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# Long-term changes in pelagic tunicates of the California Current

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## Abstract

This study analyzes interannual variability in springtime carbon biomass of pelagic tunicates (salps, doliolids, pyrosomes, and appendicularians) over the period 1951–2002 from CalCOFI zooplankton samples taken in the southern sector of the California Current System. The results provide evidence for ecosystem changes between 1976 and 1977 and perhaps between 1998 and 1999. A cool-phase group of salps (*Salpa maxima*, *Pegea socia*, *Cyclosalpa bakeri*, and *Cyclosalpa affinis*) that was present between 1951 and 1976 was nearly undetectable in Southern California waters during the warm phase of the California Current (1977–98). *C. bakeri* and *C. affinis* then re-appeared in 2001. A persistent group of salps (*Salpa aspera*, *Salpa fusiformis*, *Thalia democratica*, *Ritteriella picteti*, *Iasis zonaria*) was observed throughout the study period. The cool-phase species tend to be distributed in mid-latitudes, while the distributions of the persistent species extend to equatorial waters. The cool-phase species have been reported to show little evidence of diel vertical migration, while most of the persistent species are reported to be diel migrants. No distinct multi-decadal patterns were observed in the dominant doliolid *Doliolletta gegenbauri*, but the rarer subtropical doliolid *Doliolum denticulatum* was present predominantly during the warm phase of the California Current. The recurrence patterns and biogeographic distributions of both salps and doliolids suggest that the warm phase of the California Current was accompanied by at least some intervals of anomalous transport “seeding” organisms from the south. Variations in total pyrosome and total appendicularian carbon biomass are not clearly related to long-term trends in the water column, although the highest pyrosome biomass occurred in earlier decades and appendicularian biomass has increased since 1999. Long-term changes in the biomass of pelagic tunicates appear to be chiefly responsible for the previously documented long-term decline in California Current total zooplankton biomass. The pattern of decline appeared to reverse in 1999, with a shift to cooler temperatures, somewhat reduced thermal stratification, and an increase in biomass of total zooplankton and of pelagic tunicates.

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## 1. Introduction

Relationships between variations in climate and marine ecosystems of the Northeast Pacific have been recognized at least since the pioneering

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studies of El Niño (see Sette and Issacs 1960). In recent years, attention has increasingly focused on longer-term variability of the ecosystems of the North Pacific (Venrick et al., 1987; Ebbesmeyer et al., 1991; Latif and Barnett, 1994; Roemmich and McGowan, 1995a,b; Beamish et al., 1997; Hare and Mantua, 2000; Moser et al., 2001; Rebstock, 2002) and North Atlantic (Fromentin and Planque, 1996; Beaugrand et al., 2002; Reid and Beaugrand, 2002). There is growing interest in the possibility that marine populations and ocean climate may persist in alternative states for protracted periods of 2–3 decades or more, followed by relatively rapid transitions to a new ecosystem state. Such alternative ecosystem states or ‘regimes’ (*sensu* Issacs, 1976) and associated ‘regime shifts’ have been identified in the North Pacific. The best evidence for such ecosystem state changes comes from concerted changes in meteorological, oceanographic, and biological variables during the winter of 1976–77 (Ebbesmeyer et al., 1991; Trenberth and Hurrell, 1994; Anderson and Piatt, 1999; but see Rudnick and Davis, 2003). These studies opened the question of whether ecosystem shifts also occurred around other nodal points in the 20th century. Mantua et al. (1997) found evidence of reversals in the Pacific Decadal Oscillation (PDO) index in 1925, 1947, and 1977. Hare and Mantua (2000; see also Rebstock, 2002) suggested that another change may have occurred in 1989–90. It has been proposed that the continued persistence of cool conditions in the NE Pacific after 1998 may represent another transition to a new ecosystem state (Schwing and Moore, 2000; Schwing et al., 2002a).

Mantua et al. (1997) called attention to the apparent out-of-phase oscillations of Alaska salmon catches and those farther south off Washington and Oregon. Regional catches off Alaska and Washington/Oregon are correlated with the PDO index, but with opposite signs (see also Batchelder et al., 2002). Chelton and Davis (1982) had proposed that ocean circulation into the subpolar gyre and the California Current fluctuate out-of-phase, and Hollowed and Wooster (1992) extended this idea to suggest that there are two main states of atmospheric circulation in the northern North Pacific that depend on the position and

intensity of the Alaska low pressure system. Intensification of the Aleutian low increases winds and intensity of ocean circulation into the Gulf of Alaska and weakens circulation into the California Current (Graham, 1994; Miller et al., 1994; Trenberth and Hurrell, 1994). Brodeur et al. (1996) suggested that out-of-phase circulation in the Alaskan gyre and California Current generates long-term trends in zooplankton biomass of opposite sign, with biomass increases in the Gulf of Alaska in the 1980s concurrently with biomass decreases in the California Current (Roemmich and McGowan, 1995a, b).

