

Coherence of long-term variations of zooplankton in two sectors of the California Current System

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Received 5 March 2007; accepted 13 July 2007

Available online 27 July 2007

Abstract

We analyzed long-term (56-year) variations in springtime biomass of the zooplankton of the California Current System from two primary regions sampled by CalCOFI: Southern California (SC) and Central California (CC) waters. All organisms were enumerated from the plankton samples and converted to organic carbon biomass using length–carbon relationships, then aggregated into 19 major taxa. Planktonic copepods dominate the carbon biomass in both SC (59%) and CC (46%), followed by euphausiids (18% and 25% of mean biomass in SC and CC, respectively). Pelagic tunicates, especially salps and doliolids, constituted a higher fraction of the biomass in CC (13%) than in SC (5%). There was no long-term trend detectable in total zooplankton carbon biomass, in marked contrast to a decline in zooplankton displacement volume in both regions. The difference between these biomass metrics is accounted for by a long-term decline in pelagic tunicates (particularly salps), which have a relatively high ratio of biovolume:carbon. The decline in pelagic tunicates was accompanied by a long-term increase in water column density stratification. No other taxa showed a decline over the duration of the study, apart from salps and pyrosomes in SC and doliolids in CC. Some zooplankton taxa showed compensatory increases over the same time period (ostracods, large decapods, and calycophoran siphonophores in both SC and CC; appendicularians and polychaetes in SC). Two tests for ecosystem shifts, a sequential algorithm and the cumulative sum of anomalies (CuSum) approach, failed to detect changes in 1976–1977 in total carbon biomass, displacement volume, or most individual major taxa, suggesting that aggregated biomass is an insensitive indicator of climate forcing. In contrast, both techniques revealed a cluster of step-like changes associated with the La Niña of 1999. The major El Niño's in the past half century have consistently depressed total zooplankton biomass and biomass of many major taxa in both SC and CC, although such effects are transitory. Much, but not all, of the interannual variability in zooplankton is shared between the Southern and Central California sectors of the California Current System.

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Keywords: Decadal change; Regime shifts; Zooplankton; Copepods; Euphausiids; Pelagic tunicates; Salps; Northeast Pacific; California Current

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1. Introduction

The California Current System (CCS) experiences climate variability at multiple time scales, ranging from the annual (Sydeman et al., 2006; Mackas et al., 2006) to the millennial (Field et al., 2006) and beyond. A major challenge in interpreting the temporal variability in this ocean environment is to understand the effects of processes acting and interacting on these multiple scales. However, it is apparent that characterizing physical climate variables alone is inadequate for understanding and forecasting trajectories of plankton ecosystems. The temporal dynamics of populations do not usually show linear tracking of climate forcing, but typically reflect nonlinear interactions within and among species (Hsieh et al., 2005). An exception appears when the organisms' generation times are closely synchronized with the dominant time scale of environmental forcing (Hsieh and Ohman, 2006). Hence, ecosystem research programs need to characterize the variations of the populations of interest, rather than relying on physical climate variables as surrogate indices.

This need for adequate characterization of the biotic properties of ocean ecosystems focuses attention on the very limited number of research programs that have sufficient continuity to address ecological responses on time scales of several decades. In the Northeast Pacific the program that stands out in this regard is CalCOFI (the *California Cooperative Oceanic Fisheries Investigations*). Since 1949, CalCOFI cruises have been conducted in the CCS, providing a rich empirical foundation for understanding biotic changes on a multi-decadal scale. An important component of CalCOFI is the simultaneous resolution of spatial and temporal changes in the ecosystem, together with high quality physical and chemical measurements. Unlike measurement programs that focus on one location or a limited number of geographic points in space, CalCOFI samples a broader geographic area. Although the coverage of cruises has changed considerably over time (e.g., Hewitt, 1988), even in years of minimal spatial coverage CalCOFI has sampled a minimum of 66 stations over ca. 200,000 km² of ocean surface. Other significant programs in the Northeast Pacific are reported in Mackas et al. (2006).

The long-term decline in zooplankton biomass (as measured by bulk displacement volume) observed in Southern California waters from CalCOFI samples (Roemmich and McGowan, 1995a,b) begged the question how different taxonomic groups may have changed over time. Calanoid copepods analyzed between 1951 and 1999 suggested long-term stability of copepod species composition and abundance (Rebstock, 2001), in marked contrast to the result from zooplankton displacement volume. Also contrasting with the trend in displacement volume, none of the eight dominant euphausiid species analyzed by Brinton and Townsend (2003) showed temporal declines. Instead, responses varied by species, with some subtropical euphausiids (notably the coastal *Nyctiphanes simplex*) showing a distinct increase in 1977 at the onset of a warm phase of the Pacific Decadal Oscillation (Brinton and Townsend, 2003). Mesopelagic larvae of southern offshore species of fishes also increased markedly in the Southern California Bight region after 1977 (Smith and Moser, 2003) and the geographic center of hake spawning shifted northward ca. 100 km (Hsieh, 2005). However, Lavaniegos and Ohman (2003) presented evidence from the Southern California region that pelagic tunicates did decline over the same time scale as displacement volume. Contributing to the temporal trend, one component of the salp assemblage, the cool-phase species present in 1951–1976, was nearly undetectable during the warm phase (1977–1998). These authors also found evidence of a possible change of this pattern in 1999. Colebrook (1977) found pronounced changes in major taxonomic groups through the El Niño cycle of 1955–1959, observing considerable coherence both among taxa and geographic subregions. Chelton et al. (1982) analyzed the covariability of zooplankton displacement volume with an index of southward transport on an interannual time scale and Roesler and Chelton (1987) extended this analysis to include spatial differences within the California Current System. However, there has been no comprehensive analysis of all mesozooplankton taxa, expressed in common units of biomass, that would permit the contribution of different taxa to multi-decadal trends to be assessed.

Therefore the present paper addresses the following central questions. Is the long-term decrease of zooplankton displacement volume also observed in terms of organic carbon biomass? Is the response similar among all major zooplankton taxa? Are long-term changes in zooplankton biomass and composition coherent between two major regions of the California Current System? Are there abrupt temporal changes in major taxa of zooplankton consistent with an interpretation of ecosystem shifts? We addressed these questions with the CalCOFI springtime zooplankton samples collected between 1951 and 2005 in Southern California and

Central California waters. The possible seasonal bias of the results is investigated with two seasonal sample series.

2. Methods

2.1. Sampling

The macrozooplankton samples analyzed were from CalCOFI springtime cruises for the period 1951–2005 plus all cruises available for the years 1969 and 1984. The latter two years were selected to describe seasonal variations before and after the 1976–1977 climate shift, both in El Niño-neutral years. Spring cruises (usually April, range: March–May) were the focus because they provided the best interannual coverage, attention to a single season permitted us to address interannual rather than seasonal variability, and because this is an important time period of fish spawning. The two study regions selected were off Southern California (lines 80 through 93, to station 70; Fig. 1) and Central California (lines 60 through 70, to station 90). The Central California stations chosen for analysis extended further offshore because of evidence for cross-shore extent of coastal filaments (e.g., Abbott and Zion, 1987). Many fewer spring cruises were conducted in Central California, particularly in the mid-1980s to 1990s, because of financial constraints and the southward contraction of the center of spawning of the California sardine. In both regions, sampling was carried out only every third year in the late 1960s to early-mid 1970s. All zooplankton tows were double oblique with calibrated flow meters mounted in the net mouth. Samples were fixed in sodium borate-buffered formaldehyde, displacement volume determined ashore (Kramer et al., 1972) after removal of fish larvae and adults, and samples archived in the Pelagic Invertebrates Collection of the Scripps Institution of Oceanography. Displacement volume used here is the total displacement volume inclusive of large organisms >5 ml individual biovolume. The net type and depth of tow changed: from 1951 to 1968 a 1-m diameter ring net with 0.55 mm mesh was towed to a depth of 140 m; between 1969 and 1977 a 1-m ring net with 0.505 mm mesh was towed to 210 m; and from

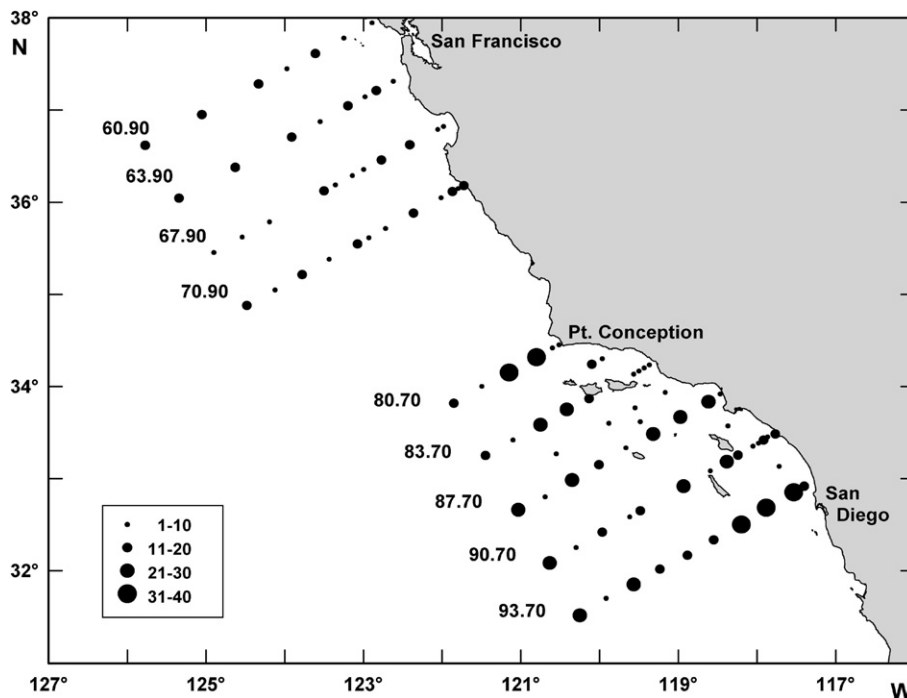


Fig. 1. Station locations for springtime CalCOFI cruises analyzed herein, 1951–2005. Stations are numbered at the offshore end of each line (line.station number). The Central California region defined here comprises lines 60 through 70 and Southern California, lines 80 through 93. Symbol diameter is proportional to the number of times each station is represented in the present zooplankton time series.

December 1977 to present a 0.71-m diameter bongo net with 0.505 mm mesh was towed to 210 m (Ohman and Smith, 1995). CalCOFI samples from 1949 to 1950 were not analyzed because of the shallower tow depth (70 m).

2.2. Zooplankton enumeration

For most taxa, samples within a cruise were pooled for purposes of enumeration, except for 14 cruises in Southern California (SC) and 4 cruises in Central California (CC), where samples were analyzed individually by station in order to assess spatial variability and its stability over time. Euphausiids were enumerated from all samples individually and these data were kindly provided by Brinton and Townsend (2003, updated). For each cruise, only samples collected at night (1 h after sunset until 1 h before sunrise) within the study region were analyzed. Stations shallower than 140 m (1951–1968) or 210 m (1969–2005) were omitted from pooled samples. The total number of nighttime samples selected for SC was 619 (8–19 per cruise) and 266 for CC (2–16 per cruise).

Large organisms (>25 mm total length) were counted from each entire sample, identified, and sized. These organisms were removed from the samples prior to pooling. A volume of each sample corresponding to 50 m³ of seawater filtered was then removed and combined into a pooled sample for each cruise (Rebstock, 2001). The samples we analyzed from Southern California were the same samples analyzed by Rebstock, although her analyses stopped in 1999 while the present analyses continue through 2005 and also include Central California. One quarter of each pooled sample was counted. In nonpooled samples, 1/8 was analyzed. All zooplankton were identified to the lowest taxonomic level practical for our expertise (over 400 taxa; usually species) and measured to the nearest mm, then aggregated into 19 (or fewer) major holoplankton taxa for the purposes of the present paper.

Counts were standardized to individuals m⁻² of sea surface because such values are less subject to bias than volumetric values (individuals m⁻³) when there are differences in maximum sampling depth (Ohman and Lavaniegos, 2002). A Mann–Whitney *U* test tested for increased biomass after 1968 as a consequence of the increase in sampling depth from 140 to 210 m. No consistent change in biomass in both regions was detected for any taxa except ostracods, chaetognaths, and large decapods (*P* < 0.05), suggesting increases in these three could reflect an artifact of the deeper sampling depth. Abundances of salps prior to 1978 were multiplied by a net factor of 2.68, as salps are better collected by the bongo net (Ohman and Lavaniegos, 2002). Euphausiids were multiplied by species-specific net factors reported in Brinton and Townsend (1981).

2.3. Length–carbon relationships

Abundances within size classes were converted to organic carbon biomass by applying carbon–length regressions or a combination of dry mass–length regressions and carbon percentage from the literature. Since the zooplankton categories analyzed are mixtures of species, we estimated carbon–length relationships using values of carbon content from diverse species, giving preference to those inhabiting the North Pacific. Data sources as well as the regression relations for each taxon are in the electronic [supplement materials](#) (Supplement Tables 1–3, Supplement Fig. 1). Only the largest organisms (the genera *Gennadas* and *Pasiphaea*) were included in the category large decapods. Heteropods, chondrophores, and polychaetes of the family Alcipidae were excluded from the present analyses due to a lack of data required for carbon conversion.

All carbon biomass data were $\log_{10}(x + 1)$ transformed and then the mean and 95% confidence interval calculated for the cruises (14 in SC and 4 in CC) where station samples were analyzed individually. Carbon anomalies were calculated after removing the long-term mean (1951–2005) of each region.

2.4. Physical indices

Density stratification was calculated as the difference in σ_t between a depth of 150 m and 10 m, for each CalCOFI station within the two sampling regions. A spring cruise mean $\pm 95\%$ C.L. was then calculated for all stations for which temperature, salinity, and density were available (SC: median of 27 stations per

cruise, range: 6–38; CC: median of 19 stations per cruise, range: 7–45). These measurements were available for 46 years in SC and 21 years in CC.

Monthly sea level measurements near San Diego (32°42.8'N, 117°10.4'W) and San Francisco (37°48.4'N, 122°27.9'W) were obtained from the University of Hawai'i Sea Level Center (<http://ilikai.soest.hawaii.edu/uhscl/>). The average seasonal cycle was then removed from these data, followed by removal of a linear trend. The resulting anomalies of de-trended sea level were used as a mid-latitude index of El Niño. The Southern Oscillation Index (SOI, from the Climate Prediction Center of the U.S. National Weather Service, <http://www.cpc.ncep.noaa.gov/data/indices/soi>) was used as a remote, tropical index of El Niño. The Northern Oscillation Index (NOI, from the Environmental Research Division of NOAA's Southwest Fisheries Science Center; Schwing et al., 2002) is an index of extratropical forcing and is available at http://las.pfeg.noaa.gov/las6_5/servlets/dataset. From the same web site we obtained the Bakun upwelling index for two locations centered on 33°N, 119°W and 36°N, 122°W. Mantua et al.'s (1997) index of the Pacific Decadal Oscillation is available at ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest.

