Dugdale, 2000; Bruland et al., 2001). Furthermore, physical factors such as light regime, water temperature, and horizontal current velocity may play important roles in controlling primary production as well as the metabolism, development, dispersal, and survival of secondary consumers (Polovina et al., 1995; Gargett, 1997; Laws et al., 2000). Such physical effects on predator abundance (e.g., fish) could in turn result in "top down" controls on the abundance and composition of their lower trophic level prey such as zooplankton (Rice, 2001), in contrast to the preceding "bottom-up" control of animal abundance via primary production. Establishing which if any of the preceding mechanisms are responsible for the observed climate and biology covariations has proven difficult, due at least in part to frequent spatial or temporal mismatches in relevant climate, ocean, and ecosystem observations.

Variation of $^{15}N/^{14}N$ in consumer biomass could play a role in addressing the preceding issues. For example, in the N. Pacific plankton $^{15}N/^{14}N$ has been shown to vary spatially, temporally, and historically, with the underlying causes of such variations stemming from changes in specific nitrogen sources, denitrification, utilization efficiency, trophic transfer, and/or degree of recycling (Mullin et al., 1984; Saino and Hattori, 1987; Goering et al., 1990; Wu et al., 1997; Rau et al., 1998; Pride et al., 1999; Altabet et al., 1999; Hirons et al., 2001). $^{15}N/^{14}N$ variations in a specific, low-trophic-level plankton population therefore could be used at least as a qualitative measure of variation in some aspect of nitrogen sources and dynamics integrated over the residence time of N in such tissues. It thus would be relevant to measure temporal variations in plankton $^{15}N/^{14}N$ over long-time scales and to determine the correlation between these and various measures of local, regional, and larger scale physical forcing. In this way climate effects on local N dynamics could at least be qualitatively addressed.

For example, it has been shown at several locations in the NE Pacific that plankton $^{15}N/^{14}N$

is loosely related to biological nitrate utilization efficiency (Wu et al., 1997; Rau et al., 1998; Altabet et al., 1999). If vertical advection controls nitrate supply and the degree of nitrate utilization, this would be evident in a negative relationship between plankton $^{15}N/^{14}N$ and, for example, upwelling intensity. Secondly, changes in horizontal advection and mixing of source waters containing contrasting inorganic nitrogen concentrations and $^{15}N/^{14}N$ would affect planktonic $^{15}N/^{14}N$ in local environments. Of particular relevance here is the northerly and variable excursions of partially denitrified and ^{15}N-enriched eastern subtropical Pacific water along the California coast (Liu and Kaplan, 1989; Altabet et al., 1999; Castro et al., 2001). Variations in the intensity of warm, nutrient-poor water impinging from the south are associated with significant nutrient and biological perturbations along the California coast (Chelton et al., 1982; Chavez, 1996; Bograd and Lynn, 2001). Conversely, long-term changes in the sources and cycling of N observed in the N. Pacific gyre (Karl, 1999; Limsakul et al., 2001; Keller et al., 2002) could impart N isotopic variation in waters which can intrude into the California Current from the west.

There also can be secondary increases in consumer $^{15}N/^{14}N$ as the consumer's trophic distance from the base of the food web increases (e.g., Minagawa and Wada, 1984; Checkley and Miller, 1989). Non-parallel or non-coherent changes in $^{15}N/^{14}N$ over time among consumer species could then imply that relative trophic distances among those consumers had temporally changed. A climate effect on trophic structure therefore would be evident if such interspecific variations in $^{15}N/^{14}N$ were correlated with indices of climate or oceanographic conditions.

Accordingly, we measured $^{15}N/^{14}N$ variations both within and among four species of zooplankton sampled near Monterey Bay, California, over the past 51 years. We sought to test whether $^{15}N/^{14}N$ in animal tissues remained constant over time, or alternatively, responded to the significant interannual and lower frequency forcing known in the NE Pacific. This provides a limited test of the hypothesis that N cycling and trophic structure in this coastal location vary at interannual to interdecadal time-scales and are affected by physical processes.

The zooplankton species we consider are the copepods *Calanus pacificus californicus* Brodsky (hereafter *C. pacificus*) and *Eucalanus californicus* Johnson. The former species is a California Current System (CCS) endemic and the latter a Transition Zone species (Fleminger and Hulsemann, 1973). Both are particle-grazers and are among the numerically dominant copepods in the CCS (Fleminger, 1967; Ohman et al., 1998; Rebstock, 2001). The chaetognaths are *Sagitta bierii* Alvariño and *S. euneritica* Alvariño (retaining the generic assignment *Sagitta*, but see the discussion in Bieri, 1991), both of which are obligate carnivores. The geographic ranges of both chaetognaths species overlap extensively in the CCS (Alvariño, 1965), although *S. bierii* is more broadly distributed in offshore and tropical waters (Pierrot-Bults and Nair, 1991), while *S. euneritica* is restricted to more nearshore waters (Alvariño, 1965; Bieri, 1959 as *S. friderici*). These two species are typically the most abundant chaetognaths in the California Current (Alvariño, 1992).

2. Methods

2.1. Sampling

Zooplankton were sampled in the central California region offshore of Monterey Bay, at line 67, station 55 (36°37′N, 122°25′W; 20 km west of Monterey, CA) or at an adjacent station. Samples were taken with a 0.55 mm mesh, 1-m diameter ring net between 1951 and 1977 and with a 0.505 mm mesh, 0.71-m diameter bongo net from 1978 to present (Ohman and Smith, 1995). Nets were fished double obliquely to 140 m from 1951 to 1968 and to 210 m in following years (Ohman and Smith, 1995). Collections were fixed in a 3.7% solution of sodium borate-buffered formaldehyde in seawater.

Preliminary analyses suggested that the $^{15}N/^{14}N$ of both *C. pacificus* and *E. californicus* varies seasonally, thus we restricted our time series analysis to only the springtime cruises (in March, April, or May), which also were more routinely

conducted than at any other time of year. We utilized CalCOFI springtime zooplankton samples where available between 1951 and 1999, supplemented by zooplankton samples taken along CalCOFI line 67 by the Monterey Bay Aquarium Research Institute (MBARI) from 1999 to 2001, and provided to us by F. Chavez and B. Marinovic. The latter cruises used CalCOFI style bongo nets and the same protocols for zooplankton collection and fixation.

To analyze spatial variability in the geographic locale of station 67.55, and to assess within-sample variation in ^{15}N composition of different lots of copepods, *Calanus pacificus* were sorted from samples taken at 5 stations (67.55, 67.60, 67.65, 70.60, 70.53) on cruise 7203 (March 1972) occupied over a 2-day time period. Four replicate lots of 10 animals were sorted from each sample, dried, and analyzed as indicated below.

To assess the effects of long-term formaldehyde preservation on the stable isotope composition of zooplankton, we compared the $\delta^{15}N$ of adult female *Calanus pacificus* and *Eucalanus californicus* that had been preserved for 11 years with animals deep-frozen for the same period of time. The collection locality was in the southern sector of the CCS, at station 19 ($32°57'N$, $121°3.8'W$) on cruise Fronts 88, on 31 August 1988 (Venrick et al., 1991). Samples were collected with paired bongo nets on a frame towed to 210 m. The catch of one bongo net was immediately frozen in liquid nitrogen aboard ship, then transferred to a $-80°C$ freezer ashore for long-term storage, while the catch from the second bongo net was fixed in buffered formaldehyde according to standard CalCOFI protocols. Five to 10 lots of 5–10 animals from each treatment were sorted and analyzed as described below.

