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PII: S0967-0637(11)00200-7
DOI: doi:10.1016/j.dsr.2011.11.003
Reference: DSRI 2027

To appear in: *Deep–Sea Research I*

Received date: 20 December 2010
Revised date: 1 November 2011
Accepted date: 12 November 2011

Cite this article as: Mark D. Ohman, Greg H. Rau and Pincelli M. Hull, Multi-decadal variations in stable N isotopes of California Current zooplankton, *Deep–Sea Research I*, doi:10.1016/j.dsr.2011.11.003

Multi-decadal variations in stable N isotopes of California Current zooplankton

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Keywords: stable N isotopes, El Niño, California Current System, copepods, chaetognaths, climate change

Abstract

We analyzed variations in naturally occurring $\delta^{15}N$ in four species of zooplankton as an index of climate influences on pelagic food web structure in a major eastern boundary current ecosystem. Our analyses focused on two species of particle-grazing copepods (*Calanus pacificus* and *Eucalanus californicus*) and two species of carnivorous chaetognaths (*Sagitta bierii* and *S. euneritica*), drawing on the CalCOFI zooplankton time series from both the southern and central sectors of the California Current System. We detected a significant difference between regions in average stable N isotope content of the two species of copepods, with $\delta^{15}N$ elevated by 0.5-1.1 per mil in the southern region, but no regional differences in the isotopic content of the chaetognaths. We address climate influences over a 54-year time period, on three different time scales: interannual (dominated by ENSO), decadal, and multi-decadal. Three of four species showed evidence of an ENSO-related isotopic shift toward increased ^{15}N during El Niño conditions. In addition, in Southern California waters, *C. pacificus* and *S. euneritica* showed elevated $\delta^{15}N$ in the warm phase of the NE Pacific between 1978-1998 relative to the preceding and following time periods. When considered over the entire 5½ decades treated here, for most species there was remarkable long-term stability in stable isotope content in both southern and central California waters, despite interannual and decadal perturbations. Only *E. californicus* in the southern sector showed a significant downward secular trend in $\delta^{15}N$. Variability of $\delta^{15}N$ in 3 species covaried with the average nitrate concentration in the mixed layer, suggesting altered nitrate utilization at the base of the food web as a primary mechanism underlying interannual changes in zooplankton isotopic content.

1. Introduction

Discerning the effects of climate change on planktonic food webs is hampered by the relatively short temporal record that exists in most ocean regions. Important studies of zooplankton assemblages extend back several decades in a limited number of cases (Mackas and Beaugrand, 2010). Among these, CalCOFI (the *California Cooperative Oceanic Fisheries Investigations*) is an unusual resource, as it has conducted nearly continuous surveys in the California Current System (CCS) since 1949, combining extensive sampling of the mesozooplankton and ichthyoplankton together with well calibrated measurements of the physical and chemical environment (Bograd et al., 2003; Ohman and Venrick, 2003). From these, and other studies, it has been possible to document the effects of climate forcing on the epipelagic food web in the Northeast Pacific on at least three time scales during the 20^{th}–21^{st} centuries: long-term secular trends, decadal variations, and interannual perturbations. Long-term declines have been detected in the biomass of pelagic tunicates (Lavaniegos and Ohman, 2007), in parallel with increased surface temperatures (Roemmich, 1992) and increased stratification of the water column (Kim and Miller, 2007). Progressive, long-term decreases in optical transparency together with increases in chlorophyll-*a* have also been reported (Aksnes and Ohman, 2009). In addition to these and other secular trends, multi-decadal scale plankton variations in the CCS have been associated with changes in the Pacific Decadal Oscillation (PDO, Brinton and Townsend, 2003) and the North Pacific Gyre Oscillation (NPGO, DiLorenzo et al., 2008). On an interannual time scale, changes in the NE Pacific are dominated by the El Niño-Southern Oscillation (ENSO, e.g., Kahru and Mitchell, 2002; Lavaniegos and Ohman, 2007). Teasing apart the interacting influences of secular trends, decadal variations, and interannual perturbations on marine ecosystems becomes possible only with a sustained, interdisciplinary research program.

Analyses of 2-3 decades of variation in zooplankton assemblages from British Columbia to Baja California suggest that there can be considerable spatial coherence in zooplankton variability across this broad latitudinal scale (Batchelder et al., 2002; Mackas, 2006). Nevertheless, the California Current System (CCS) spans as much as 20-25° of latitude and the dominant climate influences on pelagic food webs can differ in different sectors of the CCS (e.g., Mackas, 2006). In some years, there are pronounced regional differences in timing of upwelling and ecosystem responses (e.g., Sydeman et al., 2006; Mackas et al., 2006; Bograd et al., 2009). On a smaller scale Lavaniegos and Ohman (2007) analyzed the extent of coherence of variations of zooplankton carbon biomass between Central California and Southern California waters and observed that approximately half of the variance was held in common between the two regions. On the same geographic scale Roesler and Chelton (1987) suggested that the total zooplankton biomass (as displacement volume) in Central California region is influenced more by advection of biomass from the north and the Southern California region more by local responses. Model hindcasts illustrate that source waters that upwell along the coastal boundary may come from somewhat different sources during the positive and negative phase of the PDO (Chhak and Di Lorenzo, 2007) and a model forecast suggests that nitrate concentrations may increase in the future (Rykaczewski and Dunne, 2010). In the northern part of the CCS, upwelling variations are more closely associated with the PDO, while in the southern region, the NPGO has greater influence (Di Lorenzo et al., 2008).

To evaluate the effects of climate forcing on zooplankton assemblages and regional-scale variations in such responses, it would be desirable to have measures of instantaneous growth and mortality rates of zooplankton extending back several decades. Such data do not exist and at present it is not feasible to reconstruct them from archived samples. As an alternative, here we use zooplankton stable N isotope content as an index of zooplankton responses to different time scales of climate forcing. Unlike measures of population biomass or stage structure, which integrate across the life history of the target population, stable isotopes are an indication of the cumulative influences of nutrient sources, metabolic fractionation, and diet on the tissue composition of individuals up to the time of their capture. Our approach entails analysis of whole animal N isotopes, focusing on two species of particle-grazing copepods close to the base of the food web (*Calanus pacificus* and *Eucalanus californicus*) and two species of chaetognaths (*Sagitta bierii* and *S. euneritica*), the latter both carnivores.

Previous results based entirely on sampling in the central California sector of the California Current System showed that three of these four species of zooplankton had enriched ^{15}N during springtime cruises of El Niño years, but reverted to previous values thereafter (Rau et al., 2003). In the same study, two species showed enrichment during the positive phase of the PDO. Rau et al. (2003) proposed three mechanisms to account for such isotopic enrichment: increased inorganic nitrate utilization by phytoplankton relative to supply via Rayleigh isotope fractionation; possible food chain elongation and increased carnivory during El Niño; and increased importance of ^{15}N-rich nitrate originating from denitrified waters advected northward from the Eastern Tropical Pacific. Those three mechanisms could not be differentiated in that study. We address them here with a different and greatly expanded data set, arising from new measurements of zooplankton stable isotopes from the Southern California region, where the temporal sampling is more complete than in the Central California region. In this context, we also relate measured zooplankton $^{15}N/^{14}N$ to nitrate concentration in the surrounding waters.

2. Material and Methods

Zooplankton were collected with 0.5 mm mesh double oblique tows with a 1-m diameter ring net from 1951-1977 and afterwards with a 0.71-m diameter bongo net. The sampling depth extended from 140-0 m until 1969, and thereafter from 210-0 m, at stations on the sampling grid of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) as detailed in Ohman and Smith (1995). Our stable isotope sampling in the southern California sector of the CCS used individuals collected at a group of stations along 5 CalCOFI transects from lines 80 through 93, extending from shore to station 70, inclusive (see station map in Lavaniegos and Ohman, 2007). Samples were preserved in formaldehyde-seawater buffered with sodium tetraborate and archived in the Pelagic Invertebrates Collection of the Scripps Institution of Oceanography. Only springtime (March-May) nighttime samples were analyzed, following sample pooling. In brief, the pooling entailed selecting all nighttime CalCOFI zooplankton samples in the geographic region of interest, removing an aliquot from each sample corresponding to 50 m^3 of water filtered in the ocean, then combining these aliquots into a single pooled sample for each cruise (procedure detailed in Rebstock (2001) and Lavaniegos and Ohman (2007)). From these pooled samples, approximately 30 individuals of each of two species of copepods (*Calanus pacificus* and *Eucalanus californicus*, adult females only for both taxa) and two species of chaetognaths (*Sagitta bierii* and *S. euneritica*, all size classes captured), were removed, identified, measured, rinsed in a small volume of Milli-Q water, and dried at 55º C for 24 h in clean tin boats in lots of 5-10 individuals per boat. These taxa were selected because of their numerical abundance and high frequency of occurrence across the time series, and the contrast between copepods and chaetognaths in diet and trophic level. Spring cruises were selected because this is the season that has been most consistently sampled and because it is the period of peak upwelling (Aksnes et al., 2007). Restricting our analyses to springtime reduced influences of seasonal variations. Copepod prosome lengths and chaetognath total lengths (N ~30 per sample) were measured with an ocular micrometer in a dissecting microscope. Chaetognaths for stable isotope analysis were identified to species by A. Pierrot-Bults (University of Amsterdam). In situ abundances of adult female *C. pacificus*, *E. californicus*, and total chaetognaths (chaetognath species were not differentiated in those enumerations) are expressed as individuals per m^2,by multiplying the density per m^3 by the maximum depth of each tow, as explained in Lavaniegos and Ohman (2007).