Such analyses of long-term changes in North-east Pacific zooplankton have been based primarily on measures of composite zooplankton biomass (Roemmich and McGowan, 1995a, b; Brodeur et al., 1996; Lavaniegos et al., 1998; but see Mackas et al., 1998; Lavaniegos and Ohman, 1999; Rebstock, 2001, 2002; Brodeur et al., 2002). Bulk zooplankton biomass is comprised of organisms representing as many as four trophic levels as well as widely different morphologies, body sizes, ratios of carbon:wet biomass, life histories, growth rates, and biogeographic distributions. Such diverse organisms are unlikely to respond in a uniform manner to environmental forcing, and thus the aggregated biomass of such disparate taxa is unlikely to be a sensitive indicator of environmental change. It has been hypothesized that specific zooplankton taxa may promote strong links between variations in physical processes and fish populations, while other zooplankton species may filter the environmental variability and translate little of it into variability in growth of fish populations (Runge, 1988). Hence, analysis of the specific members of zooplankton assemblages is also important from the perspective of the linkages between zooplankton and the recruitment of planktivorous fishes.

Pelagic tunicates can be conspicuous members of zooplankton assemblages. When abundant, their relatively large size and high water content make them significant contributors to total wet biomass. Moreover, individuals have high filtration rates and remove small planktonic microorganisms with relatively high efficiency (Alldredge and Madin, 1982; Kremer and Madin,

1992; Drits et al., 1992; Madin and Deibel, 1998). Grazing by pelagic tunicates and vertical transfer of organic matter through production of appendicularian houses (Gorsky and Fenaux, 1998) or unusually rapidly sinking fecal pellets (Bruland and Silver, 1981) can play a significant role in biogeochemical fluxes (Michaels and Silver, 1988; Drits et al., 1992; Andersen, 1998). High population growth rates of salps (Madin and Deibel, 1998), doliolids (Deibel, 1982; Gibson and Paffenhöfer, 2000), and appendicularians (Hopcroft and Roff, 1995) can lead to high abundances over large areas. Swarms of salps, in particular, can be of enormous geographic extent. In the California Current, a swarm of *Thalia democratica* extended over 9000 km<sup>2</sup> (Bernier, 1967). Extensive regions of high salp abundances also have been reported in the northern North Atlantic (Fraser, 1961), the Agulhas Bank region (De Decker, 1973), and elsewhere. Silver (1975) suggested that relatively subtle biological differences in microhabitats may exist for California Current salps that occur in the same geographic area.

In the present study, we analyze long-term changes in pelagic tunicates (salps, doliolids, pyrosomes, and appendicularians) in the California Current system (CCS) based on CalCOFI springtime zooplankton samples collected between 1951 and 2002 in Southern California waters. Our analysis is based on annual analysis of populations that may have considerable intra-annual variability. We examine lower frequency variations in pelagic tunicates in the context of long-term changes in physical properties of the water column. We also analyze temporal variations of hyperiid amphipods, which are crustacean parasitoids that frequently use tunicates as host organisms (Harbison, 1998; Laval, 1980; Lavaniegos and Ohman, 1999). We test the hypothesis of no significant long-term variability in tunicate assemblages of the CCS.

## 2. Methods

Our analysis is based on macrozooplankton samples collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI), in the

Southern California Bight and region offshore to station 70, inclusive (Fig. 1). The zooplankton samples used in this study were from CalCOFI springtime cruises for the period 1951–2002. Although samples were taken at other times of year, springtime samples were selected in order to obtain the best interannual coverage and longest record. Sampling methods are described in detail in Ohman and Smith (1995). Briefly, a 1-m diameter ring net with 0.55 mm mesh was towed to a depth of 140 m from 1951 to 1968, a 1-m ring net with 0.505 mm mesh to 210 m from 1969 to 1977, and a 0.71-m diameter bongo net with 0.505 mm mesh was towed to 210 m from December 1977 to present. All plankton tows were double oblique with calibrated flow meters mounted in the net mouth.

Samples within a cruise were pooled for purposes of enumeration, except for 14 cruises where samples were analyzed individually by station in order to assess spatial variability and its stability over time. For each cruise, only samples collected at night (1 h after sunset until 1 hr before sunrise) within the study region (Fig. 1) were analyzed. Stations shallower than 140 m (1951–68) or 210 m (1969–2002) were omitted from pooled samples. A total of 577 samples was selected (8–19 per cruise).

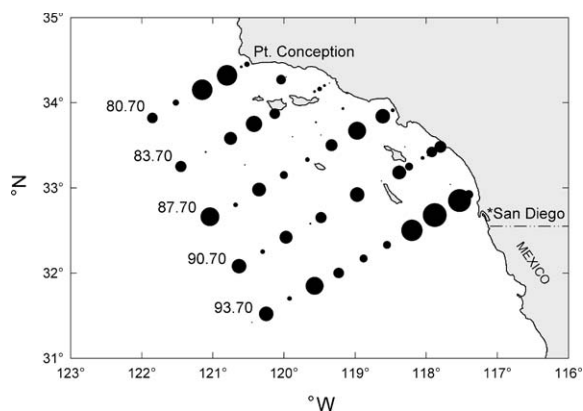


Fig. 1. Station locations and sampling effort for springtime CalCOFI cruises, 1951–2002. Symbol sizes are proportional to the number of times a station was sampled at night and included in this analysis. CalCOFI stations are numbered at the offshore end of each line (line.station number) considered in this study.