2.2. Stable isotope analysis

Individual copepods and chaetognaths were removed from sample aliquots with no selection bias, other than avoiding damaged animals. In the case of chaetognaths, individuals that contained obvious prey items in the gut were excluded. Only the adult female stage of copepods was analyzed in this study. Zooplankton were measured under a dissecting microscope with an ocular micrometer, rinsed in Milli-Q water, then transferred to clean tin boats in lots of 5–10 individuals of the same species. Samples were dried for 24 h at 55°C, then isotopically analyzed at NASA-Ames Research Center using either break-seal combustion or continuous flow isotope ratio mass spectrometry (e.g., Rau et al., 1989, 1990). When possible replicate analyses were conducted for each species and treatment or sampling date. $^{15}N/^{14}N$ was reported as $\delta^{15}N$ where by convention: $\delta^{15}N = [R_{(sample)}/R_{(standard)} - 1] \times 1000$ (‰) and where $R = {}^{15}N/{}^{14}N$, and "standard" = air N_2, respectively. Also measured was $\delta^{13}C = [R_{(sample)}/R_{(standard)} - 1] \times 1000$ (‰) and where $R = {}^{13}C/{}^{12}C$, and "standard" = Peedee Belemnite. The analytical precision (1 standard deviation) of these measurements was approximately 0.2‰.

2.3. Physical/climate data

Physical time series representing both remote and local forcing in the region were obtained from the following sources. For the Scripps pier temperature record, the springtime mean temperature was computed as the March–April–May average and anomalies computed from the long-term spring average. The average annual Pacific Decadal Oscillation (PDO; Mantua et al. 1997) index was obtained from http://tao.atmos. washington.edu/pdo/. Higher positive values of the PDO index indicate higher temperatures in the Northeast Pacific north of 20°N. The average annual Northern Oscillation Index (NOI), the difference in sea-level pressure anomalies between the North Pacific high and Darwin, Australia (Schwing et al., 2002) was obtained from "www.pfeg.noaa.gov/products/PFEL/modeled/ indices/NOIx/noix.html". Annual PDO and NOI indices were highly correlated ($P < 0.0001$), but with opposite sign. We consistently found the PDO to explain more of the variance in our data than the NOI. Winter averages of the Southern Oscillation Index (SOI), the difference in sea-level pressure between Tahiti and Darwin, were calculated from the anomalies obtained at "http:// www.cpc.ncep.noaa.gov/data/indices". Strong negative values indicate equatorial El Niños.

The Bakun wind-driven upwelling index for 36°N, 122°W was obtained from www.pfeg.noaa. gov/products/PFEL/modeled/indices/upwelling. html and calculated as the spring average (March–April–May), then anomalies computed from the long-term mean spring average. Positive values indicate stronger upwelling. Sea-level height at the San Francisco station was obtained from http:// ilikai.soest.hawaii.edu/uhslc/products.html. The seasonal mean was subtracted from each monthly value, then a linear trend subtracted to give anomalies from the long-term trend. Winter (Dec–Jan–Feb) anomalies of sea level were then averaged. The Aleutian Low Pressure Index (ALPI) was obtained from www.pac.dfo-mpo.gc. ca/sci/sa-mfpd/climate/clm_indx_alpi.htm. Positive values of ALPI indicate a strong Aleutian low pressure system.

We used a General Linear Model to select the best predictor variables for the observed variations in zooplankton stable isotopes and zooplankton body size. Anomalies from the long-term mean of δ^{15}N of each of the four species, or anomalies of body lengths, were regressed against the physical variables noted above. A forward stepwise procedure was used, with α to enter or remove = 0.05 (Systat 10.2). This procedure takes into account the partial correlation structure among potential predictor variables (Sokal and Rohlf, 1995). Although a model II regression (Sokal and Rohlf, 1995) would be more appropriate for these data, we are not aware of a model II multiple regression fitting procedure. P-values were corrected for serial autocorrelation using the method of Dutilleul (1993) when a single predictor variable was found.

3. Results

Long-term preservation in a formaldehyde–seawater solution had a negligible effect on the N isotope content of either *Calanus pacificus* or *Eucalanus californicus*, but appreciably altered the C isotope content of both species (Table 1). The slight increase in δ^{15}N of 0.3‰ observed after 11 years is comparable to the results from Mullin et al. (1984) after 2 years of preservation in a formaldehyde–seawater solution, suggesting that any changes occur relatively quickly upon fixation and thereafter the N isotopic content remains stable. As has been previously reported for formalin-stored samples (Sarakinos et al., 2002), δ^{13}C declined substantially in preserved copepods, with greater variability among replicates than for N isotopes and larger differences between species. Hence, we do not consider δ^{13}C further. In our time series study, there was no relationship between δ^{15}N of the four species of zooplankton and any of the following properties: the age of the plankton samples, sample pH, or the proportion of the sample jar that contained plankton biomass ($P > 0.05$ for all comparisons, $60 \leqslant N \leqslant 77$). We therefore infer that the δ^{15}N measured in preserved animals over the 51-year period largely reflects the

Table 1
Test for differences in the stable isotope content of frozen vs. preserved copepods, after 11 years

Treatment	Frozen (‰) $x \pm 95\%$ (N)	Preserved (‰) $x \pm 95\%$ (N)	Average difference (‰)	P-value
δ^{15}N				
C. pacificus	10.28 ± 0.21 (9)	10.59 ± 0.19 (10)	0.31	< 0.05
E. californicus	9.60 ± 0.46 (5)	9.88 ± 0.22 (8)	0.28	> 0.10
δ^{13}C				
C. pacificus	-18.46 ± 0.34 (9)	-20.94 ± 0.36 (10)	-2.48	< 0.00001
E. californicus	-19.94 ± 0.67 (5)	-21.52 ± 0.35 (8)	-1.58	< 0.001

Aliquots of copepods from the same net collection were either frozen at sea and maintained in liquid nitrogen or fixed and maintained in a solution of 3.7% formaldehyde–seawater until analysis. P-value reports the result of a Student's t-test.

natural isotopic variability of the selected zooplankton species in the region sampled.

We examined the variability in $\delta^{15}N$ attributable to within-station sample replication and to between-station differences in situ. The average difference in $\delta^{15}N$ of *Calanus pacificus* between four lots of 10 animals drawn from the same plankton sample was 0.27‰, while the average difference between five stations sampled in the same geographic area was 0.43‰. Significant differences among stations were resolvable using a 1-way ANOVA ($P < 0.01$, Fig. 1). The magnitude of the differences observed in the time series study is appreciably greater than the variability among stations.