For analysis of spatial variability of zooplankton stable N isotopes, zooplankton from multiple stations sampled in Southern California waters were analyzed in a manner analogous to Rau et al. (2003). For this purpose, the 4 species of zooplankton were sorted as above from stations 80.55, 83.55, 87.50, 90.53, and 93.70 from April 1951 (cruise 5104) and from stations 80.70, 83.60, 87.60, 90.60, and 93.28 from April 1978 (cruise 7804; see map in Lavaniegos and Ohman, 2007). Triplicate analyses were performed for each species from each station whenever the number of specimens available permitted.

Zooplankton stable isotopes were analyzed on a Thermo Delta plus XP isotope ratio mass spectrometer in the Analytical Facility of the Scripps Institution of Oceanography, calibrated against an acetanilide standard. Triplicate samples were analyzed for each species and sampling date, wherever possible. $^{15}N/^{14}N$ is reported in the standard $\delta^{15}N$ notation, with $\delta^{15}N$ = $[R_{sample}/R_{standard} -1] \times 1000$ (per mil), where $R={}^{15}N/^{14}N$ and "standard" = air N_2. Analytical precision of the measurements was approximately 0.1 per mil. Isotope values were corrected for N blanks from clean tin boats. Our previous experiments demonstrated that zooplankton N isotopes show a negligible change upon long-term (11 year) preservation in buffered formaldehyde when fixation and preservation methods are standardized over time (Rau et al., 2003). These results confirm earlier results of Mullin et al. (1984) and the subsequent analyses of Hannides et al. (2009), both based on shorter duration experiments. C isotopes from formaldehyde-preserved specimens are variable and unreliable (Rau et al., 2003).

For comparison of our new results from Southern California from 1951-2004 with results from Central California, we extended previously published analyses for the spring cruises from Central California (Rau et al. 2003, from 1951-2001) to the years 2002-2004. We employed identical methods as before, using nighttime samples from CalCOFI stations 50, 55, or 65 on line 67 in the outer Monterey Bay region. In total, zooplankton stable N isotopes were analyzed from 46 spring cruises in Southern California and 34 spring cruises in the Central California region; the latter number is lower because Central California was sampled infrequently during the mid-1980's-1990's. Linear regressions testing for trends through time employed the mean values for each spring, so as not to bias regressions by slightly unequal sample sizes among years.

Hydrographic data were obtained from the CalCOFI archive (http://calcofi.net/) for the same regions as the zooplankton. Nitrate measurements as a function of depth were available from spring cruises in the Southern California region in 1969, 1972, 1978, 1981, 1983, and 1984-2004 and were averaged over depths from 10-50 m as a representative average of mixed layer concentrations. Too few nitrate data were available from spring cruises in Central California to evaluate time series relationships with zooplankton ^{15}N from that region. Other physical oceanographic time series and climate indices were obtained from sources specified in Rau et al. (2003). The North Pacific Gyre Oscillation index (Di Lorenzo et al., 2008) originated from www.o3d.org/npgo/. A general linear model was fitted using the forward stepwise algorithm in Systat software.

We use the taxonomic designation *Calanus pacificus* Brodsky, although the species in our sampling domain is known to be *C. pacificus californicus* (Fleminger, 1985; Nuwer et al., 2008). We refer both chaetognath species to the genus *Sagitta* (*S. bierii* and *S. euneritica*), while recognizing that alternative generic divisions have been proposed (e.g., Bieri, 1991).

3. Results

3.1. Southern California compared with Central California

The long-term average stable N isotope content of the two copepod species was systematically lower than that of the chaetognaths, although δ^{15}N of the two chaetognaths differed substantially from each other (Fig. 1). *Sagitta bierii* was isotopically heavier than *S. euneritica* in both Southern and Central California waters ($p < 0.001$, Wilcoxon matched pairs test). As found in Central California alone (Rau et al., 2003), the difference in δ^{15}N between the two chaetognath species (1.6-2.4 per mil) was as great as the difference between the two copepod species and *S. euneritica* (1.0-2.3 per mil).

Considering differences between regions, both species of copepods were significantly enriched in ^{15}N in Southern California relative to Central California waters ($p < 0.01$, Mann-Whitney U test, for this and remaining tests in this paragraph), averaging 0.52 (*Calanus pacificus*) to 1.1 (*Eucalanus californicus*) per mil higher in the south (Fig. 1). In contrast, neither chaetognath species exhibited significant differences between regions in stable N isotope content ($p > 0.05$). Average body size was larger in Central California for both chaetognath species and for *E. californicus*, but not for *C. pacificus* (Fig. 2). Long-term average abundances of *C. pacificus* and total chaetognaths (the chaetognath species were not differentiated for total abundance measurements) were greater in Southern California and abundances of *E. californicus* higher in Central California ($p < 0.05$, Fig. 3).

No significant within-cruise heterogeneity of $\delta^{15}N$ was detected in 6 of 8 comparisons across two cruises (Suppl. Fig. 1, $p > 0.05$, Kruskal-Wallis 1-way ANOVA). However, spatial differences were resolvable for *E. californicus* and *S. bierii* on cruise 5104 ($p < 0.05$, Kruskal-Wallis). Such within-cruise spatial differences are not resolved by our procedure of sample pooling in our time series study, however our procedure results in a value that is generally comparable to the mean of spatial replicates. The 95% confidence interval of the cruise mean pooled value nearly always included the individual sample means (Suppl. Fig. 1). As with our previous study (Rau et al., 2003), we conclude that the interannual differences we detected generally exceeded the magnitude of spatial variations on a single cruise.

We examined the covariability of stable isotope content between Southern and Central California waters for each species. Interannual variations in stable isotope content in the two regions were correlated for *C. pacificus* ($p < 0.05$, Spearman's rank) and *S. bierii* ($p < 0.05$), and marginally for *E. californicus* ($0.05 < p < 0.10$), but not for *S. euneritica* ($p > 0.20$).

3.2. Temporal changes

In three of four species, the $\delta^{15}N$ of Southern California zooplankton showed no linear trend over 5½ decades ($p > 0.05$, Fig. 4). However, *Eucalanus californicus* exhibited a significant decline in $\delta^{15}N$ ($p < 0.001$, Fig. 4) over this period. *E. californicus* also differed from the other species in showing greater variability of replicate analyses of $\delta^{15}N$ (Fig. 4) and greater interannual variability (Table 1). $\delta^{15}N$ of *S. euneritica* was somewhat lower and more variable in the early 1960's than at other time points (Fig. 4), although this was not an anomalous time period for any of the other three species in Southern California (Fig. 4), or for *S. euneritica* in Central California (Suppl. Fig. 2). The long-term stability of the stable isotope content of three of four zooplankton species in Southern California parallels the stability observed for all four species in Central California (Suppl. Fig. 2, updating Rau et al., 2003).

Body sizes were also relatively stable for most species, with no linear trend detectable for any but *S. euneritica*, which showed a slight decrease in average body length over time ($p < 0.05$, Fig. 5). Body sizes in Central California showed no linear trend over time (Suppl. Fig. 3). Abundances of total chaetognaths and *Calanus pacificus* did not show a linear change with time in either Southern California or Central California (Suppl. Fig. 4). Only *E. californicus* revealed a change in average abundance, with a significant increase in Southern California waters ($p < 0.05$), but not in Central California waters ($p > 0.10$). This increase could perhaps be described by a step function increase in 1977, coinciding with the timing of the putative North Pacific ecosystem shift (Mantua et al., 1997), rather than a progressive linear change through time (Suppl. Fig. 4).

Variations in stable isotope content of the 4 species are evaluated with respect to changes in the sign of the Pacific Decadal Oscillation (PDO) in figure 6. In Southern California, *C. pacificus* and *S. euneritica* exhibited significantly elevated $\delta^{15}N$ during the warm phase of the California Current System (1977-1998) relative to the time period before and after (Fig. 6a,d, $p < 0.05$, Mann-Whitney U). *S. bierii* showed no significant difference between time periods (Fig. 6c, $p > 0.30$), while *E. californicus* $\delta^{15}N$ exhibited a progressive decline over time (Fig. 6b), as expected from figure 4. In Central California, none of the species showed significant changes in $\delta^{15}N$ during the warm phase (Fig 6, $p > 0.10$).