Large tunicates (>25 mm total length) were counted and identified to species from the complete sample. These and other large organisms were removed from the samples prior to pooling. A volume of each sample corresponding to 50 m<sup>3</sup> of seawater filtered was removed and combined into a pooled sample for each cruise (Rebstock, 2001). One quarter of each pooled sample was counted. In nonpooled samples, 1/8 was analyzed. Pelagic tunicates (salps, doliolids, pyrosomes, and appendicularians) were enumerated and measured to the nearest mm. Salps and doliolids were identified to species, with reference to Fraser (1947, 1981); Yount (1954); Foxton (1961), and Godeaux (1998). Appendicularians and pyrosomes were enumerated only by size class. Hyperiid amphipods also were counted and identified to species (following Brusca, 1981 and Vinogradov et al., 1996). The same pooled samples were used, but the entire sample was enumerated. As pooling samples affects abundance estimates of rare organisms (Ohman and Lavaniegos, 2002), only the five most abundant hyperiid species were selected to investigate associations with tunicate hosts.

Counts were standardized to individuals m<sup>-2</sup> of sea surface because such values are less subject to bias than volumetric values (individuals m<sup>-3</sup>) when there are differences in maximum sampling depth. A one-tailed 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 increase in biomass in the later period was detected for any taxa except the hyperiid amphipods *Eupronoe minuta* ( $P < 0.001$ ) and *Primno brevidens* ( $P < 0.05$ ), total appendicularians ( $P < 0.05$ ), and *Doliolum denticulatum* ( $P < 0.05$ ), although only *E. minuta* would be considered significant if corrected for multiple testing. The increased biomass of the two hyperiid amphipods began in 1969 and was sustained for most of the subsequent period; hence this change probably is an artifact of increased sampling depth. Increased biomass of appendicularians appears to be influenced mainly by sharp changes beginning in 1999, rather than at an earlier date. *D. denticulatum* was not detectable after 1998; hence true long-term changes appear not to be influenced by sampling depth.

Abundances of salps prior to 1978 were multiplied by a net factor of 2.68, as salps are collected better by the bongo net (Ohman and Lavaniegos, 2002). The abundance of tunicates was converted to carbon biomass by applying length-carbon regressions by species (Table 1). In applying these regression relationships derived from live lengths (Madin and Deibel 1998), we have not attempted to correct for shrinkage of specimens in preservative (Madin et al., 1981). Hence, our estimated C biomass may be somewhat low, but consistently so across the time series. In our counts, zooids from both solitary and aggregate generations are mixed, therefore we used the most suitable regression covering the appropriate size range for each species. For hyperiids the relation  $Y = 10.91(X)^{1.54}$  was used, where  $Y = \mu\text{g C}$  and  $X = \text{body length (mm)}$ . This function was derived from the dry mass to size relation for *Themisto japonica* (Ikeda, 1990) and percentage of organic carbon proposed by Ikeda and Shiga (1999). All carbon biomass data were  $\log(x + 1)$  transformed and then the mean and 95% confidence interval calculated for the 14 cruises where samples were analyzed individually.

Two measurements of composite zooplankton biomass were used, total displacement volume and small displacement volume. The first is determined by measuring the displacement volume of all material in plankton sample and the latter after removal of specimens of individual biovolume larger than 5 ml (Smith and Richardson, 1977). Displacement volume measurements prior to 1978 were corrected by the net factor of 1.366 arrived at by Ohman and Smith (1995) to correct for the reduced collection of biomass by the ring net.

The relationship between tunicate or total zooplankton biomass and environmental variables was investigated using a general linear model (SYSTAT v. 10.2) fitted using a stepwise forward procedure with alpha-to-enter and alpha-to-remove = 0.05. Three large-scale and nine local variables were used as independent variables (Table 2). The Pacific Decadal Oscillation Index (annual mean) is based on the first empirical orthogonal function of sea-surface temperature in the North Pacific north of 20°N (Mantua et al., 1997). The Aleutian Low Pressure Index (Beamish