The average $\delta^{15}N$ of the four species of zooplankton differed significantly (Fig. 2), with the values for the two copepod species consistently lower than those for the two chaetognaths. The difference between median values of the two copepod species was 0.20‰, while the average
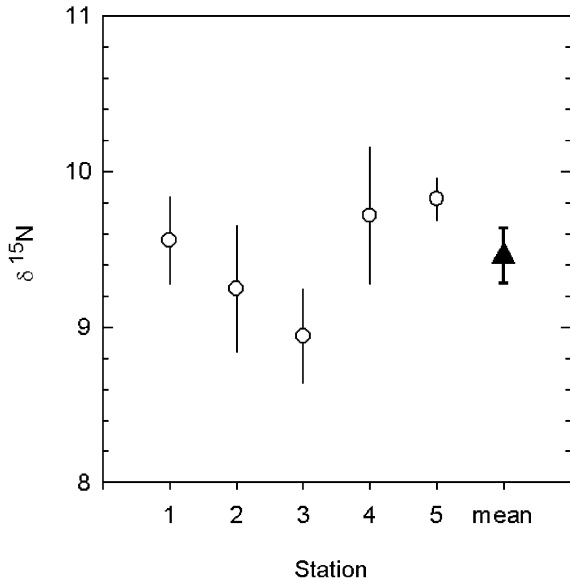

Fig. 2. Overall average values of $\delta^{15}N$ of two species of copepods (*Eucalanus californicus* and *Calanus pacificus*) and two species of chaetognaths (*Sagitta euneritica* and *S. bierii*). Data from all sampling dates (between 28 and 31 springtime cruises) are combined. Box plots: wide horizontal lines indicate median, 25%tile, and 75%tile, stems indicate 10%tile and 90%tile, and dots indicate the 5%tile and 95% tile of the observed values.

difference between the chaetognath *S. euneritica* and the copepod *C. pacificus* was 2.12‰ and between *S. bierii* and *C. pacificus* was 3.91‰.

Fig. 3 illustrates interannual variations in springtime $\delta^{15}N$ of the four species investigated between the years 1951 and 2001. Interannual differences in mean $\delta^{15}N$ of the four species were significantly ($P < 0.001$) but not completely correlated with one another (Kendall's coefficient of concordance $= 0.71$). There was no evidence of a linear trend with time in the stable N isotope content of any of the four species ($P > 0.10$, linear regression analysis). For all species, the $\delta^{15}N$ in spring 2001 was quite similar to that of animals collected 51 years earlier.

We tested for the possibility of regime-related shifts in stable N isotope content of the four species by defining three time periods: 1951–1975, 1978–1998, and 1999–2001. The null hypothesis of no difference among time periods in $\delta^{15}N$ was then tested with a Kruskal–Wallis 1-way ANOVA. Significant differences in $\delta^{15}N$ among the three time periods were detected only for *Sagitta bierii* ($P < 0.01$), with the 1999–2001 mean significantly lower than the other periods for this species (Fig. 4, which also depicts the non-significant trend in *S. euneritica*, $P > 0.05$). This statistical

Fig. 1. Variability of $\delta^{15}N$ of *Calanus pacificus* (mean $\pm$ 95% C.L.) at 5 CalCOFI stations over 2 days on cruise 7203. Station numbers, sampling dates, and [times] are: (1) 67.55, 6 March 1972 [0728], (2) 67.60, 6 March [1140], (3) 67.65, 6 March [1348], (4) 70.60, 8 March [0116], and (5) 70.53, 8 March [0532]. Also shown are the overall mean $\pm$ 95% confidence interval for all values combined.
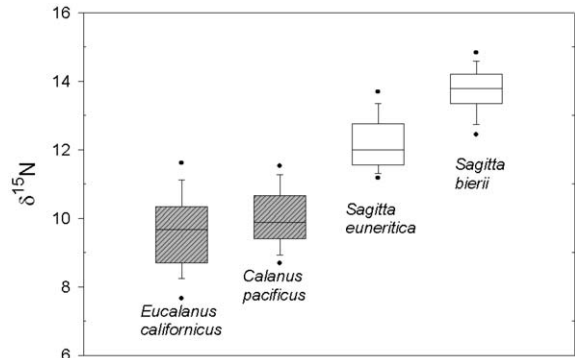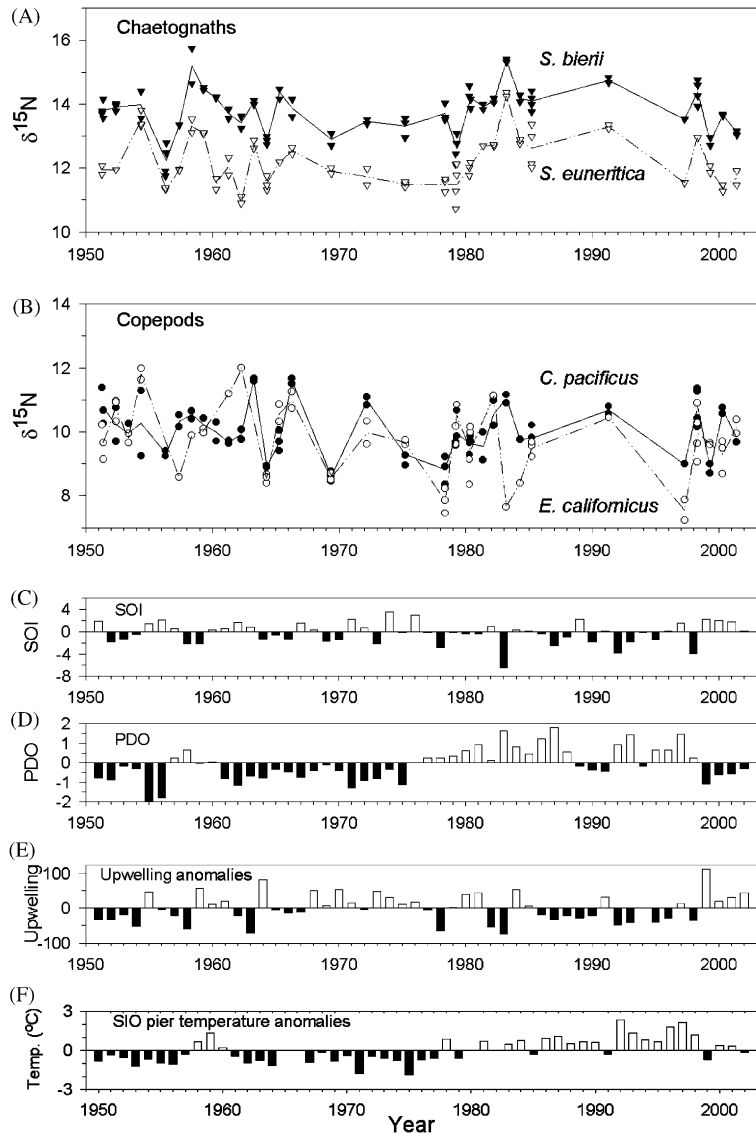
Fig. 3. Interannual variations in springtime δ^{15}N of (A) the chaetognaths *Sagitta bierii* (filled) and *Sagitta euneritica* (open) and (B) adult females of the copepods *Calanus pacificus* (filled) and *Eucalanus californicus* (open) in the central California region. Lines connect the average values on each sample date to illustrate general δ^{15}N temporal variability within species. Due to low temporal sampling resolution, these lines should not be used to interpolate δ^{15}N between sampling dates. Interannual variations in (C) the Southern Oscillation Index, (D) the Pacific Decadal Oscillation index, (E) anomalies from the long-term mean of a coastal upwelling index for 36°N, 122°W, and (F) near surface water temperature anomalies at Scripps Pier.

analysis was repeated omitting the El Niño years 1958, 1983, and 1998, and again *S. bierii* was the only species for which δ^{15}N showed significant heterogeneity among time periods ($P < 0.05$). Some caution is needed, however, in making the

inferences about regime shifts in our δ^{15}N data, considering that samples were not randomly or uniformly sampled within the time periods, and the duration and thus sample size of the most recent period (1999–2001) was relatively small.
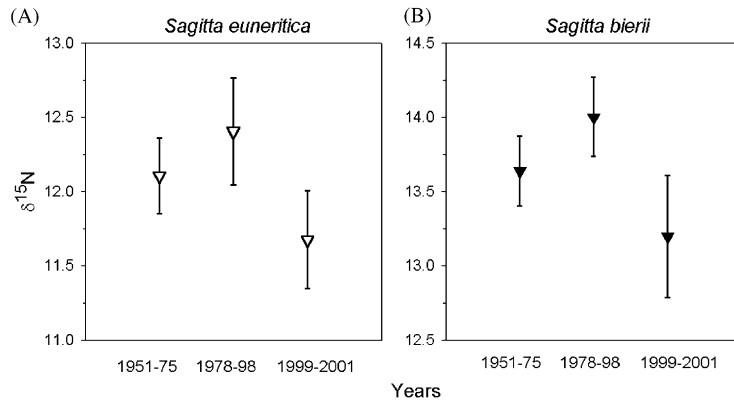
Fig. 4. $\delta^{15}N$ of the chaetognaths (A) *Sagitta bierii* and (B) *Sagitta euneritica* in three time periods: 1951–1975, 1978–1998, and 1999–2001. Mean$\pm$95%.