Our consideration of the effects of interannual forcing focused on the effects of ENSO. For *C. pacificus*, *S. bierii*, and *S. euneritica* there was a consistent tendency toward heavier isotopic content in El Niño conditions and often lighter isotopic content in La Niña conditions relative to El Niño-neutral years (Fig. 7). Comparison of $\delta^{15}N$ in strong El Niño springs (1958, 1983, 1992, 1998) in relation to all other years showed that in Central California waters, ^{15}N was enriched during El Niño in 3 species: *C. pacificus* ($p = 0.056$, Mann-Whitney U), *S. bierii* ($p < 0.05$), and *S. euneritica* ($p < 0.05$).. In Southern California, *C. pacificus* ($p < 0.01$) and *S. bierii* ($p = 0.061$) showed elevated ^{15}N during strong El Niño's (Fig. 7), but not the other two taxa. *S. euneritica* occurs in low abundance during El Niño years, hence it was difficult to find enough specimens to conduct adequate replication. There was no evidence of isotopic enrichment during El Niño conditions for *E. californicus* in either region ($p > 0.05$). The chaetognaths tended to show a larger El Niño-related elevation in $\delta^{15}N$ in Central California (1.3-1.4 per mil) than in Southern California waters (0.5 per mil, Fig. 7).

A general linear model evaluated the relationship between stable isotope values of zooplankton from the Southern California region and different climate variables (upwelling index, SOI, PDO, NOI, transport anomalies, NPGO), as described previously for Central California (Rau et al., 2003) but with the addition of the NPGO as an independent variable (Di Lorenzo et al., 2008). Although statistically significant relationships were detected, none explained more than 17% of the variance in the data and are not considered further.

3.3. Isotopic content in relation to nutrient supply

We analyzed temporal changes in isotopic content in relation to nitrate concentration averaged over the upper 10-50 m, in order to assess the possible role of nutrient supply to phytoplankton in altering the stable isotope content of California Current zooplankton. This analysis could be conducted only for Southern California where the time series measurements of dissolved nitrate were sufficiently complete. $\delta^{15}N$ of *Calanus pacificus, Eucalanus californicus*, and *Sagitta euneritica* varied inversely with average nitrate concentration ($p < 0.05$, Fig. 8). *S. bierii* $\delta^{15}N$ did not covary with nitrate concentration ($p > 0.80$).

4. Discussion

4.1. Regional differences

Increased $^{15}N/^{14}N$ in copepods in Southern California (SC) relative to Central California (CC) waters is consistent with the lower springtime mixed layer nitrate concentrations in the southern part of the California Current System (Table 2). Both copepod species are particle-grazing suspension feeders whose diet is comprised of microplankton dominated by larger phytoplankton (Mullin and Brooks, 1967; Smith and Lane, 1991; Ohman et al., 1998). Because phytoplankton δ^{15}N can be inversely related to nitrate concentration via nitrate utilization and Rayleigh isotope fractionation (e.g., Waser et al., 1998; Rau et al., 1998), together with isotopic fractionation due to recycling (Checkley and Miller, 1989), the enrichment in copepod ^{15}N in SC waters would be consistent with greater nitrate utilization and lower nitrate concentrations in this region. Indeed, within the SC region, δ^{15}N in three of four species is negatively correlated with nitrate concentration, with trends similar to those predicted by a Rayleigh isotope fractionation model (Fig. 8). Unfortunately an equivalent nitrate record of sufficient duration is not available for CC waters. As in our regional differences in zooplankton δ^{15}N, Altabet et al. (1999) also reported slightly higher mean δ^{15}N in sinking particulate organic matter in SC waters (8.0 ‰) relative to that in Monterey Bay (mean = 7.8 ‰,). However, they concluded that mixed layer source nitrate δ^{15}N (elevated by partially denitrified subsurface water advected from the south) and nitrate utilization were on average similar in both regions.

A lack of regional differences in δ^{15}N of the chaetognaths may be attributed to the generally longer life span of chaetognaths relative to epipelagic copepods, hence a larger region of oceanographic influence during the course of their ontogeny. The body tissue N of the chaetognaths collected in one region may be influenced by geographically distant prey encountered earlier in their development. Also, while the chaetognaths are obligate predators that feed mainly on copepods (Feigenbaum, 1991), the two copepod species studied here do not constitute their only prey. The abundance of total chaetognaths is positively correlated with the abundance of *C. pacificus* plus *E. californicus* in our study sites ($p < 0.001$, Suppl. Fig. 5), but the association is weak and there is considerable unexplained variability that suggests that other prey species also influence these predators' tissue composition and abundance.

The elevated ^{15}N content of *Sagitta bierii* relative to *S. euneritic*a (Rau et al., 2003) is here found to be a consistent interspecific difference in both SC and CC, and over time. *S. bierii* has a somewhat deeper range of vertical habitat and larger average body size than *S. euneritica*. In addition, Thuesen and Childress (1993) commented on the two-fold higher activity of the metabolic enzyme pyruvate kinase (but not citrate cynthase) in *S. bierii*. They suggested that *S. bierii* is the more active of the two chaetognath species, perhaps leading to differences in prey capture ability and composition of the diet. In addition, if, by analogy with pyruvate kinase activity, proteolytic and other enzyme activity involved in nitrogen metabolism were markedly elevated in *S. bierii*, this could potentially lead to greater isotopic fractionation and elevated tissue ^{15}N content in *S. bierii* relative to *S. euneritica*.

The correlated variability of stable N isotopes in Central and Southern California waters, for the copepods and one of the chaetognath species, recalls the coherence of carbon biomass variations of both copepods and chaetognaths between the two regions (Lavaniegos and Ohman, 2007). These results suggest some degree of common response to remote forcing in Central and Southern California but, as with the biomass variations, some but not all of the variance was shared.

4.2. Temporal Changes

With the exception of one species in Southern California waters, overall we observed long-term stability of zooplankton stable N isotopes. After 5½ decades, the average stable N isotope content was comparable to initial starting values in 1951. This observation confirms earlier results from a slightly shorter and more irregular time series for the Central California region alone, and extends it to the better sampled southern California region. These results imply that despite ocean perturbations on multiple time scales, including decadal and interannual variations that alter both stable isotope content (Rau et al., 2003; present results) and abundances of marine zooplankton (Rebstock, 2001; Lavaniegos and Ohman, 2003; 2007; Mackas et al., 2006; Peterson, 2009) there is considerable resilience in the trophic position of most zooplankton taxa. To the extent that stable isotope content of zooplankton is indicative of food web structure, these results suggest a relative stability of basic pathways of energy flow, and the sources and cycling of nitrogen in the California Current System pelagic food web. This result corroborates Rebstock's (2001) analysis of copepod community composition, which exhibited substantial, but reversible, declines in community percent similarity during several ENSO events, with an overall long-term stability of the copepod community over multiple decades. These results are also consistent with the overall similarity of euphausiid species composition in the CCS over multiple decades (Brinton and Townsend, 2003), despite interannual and decadal-scale fluctuations. In contrast, a long-term decline in salps has been detected in this region (Lavaniegos and Ohman, 2007). One implication of the stability of other members of the food web despite a decrease in salp biomass is that salps, when considered across broad temporal-spatial averages, apparently do not exert sufficient sustained grazing pressure to alter the growth rate of other potentially competing metazoan plankton in this region (cf. Hereu et al., 2006). It is also possible that the sample pooling procedure we employed (cf. Lavaniegos and Ohman, 2007) reduced our ability to detect variability within our study regions, although the correspondence between our individual station analyses and pooled analyses suggests this was not a major bias.

The exception to the pattern of relative stability is the long-term δ^{15}N decline seen in *Eucalanus californicus* in SC waters. As adults, both *E. californicus* and *C. pacificus* reside in epipelagic waters in springtime, though there are subtle, but important, differences in the vertical habitat occupied. *C. pacificus* live in the mixed layer in spring in this region (Mullin and Brooks, 1970; Ohman et al., 1998; Johnson and Checkley, 2004), as they do elsewhere in their range (e.g., Frost, 1988). In contrast to *C. pacificus*, during spring-summer *E. californicu*s lives somewhat deeper in the water column, just below the mixed layer (Ohman et al., 1998). This vertical distribution recalls that of its congener *Eucalanus bungii* in the Subarctic Pacific, which, together with *Neocalanus cristatu*s, resides somewhat deeper than other particle-grazing copepods (*Neocalanus plumchrus* and *N. flemingeri*, Mackas et al., 1993), although *E. bungii* adults can occur near the surface in spring in the Oyashio region (Yamaguchi et al., 2010).