Table 1  
Regressions used to estimate carbon content of pelagic tunicates

Species	Generation	Size range (mm)	Regression	Source
<i>Cyclosalpa affinis</i>	Sol	9–153	$\mu\text{g C} = 10.91 (\text{mm})^{1.54}$	Madin et al. (1981)
<i>Cyclosalpa bakeri</i>	Both	10–100	$\mu\text{g C} = 5.10 (\text{mm})^{1.75}$	Madin and Purcell (1992)
<i>Iasis zonaria</i>	Agg	11–50	$\mu\text{g C} = 1.00 (\text{mm})^{2.26}$	Madin and Deibel (1998)
<i>Pegea socia</i>	Agg	29–91	$\mu\text{g C} = 0.47 (\text{mm})^{2.22}$	Madin et al. (1981)
<i>Ritteriella retracta</i> <sup>a</sup>	Sol	30–73	$\mu\text{g C} = 0.20 (\text{mm})^{2.60}$	Madin and Deibel (1998)
<i>Salpa aspera</i>	Sol	15–75	$\mu\text{g C} = 3.00 (\text{mm})^{1.81}$	Madin and Deibel (1998)
<i>Salpa fusiformis</i>	Sol	10–55	$\mu\text{g C} = 1.40 (\text{mm})^{2.05}$	Madin and Deibel (1998)
<i>Salpa maxima</i>	Agg	3–93	$\mu\text{g C} = 1.01 (\text{mm})^{2.06}$	Madin et al. (1981)
<i>Thalia democratica</i>	Both	0.5–12	$\mu\text{g C} = 1.62 (\text{mm})^{1.93}$	Heron et al. (1988)
<i>Doliolletta gegenbauri</i>	Two	2.5–8.5	$\mu\text{g C} = 0.51 (\text{mm})^{2.28}$	D.M. Gibson (pers. comm.) <sup>b</sup>
<i>Pyrosoma atlanticum</i>		Not specified	$\mu\text{g C} = 12.54 (\text{mm})^{1.90}$	Andersen and Sardou (1994) (modified) <sup>c</sup>
<i>Oikopleura dioica</i> <sup>d</sup>		1–11	$\mu\text{g C} = 0.49 (\mu\text{g DW})^{1.12}$	Gorsky et al. (1988)

Sol is the solitary generation and Agg the aggregate generation.

<sup>a</sup> Applied to *Ritteriella picteti* in the present study.

<sup>b</sup> Based in part on results in Gibson and Paffenhöfer (2000). Also used for *Doliolum denticulatum* in the present study.

<sup>c</sup> The relationship between length and dry mass from Andersen and Sardou, (1994) was  $\text{mg DW} = 0.111 (\text{mm})^{1.90}$ , which was converted to carbon assuming 11.3% of dry mass from Gorsky et al. (1988).

<sup>d</sup> Used for all appendicularians in the present study. Additional functions for *Oikopleura longicauda* (Fenaux and Gorsky, 1983) were required to estimate dry mass [ $\text{DW} = 0.111 (\text{TL})^{1.90}$ ] and trunk length [ $\text{TA} = 3.77 (\text{TL})^{0.846}$ ], where DW = dry mass ( $\mu\text{g}$ ), TL = trunk length (mm), and TA = tail length (mm).

Table 2  
Environmental variables used in multiple regression analysis

Variable	Source
Pacific Decadal Oscillation Index (annual mean)	Mantua et al. (1997) <sup>a</sup>
Aleutian Low Pressure Index	Beamish et al. (1997) <sup>b</sup>
Southern Oscillation Index (winter mean)	NOAA Climate Prediction Center <sup>c</sup>
San Diego Sea Level, winter anomalies (secular trend removed)	University of Hawaii Sea Level Center <sup>d</sup>
Upwelling Index (33°N, 119°W), spring anomalies	NOAA Pacific Fisheries Environmental Laboratory <sup>e</sup>
Alongshore transport, line 90, winter anomalies derived from CalCOFI data	D. Roemmich (pers. comm.)
10 m temperature anomalies	CalCOFI <sup>f</sup>
10 m salinity anomalies	CalCOFI <sup>f</sup>
150 m temperature anomalies	CalCOFI <sup>f</sup>
150 m salinity anomalies	CalCOFI <sup>f</sup>
Thermal stratification anomalies (10–150 m)	CalCOFI <sup>f</sup>
Salinity stratification anomalies (10–150 m)	CalCOFI <sup>f</sup>

<sup>a</sup> [www.atmos.washington.edu/~mantua/abst.PDO.html](http://www.atmos.washington.edu/~mantua/abst.PDO.html).

<sup>b</sup> [www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/climate/clm\\_indx\\_alpi.htm](http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/climate/clm_indx_alpi.htm).

<sup>c</sup> [www.cpc.ncep.noaa.gov/data/indices/](http://www.cpc.ncep.noaa.gov/data/indices/).

<sup>d</sup> [www.nodc.noaa.gov/woce\\_v2/disk09/fast\\_del](http://www.nodc.noaa.gov/woce_v2/disk09/fast_del).

<sup>e</sup> [www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html](http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html).

<sup>f</sup> [www.calcofi.org/data/data.html](http://www.calcofi.org/data/data.html).

et al., 1997) measures the relative intensity of the Aleutian low pressure system of the North Pacific (Dec.–Mar). The Southern Oscillation Index is based upon atmospheric pressure differences between Tahiti and Darwin, and here we use a winter mean (Dec.–Feb.) as a proxy for El Niño in the tropics. For an indicator of El Niño in our mid-latitude region, we used San Diego sea-level winter anomalies (Dec.–Feb.), calculated after removal of the seasonal cycle and the secular trend.

Upwelling index anomalies were calculated for the Mar.–May time period (see ([www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html](http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html))). North–south transport between 0 and 200 m was calculated from CalCOFI hydrographic sections along CalCOFI line 90 from shore out to station 80 (D. Roemmich, pers. comm.). Winter anomalies (Jan.–Mar.) were then computed from these data. We computed indices of thermal and salinity stratification between 10 and 150 m depth from vertical profiles at all CalCOFI and related cruises within our sampling domain for springtime. Station-specific anomalies of temperature and salinity values were computed from the long-term means at each individual station within our sampling domain, and then the anomalies at each station averaged by cruise. Sea-surface temperature (SST) at the Scripps Pier (32.7°N, 117.2°W), was used to illustrate temperature variability in the region, but was not used in the multiple regression analysis. The average seasonal cycle from 1951 to 2002 was subtracted from each monthly mean temperature, the long-term secular trend removed using linear regression, and a 13-month running mean calculated.