2.5. Data analysis

For statistical comparisons between Southern California (SC) and Central California (CC), only the 32 years in common were considered and the zooplankton anomalies for SC were therefore recalculated. Spearman rank order correlation analysis was carried out between carbon anomalies of the two regions. Geometric means among different time periods were compared with the nonparametric Kruskal–Wallis test. Two approaches were used to test for abrupt changes in zooplankton time series, but only for the Southern California time series for which there were many fewer years with missing data. The sequential *t*-test of Rodionov (2004) was calculated for time series of carbon anomalies of each major taxon, using a minimum regime length $l = 10$ y, $\alpha = 0.05$, and Huber's weighting parameter of 3 (i.e., allowing anomalies of up to 3 standard deviations to have equal weights). Cumulative sums of anomalies (CuSum; Beamish et al., 1999; Rebstock, 2002) were plotted and examined visually for changes in slope. Abrupt changes in slope reflect changes in the underlying time series.

Secular trends in biomass of the major taxa were investigated using linear regression analysis on log-transformed data of organic carbon. Because most taxa are relatively short-lived, with generation times of weeks to a few months, serial autocorrelation of annual samples was unlikely. To analyze co-variability among taxa, Principal Component Analysis (PCA) was performed using results from both SC and CC (Systat v. 11). PCA was done with standardized, log-transformed carbon biomass data by first subtracting the overall mean for each taxon and then dividing by the standard deviation.

A General Linear Model (GLM) was used to explore the co-variation of log-transformed zooplankton biomass with several physical variables, including water column density stratification (cruise average) measured from CalCOFI cruises in the same region where the zooplankton were sampled, detrended sea level anomaly (DSL, December–January–February average) as a mid-latitude index of El Niño, the Southern Oscillation Index (SOI, December–January–February average) as a tropical index of El Niño, the annual average of the Northern Oscillation Index (NOI), annual average of the Pacific Decadal Oscillation Index (PDO), and the Bakun Upwelling Index (BUI, April–May–June average). Total organic C, displacement volume, and each of the major taxa of zooplankton were used as a dependent variable in a separate GLM analysis. A forward stepwise fitting method was used, with α -to-enter and α -to-remove = 0.05 (Systat v. 11). Stepwise multiple regression accounts for partial correlation between variables.

3. Results

3.1. Relation between biomass as organic carbon and displacement volume

Springtime zooplankton biomass as total organic carbon shows considerable variability from year to year (Fig. 2a and b). In Southern (SC), carbon biomass declined during major El Niño's (note 1958, 1972, 1978, 1983, 1992–1993, 1998), but usually recovered to the long-term mean within one or two years. El Niño-related

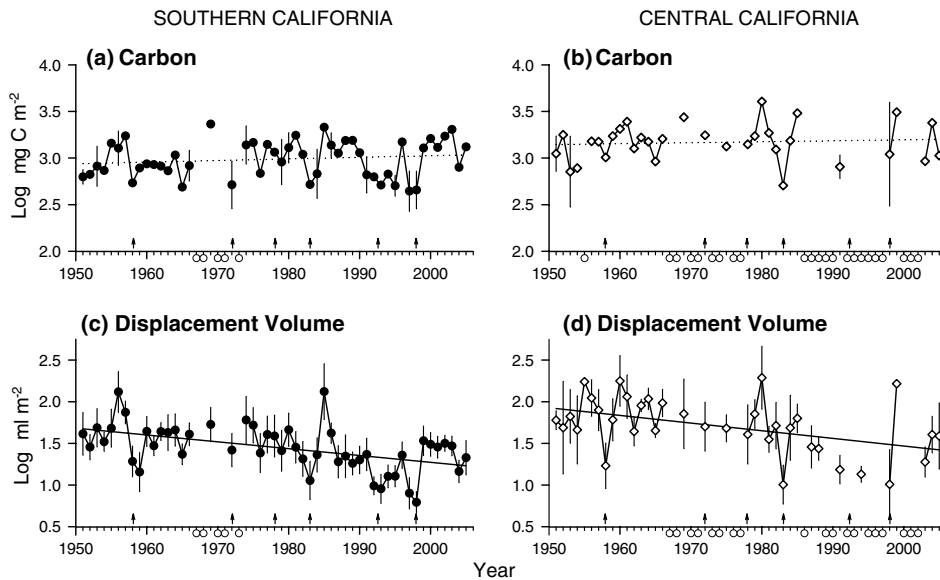


Fig. 2. Interannual variation in total zooplankton biomass expressed as (a and b) organic carbon and (c and d) displacement volume, from springtime CalCOFI cruises from Southern California (SC; a and c) and Central California (CC; b and d). El Niño years, defined from Fig. 11 below, are identified with upward facing arrows. Open circles below the y-axis indicate no springtime samples available, in this and subsequent figures.

depression of carbon biomass also occurred in Central California (CC), to the extent the more discontinuous data set permits assessment. There was an abrupt increase in carbon biomass in 1999, following the strong El Niño of 1998. There was no significant long-term trend in total organic carbon biomass in either region over the 55 year period of sampling ($P > 0.30$, linear regression).

In marked contrast, zooplankton biomass from the same plankton samples but expressed as displacement volume showed highly significant temporal declines ($P < 0.005$, Fig. 2c and d). Between 1951 and 2005, the average springtime displacement volume decreased by 64.1% in SC and 68.2% in CC. Displacement volume also showed transient decreases during major El Niño's and sharp increases in the La Niña of 1999. The temporal variability in displacement volume (DV) was considerably higher than that of organic carbon (C), for both SC (16.9% DV vs. 6.6% C) and CC (20.2% DV vs. 6.3% C; in both regions variability expressed as the coefficient of variation of log-transformed data, considering only the 32 years of common sampling). Neither measure of zooplankton biomass displayed an abrupt shift at or near 1976–1977 (Fig. 2).

There was a highly significant positive relationship between biomass as organic carbon and displacement volume (Fig. 3a, $r^2 = 0.503$, $P < 0.0001$, Model II regression), which may seem surprising in light of the contrasting temporal trends observed in Fig. 2. However, the positive relationship between these two measures of biomass accounts for only half the variance in either and masks an important temporal change. Examination of the residuals of the Model II regression (Fig. 3b) show a significant temporal trend ($P < 0.0001$). For the earlier part of the time series (1951–1976), in the cooler state of the Pacific Decadal Oscillation (PDO), there was lower carbon biomass than expected from measured displacement volume. In the warmer phase of the PDO (1977–1998) and then more recently from 1999 to 2005, there was progressively higher carbon biomass than expected from displacement volume. This trend suggests a diminished contribution over time from organisms with a high ratio of biovolume:carbon.

3.2. Contribution of major taxa to zooplankton biomass

The average organic carbon biomass of zooplankton ranged between 440 and 2307 mg C m⁻² during 1951–2005 off Southern California, with a geometric mean of 971 mg C m⁻². In the complete data set for SC ($N = 50$ years), three main taxa (copepods, euphausiids, and chaetognaths) comprised 90% of the carbon bio-

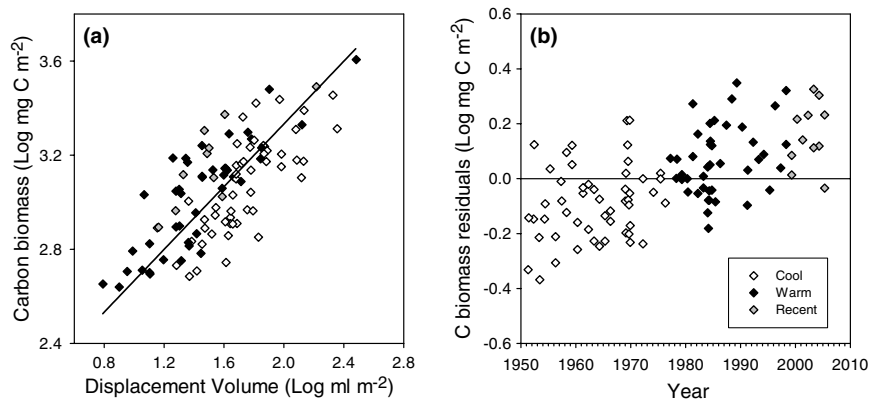


Fig. 3. (a) Relationship between zooplankton carbon biomass (C) and displacement volume (DV) based on spring means from both Southern and Central California. (b) Relationship between the regression residuals from panel (a) and year. Symbols represent the different climate periods: cool (1951–1976), warm (1977–1998), and recent (1999–2005). Model II regression: $\text{Log } C = 0.6664 * (\text{logDV}) + 1.9997$, $r^2 = 0.538$, $P < 0.00001$.

mass, while all pelagic tunicates together (salps, doliolids, appendicularians, and pyrosomes) accounted for only 3.4%, and the remaining zooplankton 6.9%, of the total.

In order to compare Central and Southern California, we consider only those years with observations in both areas ($n = 32$, Fig. 4). The geometric mean of SC biomass using the reduced data set remained similar (935 mg C m^{-2}) to that estimated for the entire series, while carbon biomass in CC averaged 1468 mg C m^{-2} . That is, on average, the organic carbon biomass is 57% higher in CC compared to SC. Copepods and euphausiids were the dominant contributors to zooplankton biomass in both regions, although copepods and chaetognaths made a relatively greater contribution in the south (Fig. 4a) and euphausiids and pelagic tunicates constituted an appreciably larger fraction in the north (Fig. 4b).

Absolute biomass in 12 of 19 taxa, in addition to total organic C, was significantly higher in CC than in SC (Table 1). Among the primary taxa lacking inter-regional differences were copepods and chaetognaths. Euphausiids showed higher carbon biomass in Central California, with mean biomass double that for SC (Table 1). More impressive differences were observed in two groups of tunicates. Salp biomass was almost triple and doliolid biomass almost 10-fold higher in CC than SC ($P < 0.05$).

The proportional composition of different taxa to zooplankton carbon biomass varied from year to year (Fig. 5a and b). In SC, pelagic tunicates as a fraction of the total decreased over time ($P < 0.05$,

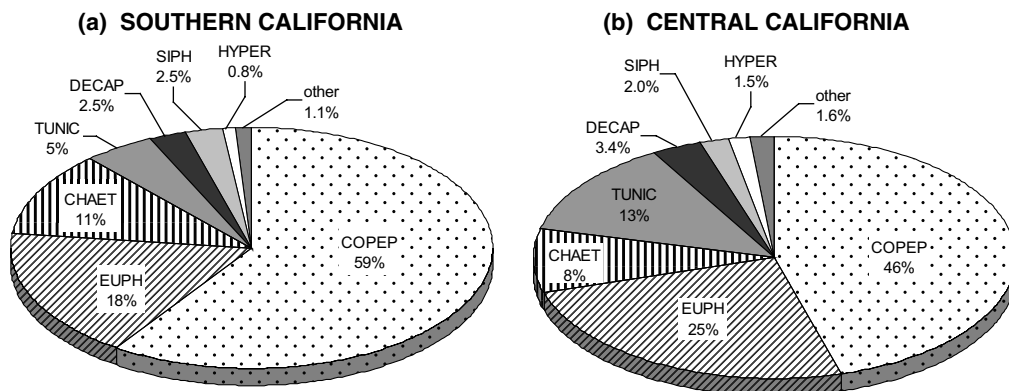


Fig. 4. Proportion of carbon biomass contributed by primary zooplankton taxa from (a) Southern California and (b) Central California, based on geometric means of all springs sampled in common ($N = 32$ for both regions).

Table 1

Geometric mean carbon biomass (mg C m^{-2}) of major taxa in two regions of the California Current System (Southern California and Central California), associated P -value of the Mann–Whitney U test comparing means between regions, Spearman rank correlation (r_s) between regions, and P -value of r_s ($P < 0.05$ in boldface, $N = 32$)

Taxon	Southern California (mg C m^{-2})	Central California (mg C m^{-2})	U test P -value	r_s	r_s P -value
Copepods	476.5	544.6	0.264	0.455	0.009
Euphausiids	141.0	294.0	0.000	0.290	0.107
Chaetognaths	90.1	100.7	0.326	0.651	0.000
Sergestids	16.4	32.2	0.014	0.110	0.548
Salps	14.9	41.1	0.047	0.376	0.034
Calycophoran siphonophores	12.9	9.5	0.057	0.226	0.214
Hyperiid	6.4	18.0	0.000	0.152	0.406
Physonect+cystonect siphonophores	4.9	11.1	0.002	0.339	0.057
Ostracods	4.1	6.2	0.015	0.163	0.371
Appendicularians	3.6	3.5	0.764	0.307	0.088
Doliolids	2.7	25.5	0.000	0.332	0.063
Large decapods	1.9	2.2	0.826	0.414	0.018
Hydromedusae	1.3	2.8	0.000	−0.036	0.847
Polychaetes	1.2	4.9	0.000	0.367	0.039
Thecosome pteropods	1.1	2.4	0.005	0.063	0.730
Ctenophores	0.9	1.2	0.196	0.049	0.788
Pyrosomes	0.5	0.8	0.764	0.552	0.001
Gymnosome pteropods	0.2	0.7	0.001	0.262	0.148
Scyphomedusae	0.1	0.1	0.010	−0.019	0.916
Total carbon biomass	934.9	1468.2	0.000	0.404	0.022

linear trend) and other zooplankton taxa increased in relative importance ($P < 0.05$). In CC, there was also a tendency for the proportion of pelagic tunicates to decrease over time, although this was not significant ($P > 0.10$).

Total carbon biomass grouped by climatic periods showed similar log-means for the cool and warm phases (1951–1976 and 1977–1998, respectively) in Southern California (Fig. 5c), while the period from 1999 to 2005 had the highest log mean. However, differences in total carbon among these three time periods were not significant ($P > 0.05$, Kruskal–Wallis nonparametric ANOVA). Nevertheless, some taxa considered separately showed differences among these three periods, suggesting that changes in carbon biomass of some taxa compensated for reciprocal changes in other taxa. Copepod biomass during the recent years (1999–2005) was significantly higher than in the cool period ($P < 0.05$, Mann–Whitney U test) and also higher than in the warm period ($P = 0.05$), with no differences between cool and warm periods ($P > 0.10$). Tunicate biomass exhibited a significant decrease from the cool to warm periods ($P < 0.05$). Despite the differences in absolute carbon in these two taxa, the proportion of copepods, euphausiids, and chaetognaths was relatively stable through time, representing 87–91% of the total zooplankton (Fig. 5e). Considering only the 32 years for which there are data for both SC and CC, total carbon showed significant differences between regions only during the cool period ($P < 0.01$, Fig. 5d). In CC the mean carbon biomass of the three periods did not differ ($P > 0.10$). No significant changes were found among time periods for absolute biomass of each of the four main taxa, although their relative proportions changed, suggesting a progressively smaller contribution of tunicates to total biomass in both regions through time (Fig. 5f).