An expected consequence of residence below the mixed layer in the California Current System is that the phytoplankton prey available to *E. californicus* would likely come from a somewhat deeper depth than those commonly encountered by *C. pacificus* (or would arrive in the form of sinking particles). Deeper-dwelling prey would be closer to the nitracline region where light-limited nitrate utilization and hence nitrate and plankton δ^{15}N would be lower. Both Liu and Kaplan's (1989) results from Southern California and Wankel et al.'s (2007) results from Monterey Bay show δ^{15}N of nitrate decreases with depth in the upper 100-150 m of the water column, for stations with well oxygenated waters. A depth-dependent decrease in $\delta^{15}NO_3$ has also been documented in the oxic Subarctic Pacific (Wu et al., 1999). While Sigman et al. (2005) showed that $\delta^{15}NO_3$ increases with depth to a maximum at about 300 m depth, that gradient was most pronounced in hypoxic waters of the Baja California and Southern California coast that are sites of denitrification. As nearly all of our study regions have oxic water columns, the results of Liu and Kaplan (1989), Wankel et al (2007), and Wu et al. (1999) appear most applicable to our regions, with the consequent expectation of lower $\delta^{15}N$ of nitrate just below the mixed layer. We infer, but do not have direct evidence, that deeper-dwelling phytoplankton would also be lower in $\delta^{15}N$. We note that previous vertical profiles of $\delta^{15}N$ of suspended particulate matter (SPM) do not consistently support the idea of ^{15}N-depleted food source at depth (e.g., Saino and Hattori, 1987; Benner et al., 1997; Wu et al., 1999), however these profiles may not be reflective of physiologically active phytoplankton. If copepods feed selectively on living cells over detrital material (cf. Cowles et al., 1988), their tissue composition would be better reflected by the living cells than by total SPM.

Recently it has been noted that there has been a long-term shoaling of the nitracline and increase in chlorophyll-*a* concentration in the specific region that we have studied here (Aksnes and Ohman 2009). Our results above, in figure 8, suggest that $\delta^{15}N$ of *E. californicus* varies inversely with average nitrate concentration. Hence a shoaling of the nitracline would be expected to result in somewhat higher nitrate concentrations, especially at the subsurface depths where *E. californicus* feeds, and consequently a lower isotopic content of tissues. (We note that the deeper sampling depth beginning in 1969 would not have affected our results because zooplankton sampling extended well below the nitracline both before and after this date.) Such an effect would not be evident in the shallower-dwelling *C. pacificus.* A slow, but progressive trend toward ingestion of isotopically lighter prey would be consistent with the isotopic lightening of *E. californicus*. The requisite vertically resolved samples of changes in stable N isotope content of suspended particulate matter over time are not available to evaluate this hypothesis directly. However, the extent to which the diet of *E. californicus* depends on isotopically lighter, nitrate-rich prey could be tested in situ.

A long-term decline in δ^{15}N of *E. californicus* was not observed in CC waters, perhaps because of small differences in vertical habitats occupied in the two regions or a less pronounced change in nitracline shoaling or stratification in Central California waters. The lack of change in isotopic content in CC parallels the lack of long-term change in numerical abundance, in contrast to SC waters where *E. californicus* increased in abundance as well as becoming isotopically lighter over time.

We detected perturbations to zooplankton stable isotope content on both decadal and interannual time scales, despite the relative stability of most species' isotopic signatures over the entire time series. The enrichment in ^{15}N of *C. pacificus* and *S. euneritica* during the warm phase of the Northeast Pacific (i.e., the time period of mainly positive values of the PDO between 1978-1998) would be consistent with reduced nitrate fluxes during the warmer surface ocean conditions, accompanied by reduced nitrate supply relative to demand by phytoplankton, leading to elevated ^{15}N. No such decadal-scale variation was detectable in the CC region, although previous results based on a slighter shorter time series suggested that *S. bierii* in CC showed significant enrichment during the warm phase of the PDO (Rau et al., 2003). The more variable ^{15}N content of CC chaetognaths in the most recent years analyzed modified the statistical significance of the previous result.

On the interannual time scale, El Niño-La Niña variations influenced the stable N isotopes of *C. pacificus* and the two chaetognath species. ^{15}N of some species zooplankton was enriched in El Niño conditions in both SC and CC. For the chaetognaths, the magnitude of the El Niño-related enrichment was greater in the Central California region. If the mechanism proposed above (i.e., reduced nitrate fluxes) were responsible for this enrichment, we would anticipate a larger El Niño-related suppression of nitrate fluxes in CC waters than in SC waters. We do not have measurements of nitrate fluxes, but from the limited comparison of nitrate concentrations available in Table 2 it may be seen that the areally-averaged El Niño-related reduction in nitrate concentration was indeed somewhat greater in CC waters (59%) in comparison with SC waters (38 %).

4.3. Relationship to nutrient availability

Regional differences, as well as interannual and decadal variations in zooplankton ^{15}N content, appear consistent with spatial and temporal variability in the importance of nitrate nutrition for the phytoplankton at the base of the food web, accompanied by Rayleigh isotope fractionation. While it remains possible that trophic elongation, through increased ingestion of microzooplankton by the suspension-feeding copepods, could be a contributing factor to the isotopic variations detected here, recent evidence appears to rule out this explanation. Décima (2011), analyzing compound-specific stable isotopes across the 1998-1999 El Niño-La Niña transition, found that source as well as trophic amino acids in *C. pacificus* were enriched in ^{15}N during El Niño, resulting in no change in the copepods' trophic level. These results are in agreement with our findings of the importance of nitrate availability in explaining zooplankton isotopic variation.

An increased influx of isotopically heavier nitrate originating in waters of the eastern tropical Pacific (Liu and Kaplan, 1999; Sigman et al., 2005) could also potentially alter the $\delta^{15}N$ of phytoplankton and hence their consumers (cf. Rau et al., 2003). However, Chhak and DiLorenzo (2007) have illustrated that source waters upwelled into the CCS tend to come from shallower depths and more northerly sources in the positive phase of the PDO. Hence advection of high $\delta^{15}NO_3$ from the south seems unlikely to explain our PDO-related ^{15}N results. Furthermore, the slope of the relation between zooplankton $\delta^{15}N$ and nitrate concentration is considerably shallower and the $\delta^{15}N$ values considerably lower than would be expected if this relation were governed solely by the degree of denitrification occurring prior to the delivery of nitrate to the mixed layer. An additional potential mechanism for regional and temporal variation in zooplankton ^{15}N is a possible long-term increase in nitrate concentration coming from the central North Pacific (Rykaczewski and Dunne, 2010). However, the isotopic effect of such a projected trend would depend upon the $\delta^{15}N$ of NO_3 in source waters and, in any case, is not consistent with the differences in $\delta^{15}N$ that we have observed among different zooplankton species.

On the interannual time scale, for horizontal advection of high $\delta^{15}NO_3$ water to explain ENSO-related enrichment in zooplankton ^{15}N there would need to be consistent influxes of southerly waters in all El Niño's. While such influxes frequently do occur, recent evidence suggests that this is not always the case, because El Niño may sometimes propagate into this region via atmospheric teleconnections rather than oceanic advection (Todd et al., 2011). Furthermore, the hypothesis of altered advection is not consistent with the lack of El Niño-related enrichment in *E. californicus*. This somewhat deeper-dwelling species should be more strongly influenced if there were a lateral influx of subsurface ^{15}N-enriched nitrate during El Niño conditions.

Definitive resolution of the mechanisms through which ENSO, decadal variations, and long term ocean stratification influence zooplankton stable isotopes would require complete time series of isotopic content of dissolved nitrogen sources, phytoplankton, and microzooplankton prey, combined with experimental feeding studies. An alternative approach would be to carry out amino acid-specific stable N isotope analyses (e.g., McClelland and Montoya, 2002; Hannides et al. 2009; Décima, 2011) in order to distinguish between differences in nitrogen sources utilized by phytoplankton and altered diets of zooplankton. Although a powerful approach, it is much more lab intensive than the bulk analyses that we carried out here. Thus far, amino acid-specific N isotopic analyses suggest that trophic relationships in marine zooplankton are relatively stable, in contrast to the variability in environmental δ^{15}N. McClelland et al. (2003) reported a stable trophic structure among zooplankton size classes along a tropical North Atlantic transect. A recent amino acid-specific study of four copepod species in the North Pacific Subtropical Gyre for three years (1995, 2000, 2005) found consistent trophic level assignments and reproducible summer-winter differences in these years (Hannides et al., 2009). Décima's (2011) results for *Calanus pacificus* also suggest trophic stability. The variation in whole organism nitrogen isotopes observed in both North Atlantic and North Pacific studies was attributed to variation in source water nitrogen or basal food web δ^{15}N (McClelland et al., 2003; Hannides et al., 2009), rather than to a change in food web structure.