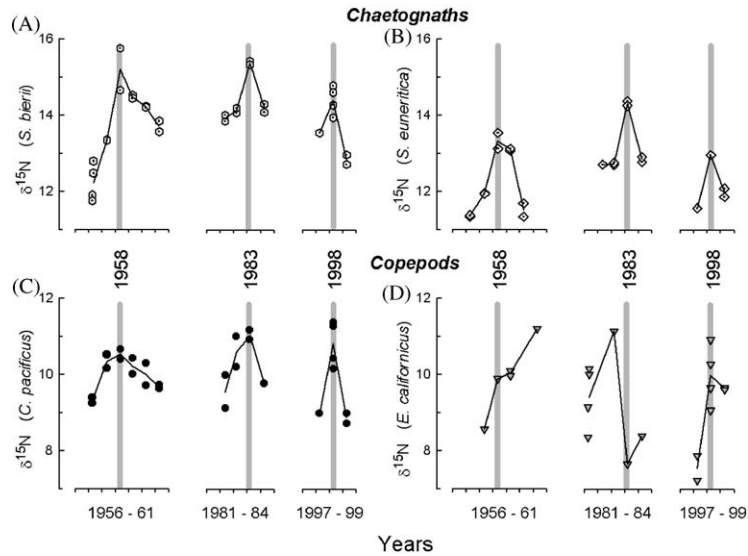Fig. 5. $\delta^{15}N$ of (A) *Sagitta bierii*, (B) *Sagitta euneritica*, (C) *Calanus pacificus* and (D) *Eucalanus californicus* for the springtime cruises during years preceding, during, and following three major El Niño events (1958, 1983, and 1998). Vertical bars highlight the principal El Niño years.

We tested for the effects of El Niño on stable N isotope content of the four species by considering springs immediately before, during, and after the three major El Niños for which we have samples. These are the major El Niños of the second half of the 20th century (i.e. springs of 1958, 1983, and 1998). $\delta^{15}N$ of each of the four species in this sequence of years, plus an additional year on either side where available, is illustrated in Fig. 5. For three of the four species (*S. bierii*, *S. euneritica*,

and *C. pacificus*) there was a consistent, significant ($P \leqslant 0.02$, Mann–Whitney U-test) enrichment in ^{15}N during the El Niño years in comparison with the 1 year immediately preceding and following. There was no significant change in the case of *E. californicus* ($P > 0.50$).

A general linear model fitted with a stepwise multiple regression (MR) procedure was used to assess the covariation of the $\delta^{15}N$ of each of the four species with time series of the various

Table 2
Multiple regression equations relating zooplankton δ^{15}N to environmental variables

Species	Intercept	Slope	Independent variable	r^2	P
S. bierii	-0.053 ± 0.208	-0.166 ± 0.113	SOI	0.417	<0.001
		0.300 ± 0.261	Temp		
S. euneritica	-0.058 ± 0.240	-0.232 ± 0.125	SOI	0.329	<0.001
C. pacificus	-0.012 ± 0.246	-0.009 ± 0.006	UPW	0.258	<0.01
E. californicus	-0.117 ± 0.388	-0.914 ± 0.525	PDO	0.330	<0.05

A general linear model fitted with a stepwise, forward procedure. The anomalies of δ^{15}N of each species were found to be best predicted by 1 or in one case 2 of the following independent variables: SOI (Southern Oscillation Index), Temp (SIO pier temperature), UPW (anomalies of coastal upwelling index), or PDO (Pacific Decadal Oscillation Index). Table entries are the fitted coefficient $\pm$ 95% confidence interval. P indicates the overall significance of the regression equation, corrected for serial autocorrelation (Dutilleul, 1993). Variables found not to contribute significantly to δ^{15}N prediction were: ALPI, Sea Level anomalies, Northern Oscillation Index.

environmental variables. For each MR, anomalies of δ^{15}N from the long-term mean were regressed against ALPI, SOI, PDO, and NOI indices, as well as anomalies of Sea level, Upwelling Index, and SIO pier temperature. Anomalies were calculated from the mean for the period 1951–2001 for the latter three variables, and the index values themselves used for the former four. For each species, significant relationships between δ^{15}N and environmental variables were found ($P \leqslant 0.05$, Table 2), but only one or two variables for each species was found to be a statistically significant predictor of δ^{15}N anomalies, and these variables differed among taxa. For *Calanus pacificus*, δ^{15}N showed an inverse relationship with the coastal upwelling index (Table 2). The isotopic content of *Eucalanus californicus* was inversely related to the PDO index. Both chaetognaths' isotopic content varied inversely with the Southern Oscillation Index, an indicator of El Niño, and SIO pier temperature also explained some of the residual variance in *S. bierii* δ^{15}N. ALPI, Sea Level, and NOI did not explain significant δ^{15}N variability in any of the species. Plots of the anomalous stable isotope content of each of the four species in reference to predictions from the multiple regression equation may be seen in Fig. 6. Although trends are apparent, only a portion of the isotopic variability in each species is accounted for by the observed regressions.

We also analyzed long-term variations in body size of the four zooplankton species, from samples from which stable isotopes were measured. There was no evidence of a simple linear trend with time in mean body length of any of the four species (Fig. 7, $P > 0.20$, linear regression analysis). Interannual differences in average body length of the four species were somewhat correlated $P = 0.05$, Kendall's coefficient of concordance = 0.55). The coefficient of variation (c.v.) of springtime mean prosome lengths of copepods (4.5% and 2.5% for *C. pacificus* and *E. californicus*, respectively) was smaller than the c.v. of total lengths of chaetognaths (6.7% and 9.6% for *S. bierii* and *S. euneritica*). Copepods show determinate growth, and thus body length remains essentially fixed after the terminal molt to the adult stage. Chaetognaths, however, show indeterminate growth, and thus body size variations reflect different age compositions from sample to sample, as well as variations in environmental conditions that influence the body size of individuals. Variations in body length were uncorrelated with variations in δ^{15}N for 3 of the 4 species ($P > 0.10$), but a weak negative relationship was detected for *E. californicus* ($r = -0.376, P = 0.05$).