Closer inspection of the copepod time series (Fig. 6a) indicated high variability between 1951 and 2005 in SC with spring means varying between 138 and 1625 mg C m^{-2} . Negative or positive anomalies were not consistently associated with the cool or warm climate periods. Negative anomalies were associated with the El Niños of 1972, 1982–1983, 1992–1993 and 1997–1998, but not with El Niño 1958–1959 or 1978. An interesting feature of the copepod time series was the episode of low values during the 1990s, followed by a period of positive anomalies after 1998. The depressed biomass during the 1990s was also observed in euphausiids (Fig. 6b), chaetognaths (Fig. 6c), and tunicates (Fig. 6d). The biomass of all four of these dominant taxa also

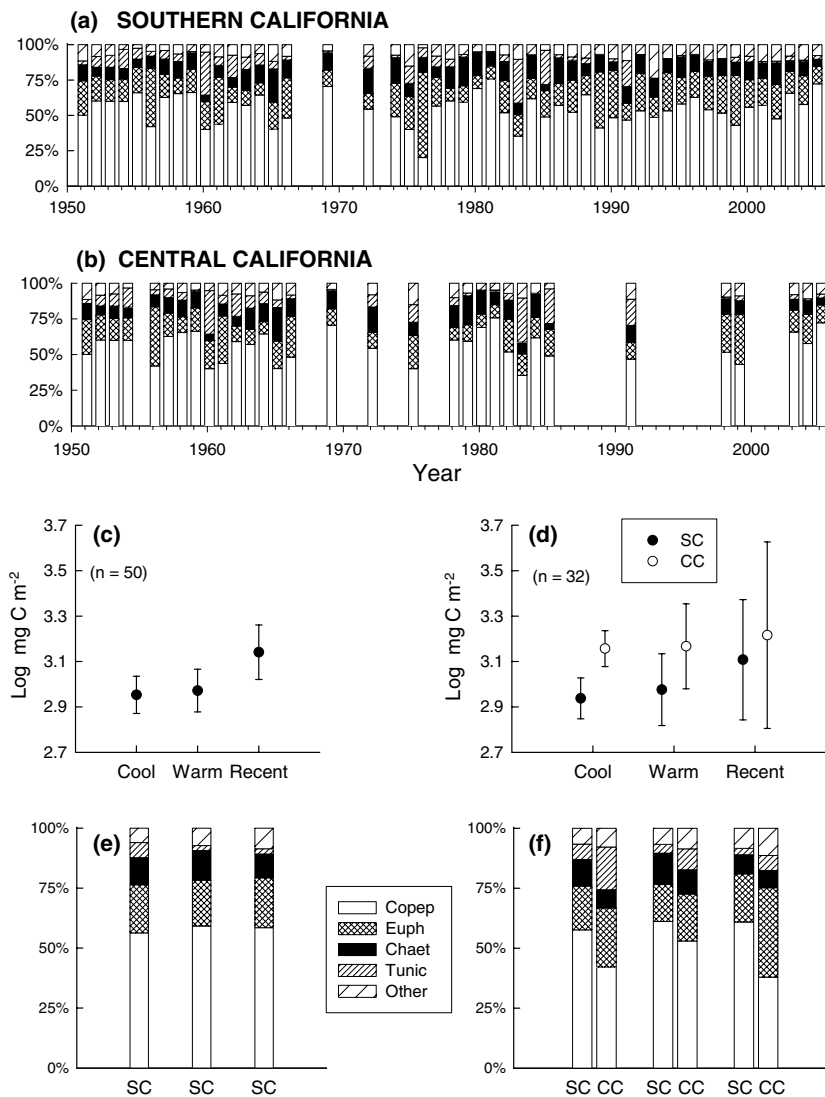


Fig. 5. Temporal variation in proportional taxonomic composition of dominant zooplankton taxa and in total zooplankton carbon biomass. Interannual variations in proportional composition in (a) Southern California and (b) Central California. Mean biomass $\pm 95\%$ confidence intervals in three climate periods (cool [1951–1976], warm [1977–1998], and recent [1999–2005]) in (c) Southern California alone and (d) Southern California compared with Central California. Average proportions of the dominant taxa in the three climate periods in (e) Southern California alone and (f) Southern California compared with Central California in each of the three time periods. Southern California (SC) results shown in (c) and (e) are for the complete data set ($n = 50$); while in (d) and (f) only the years in common ($n = 32$) with Central California (CC) are used for comparison between regions. Primary taxa included are copepods, euphausiids, chaetognaths, pelagic tunicates, and all other taxa combined.

increased after 1998. Tunicates exhibited a different pattern, with the most consistent positive anomalies in the cool phase.

Common to all four dominant taxa in SC was a relatively abrupt reversal of anomalies in 1999. Similar changes occurred in this La Niña year for hyperiid amphipods, polychaetes, appendicularians, physonect+cystonect siphonophores, and ctenophores (see Supplement Figs. 2–7).

Linear regressions of carbon biomass through time revealed no temporal trend in three (copepods, euphausiids, and chaetognaths) of the four dominant taxa in both regions (Figs. 6,7a,b,c). In contrast, the tunicates exhibited a similar decreasing trend in both SC and CC, although the trend was significant at $P < 0.05$ in

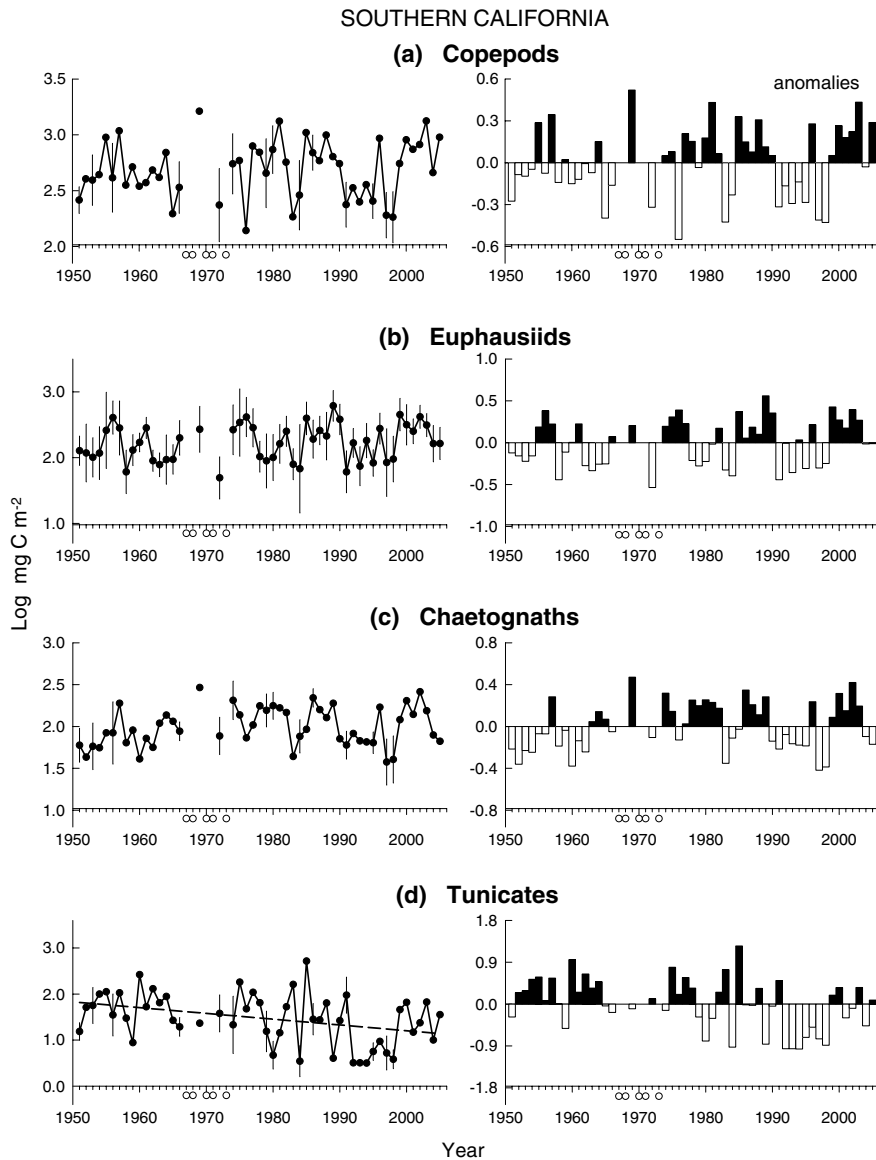


Fig. 6. Interannual variation in organic carbon biomass of the dominant zooplankton constituents in springtime CalCOFI cruises in the Southern California region: (a) copepods; (b) euphausiids; (c) chaetognaths; (d) tunicates. Mean \pm 95% confidence intervals in years when individual samples enumerated; anomalies illustrate departures from the mean of 1951–2005, in this and subsequent figures. Dashed line indicates linear regression significant at $P < 0.050$.

SC (Fig. 6d) and $P < 0.065$ in CC (Fig. 7d). Similar regressions for individual tunicate taxa (salps, doliolids, appendicularians, pyrosomes) and taxa that made smaller contributions to the total zooplankton carbon biomass are shown in the appendix (Supplement Figs. 2–7). Salps showed significant temporal declines in SC (Suppl. Fig. 4e), doliolids a decline in CC (Suppl. Fig. 5d), and pyrosomes a decline in SC (Suppl. Fig. 4f). Appendicularians showed a long term increase in SC (Suppl. Fig. 4c) but not in CC (Suppl. Fig. 5c). Three taxa showed a significant temporal increase in both regions (ostracods, large decapods, and calycophoran siphonophores). Of these, ostracods and large decapods showed a significant increase in biomass after 1968 in both SC and CC, suggesting that this apparent change could be an artifact of increased sampling depth. A temporal increase was detected for polychaetes from SC (Suppl. Fig. 2e).

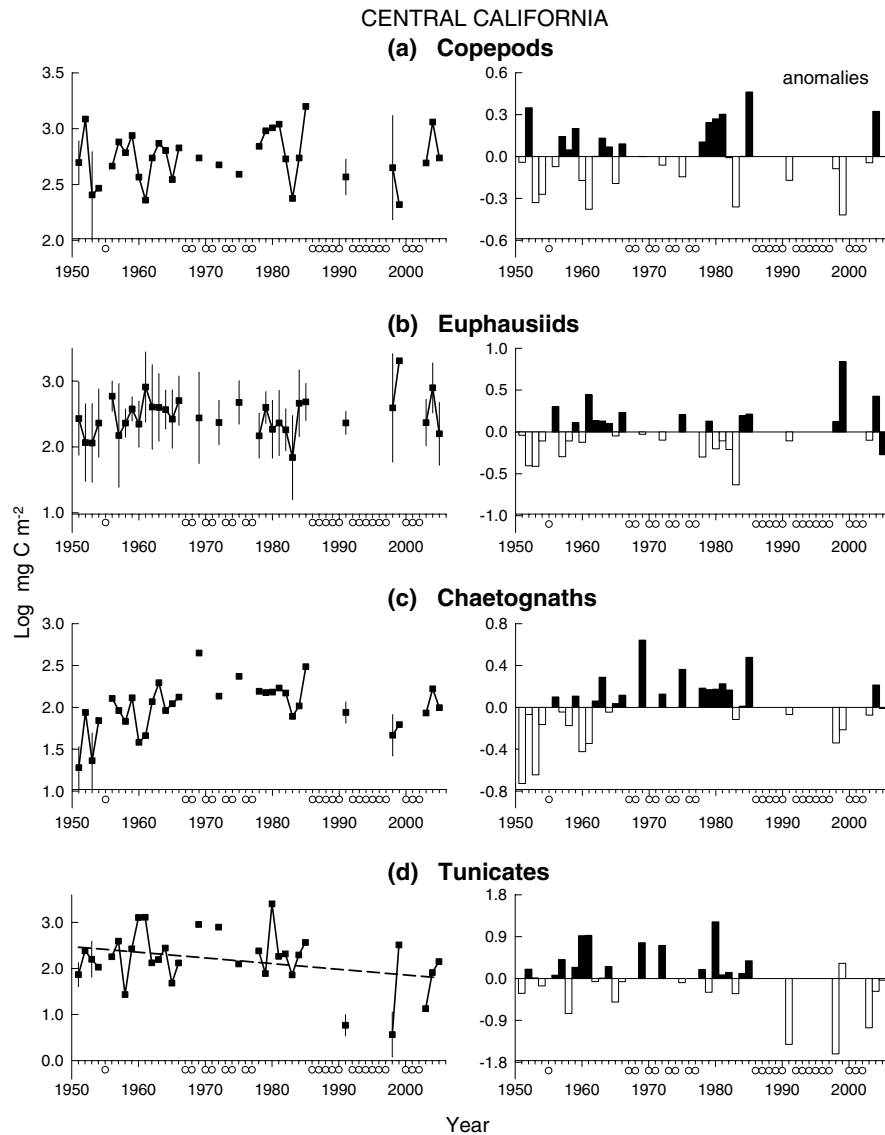


Fig. 7. Interannual variation in organic carbon biomass of the dominant zooplankton constituents in springtime CalCOFI cruises in the Central California region: (a) copepods; (b) euphausiids; (c) chaetognaths; (d) tunicates. Dashed line indicates linear regression significant at $P < 0.065$.

3.3. Coherence between Southern and Central California

In addition to comparing absolute carbon biomass and temporal trends between regions, we wish to assess whether zooplankton assemblages in the two regions show a coherent response on interannual time scales. Spearman correlation based on carbon biomass anomalies indicated similar responses between regions for total zooplankton carbon and six of the major taxa ($\alpha = 0.05$, Table 1). Thus, copepods, the most important contributor to carbon biomass, varied through time in a similar manner in both SC and CC, along with chaetognaths, large decapods, salps, pyrosomes, and polychaetes. The physonect+cystonect siphonophores, euphausiids, appendicularians, and doliolids showed probabilities between 0.1 and 0.05. These results suggest that much of the interannual variation in biomass of the primary suspension feeders and the most important group of predators is correlated in SC and CC.