5. Conclusions

Stable N isotope content of preserved zooplankton can provide an index of the response of plankton communities to climate forcing on different time scales. We found variations in $\delta^{15}N$ of both particle-grazing copepods and carnivorous chaetognaths associated with ENSO and with PDO-scale forcing. These isotopic changes in the zooplankton are consistent with variations in nutrient availability at the base of the food web. Despite these strong perturbations to the upper ocean environment and planktonic food web, in most cases there was no progressive secular change in isotopic content over 5½ decades. This implies resilience of the food web to external forcing. Most changes measured in stable isotope content were reversible, at least in response to the magnitude of variation that has been experienced thus far. It is not known whether thresholds may exist that, once crossed, may give rise to markedly different responses in the future (e.g., Hsieh et al., 2005; Scheffer et al., 2009). In contrast, the copepod *Eucalanus californicus* in Southern California waters demonstrated a progressive decrease in $\delta^{15}N$ over multiple decades, which is consistent with a previously documented shoaling of the nitracline.

6. Acknowledgments

We thank Annelies Pierrot-Bults for identifying chaetognaths for stable isotope analyses and Bruce Deck for his careful analytical work on the mass spectrometer. Ginger Rebstock and Bertha Lavaniegos conducted the zooplankton enumerations. We thank Annie Townsend for her sterling work in the SIO Pelagic Invertebrates Collection and the CalCOFI seagoing technicians for their unflagging work at sea; without both, this study would not have been possible. Moira Décima and the anonymous reviewers provided helpful comments. Supported initially by the U.S. GLOBEC research program and completed as part of the California Current Ecosystem LTER site, both funded by the NSF. A contribution of the Pelagic Invertebrates Collection of SIO.

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Figure Legends

Fig. 1. Average $\delta^{15}N$ of four zooplankton species (copepods *Calanus pacificus* and *Eucalanus californicus*, and chaetognaths *Sagitta euneritica* and *Sagitta bierii*) in two regions of the California Current System (Southern California = solid, Central California = open). Box boundaries indicate the 25th and 75th percentiles of the distribution of values, horizontal line indicates the median, whiskers the 10th and 90th percentiles, and dots the outliers. Asterisks indicate significant differences between regions ($p < 0.05$, Mann-Whitney U).

Fig. 2. Average body length of four zooplankton species in two regions of the California Current System (Southern California = solid, Central California = open). Prosome length of the copepods a) *Calanus pacificus*, b) *Eucalanus californicus*, and total length of the chaetognaths c) *Sagitta bierii*, and d) *Sagitta euneritica*. Asterisks indicate significant differences between regions ($p < 0.05$, Mann-Whitney U). Others details as in Fig. 1.

Fig. 3. Average abundance of two copepod species and total chaetognaths in two regions of the California Current System (Southern California = solid, Central California = open). Asterisks indicate significant differences between regions ($p < 0.05$, Mann-Whitney U). Others details as in Fig. 1.

Fig. 4. Long-term variation in $\delta^{15}N$ of four zooplankton species in Southern California waters, and p-value of a test of departure of the slope of a linear trend from zero, together with r^2. a) *Calanus pacificus* ($p>0.10$, $r^2=0.02$), b) *Eucalanus californicus* ($p<0.001$, $r^2 = 0.35$, solid regression line) c) *Sagitta bierii* ($p>0.10$, $r^2=0.04$), and d) *Sagitta euneritica* ($p>0.05$, $r^2=0.08$). Sample size was 46 for all regressions. Mean ± 95% C.I.

Fig. 5. Long-term variation in body length of four zooplankton species in Southern California waters, and p-value of a test of departure of the slope of a linear trend from zero, together with r^2. Prosome length of the copepods a) *Calanus pacificus* ($p>0.10$, $r^2=0.01$) , b) *Eucalanus californicus* ($p>0.10$, $r^2=0.02$), and total length of the chaetognaths c) *Sagitta bierii* ($p>0.10$, $r^2=0.01$), and d) *Sagitta euneritica* ($p<0.05$, $r^2=0.09$, solid regression line). Sample size was 46 for all regressions. Mean ± 95% C.I.

Fig. 6. Decadal variation in zooplankton $\delta^{15}N$ across three time periods (**1**= 1951-1976, **2** = 1977-1998, **3** = 1999-2004) in Southern California (a-d) and Central California (e-h) waters. a,e) *Calanus pacificus*, b,f) *Eucalanus californicus*, c,g) *Sagitta bierii*, and d,h) *Sagitta euneritica*. Mean ± 95% C.I.

Fig. 7. Interannual variation in zooplankton $\delta^{15}N$ in three phases of ENSO: **neutral**= El Niño-neutral years, **Niña** = La Niña years, **Niño** = strong El Niño years (Southern California = solid, Central California = open). a) *Calanus pacificus*, b) *Eucalanus californicus*, c) *Sagitta bierii*, and d) *Sagitta euneritica*. Mean ± 95% C.I.

Fig. 8. Relationship between zooplankton $\delta^{15}N$ and average nitrate concentration (10-50 m) in Southern California waters. a) *Calanus pacificus*, b) *Eucalanus californicus*, c) *Sagitta bierii*, and d) *Sagitta euneritica*. Solid lines indicate regressions significant at $p < 0.05$ (slope differs from 0). Dotted lines denote Rayleigh model fits where initial source $[NO_3^-] = 25\ \mu M\ L^{-1}$ (Liu and Kaplan, 1989; Sigman et al., 2005), source nitrate $\delta^{15}N = 8‰$ (Liu and Kaplan, 1989; Sigman et al., 2005), instantaneous isotope fractionation by phytoplankton nitrate uptake = 5‰ (Waser et al., 1998; Altabet et al., 1999), phytoplankton $\delta^{15}N = \delta^{15}N$ of the accumulated biomass product predicted by the model, and in each species zooplankton $\delta^{15}N$ is trophically elevated above

predicted phytoplankton δ^{15}N by a specified constant amount: C.p. +4.2‰, E.c. +3.7‰, and S.e. +5.5‰.

Tables

Table 1. Coefficient of variation (c.v.= standard deviation/mean) of annual mean δ^{15}N for four species of zooplankton in two regions of the California Current System.

Species	Southern California (c.v.)	Central California (c.v.)
Calanus pacificus	0.07	0.08
Eucalanus californicus	0.12	0.12
Sagitta bierii	0.03	0.05
Sagitta euneritica	0.08	0.06

Table 2. Comparison of Southern California and Central California waters with respect to average springtime temperature and nitrate in the upper 10-50 m. El Niño-neutral springs (cruises 8404 and 0704) compared with an El Niño spring (cruise 9804). Southern CA stations included CalCOFI lines 80-93.3 and Central CA lines 60-70, from shore out to station 70. Table entries are the mean ± 95% C.I.

	El Niño-neutral Spring		El Niño Spring	
	Temp (°C)	NO_3 (μM L^{-1})	Temp (°C)	NO_3 (μM L^{-1})
Southern CA	13.4 ± 0.3	5.0 ± 1.4	14.3 ± 0.4	3.1 ± 1.4
Central CA	10.4 ± 0.6	14.7 ± 4.1	12.4 ± 1.1	6.0 ±6.4

Research Highlights for:

Multi-decadal variations in stable N isotopes of California Current zooplankton

M. D. Ohman, G. H. Rau, P. Hull

- Some zooplankton species analyzed show El Nino-related enrichment in 15N
- Zooplankton d15N covaries with nitrate concentration, consistent with Rayleigh fractionation
- 3 of 4 zooplankton species show long-term stability of stable N isotopes over 54 years
- d15N of 1 copepod decreased over 54 years, associated with a shoaling nitracline