When body lengths were considered in three periods corresponding to hypothesized regimes, as above, there were no differences in average body lengths among the 3 periods ($P > 0.05$ for each of the four species, Kruskal–Wallis ANOVA). Although the average body lengths of all 4 species tended to be lower during El Niño years, an El Niño-related decrease in body length was significant only for *S. bierii* ($P < 0.05$). Attempts to use multiple regression analysis to explain
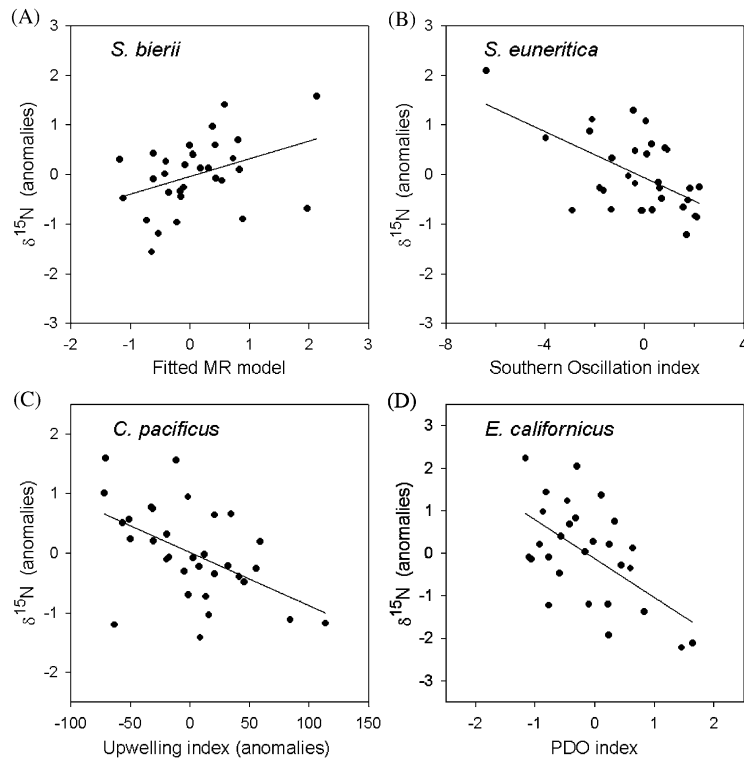
Fig. 6. Anomalies of δ^{15}N of each of four species (points) plotted against the predictor variables resulting from stepwise multiple regression analysis (see Table 2). In the case of *Sagitta bierii*, where two variables entered the equation, observations are plotted against the fitted regression model.

anomalies in body length as a function of ALPI, SOI, NOI, PDO, sea level, upwelling index anomalies, and SIO pier temperature anomalies explained little or none of the variation in body sizes. No variables entered the regression equations for 3 species. A weak relationship was detected between *S. bierii* length anomalies and S.F. sea-level anomalies, although this relationship explained only 20% of the variance in chaetognath total length.

4. Discussion

We observed no significant long-term trend in the δ^{15}N or body size of any of the four species of zooplankton on a time scale of five decades (Figs. 3a,b and 7). In the only other δ^{15}N records for this time frame and hemisphere of which we are aware, significant, long-term trends in δ^{15}N also were not found in sea lion and seal bone collagen sampled from the Bering Sea and Gulf of Alaska (Hirons et al., 2001). In contrast, starting in the late 1960s Schell (2001) found a progressive, several per mil decline in average bowhead whale baleen δ^{15}N in the Bering and Chukchi Seas.

In our study ^{15}N enrichment occurred transiently during El Niños, but relatively quickly reverted to pre-El Niño values (Fig. 5). More subtle, lower-frequency variations occurred in the chaetognaths, but the isotopic values measured in 2001 were quite similar to those measured in 1951 (Fig. 3a and b). Thus, despite perturbations on different time scales, there is considerable consistency of isotopic values, and by implication, relative consistency of N dynamics and food web structure over an extended period of time in the California Current System. This result agrees with
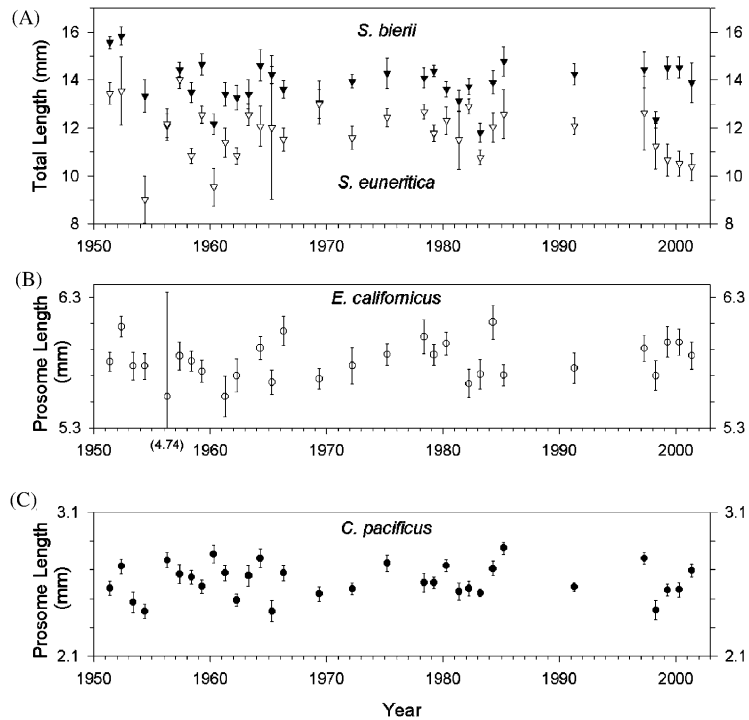
Fig. 7. Interannual variations in springtime body lengths for (A) *Sagitta bierii* and *S. euneritica* (total length), (B) *Eucalanus californicus* adult females (prosome length), and (C) *Calanus pacificus* adult females (prosome length). Mean±95%.

the findings of Rebstock (2001), who analyzed long-term variability in assemblages of calanoid copepods in a more southerly region of the California Current and observed that the dominance structure of the copepod fauna remained relatively stable between 1951 and 1999.

The pronounced, El Niño-related enrichment in ^{15}N in three of the four zooplankton species (Fig. 5) could have a number of causes. If elevated δ^{15}N during El Niños is interpreted as an elevation in relative nitrate utilization (increased nitrate demand relative to supply; Wu et al., 1997; Rau et al., 1998), this would be consistent with an El Niño-related reduction in nitrate availability in this region (Chavez, 1996). This reduced nitrate availability would need to be proportionally greater than changes in nitrate demand by primary production. Indeed, during one El Niño period, Chavez (1996) observed a decline in Monterey Bay nitrate concentration that was many times greater than the concurrent decline in primary production,

implying significantly greater nitrate utilization (Kudela and Chavez, 2000). The elevation of δ^{15}N of *C. pacificus* during El Niños appears to be related to the decreased upwelling intensity during such events (cf. Fig. 6). That *Eucalanus californicus* δ^{15}N is relatively low and does not display a consistent trend in δ^{15}N during El Niño periods (Fig. 5d) may reflect the different vertical distribution and life history of this copepod species. While *C. pacificus* females are typically in near-surface waters at night, *E. californicus* tends to be more abundant just below the surface mixed layer (Ohman et al., 1998). Also, adult female *E. californicus* have been found to enter a resting state at some times of year (Ohman et al., 1998). Entering into a resting stage as an adult would tend to decouple *E. californicus* δ^{15}N from the short-term effects of nutrient demand/supply dynamics occurring locally, and thus their tissue isotopic content may reflect feeding processes conducted elsewhere or at different times.