Principal Component Analysis was also utilized to analyze the dominant modes of variability over time. The four first principal components extracted from the matrix of spring means of 19 major taxa explained 59.5% of the total variance. The first principal component (PC1) accounted for 30.3% of the variance in inter-annual springtime variations in the two regions, with relatively high loadings on most taxa: doliolids, polychaetes, physonect+cystonect siphonophores, sergestids, large decapods, copepods, hydromedusae, euphausiids, hyperiid amphipods, and chaetognaths (Table 2). These include a variety of suspension-feeding taxa together with covarying carnivores. PC2 explained 11.8% of the variance, with strong positive loadings by salps and hyperiid amphipods and inverse loadings with calycophoran siphonophores and chaetognaths. PC3 accounted for 9.8% of the variance, with strong positive loadings by ctenophores, pyrosomes, and appendicularians and inverse loadings on sergestids, large decapods, and scyphomedusae. PC4 explained a further 7.6% of the variance, with highest positive loadings on thecosome pteropods and ostracods, and relatively high negative loadings on sergestids, large decapods, and pyrosomes.

The time series of PC1, PC3, and PC4 (CC) showed no significant trend with time ($P > 0.05$, Fig. 8), although PC4 (SC) showed a weak temporal increase ($P < 0.05$). In the case of PC1, the mean values were somewhat higher in CC than SC because of the generally higher biomass in the former region. PC2 exhibited negative trends with time in both regions, primarily reflecting the long-term decline in salps.

3.4. Zooplankton variability in relation to physical variables

3.4.1. Physical ocean characteristics

In both Southern California (SC) and Central California (CC) waters, average springtime density stratification (150–10 m) has increased over the past 55 years (Fig. 9a and b). There is no significant difference in slopes in the two regions ($P > 0.05$). In addition to the temporal trend, there are pronounced interannual variations, notably a sharp decrease in stratification during the La Niña of 1999 and possibly a step-like change between 1976 and 1978, which is more apparent in SC than in CC. Thus, the overall increase described by a simple linear regression describes only part of the variance in density stratifica-

Table 2
Principal Component Analysis of major taxa of zooplankton for both Southern California and Central California

Taxon	Eigenvectors			
	PC1	PC2	PC3	PC4
Polychaetes	0.330	−0.029	−0.167	0.227
Doliolids	0.318	0.100	−0.034	−0.007
Physonects+cystonects ^a	0.307	0.111	0.169	−0.200
Sergestids	0.282	−0.125	−0.358	−0.325
Large decapods	0.279	−0.184	−0.353	−0.294
Copepods	0.275	−0.216	0.158	−0.044
Hydromedusae	0.275	0.102	0.207	0.125
Euphausiids	0.262	0.075	−0.053	−0.229
Hyperiiids	0.253	0.280	−0.030	0.179
Chaetognaths	0.252	−0.333	0.104	−0.161
Gymnosomes	0.227	0.191	0.057	0.036
Ostracods	0.212	−0.213	0.102	0.371
Appendicularians	0.196	−0.196	0.259	0.180
Thecosomes	0.178	0.248	−0.125	0.478
Ctenophores	0.099	0.191	0.546	−0.147
Scyphomedusae	0.076	−0.063	−0.263	0.235
Pyrosomes	0.070	0.172	0.300	−0.256
Salps	0.066	0.442	−0.159	0.009
Calycophorans ^a	0.008	−0.477	0.168	0.215
Cumulative variance	30.3%	42.1%	51.9%	59.5%

The bottom line indicates the cumulative percentage of the total variance explained by successive principal components (PC). Values $>|0.25|$ indicated in boldface.

^a Siphonophores.

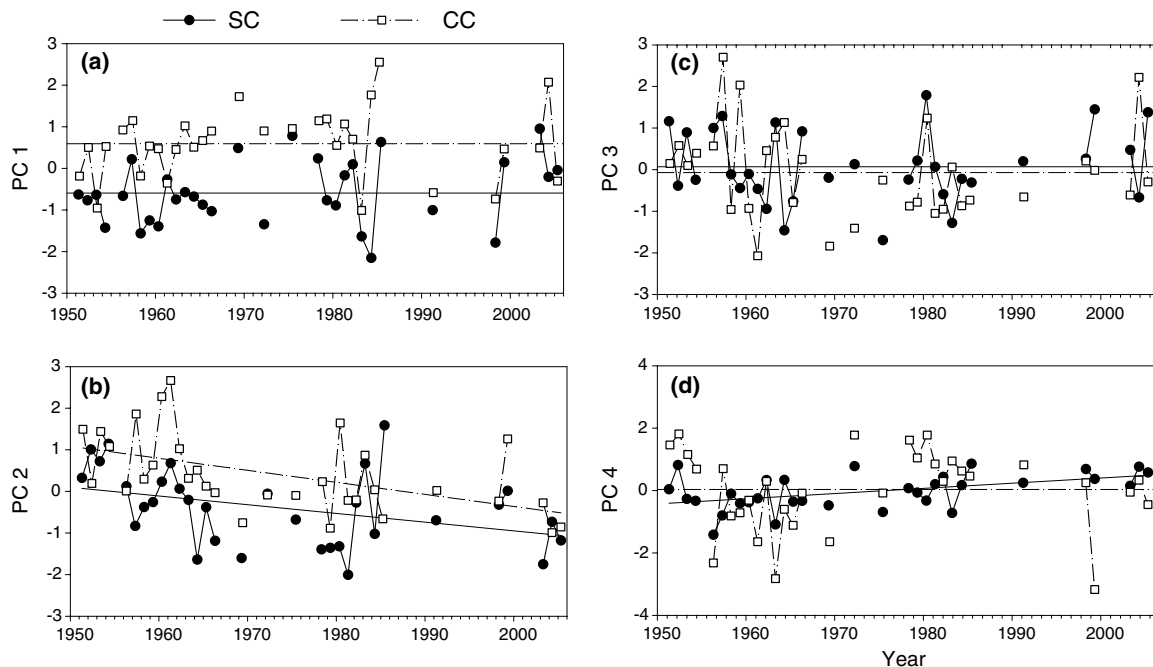


Fig. 8. Interannual variation in PCA scores for the first four principal components: (a) PC1; (b) PC2; (c) PC3; (d) PC4. Lines indicate PCA score means by region in (a), (c), and (d – Central California) and significant ($P < 0.050$) fitted linear regressions in (b) and (d – Southern California).

tion. Also, neither temperature nor salinity alone accounts for observed changes in density stratification, especially in SC. In SC, temperature stratification (10–150 m) was slightly weaker after 1999, but salinity stratification markedly stronger after 2001 (data not shown), resulting in the post-2001 increase in density stratification seen in Fig. 9a. Both temperature and salinity stratification increased in recent years off Central California, although there were many years of data missing from that region. Most of the density changes are attributable to decreased density in near-surface waters. Interannual variations in springtime density stratification are correlated between SC and CC ($P < 0.01$), with 38.4% of the variance shared between regions.

We use detrended sea level anomalies (DSLA), with the seasonal cycle also removed, as a local index of ENSO. Detrending was done with least squares linear regression. Years with DSLA off San Diego (33°N) and San Francisco (36°N) elevated above 1 standard deviation are associated with the stronger ENSO events detected along the equator by indices such as Niño 3.4 and the Southern Oscillation Index. Considering years where DSLA exceed $\pm 1SD$ for at least three successive months as El Niño years, we recognize the years of 1957–1958, 1972, 1978, 1982–1983, 1992–1993, and 1997–1998 as having El Niño expressions in California waters (Fig. 9c). The Dec.–Jan.–Feb. average DSLA, used below in our multiple regression analysis, was correlated between San Diego and San Francisco ($P < 0.0001$), with 57.4% of the variance shared between the two regions. Thus, both ENSO variations and the long-term trend in stratification are shared between Southern and Central California, but some other interannual variability is not (cf. Fig. 9c).

The Bakun upwelling index for the region centered on 33°N, 119°W (near San Diego) is similarly correlated with the index computed for 36°N, 119°W (near San Francisco), with 58.0% of variance shared between regions ($P < 0.0001$, Fig. 9d). However, the extent of agreement between regions can differ among years. For example, in El Niño conditions of 1958 and 1983, upwelling-favorable winds were more sharply depressed off CC than off SC while approximately similar decreases in upwelling favorable winds were experienced in the two regions in El Niños of 1972, 1978, 1993, and 1998 (Fig. 9d).

Hence, these physical variables suggest considerable coherence between Southern and Central California waters, with additional variations that are unique to the respective regions.

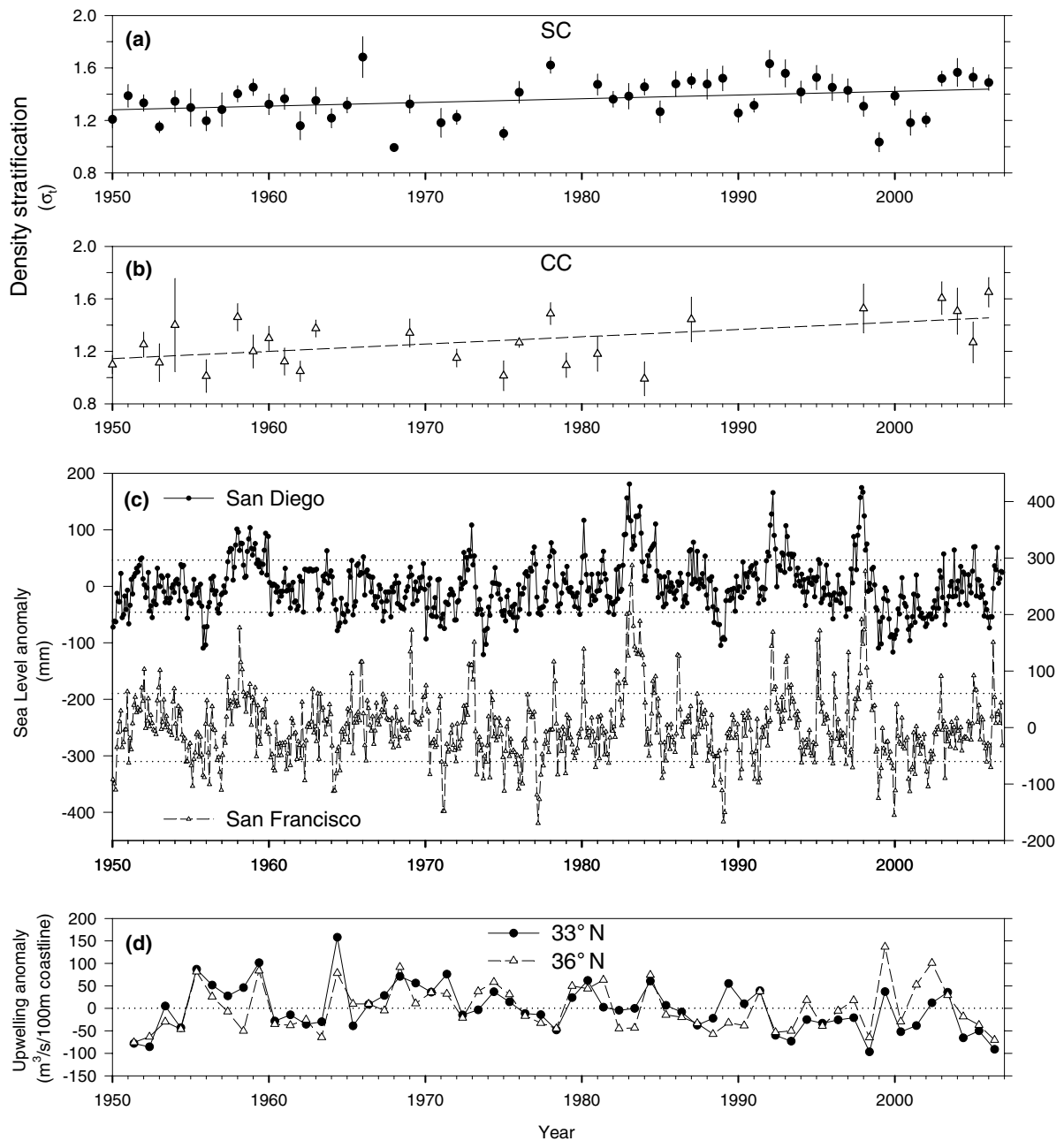


Fig. 9. Interannual variation in water column characteristics in Southern California (SC) and Central California (CC) waters. Average springtime density stratification (150–10 m) \pm 95% CI from (a) SC and (b) CC, with associated linear trends ($P < 0.050$). Detrended sea level anomalies from (c) San Diego (left axis scale, solid symbols) and San Francisco (right axis scale, open symbols), as a mid-latitude index of ENSO. Dotted horizontal lines indicate ± 1 SD around the mean. (d) Anomalies from the March–April–May mean upwelling index centered on 33°N (solid line) and 36°N (dashed line).

3.4.2. Co-variation of zooplankton and physical variables

The General Linear Model describing zooplankton biomass and six physical variables (DSLA, SOI, NOI, PDO, Bakun upwelling, and CalCOFI density stratification) generally yielded regression equations that explained no more than 10–20% of the variance in each dependent variable. The exceptions were pelagic tunicate C, for which a single variable (density stratification) explained 29.3% of the variance and zooplankton

displacement volume, for which both density stratification and NOI combined explained 33.9% of the variance. As density stratification was the principle explanatory variable in both cases, we illustrate these relationships in Fig. 10, converted to a Model II regression equation to account for the error associated with both the X and Y variables.

Three cases serve to illustrate a drawback to fitting a simple linear model, even when using a log-transformed dependent variable. For total carbon biomass, euphausiid carbon biomass, and physonect+cystonect siphonophore carbon biomass, we found a generally negative relationship with DSLA, which we use as a mid-latitude index of El Niño. However, in all cases the relationship with DSLA explained variance only at the extremes of very low or very high sea level anomalies (Fig. 11). At the lowest anomalies, to the left of the 1 standard deviation (SD) line in Fig. 11 and corresponding to La Niña conditions, all three measures of biomass (total, euphausiid, and siphonophore carbon) were higher than average. Conversely, at the highest DSLA values, to the right of the 1SD line and corresponding to strong El Niño conditions, all three measures showed a declining relationship. However, in between, within ± 1 SD of the mean, there was substantial variability that was unrelated to DSLA. This result implies nonlinear effects of El Niño: only the extreme highs and lows of the ENSO cycle are likely to influence zooplankton biomass in a measurable way.