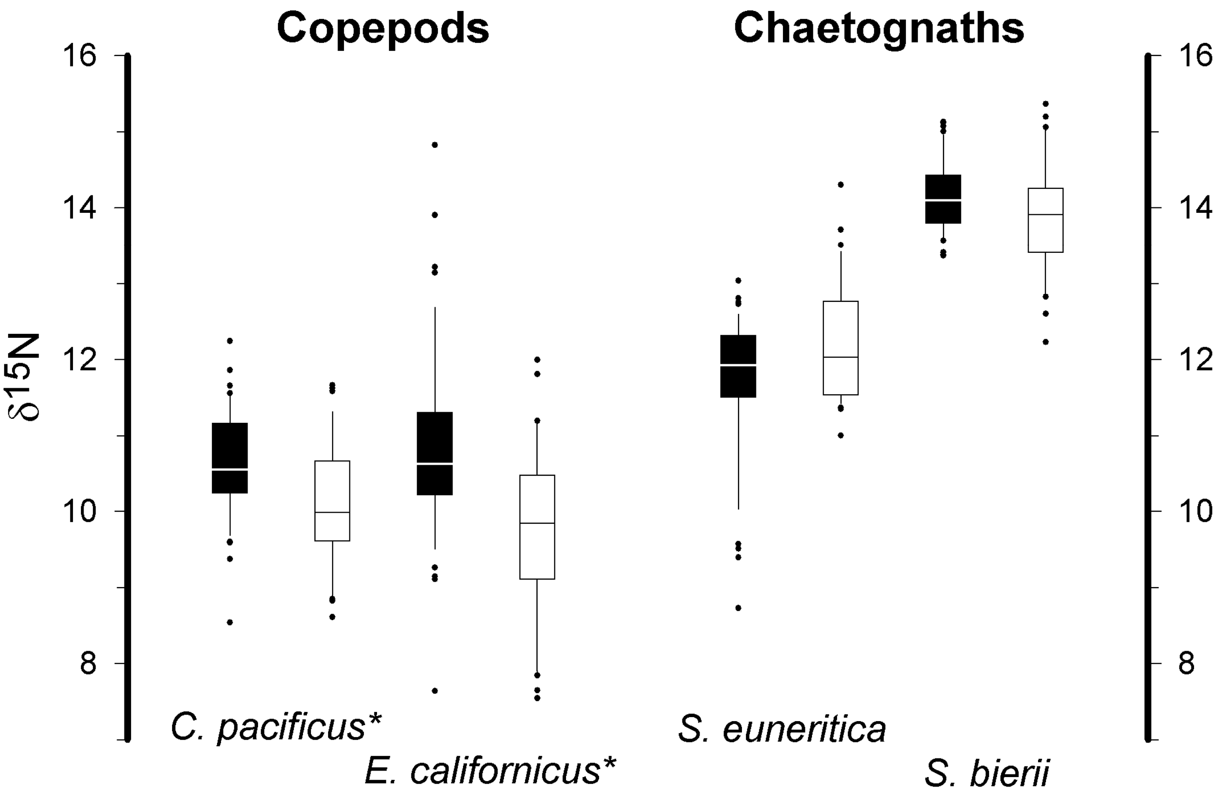


Fig. 1

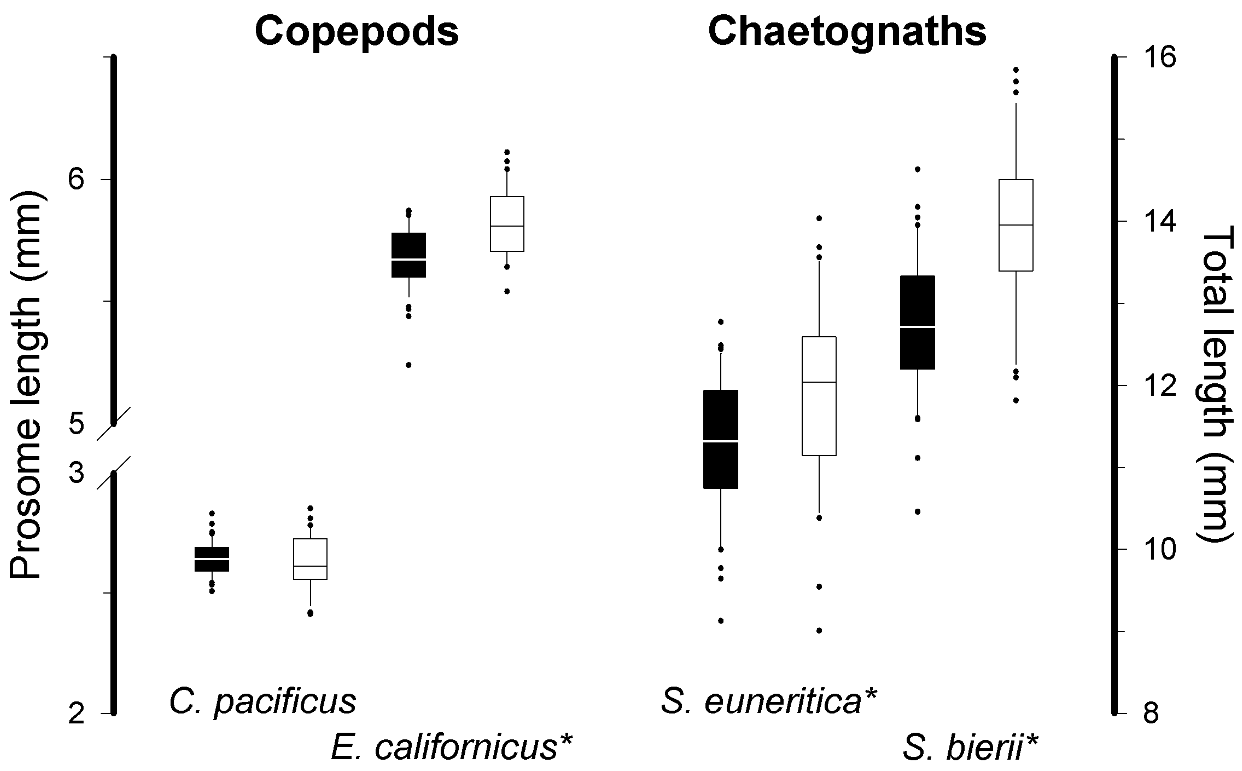

Copepods
Chaetognaths
Prosome length (mm)
Total length (mm)
6
5
3
2
16
14
12
10
8
C. pacificus
E. californicus*
S. euneritica*
S. bierii*

Fig. 2

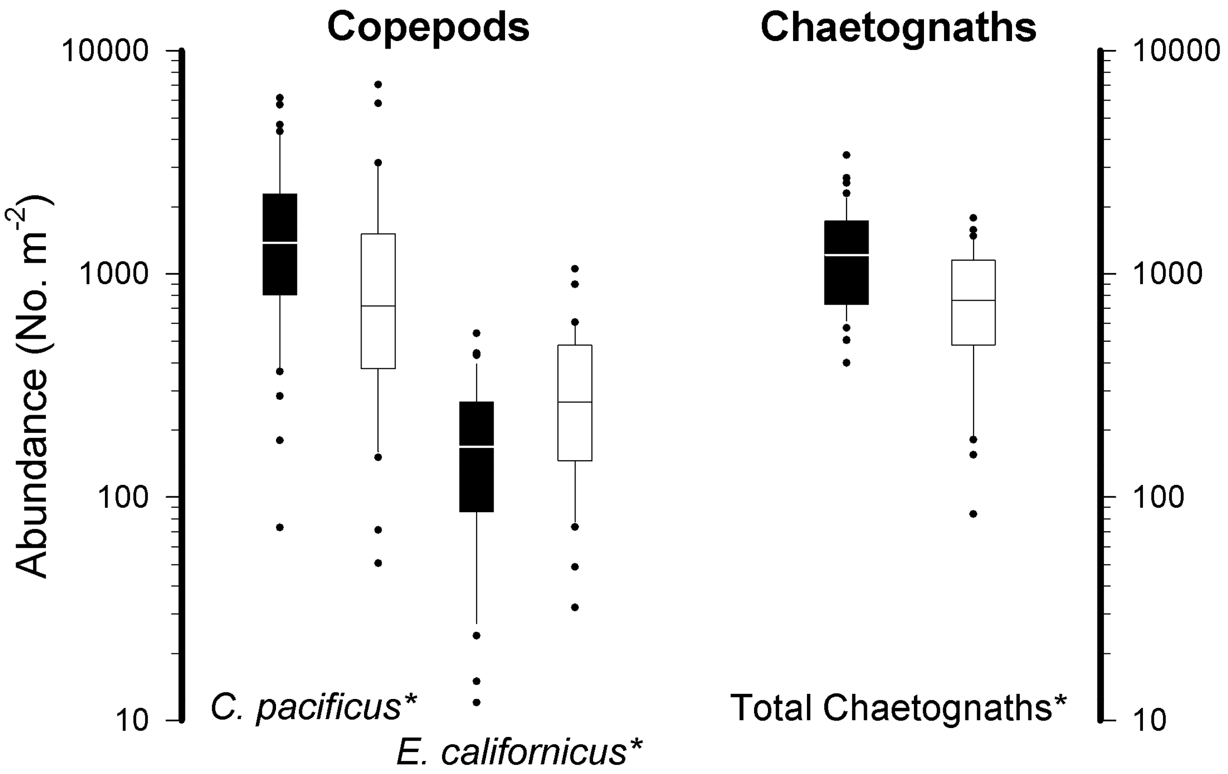

Copepods
Chaetognaths
Abundance (No. m^{-2})
10000
1000
100
10
10000
1000
100
10
C. pacificus*
E. californicus*
Total Chaetognaths*