### 3. Results

#### 3.1. Climate conditions

Anomalies of sea-surface temperature (SST) at Scripps Pier reveal appreciable, sustained warming associated with the major El Niños of 1958–59, 1982–83, 1992–93, and 1997–98 (Fig. 2a). In addition, a rapid warming event occurred between 1976 and 1977 and a precipitous, deep cooling

occurred between 1998 and 1999. Note that a linear long-term warming trend has been removed from the data in order to more readily detect other sources of variability in SST. Anomalous springtime thermal stratification in our sampling region (defined in Fig. 1) was consistent with the SST values, showing a period of somewhat lower average thermal stratification from 1951 to 1976, somewhat higher vertical stratification from 1977 until 1998, and then lower stratification again from 1999 to 2002 (Fig. 2b). The strong El Niño of 1958–59 also resulted in increased stratification. The large-scale temperature field in the North Pacific is illustrated by the Pacific Decadal Oscillation index (PDO, Fig. 2c). The predominantly cooler phase of the PDO from 1951 to 1976, followed by a warmer phase from 1977 to 1998, then a cooler phase again beginning in 1999, mirrors the patterns in local SST and regional thermal stratification. Again, the 1958–59 El Niño resulted in large-scale warming, during a cool-phase of the PDO.

Anomalous sea level at San Diego showed similar trends to SIO pier SST anomalies, increasing during major El Niños (Fig. 2d). However, sea-level anomalies were sometimes better indications than temperature of the mid-latitude influence of lesser magnitude El Niños (e.g., 1972–73 and perhaps 1977–78). Alongshore transport along CalCOFI line 90 during the El Niños of 1958–59, 1982–83, 1997–98, and to a lesser extent late 1991, became anomalously poleward for varying periods of time (Figs. 2e, D. Roemmich, pers. comm.). However, intervals of anomalously poleward transport occurred in non-El Niño years as well. Beginning in late 1998, transports were mostly anomalously southward. Note that the 3-year intervals between cruises in the 1970s makes it impossible to determine whether transports changed along with the temperature field between 1976 and 1977, as observed in Figs. 2a–c.

Springtime zooplankton biomass, as displacement volume, showed pronounced but reversible declines during the major El Niños of 1958–59, 1982–83, 1992–93, and 1997–98 (Fig. 3). On longer time scales, the decline in displacement volume that was recorded by Roemmich and McGowan (1995a, b) continued to a 50-year minimum in the