Notably, the Southern Oscillation Index never entered into a regression equation, unlike DSLA. This suggests that remote, equatorial-based indices of El Niño are less appropriate than an index derived from mid-latitudes. The Northern Oscillation Index rarely explained significant variance. The coastal upwelling index was selected as an explanatory variable for only two of the major taxa (chaetognaths and hyperiids) and explained only a small component of the interannual variability.

3.5. Tests for ecosystem shifts

The sequential test for “regime shifts” of Rodionov (2004) was first tested with the annual average of the PDO index (Mantua et al., 1997) from 1950 to 2005. It identified one distinctive shift significant at $\alpha = 0.05$, in 1977 (not shown). The same test applied to total zooplankton biomass from Southern California, as anomalies from the long-term mean organic carbon biomass, detected no shifts over the period 1951–2005 ($P > 0.05$). When applied to the major taxa individually, there were no shifts detected across 1976–1978 for any taxon (Fig. 12, filled bars; change point years are grouped into pairs). The time period for which the sequential test detected shifts for the largest number of taxa was in 1998–1999 (hyperiids, siphonophores, chaetognaths, and tunicates). Smaller numbers of taxa showed changes in 1960–1961 (ostracods), 1968–1969 (polychaetes, chaetognaths), 1990–1991 (chaetognaths), 1992–1993 (tunicates), and 2000–2001 (ostracods, medusae).

The CuSum method tested with the PDO index from 1950 to 2005 showed one abrupt, sustained change in slope in 1976 and two less pronounced changes, in 1988 and 1998, respectively (not shown). CuSum plots of

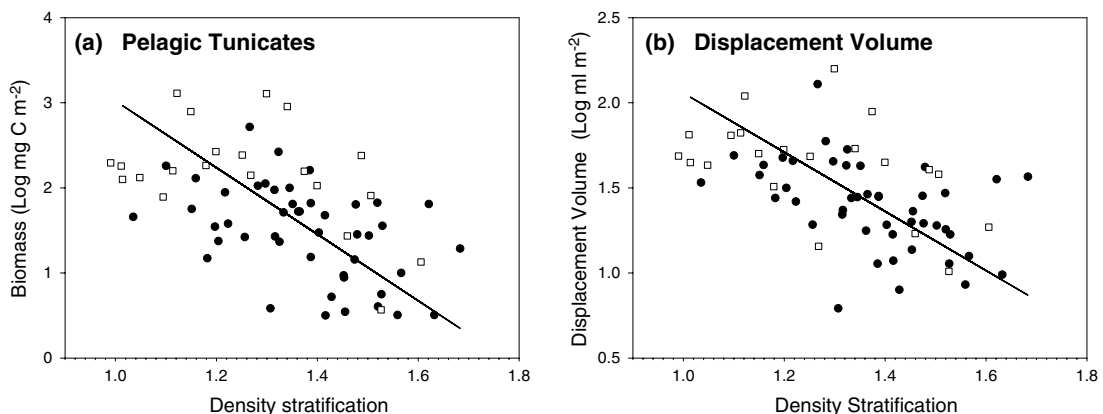


Fig. 10. Relationship between water column density stratification (STRAT) and (a) carbon biomass of pelagic tunicates (TC, Model II regression: $\text{Log TC} = -3.910 * (\text{STRAT}) + 6.929$, $r^2 = 0.293$, $P < 0.00001$) and (b) zooplankton displacement volume (DV, Model II regression: $\text{log DV} = -1.739 * (\text{STRAT}) + 3.796$, $r^2 = 0.275$, $P < 0.00001$). Solid symbols are from SC and open symbols from CC.

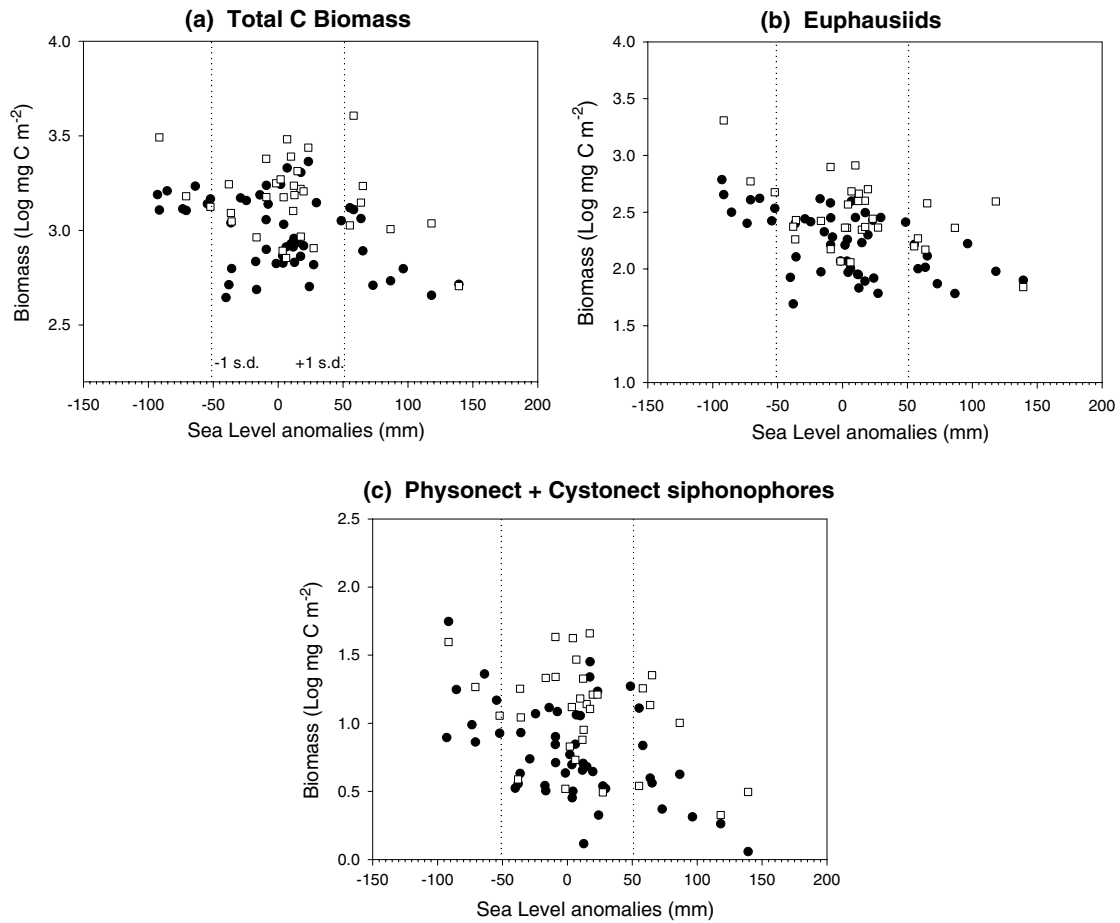


Fig. 11. Relationship between detrended sea level anomalies (DTSLA) and (a) total carbon biomass, (b) euphausiid biomass, and (c) biomass of physonect+cystonect siphonophores. Dotted vertical lines indicate ± 1 SD of the long term mean DTSLA.

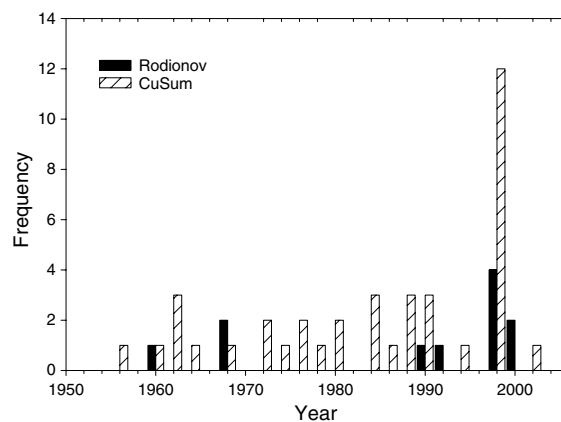


Fig. 12. Interannual variation in the frequency of taxa that showed change points in a given year by the test of Rodionov and CuSum.

total zooplankton carbon biomass anomalies showed no change in slope in 1976–1977, but slope changes in 1966, 1990, and 1998. CuSum analysis of major zooplankton taxa analyzed individually revealed no elevation of numbers of taxa with slope changes in 1976–1978 in comparison with other years (Fig. 12, hatched bars).

The most consistent result from CuSum analysis was the change in slope for all taxa analyzed in 1998–1999; in all cases the CuSum slope became positive, indicating an increase in biomass.

3.6. Seasonal variability

The preceding results are based upon analysis of interannual variations in springtime biomass, which does not consider the possibility of long-term phenological changes or different trends at other times of year. Neither plankton samples nor analytical resources were available to address these issues in a comprehensive manner, but we compared seasonal variations during one year in a cool period (1969) and one in a warmer period (1984). Both years are El Niño-neutral.

April was typically at or near the annual peak carbon biomass for copepods, apart from SC in 1984. This seasonal trend in copepods, in light of reduced seasonal variability for some other taxa, suggests that the fractional contribution of copepods to carbon biomass in the springtime series (Fig. 5) may be somewhat higher than at other times of the year. No confidence limits on biomass are available for most taxa in Fig. 13, apart from April 1984 and euphausiids, because of the procedure used for pooling samples. However, the comprehensive results from euphausiids suggest that variability observed in April 1984 is probably indicative of variations to be expected at different times of year and that spatial variability in CC is somewhat greater than in SC. There was a tendency toward highest euphausiid biomass in July–August (Fig. 13c and d). Neither chaetognaths (Fig. 13e and f) nor aggregated pelagic tunicates (Fig. 13g and h) showed pronounced seasonality, although tunicate biomass tended to be highest in late summer–autumn. The reduced seasonality in all pelagic tunicates combined partially masks out-of-phase tendencies in particular groups (see Suppl. Fig. 8). Doliolids had highest biomass in spring and summer (Suppl. Fig. 8i,j), while salp biomass tended to maxima in winter (Suppl. Fig. 8k,l). Appendicularians showed inconsistent trends in CC between years, with higher biomass in summer–fall of 1969 and spring–summer of 1984 (Suppl. Fig. 8h).

Other taxa for which biomass could have been underestimated by our spring time-series were the hyperiid amphipods (Suppl. Fig. 8a,b), thecosome and gymnosome pteropods (Suppl. Fig. 9a,b), and some gelatinous predators (Suppl. Fig. 9e–h).

Carbon biomass of all major taxa combined exhibited relatively consistent seasonal patterns between years within a region (Fig. 14a and b), though the absence of error estimates makes this only a qualitative statement. The seasonal variability of organic carbon biomass in SC was more pronounced than displacement volume (Fig. 14). Central California showed low seasonality in carbon biomass, but not displacement volume during 1969.

Overall we conclude that with some exceptions, for most individual taxa and for aggregated measures of total biomass our analyses of interannual variability focusing on springtime cruises provide a generally representative basis for understanding long-term variations at other times of year as well. Also, Brinton and Townsend (2003) show that for four out of five species of euphausiids, interannual variations in springtime abundance closely reflect those measured in winter.

3.7. Interspecific interactions

We evaluated the possibility that temporal variations in some zooplankton taxa might be controlled by variations in predation pressure. For this purpose, we considered planktonic copepods and euphausiids as predominantly suspension-feeders, although this is an obvious oversimplification of diverse dietary habits that vary among species. The predominantly predatory zooplankton taxa we considered were chaetognaths, ctenophores, medusae, siphonophores, and pelagic polychaetes. Insufficient information was available to estimate temporal variations in planktivory by fishes. The expectation under the hypothesis of predatory control is an inverse relationship between carbon biomass of copepods or euphausiids as prey and one or more of the five predatory zooplankton groups identified above. In none of the 10 pairwise comparisons was such a negative relationship found. Instead, there were significant positive relationships (Spearman's rank, $n = 82$ pairs) between copepods and several predatory taxa: chaetognaths ($r_s = 0.681$, $P < 0.001$), polychaetes ($r_s = 0.407$, $P < 0.001$), siphonophores ($r_s = 0.365$, $P < 0.001$), and medusae ($r_s = 0.414$, $P < 0.001$). Euphausiid biomass

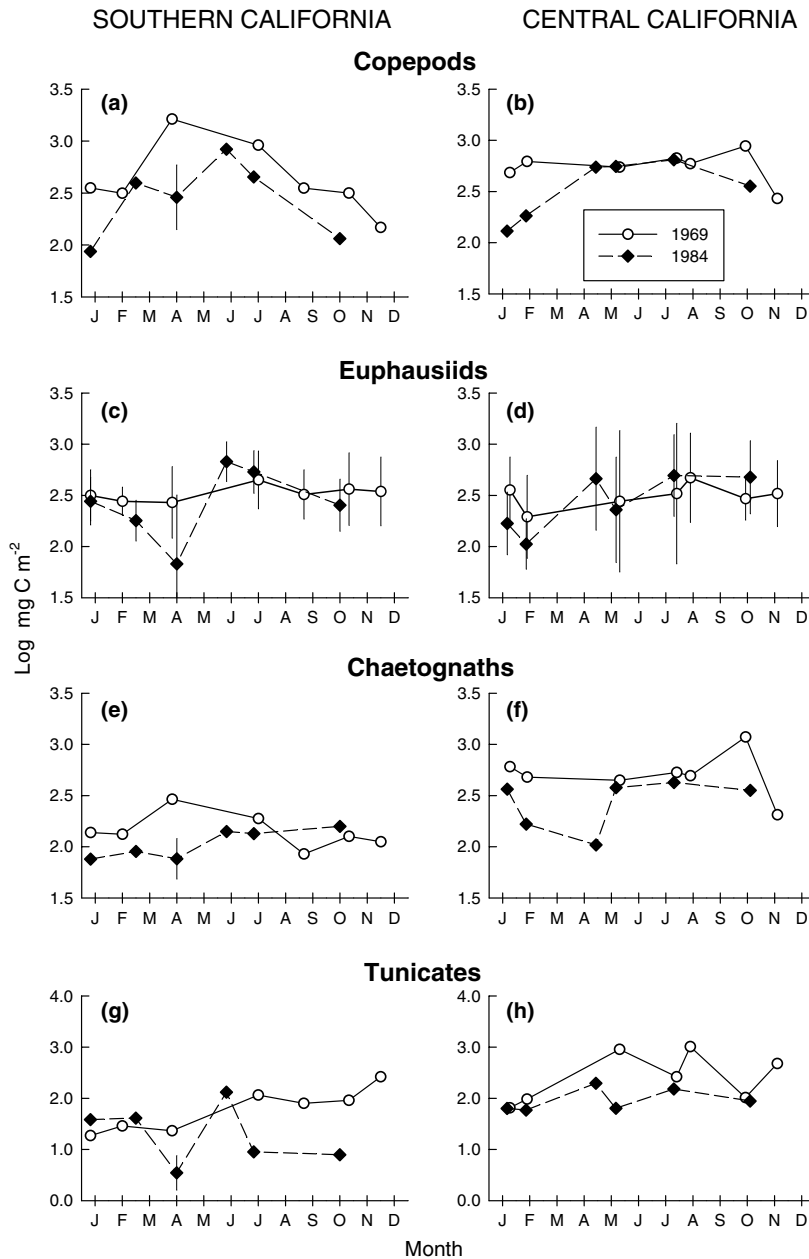


Fig. 13. Seasonal variation of organic carbon biomass for: (a and b) copepods; (c and d) euphausiids; (e and f) chaetognaths; (g and h) tunicates, from Southern (SC, left hand panels) and Central California (CC, right hand panels), during years representative of the cool (1969) and warm (1984) climate periods. Ninety-five percent confidence intervals are available from all cruises for euphausiids, but for other taxa only from April 1984 (SC) when individual samples were analyzed. The remaining points illustrate means from analysis of pooled samples.

was positively correlated with carbon biomass of polychaetes ($r_s = 0.457$, $P < 0.001$), chaetognaths ($r_s = 0.378$, $P < 0.001$), and siphonophores ($r_s = 0.233$, $P < 0.05$).