An alternate hypothesis for zooplankton $\delta^{15}N$ increases during El Niños would be that the $^{15}N/^{14}N$ of the nitrate (or relevant inorganic N substrate) in this region is influenced by variations in the contribution of N from various extra-regional water mass sources, each source having a characteristic $\delta^{15}N$. This could be relevant in waters off central California where the poleward-moving California Undercurrent brings subtropical, partially denitrified, and hence ^{15}N-enriched nitrate northward into this region (Liu and Kaplan, 1989; Castro et al., 2001). An oscillation in the intensity of this flow and its vertical advection to the surface, noted especially during El Niño periods (Chelton, 1981; Chavez, 1996), therefore could modulate surface water nitrate $\delta^{15}N$ and hence temporal $\delta^{15}N$ variability within plankton. Under non-El Niño conditions, Castro et al. (2001) found that the bulk of this partially denitrified water did not penetrate vertically above a depth of 400 m, and therefore did not affect near-coastal primary production in this region at such times. Higher zooplankton $\delta^{15}N$ during increased intrusion of subtropical waters, characteristic of El Niño periods here, therefore could reflect a change in water mass rather than a change in local N utilization and dynamics. However, barring off-setting isotope effects unique to *E. californicus*' life history or feeding (see above), the fact that this copepod species does not display a change in $\delta^{15}N$ during El Niños that is coherent with the other three taxa would seem inconsistent with this scenario.

In further discriminating between the effect on zooplankton $\delta^{15}N$ of variations in nutrient utilization versus advection of ^{15}N-enriched subtropical water, it would be useful to have concurrent measures of nitrate concentration and primary production rates. Higher zooplankton $\delta^{15}N$ during periods of high NO_3^- demand relative to supply would be indicative of nitrate utilization isotope effects caused by the biological drawdown of nitrate. Unfortunately, such measurements were not made at the stations relevant to this study until the mid-1980s, leaving a very small sample size to test. However, the concentration of total net plankton was determined for each of the sampling dates of this study. If this measure of biomass can be assumed to be a proxy for primary production and hence nitrate utilization, then higher zoo-plankton $\delta^{15}N$ should correlate with higher plankton biomass if nitrate utilization is a factor. In contrast, the $\delta^{15}N$ of each of the species is negatively correlated with total zooplankton bio-mass, and with the exception of *E. californicus*, these correlations are statistically significant ($P < 0.05$). While admittedly an indirect test, this result seems counter to that expected if nitrate utilization were relevant to zooplankton $\delta^{15}N$ variations in this region at the temporal scale of this study.

4.1. Relationships between zooplankton $\delta^{15}N$ and physical indices

If temporal variations in zooplankton $\delta^{15}N$ reflect changes in some aspect of local or regional nitrogen sources or dynamics, to what extent are these $\delta^{15}N$ records then correlated with various measures of climate and physical forcing over a common time period? What do such correlations say about the mechanisms by which $\delta^{15}N$ and by inference, N sources and cycling, are affected in this region? *Calanus pacificus* was the only species for which variations in $\delta^{15}N$ were related to the index of coastal upwelling (Fig. 6c). A negative $\delta^{15}N$ relationship with local upwelling intensity would be expected if increased vertical advection resulted in increased inorganic N availability relative to the N demand of the microplankton food base of this copepod (but note preceding observations and discussion). Upwelling intensity tends to decrease during strong El Niños, but the local upwelling-favorable winds can vary for other reasons as well. Of the two species of particle-grazing copepods, the life history of *C. pacificus* has been interpreted as showing rather strong coupling to upwelling/downwelling cycles in the CCS (e.g., Fleminger, 1985, Smith et al., 1986). In contrast, while *E. californicus* is known to increase egg production in cool, coastal filaments further north (Smith and Lane, 1991), Ohman et al. (1998) inferred that adult females of this species may enter dormancy during periods of food deprivation and thus be temporarily less dependent upon ambient primary production.

Variations in the PDO, an index of basin-wide warming north of the tropics, may influence *E. californicus* δ^{15}N (Fig. 6d) because such variability implies sustained changes in stratification and thus in nutrient supply over a longer temporal scale than coastal upwelling events.

In contrast to the copepods, δ^{15}N of the two chaetognath species is significantly related to the Southern Oscillation Index (Fig. 6a and b), an index of the strength of equatorial El Niños. The SOI reflects interannual-scale variations in the California Current, rather than the interdecadal variability reflected in the PDO. It is somewhat surprising that the PDO was not found to be a significant, independent variable in the multiple regression equation, as there was a significant decline in *S. bierii* δ^{15}N after 1998 (Fig. 3a), coincident with a switch to negative values of the PDO (Lavaniegos and Ohman, 2003), and reciprocally, the suggestion of a slight increase in δ^{15}N during the period from 1979 to 1998 when the PDO was in a positive phase. Positive phases of the PDO have been likened to a persistent El Niño-like conditions (Mantua et al., 1997). However, the lack of a relationship may reflect the relatively small magnitude of the δ^{15}N signal, the limited number of years sampled and relatively high variability, or the presence of a nonlinear relationship. The negative relation with the SOI index indicates an elevation in δ^{15}N during strong El Niños and a decrease during cooler water La Niñas. As described above the possible mechanisms for El Niño δ^{15}N elevation in these species include increased local nitrate demand:supply and/ or the horizontal advection of ^{15}N-enriched waters originating from the south. Although the chaetognaths and *C. pacificus* share a response to El Niño perturbations (Fig. 5a–c), the longer-lived, carnivorous chaetognaths would be less directly coupled to the influence of upwelling variations than the shorter-lived, particle-grazing copepod.

4.2. Interspecific $\delta^{15}N$

Averaged over the 51-year period there is a significant difference in the mean δ^{15}N among species (Fig. 2), with the two suspension feeders, *E. californicus* and *C. pacificus*, consistently having lower average δ^{15}N (9.7‰ and 9.9‰ respectively) than the two carnivores, *S. euneritica* (12.0‰) and *S. bierii* (13.8‰). Because ^{15}N is biomagnified by marine consumers (Minagawa and Wada, 1984; Checkley and Entzeroth, 1985), the δ^{15}N elevation in *Sagitta* relative to the copepods is consistent with the chaetognaths' known higher trophic position (Feigenbaum, 1991). A small trophic difference between *S. euneritica* and *S. bierii* is also suggested by the higher δ^{15}N of the latter species. *S. bierii* is consistently the larger species. Since prey size is typically related to chaetognath body size (Pearre, 1980), *S. bierii* is likely to be capable of ingesting larger-sized prey, which could include more carnivorous zooplankton, contributing to ^{15}N enrichment.

As previously noted, δ^{15}N variability among species within and across the 51-year period is not perfectly coherent (Figs. 3a,b and 5), and there is a slight divergence in longer-term δ^{15}N trends between chaetognath and copepods species (Fig. 3a and b), which could reflect small changes in relative trophic position of these species within these temporal ranges. For example, the δ^{15}N elevation seen in *C. pacificus*, *S. bierii*, and *S. euneritica* relative to *E. californicus* during El Niño periods (Fig. 5) could reflect increases in relative trophic position of the former species during such times. Indeed, greater prey diversity, lower dietary overlap, and greater dependence of prey of southern origin were observed in nekton off the NW US coast during the 1983 El Niño event (Brodeur and Pearcy, 1992).