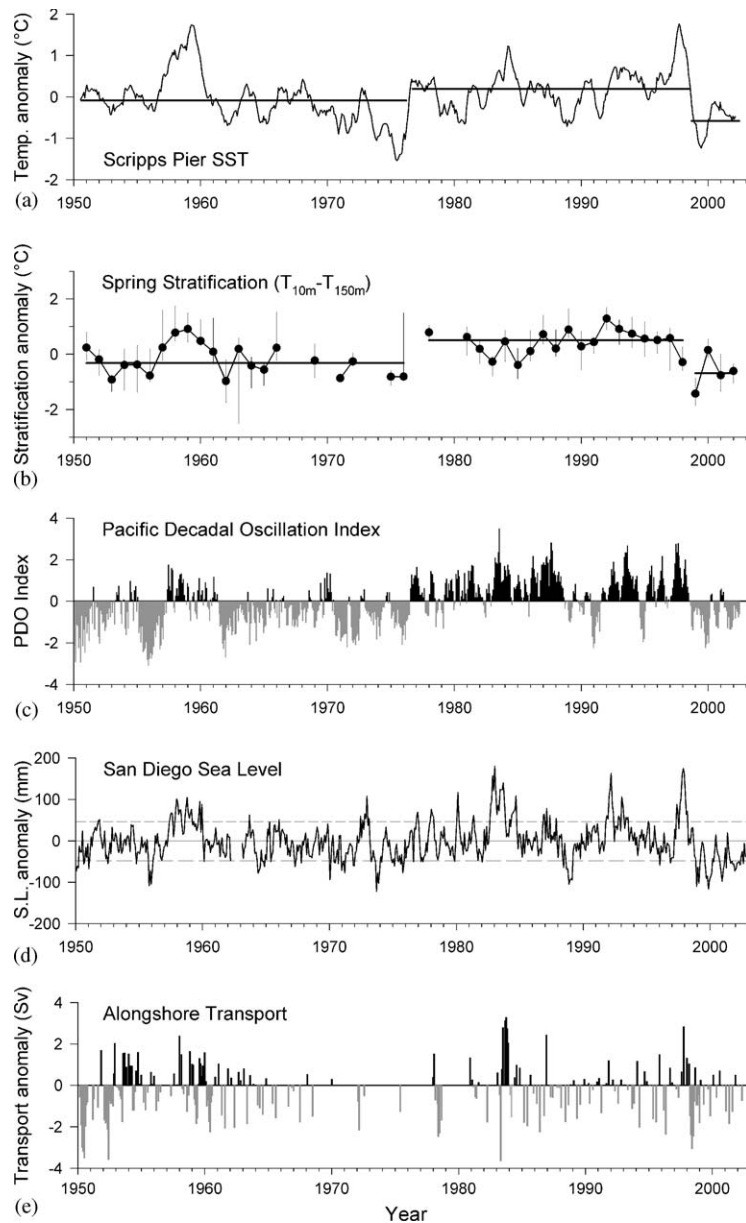


Fig. 2. Environmental conditions through the study period. (a) Sea-surface temperature (SST) anomalies at Scripps pier ( $32.7^{\circ}\text{N}$ ,  $117.2^{\circ}\text{W}$ ) obtained from a 13-month running mean, after removal of the seasonal cycle and the secular trend. Continuous lines indicate means for 1950–76, 1977–98, and 1999–2002. (b) Thermal stratification anomalies (median  $\pm$  95% nonparametric CI), measured as the difference between temperature at 10 and 150 m at each station occupied in the study region during spring CalCOFI cruises. Continuous lines indicate means for 1950–76, 1977–98, and 1999–2002. (c) Monthly values of the Pacific Decadal Oscillation index (Mantua et al., 1997). (d) San Diego sea level anomalies obtained from a 4-month running mean, after removal of the seasonal cycle and the secular trend. Dashed lines indicate  $\pm 1$  standard deviation. (e) Alongshore volume transport anomalies (Sverdrups) along CalCOFI line 90 from the coast to station 80, between 0 and 200 m, for winter months (Jan–Mar; D. Roemmich, pers. comm.). Positive indicates anomalously northward transport.

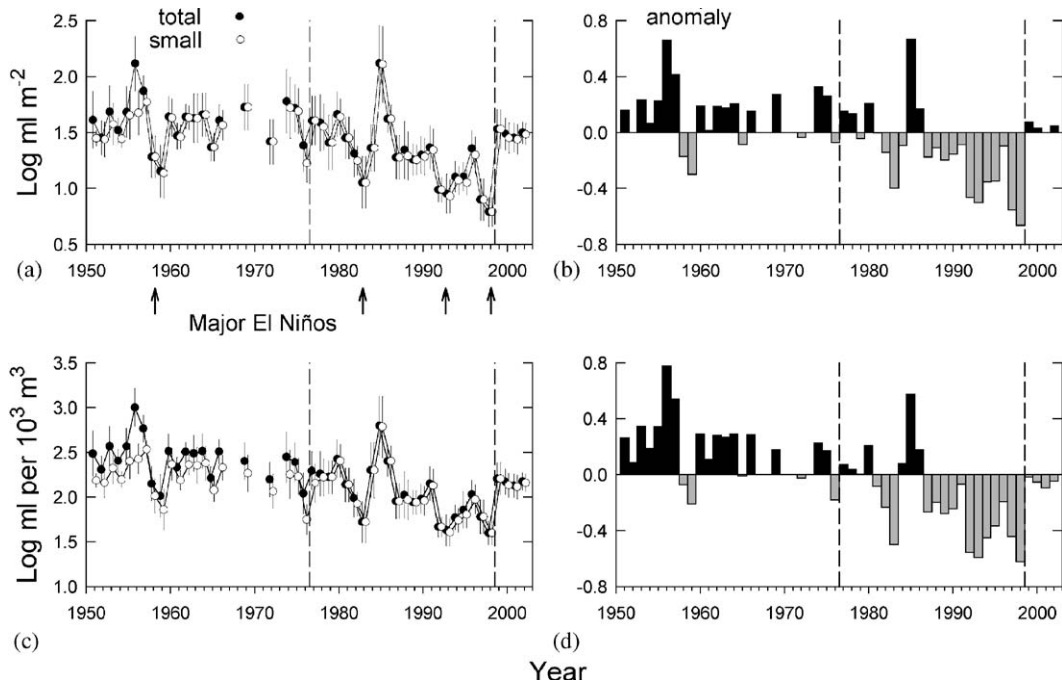


Fig. 3. Zooplankton biomass, measured as displacement volume, from springtime CalCOFI cruises. Only nighttime samples are considered. Total volume indicates displacement volume of all organisms in the sample, while small volume excludes animals of individual volume  $> 5$  ml. (a) Displacement volume per  $\text{m}^2$  of sea surface, (b) anomalies from the long-term mean of displacement volume per  $\text{m}^2$ . (c) displacement volume per  $1000 \text{ m}^3$  of sea water filtered, and (d) anomalies from the long-term mean of displacement volume per  $1000 \text{ m}^3$  of sea water filtered. Mean  $\pm 95\%$  confidence intervals; overlapping symbols offset slightly for clarity. Dashed lines illustrate hypothesized years of NE Pacific ecosystem shifts, in this and subsequent figures. Arrows indicate major El Niños in California waters.

spring of 1998, when El Niño was superimposed on a longer-term trend. However, this decline in biomass subsequently reversed to anomalously positive zooplankton biomass in springs of 1999–2002. Note that the same trends are apparent, whether we consider total zooplankton displacement volume (including organisms  $> 5$  ml) or only small displacement volume (excluding those organisms) (Fig. 3). There is no evidence suggesting a change in zooplankton biomass at or near the years 1976–77, when ocean temperature changed on several spatial scales in the NE Pacific (Fig. 2).