Most species of hyperiid amphipods are known to be parasitoids on gelatinous zooplankton hosts (Madin and Harbison, 1977; Lavaniegos and Ohman, 1999). Here we found significant correlations between total biomass of hyperiids and several potential host taxa: medusae, salps, doliolids, and physonect+cystonect siphonophores ($P < 0.005$). In all cases the correlations were positive, again suggesting that host availability affected hyperiids, but hyperiids did not suppress host biomass.

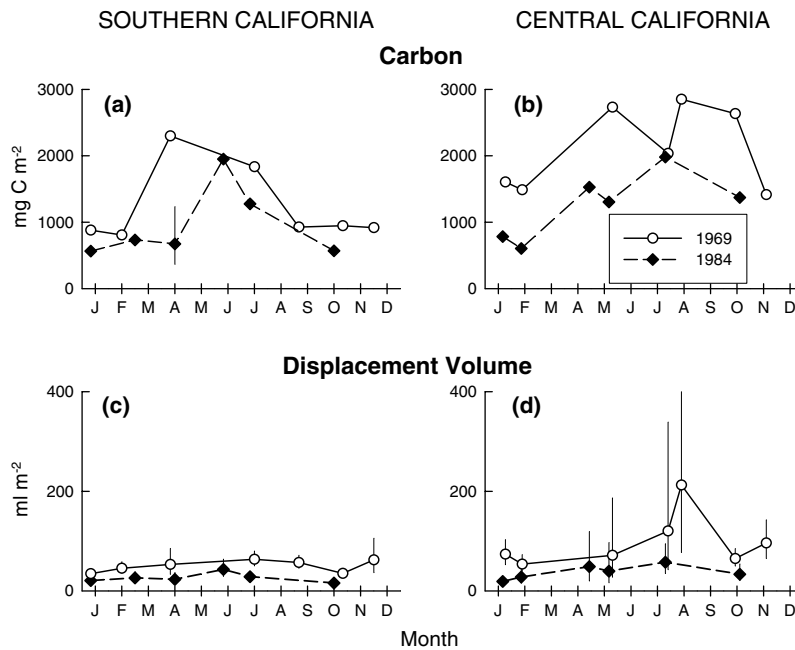


Fig. 14. Seasonal variation of organic carbon biomass for: (a and b) total zooplankton carbon biomass; (c and d) zooplankton displacement volume, from Southern California (SC, left hand panels) and Central California (CC, right hand panels), during years representative of the cool (1969) and warm (1984) climate periods. Ninety-five percent confidence intervals are available for organic carbon only from April 1984 (SC) and from all cruises for displacement volume. The remaining points illustrate means from analysis of pooled samples.

We examined relationships between potentially competing suspension-feeding pelagic tunicates and the dominant crustacean taxa (copepods and euphausiids). The expectation under the competition hypothesis is an inverse relationship between tunicates and crustaceans. However, no such relationships were found between salps, doliolids, appendicularians, and pyrosomes on the one hand and either copepod or euphausiid biomass on the other. Copepod biomass was positively related to biomass of appendicularians ($r_s = 0.590$, $P < 0.001$) and doliolids ($r_s = 0.462$, $P < 0.001$). Euphausiid biomass was positively correlated with doliolid biomass ($r_s = 0.380$, $P < 0.001$). Therefore conditions favorable to these crustacean taxa, when considered as an ensemble of different species, were in many cases also favorable to an ensemble of suspension-feeding tunicate species.

4. Discussion

4.1. Biomass as organic carbon vs. displacement volume

The striking contrast between temporal patterns of zooplankton biomass when expressed as organic carbon or displacement volume underscores the importance of taxonomically-based analyses of the zooplankton assemblage when attempting to assess responses to ocean forcing. While displacement volume is a relatively quickly executed, inexpensive measure of biomass it fails to reveal fundamental structural changes within the assemblage that may be of considerable consequence to the rest of the food web. While from displacement volume alone one might conclude that 60–70% of all zooplankton biomass had declined, in actuality most taxa showed no long term temporal trend in biomass and some increased over the 56-year study. Pelagic tunicates, and salps in particular, showed a long-term decline that accounted for the principal biomass variations observed in displacement volume. Because tunicates are gelatinous and have a very high biovolume:carbon ratio relative to most other zooplankton taxa (Bone, 1998), changes in the biomass of tunicates disproportionately influences displacement volume but has only a modest influence on organic carbon.

The differential long-term responses of salps and several other zooplankton taxa has implications for predator–prey interactions and for biogeochemical fluxes in the California Current System. Salps are generally less palatable than a variety of other zooplankton prey. Although salps may be ingested by marine turtles, hyperiid amphipods, and other predators, and Harbison (1998) has compiled a lengthy roster of fish species that may ingest them, salps nevertheless are often of lesser importance as a prey item to planktivores for a variety of reasons. Large body sizes make salps less accessible to gape-limited predators than many smaller crustacean prey. Their relative transparency (apart from pigmented guts in some taxa) should render them more difficult to locate visually and their tough outer tunic offers mechanical protection and reduces edibility. Their relatively low energy content per unit biovolume also reduces the nutritional benefit to predators. Hence, the long-term decline in salp biomass is likely to be of less direct consequence to planktivorous fish and carnivorous zooplankton than would be the case if a comparable decline occurred in highly edible crustacean zooplankton.

However, the long-term decline in salps may have a substantial influence from a biogeochemical perspective. Because of their potentially high grazing rates in swarm abundances in the California Current (e.g., Hereu et al., 2006) and extremely rapid sinking rates of fecal pellets (Bruland and Silver, 1981; Deibel, 1998), salps may contribute disproportionately to the vertical export of organic matter from surface waters into the deep ocean (Michaels and Silver, 1988). A long-term study of fluxes to the deep sea beginning in 1989 at K. Smith's Sta. M, located just north of our Southern California sampling region, shows a temporal decline in POC flux at 3500–4000 m depth, followed by an abrupt increase after 1999 (Ruhl and Smith, 2004; Smith et al., 2006), which bears a strong resemblance to the trend of salps in near-surface waters. Hence, the temporal variations in salps that we observed in the present study appear to have had consequences extending to the deep sea benthos. Although appendicularians in the Southern California region have shown a temporal increase over the past five decades, we note that the smaller *Oikopleura* and *Fritillaria* that dominated our epipelagic samples produce much smaller, more slowly sinking mucous houses than the larger deep-sea appendicularians (e.g., Bathochordaeus) and are less likely to dominate the flux of organic matter to the deep sea floor (cf. Robison et al., 2005).

The mechanism leading to a decline in pelagic tunicates, and salps in particular, is only speculative at this point. It seems unlikely that increased density stratification has a direct inhibitory effect on salps, but rather indirectly affects them through associated changes in ocean circulation, vertical mixing, or the prey field. In an earlier analysis focusing on individual tunicate species in the Southern California region alone we noted that the salp species that have declined tend to be those that are introduced into the region from higher latitudes (Lavaniegos and Ohman, 2003). This explanation of reduced seeding of populations from the north is consistent with the present results, since we find salp biomass off Central California shows a weaker long term decline than salp biomass in Southern California. Also, Bograd and Lynn (2003) suggested that since 1976 there has been somewhat weakened equatorward flow along CalCOFI line 90, just outside the Southern California Bight. In addition to alongshore transport, changes in mesoscale circulation could also affect salp biomass. Salps tend to have maximum abundances in the offshore region of the California Current System (Berner, 1967) in a region characterized by high eddy kinetic energy (e.g., Lynn and Simpson, 1987). If the probability of successful life history closure, growth, or survival of salps is influenced by mesoscale eddies, long-term changes in eddy kinetic energy (cf. Di Lorenzo et al., 2005) could influence their abundance. Alternatively, if increased density stratification is accompanied by reduced vertical mixing, reduced vertical nutrient supply, and decreased primary production, salps could become increasingly food-limited in stratified waters. However, we note that the seasonal maximum of salps in this area is in the winter, a time period of somewhat lower primary production, suggesting that direct food limitation is a less likely explanation. Late winter is also characterized by lower water column stability. The processes underlying the negative association of salp biomass with water column stratification (and possibly increased eddy energy) warrant direct investigation.

4.2. Multiple time scales of change

In addition to the long-term trend expressed in pelagic tunicates and a few other taxa (calycophoran siphonophores, ostracods, large decapods), other dominant time scales of change are represented in these time series. One is multi-decadal scale variations. Considerable attention has been paid to the Pacific Decadal Oscil-

lation (PDO; Mantua et al., 1997), although this EOF explains only about 30% of the sea surface temperature time series in the North Pacific and some suggest that other modes of ocean variability have become dominant in recent years (Bond et al., 2003). The transition from the cool to the warm phase of the PDO in 1977 was accompanied by distinct and relatively abrupt changes in the species composition of salps and doliolids (Lavaniegos and Ohman, 2003) as well as euphausiids (Brinton and Townsend, 2003). However, the present data, based on aggregated data for all species of salps, all doliolids, and all euphausiids combined within each respective taxon fail to show such changes, by either of two tests: the regime shift test of Rodionov (2004) and the CuSum test. In addition, total organic carbon biomass shows no distinct change at this time, nor does displacement volume. In the case of displacement volume, this measure has alternately been interpreted as representing a continuous decline (Roemmich and McGowan, 1995a,b) or an abrupt change in the mid-1970s (McGowan et al., 2003). A more objective analysis does not support the latter interpretation. Thus, more aggregated measures of zooplankton biomass, whether considering all species within a major taxon or all zooplankton taxa combined, are relatively insensitive metrics of some of the interdecadal time scales of ocean change that are readily resolved at the species level. The reason for this insensitivity is that there often are compensatory changes in different species, such that conditions unfavorable for one may preferentially favor a congener. The most responsive metrics of changes in ocean conditions therefore will be based upon taxonomically resolved analyses at the level of the species. In our work-in-progress, we will report on species-level variations from the present data set.

The most consistent abrupt changes that were discernable in the present record were not in 1977 or 1989 (cf. Hare and Mantua, 2000; Rebstock, 2002), but the sharp increases in biomass of many taxa in 1999, immediately following the El Niño conditions of 1997–1998. The rapid, deep cooling of the upper ocean that occurred from 1998 to 1999 was interpreted by many as the La Niña phase of the ENSO cycle, hence an interannual perturbation, while other authors concluded that this was a major ecosystem shift that represented a transition to a new, persistent ecosystem state (e.g., Peterson and Schwing, 2003). The magnitude of the variability revealed by the present analyses over a time scale of more than half a century reveal the challenges in differentiating between interannual and decadal scale changes if the data record is short.

The dominant interannual climate signal within our study site, and indeed in much of the ocean, is ENSO. In each of the major El Niño's from 1958 to 1998 there was an appreciable decrease in total zooplankton biomass (as either organic carbon or displacement volume) and in the biomass of many individual taxa. However, by the following year the biomass had typically recovered to pre-Niño levels. This result parallels results from stable N isotopes of copepods and chaetognaths off Central California that revealed a pronounced but reversible increase in heavier N isotopes of 3 of 4 zooplankton species (Rau et al., 2003), suggesting a strong perturbation to food web structure, but one that was no longer evident the following spring. It is also in accord with the analysis of Chelton et al. (1982), who illustrated the importance of interannual variations in transports associated with El Niño in altering zooplankton displacement volume over the period 1950–1979. Here, when we plotted biomass of various zooplankton taxa against a local index of El Niño (detrended sea level anomalies), it became clear that the extremes of very low sea level anomalies (La Niña conditions) or very high sea level anomalies (El Niño conditions) are associated with major excursions in the biomass of zooplankton, but the intermediate sea level anomalies are not a good predictor of biomass. Future efforts to forecast pelagic ecosystem responses to interannual perturbations may be most successful if focused on these more extreme events. We also note that the classically used large-scale indices of El Niño, such as the Southern Oscillation Index, Niño 3.4, and others, are more appropriate for tropical latitudes, while a local (mid-latitude) index is more appropriate for extra-tropical regions.

4.3. Coherence between Southern California and Central California

Copepods and euphausiids dominated zooplankton carbon biomass in both Southern California (SC, both taxa combined represented 77% of biomass) and Central California (CC, 71% of biomass), and chaetognaths represented a similar fraction of the mean biomass in both regions (11% vs. 8%, SC vs. CC). Most remaining taxa, including siphonophores, decapods, hyperiid amphipods, and others showed relatively similar contributions to total biomass in both regions. The most striking compositional difference between regions was in the tunicates, which represented 5% of the carbon biomass in SC but 13% on average in

CC. Combined with the higher average carbon biomass in CC than SC, the absolute as well as relative biomass of pelagic tunicates was appreciably greater in CC. Whether this difference is attributable to regional differences in loss/retention of organisms, mesoscale eddies, or primary production rates and food web structure remains to be determined.