However, using δ^{15}N differences among species purely as a measure of relative, interspecies trophic differences presumes that the base of the web is isotopically uniform across the spatial and temporal feeding scales of all taxa in question. Proving such conditions pertain is problematic because the corresponding δ^{15}N variations of their diets were uncharacterized. Also, trophic-level δ^{15}N effects could be obscured by: (i) potential species differences in lifespan of weeks to possibly even months, (ii) individual and taxonomic differences in horizontal movements potentially of many kilometers and vertical movements of tens of meters, and (iii) the heterogeneity in bulk plankton δ^{15}N observed at such spatial and temporal scales in

this region (this study; Mullin et al., 1984; Rau et al, 1998). As examples, it was previously noted that the resident depth of *E. californicus* can be somewhat deeper than that of *C. pacificus*. While *S. euneritica* is usually restricted to near-surface waters in the upper 100 m, *S. bierii* extends to 200–300 m depth, and deeper in more southerly waters (Alvariño, 1992). Because vertical gradients in nitrate concentration, δ^{15}N, and utilization can exist (Altabet et al., 1999) and vertical differences in zooplankton δ^{15}N have been previously observed (Rau et al., 1989), it is possible that at least some of the interspecific δ^{15}N differences and variability observed are related to depth of feeding. Physiological factors may also be at play. In particular, *S. bierii* is more muscular and has higher rates of metabolic enzyme activity per unit body mass than *S. euneritica* (Thuesen and Childress, 1993), which could enhance ^{15}N enrichment in the former species. All of the preceding circumstances demand caution in attributing species differences in δ^{15}N as evidence of trophic differences.

In summary, three of four species of dominant zooplankton in the central sector of the California showed significant enrichment in ^{15}N during major El Niños, and *S. bierii* showed suggestions of small changes in ^{15}N/^{14}N on still longer-time scales. However, there were no statistically significant secular trends in either nitrogen isotopic content or in body size for any of the four species over the 51-year time span of the study. The results suggest a long-term resilience in nitrogen sources and dynamics and in food web structure, despite the significant climatic perturbations affecting the California Current System. The differential responses by the four species to these perturbations probably reflect interspecific differences in vertical distribution, longevity, and life history. It appears that the primary mechanisms influencing variations in stable isotopes of zooplankton in this region are variability in the relative utilization of nitrate and/or local variation in the horizontal advection of ^{15}N-enriched sub-tropical waters. However, it is noteworthy that the physical forcing responsible for these ^{15}N/^{14}N changes differs among species and in the case of the chaetognaths studied, extra-regional forcing dominates.

References

Altabet, M.A., Pilskaln, C., Thunell, R., Pride, C., Sigman, D., Chavez, F., Francois, R., 1999. The nitrogen isotope biogeochemistry of sinking particles from the margin of the Eastern North Pacific. Deep-Sea Research I 46, 655–679.

Alvariño, A., 1965. Distributional atlas of Chaetognatha in the California Current region. California Cooperative Oceanic Fisheries Investigations Atlas 3, 1–291.

Alvariño, A., 1992. Distribucion batimetrica, diurna y nocturna, de diez y siete especies de quetognatos, durante las cuatro estaciones del año 1969, en aguas de California y Baja California. Investigaciones Marinas CICIMAR 7 (No. Esp. 1), pp. 1–169.

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology-Progress Series 189, 117–123.

Bieri, R., 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnology and Oceanography 4, 1–28.

Bieri, R., 1991. Systematics of the Chaetognatha. In: Bone, Q., Kapp, H., Pierrot-Bults, A.C. (Eds.), The Biology of Chaetognaths. Oxford University Press, Oxford, pp. 122–136.

Bograd, S.J., Lynn, R.J., 2001. Physical–biological coupling in the California current during the 1997–99 El Niño–La Niña cycle. Geophysical Research Letters 28, 275–278.

Brodeur, R.D., Pearcy, W.G., 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Marine Ecology-Progress Series 84, 101–119.

Brodeur, R.D., Frost, B.W., Hare, S.R., Francis, R.C., 1996. Interannual variations in zooplankton biomass in the gulf of Alaska, and covariation with California Current zooplankton biomass. California Cooperative Oceanic Fisheries Investigations Reports 37, 80–99.

Bruland, K.W., Rue, E.L., Smith, G.J., 2001. Iron and macronutrients in California coastal upwelling regimes: implications for diatom blooms. Limnology and Oceanography 46, 1661–1674.

Castro, C.G., Chavez, F.P., Collins, C.A., 2001. Role of the California undercurrent in the export of denitrified waters from the eastern tropical North Pacific. Global Biogeochemical Cycles 15, 819–830.

Chavez, F.P., 1996. Forcing and biological impact of onset of the 1992 El Niño in central California. Geophysical Research Letters 23, 265–268.

Checkley, D.M., Entzeroth, L.C., 1985. Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. Journal of Plankton Research 7, 553–568.

Checkley, D.M., Miller, C.A., 1989. Nitrogen isotope fractionation by oceanic zooplankton. Deep-Sea Research 36, 1449–1456.

Chelton, D.B., 1981. Interannual variability of the California Current—physical factors. California Cooperative Oceanic Fisheries Investigation Reports 22, 34–48.

Chelton, D.B., Bernal, P.A., McGowan, J.A., 1982. Large-scale interannual physical and biological interaction in the California Current. Journal of Marine Research 40, 1095–1125.

Conversi, A., Hameed, S., 1998. Common signals between physical and atmospheric variables and zooplankton biomass in the Subarctic Pacific. Journal of Marine Science 55, 739–747.

Dutilleul, P., 1993. Modifying the t test for assessing the correlation between two spatial processes. Biometrics 49, 305–312.

Ebbesmeyer, C.C., Cayan, D.R., McLain, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1991. 1976 step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984: Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop, April 1990. California Department of Water Resources, pp. 115–126.

Feigenbaum, D., 1991. Food and feeding behavior. In: Bone, Q., Kapp, H., Pierrot-Bults, A.C. (Eds.), The Biology of Chaetognaths. Oxford University Press, Oxford, pp. 45–54.

Fiedler, P.C., 1984. Satellite-observations of the 1982–1983 El-Niño along the United States Pacific coast. Science 224, 1251–1254.

Fleminger, A., 1967. Distributional atlas of calanoid copepods in the California Current region, Part II. California Cooperative Oceanic Fisheries Investigations Atlas 7, 1–213.

Fleminger, A., 1985. Dimorphism and possible sex change in copepods of the family Calanidae. Marine Biology 88, 273–294.

Fleminger, A., Hulsemann, K., 1973. Relationship of Indian Ocean epiplanktonic calanoids to the world oceans. In: Zeitzschel, B. (Ed.), Ecological Studies. Analysis and Synthesis, Vol. 3. Springer, New York, pp. 339–347.

Gargett, A.E., 1997. The optimal stability window: a mechanism underlying decadal fluctuations in North Pacific salmon stocks? Fisheries Oceanography 6, 109–117.

Goering, J., Alexander, V., Haubenstock, N., 1990. Seasonal variability of stable carbon and nitrogen isotopic ratios of organisms in a North Pacific bay. Estuarine Coastal and Shelf Science 30, 239–260.

Goes, J.I., Gomes, H.D., Limsakul, A., Balch, W.M., Saino, T., 2001. El Niño related interannual variations in biological production in the North Pacific as evidenced by satellite and ship data. Progress in Oceanography 49, 211–225.

Greene, K., 2002. Coastal cool-down. Science 295, 1823–1823.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence of North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47, 103–145.

Hirons, A.C., Schell, D.M., Finney, B.P., 2001. Temporal records of delta C-13 and delta N-15 in North Pacific pinnipeds: inferences regarding environmental change and diet. Oecologia 129, 591–601.

Hollowed, A.B., Hare, S.R., Wooster, W.S., 2001. Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. Progress in Oceanography 49, 257–282.

Kahru, M., Mitchell, B.G., 2000. Influence of the 1997–98 El Niño on the surface chlorophyll in the California Current. Geophysical Research Letters 27, 2937–2940.