Zooplankton biomass is illustrated in alternative units in Fig. 3, as biomass per  $\text{m}^2$  of sea surface (Figs. 3a and b) and as biomass per  $1000 \text{ m}^3$  of water filtered (Figs. 3c and d). The expression of biomass per  $\text{m}^2$  is preferred because of the change in sampling depth in 1969. When biomass density decreases sharply as a function of

depth, as it generally does in the CCS (Mullin, 1986), the deepening of the sampling from 140 to 210 m will cause an apparent decline in biomass. For example, if we consider the nighttime vertical distribution of biomass measured by Mullin (1986) in the Southern California Bight, increasing the sampling depth from 140 to 210 m will generate an apparent 19.4% decline in biomass per unit volume, but a lesser change in biomass when expressed per unit area of sea surface. The small negative anomalies in Fig. 3d in 1999–2002 are a consequence of expressing data per unit volume and become positive anomalies (Fig. 3b) when instead expressed per  $\text{m}^2$ .

### 3.2. Pelagic tunicates

We identified 10 species of salps in the study area (Table 3), although others are also known to



Table 3

Species of pelagic tunicates from the Southern California Bight and region immediately offshore

Taxon	No. of cruises	Mean biomass (mg C m <sup>-2</sup> ) mean ± 95%
Class Thaliacea		
Order Salpida		
<i>Salpa fusiformis</i> Cuvier, 1804	24	2.015 ± 0.597
<i>Salpa aspera</i> Chamisso, 1819	25	1.862 ± 0.606
<i>Salpa maxima</i> Forskål, 1775	5	0.251 ± 0.279
<i>Thalia democratica</i> (Forskål, 1775)	25	0.230 ± 0.115
<i>Cyclosalpa bakeri</i> Ritter, 1905	7	0.207 ± 0.170
<i>Pegea socia</i> (Bosc, 1802)	7	0.199 ± 0.192
<i>Iasis zonaria</i> (Pallas, 1774)	23	0.167 ± 0.096
<i>Ritteriella picteti</i> (Apstein, 1904)	10	0.135 ± 0.108
<i>Cyclosalpa affinis</i> (Chamisso, 1819)	5	0.102 ± 0.116
<i>Thetys vagina</i> Tilesius, 1802	2	0.067 ± 0.098
Order Doliolida		
<i>Doliioletta gegenbauri</i> Uljanin, 1884	47	2.777 ± 0.412
<i>Doliolum denticulatum</i> Garstang, 1933	14	0.061 ± 0.060
Order Pyrosomida		
<i>Pyrosoma</i> spp.	21	0.364 ± 0.220
Class Appendicularia	47	3.494 ± 0.325

Number of cruises in which they were present (total = 47) and mean biomass for the period 1951–2002.

occur (Berner, 1967). The most frequently occurring and also generally the most abundant were *Salpa fusiformis*, *Salpa aspera*, *T. democratica*, and *Iasis zonaria*. These four species were observed in 50–60% of the springtime cruises, while the rest of the species were found in fewer than 25%. Due to the condition of preserved specimens, about 5% could not be identified. However, half of these came from only one sample from spring 1966 and were small individuals (1 mm) with low contribution to biomass.

There was no clear pattern with respect to El Niño, as both total salp biomass (Fig. 4) and that of individual species (Figs. 5 and 6) decreased in some El Niño years and increased in others. Year-to-year variability in biomass of individual species of salps was pronounced through the 52-year period (Figs. 5 and 6). Even for the most abundant and frequently occurring species, biomass could vary by 2–3 orders of magnitude in consecutive springs.

On longer time scales, however, some salp species recurred (if intermittently) throughout the record, while others were not detected in the sampling region during the warm interval from 1977–98. Among the species observed in the region

throughout the record, *S. fusiformis* and *S. aspera* were the dominants. Blooms of these species were particularly high in some years. The largest observed for *S. aspera* was in spring 1985 with a log-mean of 2.69 (492 mg C m<sup>-2</sup>), while *S. fusiformis* proliferated in 1983 (158 mg C m<sup>-2</sup>). These two species were responsible for 21 of the 26 salp blooms exceeding 10 mg C m<sup>-2</sup> during the study period. Although it persisted through time, *S. aspera* had lower average biomass in the period 1977–98 (log-mean = 0.2) than in the preceding interval 1951–76 (log-mean = 0.7,  $P < 0.05$ , Mann–Whitney  $U$  test). *S. fusiformis* maintained more similar biomass between these two periods ( $P > 0.50$ ). In 1999 relatively high biomass was observed for both species, and even higher for *S. aspera* in 2000. *T. democratica* and *I. zonaria* also persisted through the complete period, though their biomass represented around 1% of that of *S. aspera* or *S. fusiformis* (Fig. 5). *Ritteriella picteti* was scarce after 1975, except for the pulse of this species observed in spring 1982 (Fig. 5).