As with the physical variables analyzed in the two regions (upwelling index, density stratification, detrended sea level anomalies), which showed 38–58% common variance, some, but not all of the variability between taxa was shared between SC and CC. Notably, total organic carbon and copepod C, the dominant constituent of biomass, covaried in the two regions, as did that of salps, the major contributor to pelagic tunicate biomass. Chaetognaths, the dominant carnivorous zooplankton, covaried between regions. At the other extreme, ctenophores, thecosome pteropods, and hydromedusae, all of which were relatively rare, showed almost no shared variance between SC and CC. At an α level of 0.10, 10 of the 19 major taxa analyzed showed correlated variations in the two regions, although for each individual taxon some but not all of the variance was held in common. The primary long-term trends in salps and total displacement volume were similar between regions. Overall we conclude that much of the low frequency (i.e., interannual and longer) variability in zooplankton taxa was similar between regions. Chelton et al. (1982) and Roesler and Chelton (1987) previously showed that much of the variance in zooplankton displacement volume is spatially coherent across the entire CalCOFI region.

A comparison of zooplankton variations from Baja California to Vancouver Island, including the two regions studied here, covered a broader area but much more limited temporal period (1977–2005, Mackas et al., 2006). Mackas et al. found that variations in displacement volume off Southern California were positively correlated with various measures of zooplankton biomass off Central California, Central Oregon, and Southern Vancouver Island, but uncorrelated with zooplankton biomass off northern Vancouver Island and negatively correlated with zooplankton biomass off Baja California. Those results suggest there is a domain from approximately the Southern California Bight and region immediately offshore, northward to the southern end of Vancouver Island where much of the interannual variability in zooplankton biomass is correlated. At the same time, the study pointed out that the retarded upwelling in spring–summer 2005 primarily affected the region of northern California to central Oregon, with lesser influences on the zooplankton both south and north of that region. In a related study, Sydeman et al. (2006) reported a catastrophic breeding failure of Cassin's auklet (*Ptychoramphus aleuticus*) off the Farallon Islands, near the entrance to San Francisco Bay (in our Central California domain) in spring 2005. This breeding collapse off Central California was accompanied by a marked reduction in biomass of two species of euphausiids, *Euphausia pacifica* and *Thysanoessa spinifera* that are key prey items for the seabirds. In contrast, in Southern California waters, the biomass of these same two species of euphausiids was at or above their long-term mean and the abundance of auklets was anomalously high, suggesting that the starved auklets flew south to utilize a better prey resource (Sydeman et al., 2006). These results indicate that regional differences in zooplankton do occur in the California Current System, especially when resolved at the species level, and that some consumers migrate considerable distances to take advantage of such spatial variation.

4.4. Interspecific interactions

Our results suggest that on the temporal scale of interannual variations and at the taxonomic level of major taxa, prey availability is affecting predatory zooplankton biomass more than the converse. This does not rule out the importance of strong predator control of individual species' abundances, predator influences at a finer temporal or spatial scale, or predator-induced modifications of prey behavior and morphology (Ohman, 1988a). The strongest relationship we detected was a positive relationship between chaetognath and copepod biomass, consistent with earlier suggestions (Feigenbaum and Maris, 1984; Ohman, 1986) that in temperate latitudes copepods affect chaetognaths more than chaetognath predation suppresses copepod growth. No inverse relationship was detected between salps and euphausiids as suggested in the Southern Ocean (Loeb et al., 1997) and elsewhere, although our analysis addresses lower frequency temporal variations and does not permit us to analyze smaller spatial or temporal scales where such effects could be discernable.

4.5. Caveats

The sampling methods bear some discussion. Half millimeter mesh nets were adopted by CalCOFI because of the initial focus on the ichthyoplankton and the problem of clogging of finer mesh nets in this productive upwelling region. Hence, the smaller mesozooplankton are not sampled quantitatively, including, in particular, smaller calanoid, poecilostomatoid, and cyclopoid copepods. Thus the contribution of copepods to total mesozooplankton biomass is probably even greater than detected in this study. However, use of a coarser mesh net means that nearly all of the displacement volume measured is indeed zooplankton organisms, without the significant contributions from phytoplankton and detritus that are unavoidable with smaller mesh nets. Also, the relatively large mouth diameter of the nets (1.0 m or 0.71 m) ensures that the larger mesozooplankton and micronekton are sampled more quantitatively than is the case with smaller-mouthed plankton nets and common towed samplers. Furthermore, our analysis here of only nighttime-collected samples ensures that variability due to daytime net avoidance and daytime vertical migration below the epipelagic zone does not confound our interpretation of ecosystem changes.

Although the sampling depth increased somewhat in 1969 and the net style changed in 1978, these changes appear to have had only nominal effects on the results. In the case of ostracods, large decapods, and perhaps chaetognaths, it does appear likely that the deeper sampling began collecting additional organisms, which could contribute to artifactual increases in biomass in these two taxa. However, a consistent change in 1969 in both regions was not detected for any other taxa. Also, the finding of a temporal decline in salp biomass in SC is not affected by the difference between nets (Ohman and Lavaniegos, 2002), as it remains significant ($P < 0.05$) in the absence of such a correction.

Preservation bias could exist for certain taxa. Although we have found perfectly intact ctenophores in CalCOFI samples taken in 1949, some of the ctenophores enumerated in the present samples were recognized only as comb rows and we have no way to assess possible losses of these fragile organisms associated with fixation and long-term preservation (cf. Harris et al., 2000). Salp chains and siphonophore colonies were reconstructed from individual zooids and colony parts, which we believe to provide an unbiased measure of abundance, apart from some tissue shrinkage in preservatives. If the preservation fluid becomes somewhat acidic over time, we would expect increasing losses of thecosome pteropods in progressively older samples, but this was not observed. The pH measurements reported in Bucklin and Allen (2004) are inaccurate and perhaps impossible to attain in formaldehyde solutions.

Finally, we note that the sample pooling procedure employed here enabled us to resolve interannual variations in two regions of the CCS, but not to resolve spatial variability within those regions. However, this focus on time rather than space permitted us to complete comprehensive taxonomic analyses that would not otherwise have been practical.

5. Conclusions

The major contributors to the organic carbon biomass of zooplankton in two sectors of the California Current System (Southern California and Central California) are planktonic copepods and euphausiids, neither of which shows a long-term trend over the 56-year span of springtime biomass analyzed here. In contrast, the carbon biomass of pelagic tunicates shows a long-term decline, particularly in the Southern California region. This decline, dominated by changes in salps, parallels a long-term increase in density stratification of the water column. It also explains the previously documented decline in zooplankton displacement volume, which we do not find in zooplankton organic carbon. This compositional change in the zooplankton assemblage is likely to markedly influence the rates of vertical transport of organic matter from the epipelagic zone, but to have only modest consequences for planktivorous consumers of the region.

At the level of aggregated zooplankton taxa or total zooplankton biomass, no evidence was detected for ecosystem shifts at 1976–1977 or 1989; instead, the most consistent transition point was the strong La Niña of 1999. On shorter time scales, interannual variations in zooplankton biomass and those of individual taxa are markedly affected by El Niño, with pronounced depression of biomass in El Niño years and greater than average biomass in La Niña years. Such effects are typically short-lived, with recovery within a year or two. Interannual variations in total zooplankton organic carbon biomass, as well as in biomass

of the major zooplankton taxa, are correlated between the Southern and Central California sectors of the CCS.

6. References cited in the electronic supplements

Andersen and Sardou (1994), Ayukai (1987), Barnett (1974), Batistić (2003), Böer et al. (2005), Canino and Grant (1985), Conover and Lalli (1974), Conway and Robins (1991), Curl (1962), Donnelly et al. (1993), Dagg and Wyman (1983), Fenaux and Gorsky (1983), Flint et al. (1991), Gilmer (1974), Gorsky et al. (1988), Heron et al. (1988), Hirota (1972, 1981), Hopcroft et al. (2002), Ikeda (1990), Ikeda and Shiga (1999), Kaeriyama and Ikeda (2002, 2004), Kimoto et al. (1986), Kotori (1976), Kremer et al. (1986a,b), Landry (1978), Larson (1986), Liang and Uye (1996), Lucas et al. (1995), Madin et al. (1981), Madin and Deibel (1998), Madin and Purcell (1992), Martinussen and Båmstedt (1999), Matsakis and Nival (1989), Matthews and Hestad (1977), Nagasawa (1984), Norrbin and Båmstedt (1984), Ohman (1988b), Ohman and Townsend (1998), Omori (1969), Peterson (1980), Purcell (1982), Purcell and Kremer (1983), Reeve and Baker (1975), Robertson and Frost (1977), Ross (1982), Runge (1980), Sameoto (1971), Smith and Lane (1991), Thuesen and Childress (1993), Uye (1982), Uye et al. (1983), Uye and Kayano (1994), Uye and Shibuno (1992), Uye and Shimauchi (2005), Yamaguchi and Ikeda (2000).

Acknowledgements

We thank the dedicated seagoing staff of the CalCOFI program who over the past half century collected the samples used in the present study. We give special thanks to Annie W. Townsend for her extraordinary dedication to the SIO Pelagic Invertebrates Collection and help with preparation of the samples and counting. Edward Brinton kindly provided most of the euphausiid data used in the present study. Connie Fey, Christopher Martin, Erin Rempala-Kim, and Patricia Brommer assisted with counting and preparation of samples and David Field and Alison Cawood helped with calculations of stratification. Contribution number 546 from the US GLOBEC Northeast Program, supported by the NSF (OCE 01-10300) and by NOAA, and a contribution of the California Current Ecosystem LTER site (NSF OCE 04-17616) and the Pelagic Invertebrates Collection of the Scripps Institution of Oceanography. Funding also provided by project CICESE-5702: Decadal variability in the zooplankton composition of the California Current.

Appendix A. Electronic supplements

A.1. Carbon–length regressions used to convert abundance to carbon biomass

This is a compendium of carbon–length or dry mass–length regressions newly estimated in the present study or taken from the literature in order to convert enumerations of organisms by length class to carbon biomass. [Supplement Fig. 1](#) illustrates relationships between carbon or dry mass and length that have not been published previously. [Supplement Table 1](#) indicates the regression equations and other conversion factors used for all taxa, with sources specified. [Supplement Tables 2 and 3](#) indicate the diverse species and sources of data used to derive length–C relationships for copepods and chaetognaths, respectively. To obtain a broad range of body sizes, it was often necessary to consult the literature beyond the Northeast Pacific.

A.2. Time series of carbon biomass of additional major taxa

This appendix contains additional time series of carbon biomass for major taxa other than the four primary taxa reported on in the main body of the text. Results are presented for both Southern California and Central California.

A.2.1. Interdecadal series

[Supplement Figs. 2–7](#) report interannual variations in springtime carbon biomass, together with anomalies from the long-term mean biomass (1951–2005), for each major taxon. Significant linear regressions are indi-

cated when a temporal trend was detected. These figures are complementary to Figs. 6 and 7 in the main text, which depict the four primary contributors to zooplankton biomass. y -Axis scales vary among taxa but are comparable between regions. Open circles below x -axis are years that were not sampled.

A.2.2. Seasonal series

Supplement Figs. 8 and 9 report seasonal variations in carbon biomass for each major taxon, for the years 1969 and 1984. These figures are complementary to Fig. 13 in the main text, which depicts the four primary contributors to zooplankton biomass. y -Axis scales vary among taxa but are comparable between regions.

Appendix B. Supplementary

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.pocean.2007.07.002](https://doi.org/10.1016/j.pocean.2007.07.002).

References

- Abbott, M.R., Zion, P.M., 1987. Spatial and temporal variability of phytoplankton pigment off Northern California during Coastal Ocean Dynamics Experiment-I. *Journal of Geophysical Research-Oceans* 92, 1745–1755.
- Andersen, V., Sardou, J., 1994. *Pyrosoma atlanticum* (Tunicata, Thaliacea): diel migration and vertical distribution as a function of colony size. *Journal of Plankton Research* 16, 337–349.
- Ayukai, T., 1987. Feeding by the planktonic calanoid copepod *Acartia clausi* Giesbrecht on natural suspended particulate matter of varying quantity and quality. *Journal of Experimental Marine Biology and Ecology* 106, 137–149.
- Barnett, A.M. 1974. The feeding ecology of an omnivorous neritic copepod, *Labidocera trispinosa* Esterly. Ph.D. Thesis, University of California, San Diego, USA, unpublished.
- Batistić, M., 2003. Abundance, biomass, C- and N-content of *Flaccisagitta enflata* and *Mesosagitta minima* (Chaetognatha). *Marine Ecology – Pubblicazioni della Stazione Zoologica di Napoli I* 24, 1–13.
- Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., Kurashov, V., 1999. The regime concept and natural trends in the production of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Science* 56, 516–526.
- Berner, L.D., 1967. Distributional atlas of Thaliacea in the California Current region. *California Cooperative Oceanic Fisheries Investigations Atlas* 8, 1–322.
- Böer, M., Gannefors, C., Kattner, G., Graeve, M., Hop, H., Falk-Petersen, S., 2005. The Arctic pteropod *Clione limacina*: seasonal lipid dynamics and life-strategy. *Marine Biology* 147, 707–717.
- Bograd, S.J., Lynn, R.J., 2003. Long-term variability in the Southern California Current System. *Deep-Sea Research II* 50, 2355–2370.
- Bond, N.A., Overland, J.E., Spillane, M., Stabeno, P., 2003. Recent shifts in the state of the North Pacific. *Geophysical Research Letters* 30. doi:10.1029/2003GL018597.
- Bone, Q. (Ed.), 1998. *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 1–400.
- Brinton, E., Townsend, A., 1981. A comparison of euphausiid abundances from bongo and 1-m CalCOFI nets. *California Cooperative Oceanic Fisheries Investigations Reports* 22, 111–125.
- Brinton, E., Townsend, A., 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep-Sea Research II* 50, 2449–2472.
- Bruland, K.W., Silver, M.W., 1981. Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). *Marine Biology* 63, 295–300.
- Bucklin, A., Allen, L.D., 2004. MtDNA sequencing from zooplankton after long-term preservation in buffered formalin. *Molecular Phylogenetics and Evolution* 30, 879–882.
- Canino, M.F., Grant, G.C., 1985. The feeding and diet of *Sagitta tenuis* (Chaetognatha) in lower Chesapeake Bay. *Journal of Plankton Research* 7, 175–188.
- 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.
- Colebrook, J.M., 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in California Current, 1955–1959. *Fishery Bulletin* 75, 357–368.
- Conover, R.J., Lalli, C.M., 1974. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. II. Assimilation, metabolism and growth efficiency. *Journal of Experimental Marine Biology and Ecology* 16, 131–154.
- Conway, D.V.P., Robins, D.B., 1991. Collection and chemical analysis of chaetognaths and changes due to preservation. In: Bone, Q., Kapp, H., Pierrot-Bults, A.C. (Eds.), *The Biology of Chaetognaths*. Oxford University Press, pp. 137–147.
- Curl Jr., H., 1962. Analyses of carbon in marine plankton organisms. *Journal of Marine Research* 20, 181–188.
- Dagg, M.J., Wyman, K.D., 1983. Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus*, calculated from gut contents. *Marine Ecology Progress Series* 13, 37–46.
- Deibel, D., 1998. The abundance, distribution, and ecological impact of doliolids. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 171–186.