Fig. 3

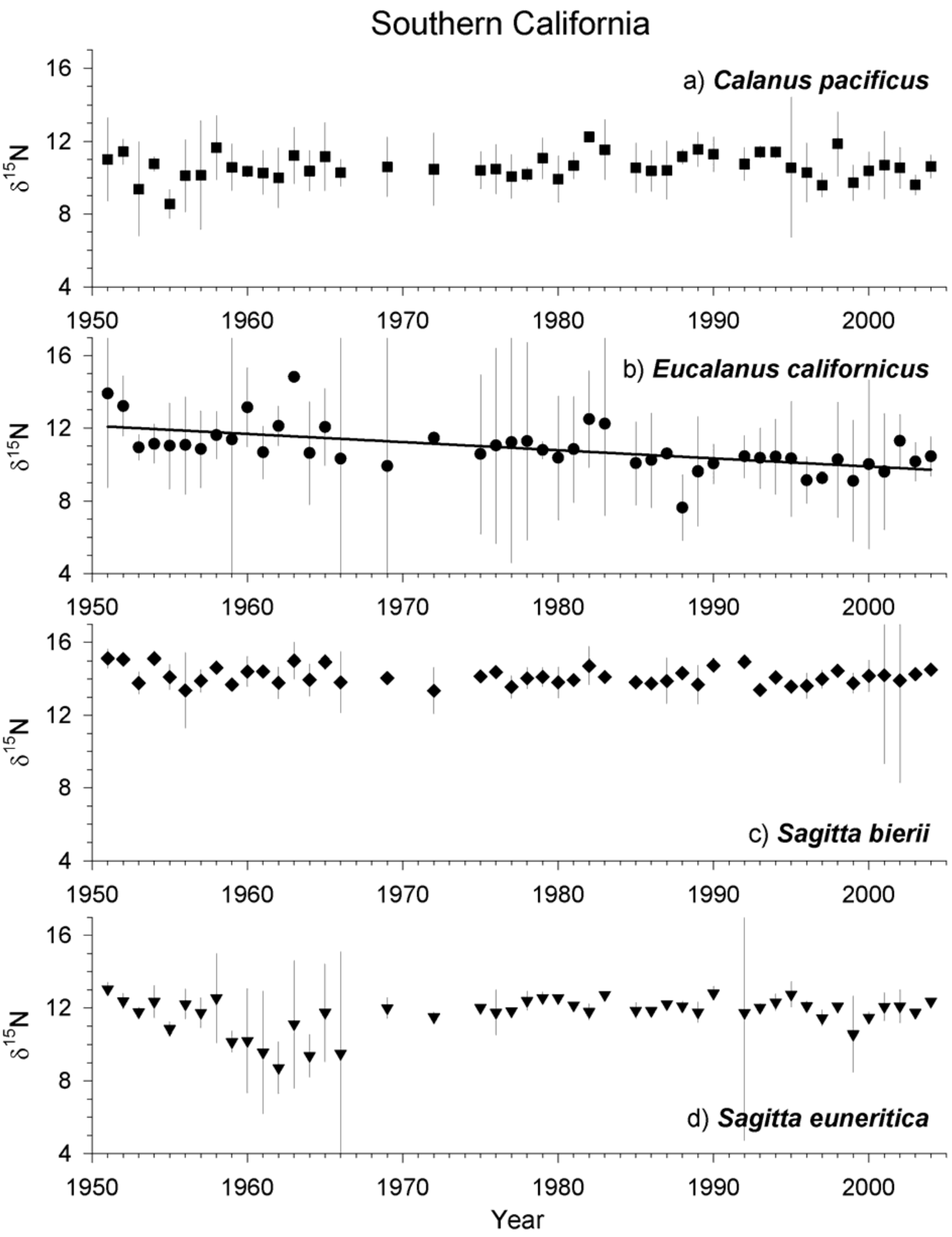

Southern California
a) Calanus pacificus
b) Eucalanus californicus
c) Sagitta bierii
d) Sagitta euneritica
δ15N
4
8
12
16
1950
1960
1970
1980
1990
2000
Year

Fig. 4

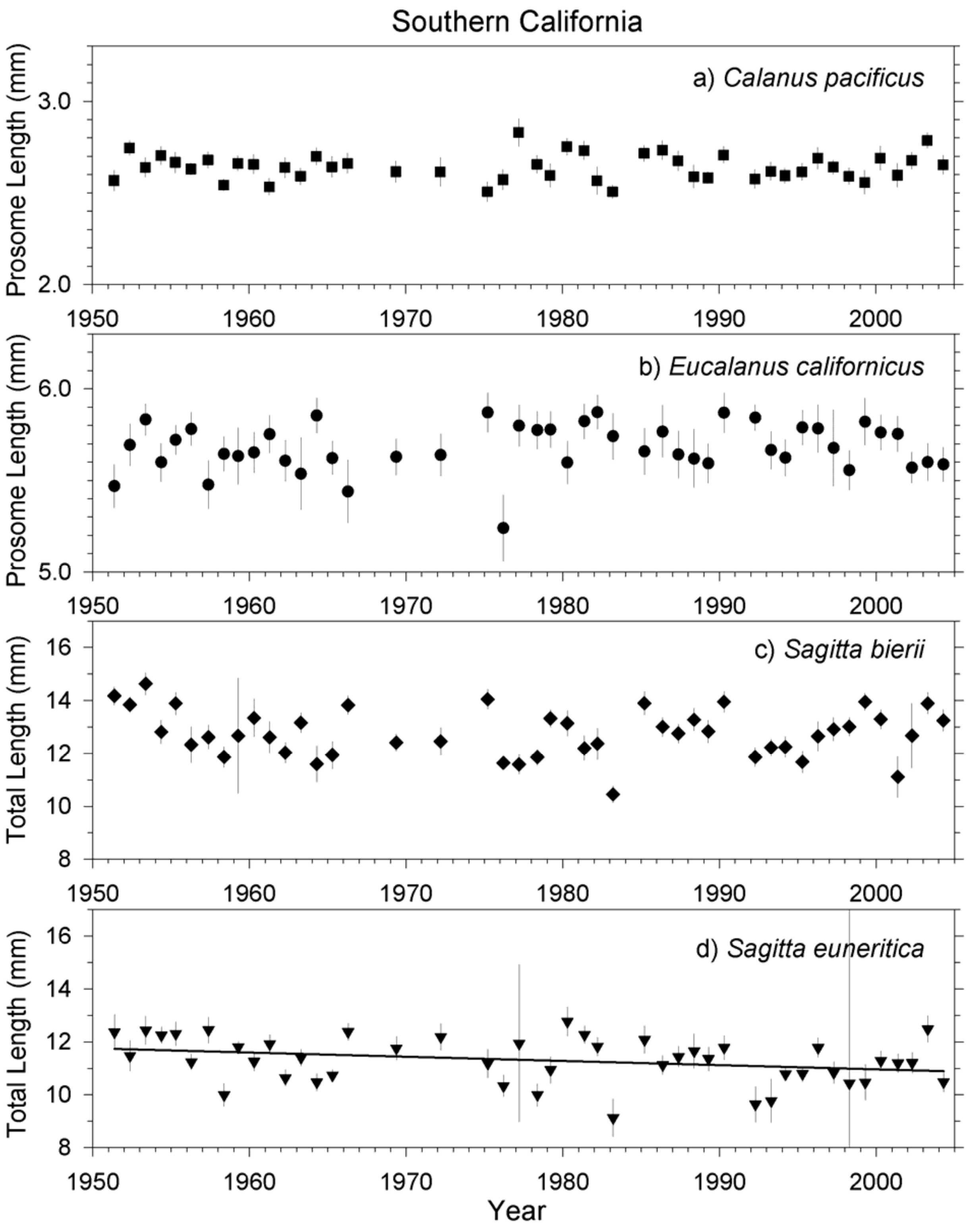

Southern California
a) *Calanus pacificus*
Prosome Length (mm)
3.0
2.0
b) *Eucalanus californicus*
Prosome Length (mm)
6.0
5.0
c) *Sagitta bierii*
Total Length (mm)
16
14
12
10
8
d) *Sagitta euneritica*
Total Length (mm)
16
14
12
10
8
1950
1960
1970
1980
1990
2000
Year