Karl, D.M., 1999. A sea of change: biogeochemical variability in the north pacific subtropical gyre. Ecosystems 2, 181–214.

Keller, K., Slater, R.D., Bender, M., Key, R.M., 2002. Possible biological or physical explanations for decadal scale trends in North Pacific nutrient concentrations and oxygen utilization. Deep-Sea Research II 49, 345–362.

Kudela, R.M., Chavez, F.P., 2000. Modeling the impact of the 1992 El Niño on new production in Monterey Bay, California. Deep-Sea Research II 47, 1055–1076.

Kudela, R.M., Dugdale, R.C., 2000. Nutrient regulation of phytoplankton productivity in Monterey Bay, California. Deep-Sea Research II 47, 1023–1053.

Lavaniegos, B.E., Ohman, M.D., 1999. Hyperiid amphipods as indicators of climate change in the California Current. In: Schram, F.R., von Vaupel Klein, J.C. (Eds.), Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998, Vol. I. Brill, Leiden, pp. 489–509.

Lavaniegos, B.E., Ohman, M.D., 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Research II, this issue (doi:10.1016/S0967-0645(03)00132-2).

Laws, E.A., Falkowski, P.G., Smith, W.O., Ducklow, H., McCarthy, J.J., 2000. Temperature effects on export production in the open ocean. Global Biogeochemical Cycles 14, 1231–1246.

Limsakul, A., Saino, T., Midorikawa, T., Goes, J.I., 2001. Temporal variations in lower trophic level biological environments in the northwestern North Pacific Subtropical

Gyre from 1950 to 1997. Progress in Oceanography 49, 129–149.

Liu, K.-K., Kaplan, I.R., 1989. The eastern tropical Pacific as a source of ^{15}N-enriched nitrate in seawater off Southern California. Limnology and Oceanography 34, 820–830.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78, 1069–1079.

McGowan, J.A., Cayan, D.R., Dorman, L.M., 1998. Climate–ocean variability and ecosystem response in the Northeast Pacific. Science 281, 210–217.

Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta 48, 1135–1140.

Mullin, M.M., Rau, G.H., Eppley, R.W., 1984. Stable nitrogen isotopes in zooplankton: some geographic and temporal variations in the North Pacific. Limnology and Oceanography 29, 1267–1273.

Ohman, M.D., Smith, P.E., 1995. A comparison of zooplankton sampling methods in the CalCOFI time series. California Cooperative Oceanic Fisheries Investigations Reports 36, 153–158.

Ohman, M.D., Drits, A.V., Clarke, M.E., Plourde, S., 1998. Differential dormancy of co-occurring copepods. Deep-Sea Research II 45, 1709–1740.

Pearre Jr., S., 1980. Feeding by Chaetognatha: the relation of prey size to predator size in several species. Marine Ecology Progress Series 3, 125–134.

Pierrot-Bults, A.C., Nair, V.R., 1991. Distribution patterns in Chaetognatha. In: Bone, Q., Kapp, H., Pierrot-Bults, A.C. (Eds.), The Biology of Chaetognaths. Oxford University Press, Oxford, pp. 86–116.

Polovina, J.J., Mitchum, G.T., Evans, G.T., 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960–88. Deep-Sea Research I 42, 1701–1716.

Pride, C., Thunell, R., Sigman, D., Keigwin, L., Altabet, M., Tappa, E., 1999. Nitrogen isotopic variations in the Gulf of California since the last deglaciation: response to global climate change. Paleoceanography 14, 397–409.

Rau, G.H., Heyraud, M., Cherry, R., 1989. ^{15}N/^{14}N and ^{13}C/^{12}C in mesopelagic shrimp from the N.E. Atlantic: evidence for differences in diet. Deep-Sea Research 36, 1103–1110.

Rau, G.H., Teyssie, J.-L., Rassoulzadegan, R., Fowler, S.W., 1990. ^{13}C/^{12}C and ^{15}N/^{14}N variations among size-fractionated marine particles: implications for their origin and trophic relationships. Marine Ecology Progress Series 59, 33–38.

Rau, G.H., Low, C., Pennington, J.T., Buck, K.R., Chavez, F.P., 1998. Suspended particulate δ^{15}N versus nitrate utilization: observations in Monterey Bay, California. Deep-Sea Research II 45, 1603–1616.

Rebstock, G.A., 2001. Long-term stability of species composition in calanoid copepods off southern California. Marine Ecology Progress Series 215, 213–224.

Rebstock, G.A., 2002. Climatic regime shifts and decadal-scale variability in calanoid copepod populations off southern California. Global Change Biology 8, 71–89.

Rice, J., 2001. Implications of variability on many time scales for scientific advice on sustainable management of living marine resources. Progress in Oceanography 49, 189–209.

Roemmich, D., McGowan, J., 1995a. Climatic warming and the decline of zooplankton in the California Current. Science 267, 1324–1326.

Roemmich, D., McGowan, J., 1995b. Sampling zooplankton: correction. Science 268, 352–353.

Saino, T., Hattori, A., 1987. Geographical variation of the water column distribution of suspended particulate organic nitrogen and its N-15 natural abundance in the Pacific and its marginal seas. Deep-Sea Research 34, 807–827.

Sarakinos, H.C., Johnson, M.L., Vander Zanden, M.J., 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. Canadian Journal of Zoology 80, 381–387.

Schell, D.M., 2001. Carbon isotope ratio variations in Bering Sea biota: the role of anthropogenic carbon dioxide. Limnology and Oceanography 46, 999–1000.

Schwing, F., Moore, C., 2000. A year without summer for California, or a harbinger of a climate shift? EOS, Transactions of the American Geophysical Union 81, 301, 304–305.

Schwing, F.B., Murphree, T., Green, P.M., 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Progress in Oceanography 53, 115–139.

Smith, P.E., Eppley, R.W., 1982. Primary production and the anchovy population in the Southern California Bight: comparison of time series. Limnology and Oceanography 27, 1–17.

Smith, S.L., Jones, B.H., Atkinson, L.P., Brink, K.H., 1986. Zooplankton in the upwelling fronts off Pt. Conception, California, pp. 195–213. In: Nihoul, J.E. (Ed), Marine interfaces ecohydrodynamics. Elsevier Oceanography Series 42, Amsterdam, The Netherlands.

Smith, S.L., Lane, P.V.Z., 1991. The jet off Point Arena, California: its role in aspects of secondary production in the copepod *Eucalanus californicus* Johnson. Journal of Geophysical Research-Oceans 96, 14849–14858.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd Edition. W.H. Freeman, New York, p. 1–887.

Thuesen, E.V., Childress, J.J., 1993. Enzymatic activities and metabolic rates of pelagic chaetognaths: lack of depth-related declines. Limnology and Oceanography 38, 935–948.

Venrick, E.L., Chereskin, T.K., Hayward, T.L., Mantyla, A.W., Niiler, P.P., Ohman, M.D., Plummer, K.M., 1991. Physical, chemical and biological data. Cruise Fronts 88, 28 August–23 September 1988. University of California, San

Diego. Scripps Institution of Oceanography, SIO Reference 91-7, p. 1–99.

White, K.K., Dugdale, R.C., 1997. Silicate and nitrate uptake in the Monterey Bay upwelling system. Continental Shelf Research 17, 455–472.

Wu, J.P., Calvert, S.E., Wong, C.S., 1997. Nitrogen isotope variations in the subarctic northeast Pacific: relationships to nitrate utilization and trophic structure. Deep-Sea Research I 44, 287–314.