- Di Lorenzo, E., Miller, A.J., Schneider, N., McWilliams, J.C., 2005. The warming of the California Current: dynamics and ecosystem implications. *Journal of Physical Oceanography* 35, 336–362.
- Donnelly, J., Stickney, D.G., Torres, J.J., 1993. Proximate and elemental composition and energy content of mesopelagic crustaceans from the eastern Gulf of Mexico. *Marine Biology* 115, 469–480.
- Feigenbaum, D.L., Maris, R.C., 1984. Feeding in the Chaetognatha. *Oceanography and Marine Biology Annual Review* 22, 343–392.
- Fenaux, R., Gorsky, G., 1983. Cycle vital et croissance de l'appendiculaire *Oikopleura longicauda* (Vogt), 1854. *Annales de l'Institut Océanographique*, Paris (N.S.) 59, 107–116.
- Field, D.B., Baumgartner, T.R., Charles, C.D., Ferreira-Bartrina, V., Ohman, M.D., 2006. Planktonic foraminifera of the California Current reflect twentieth century warming. *Science* 311, 63–66.
- Flint, M.V., Drits, A.V., Pasternak, A.F., 1991. Characteristic features of body composition and metabolism in some interzonal copepods. *Marine Biology* 111, 199–205.
- Gilmer, R.W., 1974. Some aspects of feeding in the thecosomatous pteropod molluscs. *Journal of Experimental Marine Biology and Ecology* 15, 127–144.
- Gorsky, G., Dallot, S., Sardou, J., Fenaux, R., Carré, C., Palazzoli, I., 1988. C and N composition of some northwestern Mediterranean zooplankton and micronekton species. *Journal of Experimental Marine Biology and Ecology* 124, 133–144.
- Harbison, G.R., 1998. The parasites and predators of Thaliacea. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 187–214.
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47, 103–145.
- Harris, R.P., Wiebe, P.H., Lenz, J., Skoldal, H.R., Huntley, M. (Eds.), 2000. *ICES Zooplankton Methodology Manual*. Academic, New York, pp. 1–684.
- Hereu, C.M., Lavaniegos, B.E., Gaxiola-Castro, G., Ohman, M.D., 2006. Composition and potential grazing impact of salps off Baja California during the 1997–1999 El Niño and La Niña. *Marine Ecology Progress Series* 318, 123–140.
- Heron, A.C., McWilliam, P.S., Dal-Pont, G., 1988. Length–weight relation in the salp *Thalia democratica* and potential of salps as a source of food. *Marine Ecology Progress Series* 42, 125–132.
- Hewitt, R.P., 1988. Historical review of the oceanographic approach to fishery research. *California Cooperative Oceanic Fisheries Investigations Reports* 29, 27–41.
- Hirota, J., 1972. Laboratory culture and metabolism of the planktonic ctenophore, *Pleurobrachia bachei* A. Agassiz. In: Motoda, S., Takenouti, I. (Eds.), *Biological Oceanography of the Northern North Pacific Ocean*. Idemitsu Shoten, Tokyo, pp. 465–484.
- Hirota, R., 1981. Dry weight and chemical composition of the important zooplankton in the Sentonaikai (Inland Sea of Japan). *Bulletin of Plankton Society of Japan* 28, 19–24.
- Hopcroft, R.R., Clarke, C., Chavez, F.P., 2002. Copepod communities in Monterey Bay during the 1997–1999 El Niño and La Niña. *Progress in Oceanography* 54, 251–264.
- Hsieh, C.-H., 2005. Separating environmental effects from fishing impacts on the dynamics of fish populations of the Southern California region. Ph.D. Thesis, University of California, San Diego, USA, unpublished.
- Hsieh, C.-H., Ohman, M.D., 2006. Biological responses to environmental forcing: the Linear Tracking Window hypothesis. *Ecology* 87, 1932–1938.
- Hsieh, C.-H., Glaser, S.M., Lucas, A.J., Sugihara, G., 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature* 435, 336–340.
- Ikeda, T., 1990. A growth model for the hyperiid amphipod *Themisto japonica* (Bovallius) in the Japan Sea, based on its intermoult period and moult increment. *Journal of the Oceanographic Society of Japan* 46, 261–272.
- Ikeda, T., Shiga, N., 1999. Production, metabolism and production/biomass (P/B) ratio of *Themisto japonica* (Crustacea: Amphipoda) in Toyama Bay, Southern Japan Sea. *Journal of Plankton Research* 21, 299–308.
- Kaeriyama, H., Ikeda, T., 2002. Body allometry and developmental characteristics of the three dominant pelagic ostracods (*Discoconchoecia pseudodiscophora*, *Orthoconchoecia haddoni*, and *Metaconchoecia skogsbergi*) in the Oyashio region, western North Pacific. *Plankton Biology and Ecology* 49, 97–100.
- Kaeriyama, H., Ikeda, T., 2004. Metabolism and chemical composition of mesopelagic ostracods in the western North Pacific Ocean. *ICES Journal of Marine Science* 61, 535–541.
- Kimoto, K., Uye, S., Onbe, T., 1986. Growth characteristics of a brackish-water calanoid copepod *Sinocalanus tenellus* in relation to temperature and salinity. *Bulletin of Plankton Society of Japan* 33, 43–57.
- Kotori, M., 1976. The biology of Chaetognatha in the Bering Sea and the northwestern North Pacific Ocean, with emphasis on *Sagitta elegans*. *Memoirs of the Faculty of Fisheries of the Hokkaido University* 23, 95–183.
- Kramer, D., Kalin, M.J., Stevens, E.G., Thraillkill, J.R., Zweifel, J.R., 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA TR NMFS CIRC370, U.S. Department of Commerce, Seattle, Washington, pp. 1–38.
- Kremer, P., Canino, M.F., Gilmer, R.W., 1986a. Metabolism of epipelagic tropical ctenophores. *Marine Biology* 90, 403–412.
- Kremer, P., Reeve, M.R., Syms, M.A., 1986b. The nutritional ecology of the ctenophore *Bolinopsis vitrea*: comparisons with *Mnemiopsis mccradyi* from the same region. *Journal of Plankton Research* 8, 1197–1208.
- Landry, M.R., 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. *Internationale Revue der Gesamten Hydrobiologie* 63, 77–119.
- Larson, R.J., 1986. Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *Journal of Experimental Marine Biology and Ecology* 99, 107–120.

- 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, vol. I, 1998, 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* 50, 2473–2498.
- Liang, D., Uye, S., 1996. Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. 2. *Acartia omorii*. *Marine Biology* 125, 109–117.
- Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., Trivelpiece, S., 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900.
- Lucas, C.H., Williams, D.W., Williams, J.A., Shearer, M., 1995. Seasonal dynamics and production of the hydromedusan *Clytia hemisphaerica* (Hydromedusa: Leptomedusa) in Southampton water. *Estuaries* 18, 362–372.
- Lynn, R.J., Simpson, J.J., 1987. The California Current System: the seasonal variability of its physical characteristics. *Journal of Geophysical Research* 92 (C12), 12947–12966.
- Mackas, D.L., Peterson, W.T., Ohman, M.D., Lavaniegos, B.E., 2006. Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. *Geophysical Research Letters* 33, L22S07.
- Madin, L.P., Deibel, D., 1998. Feeding and energetics of Thaliaceans. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 81–103.
- Madin, L.P., Harbison, G.R., 1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton. I. Associations with Salpidae. *Deep-Sea Research* 24, 449–463.
- Madin, L.P., Purcell, J.E., 1992. Feeding, metabolism and growth of *Cyclosalpa bakeri* in the subarctic Pacific. *Limnology and Oceanography* 37, 1236–1251.
- Madin, L.P., Cetta, C.M., McAlister, V.L., 1981. Elemental and biochemical composition of salps (Tunicata, Thaliacea). *Marine Biology* 63, 217–226.
- 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.
- Martinussen, M.B., Båmstedt, U., 1999. Nutritional ecology of gelatinous predators. Digestion rate in relation to type and amount of prey. *Journal of Experimental Marine Biology and Ecology* 232, 61–84.
- Matsakis, S., Nival, P., 1989. Elemental composition and food intake of *Phialidium* hydromedusae in the laboratory. *Journal of Experimental Marine Biology and Ecology* 130, 277–290.
- Matthews, J.B.L., Hestad, L., 1977. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway: length/weight relationship for some macroplanktonic organisms. *Sarsia* 63, 57–63.
- McGowan, J.A., Bograd, S.J., Lynn, R.J., Miller, A.J., 2003. The biological response to the 1977 regime shift in the California Current. *Deep-Sea Research Part II* 50, 2567–2582.
- Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. *Deep-Sea Research* 35, 473–490.
- Nagasawa, S., 1984. Laboratory feeding and egg production in the chaetognath *Sagitta crassa* Tokioka. *Journal of Experimental Marine Biology and Ecology* 76, 51–65.
- Norrbinn, F., Båmstedt, U., 1984. Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. *Ophelia* 23, 47–64.
- Ohman, M.D., 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. *Journal of Plankton Research* 8, 673–713.
- Ohman, M.D., 1988a. Behavioral responses of zooplankton to predation. *Bulletin of Marine Science* 43, 530–550.
- Ohman, M.D., 1988b. Sources of variability in measurements of copepod lipids and gut fluorescence in the California Current coastal zone. *Marine Ecology Progress Series* 42, 143–153.
- Ohman, M.D., Lavaniegos, B.E., 2002. Comparative zooplankton sampling efficiency of the ring net and bongo net with comments on pooling of subsamples. *California Cooperative Oceanic Fisheries Investigations Reports* 43, 162–173.
- 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., Townsend, A.W., 1998. Egg strings in *Euchirella pseudopulchra* (Aetideidae) and comments on constraints on egg brooding in planktonic marine copepods. *Journal of Marine Systems* 15, 61–69.
- Omori, M., 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. *Marine Biology* 3, 4–10.
- Peterson, W.T., 1980. Life history and ecology of *Calanus marshallae* Frost in the Oregon upwelling zone. Ph.D. Thesis, Oregon State University, USA, unpublished.
- Peterson, W.T., Schwing, F.B., 2003. A new climate regime in northeast Pacific ecosystems. *Geophysical Research Letters* 30. doi:10.1029/2003GL017528.
- Purcell, J.E., 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). *Journal of Experimental Marine Biology and Ecology* 62, 39–54.
- Purcell, J.E., Kremer, P., 1983. Feeding and metabolism of the siphonophore *Sphaeroneustes gracilis*. *Journal of Plankton Research* 5, 95–106.
- Rau, G.H., Ohman, M.D., Pierrot-Bults, A.C., 2003. Linking nitrogen dynamics to climate variability off Central California: a 51 year record based on $^{15}\text{N}/^{14}\text{N}$ in CalCOFI zooplankton. *Deep-Sea Research II* 50, 2451–2467.
- 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.
- Reeve, M.R., Baker, I.D., 1975. Production of two planktonic carnivores (chaetognaths and ctenophores) in south Florida inshore waters. *Fishery Bulletin* 73, 238–248.
- Robertson, S.B., Frost, B.W., 1977. Feeding by an omnivorous planktonic copepod *Aetideus diversens* Bradford. *Journal of Experimental Marine Biology and Ecology* 29 (3), 231–244.
- Robison, B.H., Reisenbichler, K.R., Sherlock, R.E., 2005. Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science* 308, 1609–1611.
- Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31, L09204. doi:10.1029/2004GL019448.
- 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.
- Roesler, C.S., Chelton, D.B., 1987. Zooplankton variability in the California Current, 1951–1982. *California Cooperative Oceanic Fisheries Investigations Reports* 28, 59–96.
- Ross, R.M., 1982. Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. *Marine Biology* 68, 1–13.
- Ruhl, H.A., Smith, K.L., 2004. Shifts in deep-sea community structure linked to climate and food supply. *Science* 305, 513–515.
- Runge, J.A., 1980. Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnology and Oceanography* 25, 134–145.
- Sameoto, D.D., 1971. Life history, ecological production, and an empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia. *Journal of the Fisheries Research Board of Canada* 28, 971–985.
- 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, S.L., Lane, P.V., 1991. The jet off Point Arena, California: Its role in aspects of secondary production in the copepod *Eucalanus californicus* Johnson. *Journal of Geophysical Research* 96, 14849–14858.
- Smith, P.E., Moser, H.G., 2003. Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region. *Deep-Sea Research II* 50, 2519–2536.
- Smith, K.L., Baldwin, R.J., Ruhl, H.A., Kahru, M., Mitchell, B.G., Kaufmann, R.S., 2006. Climate effect on food supply to depths greater than 4,000 meters in the northeast Pacific. *Limnology and Oceanography* 51, 166–176.
- Sydeman, W.J., Bradley, R.W., Warzybok, P., Abraham, C.L., Jahneke, J., Hyrenbach, K.D., Kousky, V., Hipfner, J.M., Ohman, M.D., 2006. Planktivorous Auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? *Geophysical Research Letters* 33, L22S09.
- Thuesen, E.V., Childress, J.J., 1993. Metabolic rates, enzyme activities and chemical compositions of some deep-sea pelagic worms, particularly *Nectonemertes mirabilis* (Nemertea; Hoplonemeritinea) and *Poeobius meseres* (Annelida; Polychaeta). *Deep-Sea Research I* 40, 937–951.
- Uye, S., 1982. Length–weight relationships of important zooplankton from the inland Sea of Japan. *Journal of the Oceanographic Society of Japan* 38, 149–158.
- Uye, S., Kayano, Y., 1994. Predatory feeding behavior of *Tortanus* (Copepoda: Calanoida): life-stage differences and the predation impact on small planktonic crustaceans. *Journal of Crustacean Biology* 14, 473–483.
- Uye, S., Shibuno, N., 1992. Reproductive biology of the planktonic copepod *Paracalanus* sp. in the Inland Sea of Japan. *Journal of Plankton Research* 14, 343–358.
- Uye, S., Shimauchi, H., 2005. Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan. *Journal of Plankton Research* 27, 237–248.
- Uye, S., Iwai, Y., Kasahara, S., 1983. Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the inland Sea of Japan. *Marine Biology* 73, 91–98.
- Yamaguchi, A., Ikeda, T., 2000. Vertical distribution, life cycle and body allometry of two oceanic calanoid copepods (*Pleuromamma scutellata* and *Heterorhabdus tanneri*) in the Oyashio region, western north Pacific Ocean. *Journal of Plankton Research* 22, 29–47.