Fig. 5

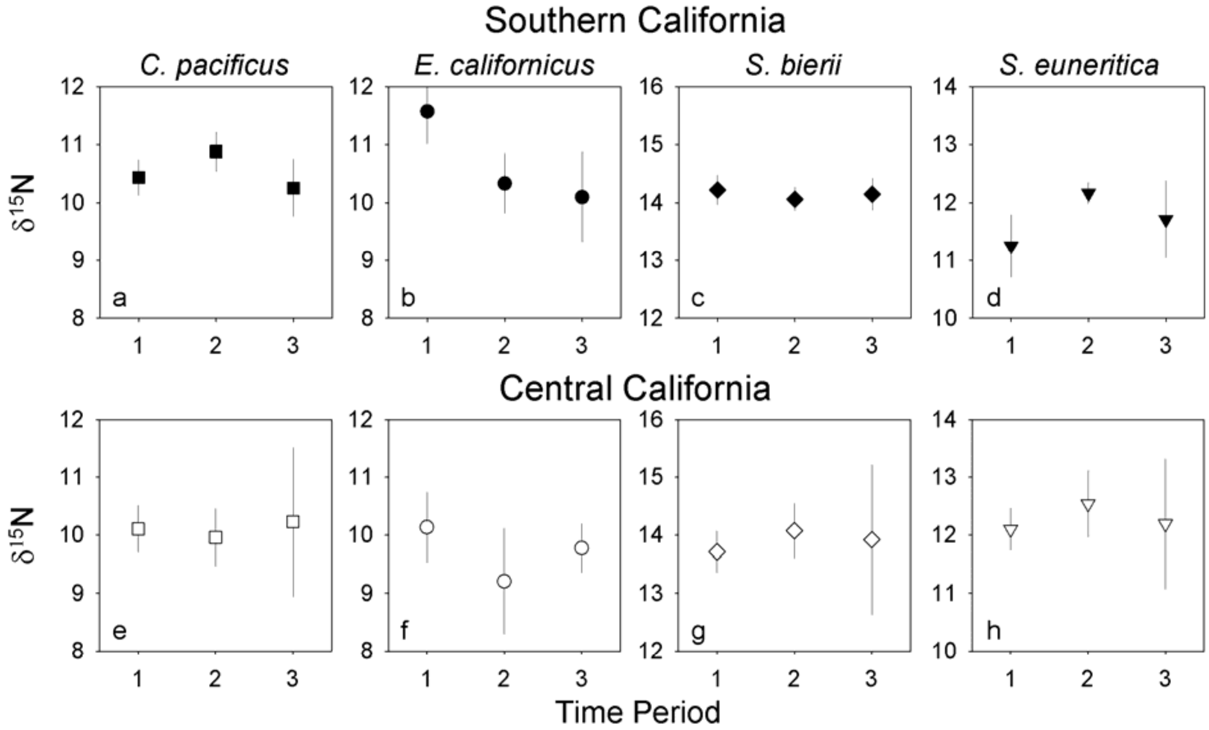
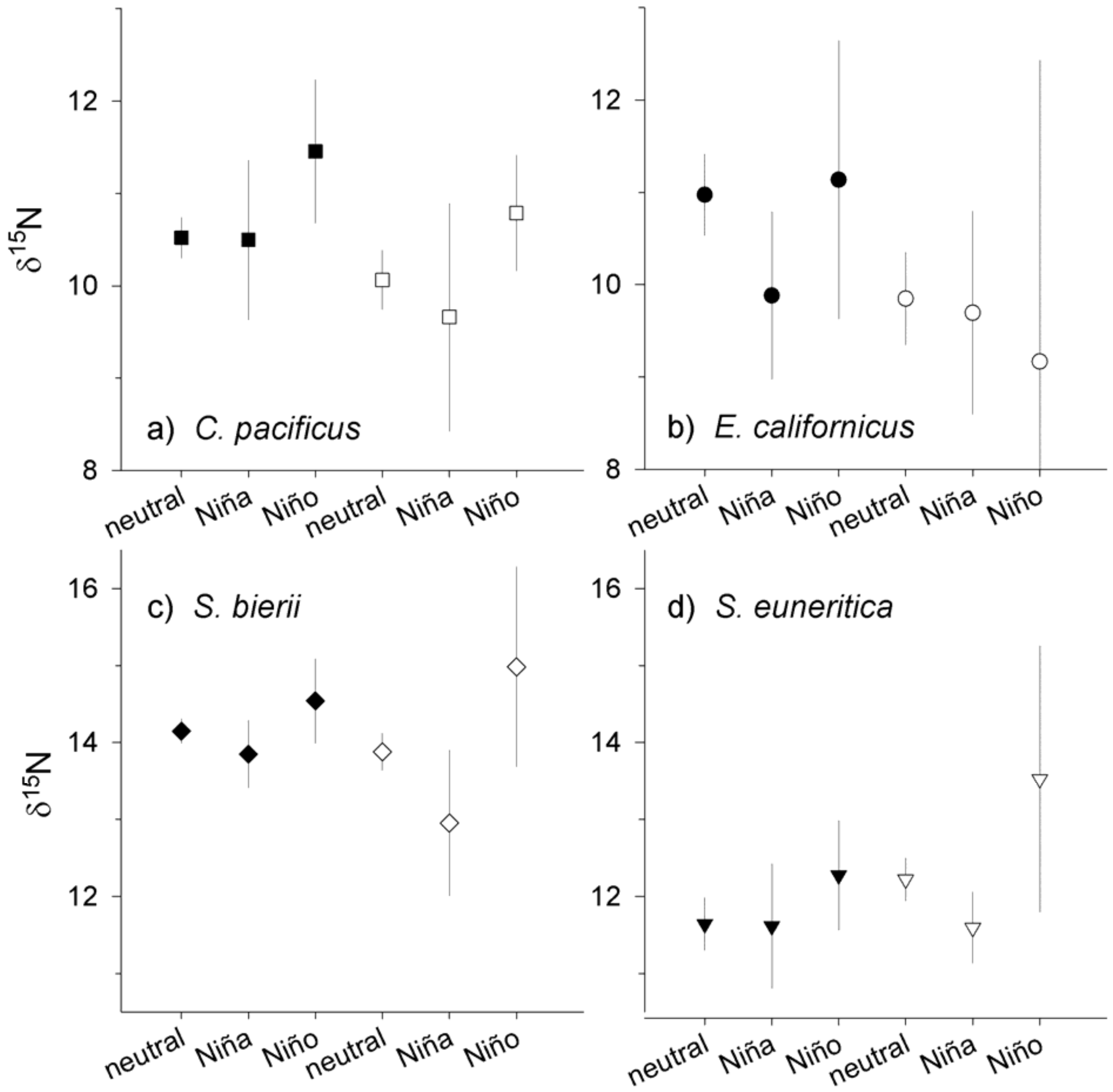

Southern California
C. pacificus
E. californicus
S. bierii
S. euneritica
$\delta^{15}N$
a
b
c
d
Central California
e
f
g
h
1
2
3
12
11
10
9
8
16
15
14
13
Time Period

Fig. 6



a) C. pacificus
b) E. californicus
c) S. bierii
d) S. euneritica
$\delta^{15}N$
$\delta^{15}N$
8
10
12
16
14
12
neutral
Niña
Niño
neutral
Niña
Niño

Fig. 7

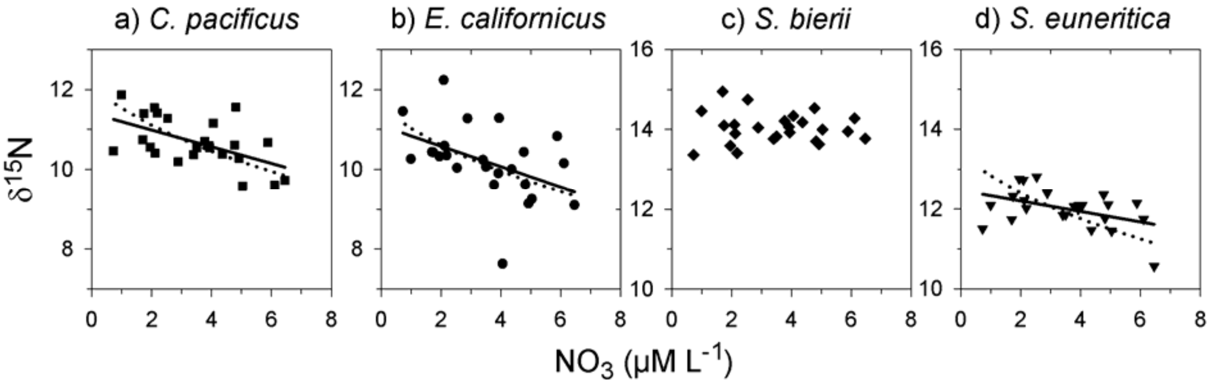

a) *C. pacificus*
b) *E. californicus*
c) *S. bierii*
d) *S. euneritica*
$\delta^{15}N$
8
10
12
16
14
12
10
0
2
4
6
8
NO_3 (µM L^{-1})

Fig. 8