The remaining four salp species were present in this area in appreciable numbers only in the first portion of the study period (Fig. 6). Some of them (*Salpa maxima*, *Pegea socia*, and *Cyclosalpa*

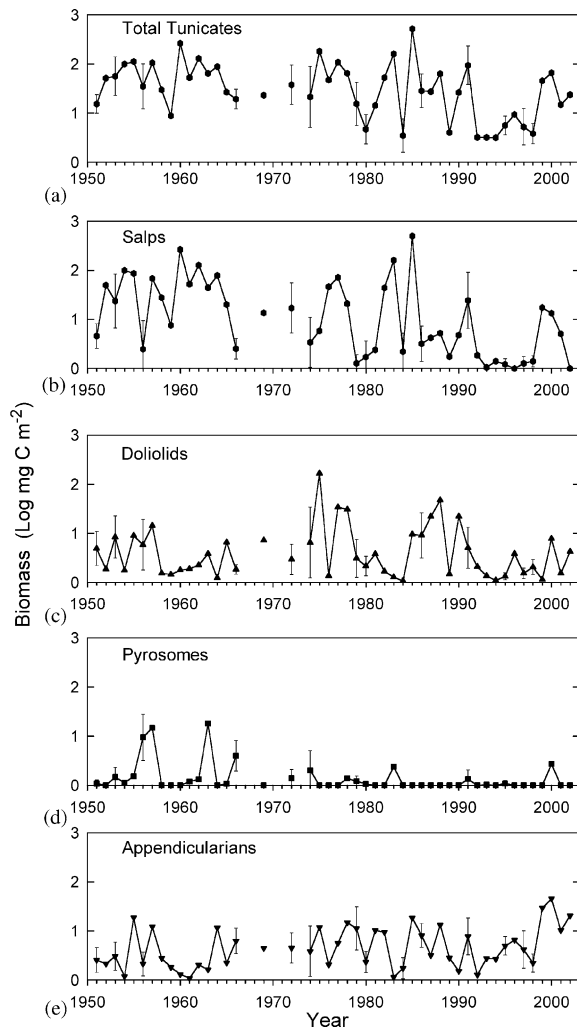


Fig. 4. Biomass, as organic carbon, through the study period of: (a) all pelagic tunicates combined, (b) salps, (c) doliolids, (d) pyrosomes, and (e) appendicularians separately.

*bakeri*) even reached biomass exceeding  $10 \text{ mg C m}^{-2}$  during 1951–76 (Fig. 6). These species and *C. affinis* essentially disappeared to undetectable levels after 1976. However, specimens of an unidentifiable species of *Cyclosalpa* were present in 1988. *C. bakeri* and *C. affinis* both reappeared in the region in 2001 (Fig. 6). *Thetys vagina* is not illustrated, as only two specimens were found (in spring of 1955 and 1964).

When salp biomass is divided into: (a) those species that were dominant in the cool-phase from

1951 to 1976, but essentially disappeared from the region from 1977 to 1998 (and may have subsequently returned after 1998), and (b) those species that persisted through the transitions into and out of cool and warm phases, the pattern is striking (Fig. 7). The cool-phase species dropped precipitously to essentially zero biomass in 1977. In contrast, the persistent species showed no change in total biomass in 1977, but declined in biomass after 1991 and increased again markedly in 1999. There was significant heterogeneity among the three time periods (1951–76, 1977–98, and 1999–2002) for the cool-phase species ( $P < 0.001$ , Kruskal–Wallis ANOVA) and weak heterogeneity for the persistent species ( $P = 0.03$ ).

The doliolids present in our springtime samples were either *Dolioletta gegenbauri* or *D. denticulatum*, although other, rarer species are also known to occur in the region (Berner, 1967). *D. gegenbauri* was present in all the cruises analyzed and was consistently the more abundant of the two species, apart from 1981 (Fig. 8a). The contribution of *D. gegenbauri* to total carbon biomass is considerable; although they are generally smaller than salps, they can be quite abundant. As with other tunicates, interannual variability of *D. gegenbauri* was pronounced, with a range from  $0.1$  to  $164 \text{ mg C m}^{-2}$  (in 1984 and 1975, respectively). Low biomass of this species was associated with the major El Niños of 1958–59, 1982–83, 1992–93, and 1997–98. There were no persistent changes in *D. gegenbauri* biomass associated with either the years 1977 or 1999. 1976 was a low biomass year.

*D. denticulatum* was considerably less abundant, less frequently observed, and showed a markedly different long-term pattern than *D. gegenbauri*. In the first 26 years, *D. denticulatum* was detected in only one spring cruise (1972) at a few stations. However, between 1977 and 1998 it occurred in several years (Fig. 8b). It has been nearly undetectable in springtime cruises in our region since the cooling of the California Current in 1998–99. There was significant heterogeneity among the three time periods (1951–76, 1977–98, and 1999–2002) for *D. denticulatum* ( $P < 0.05$ , Kruskal–Wallis) but not for *D. gegenbauri* ( $P > 0.50$ ).

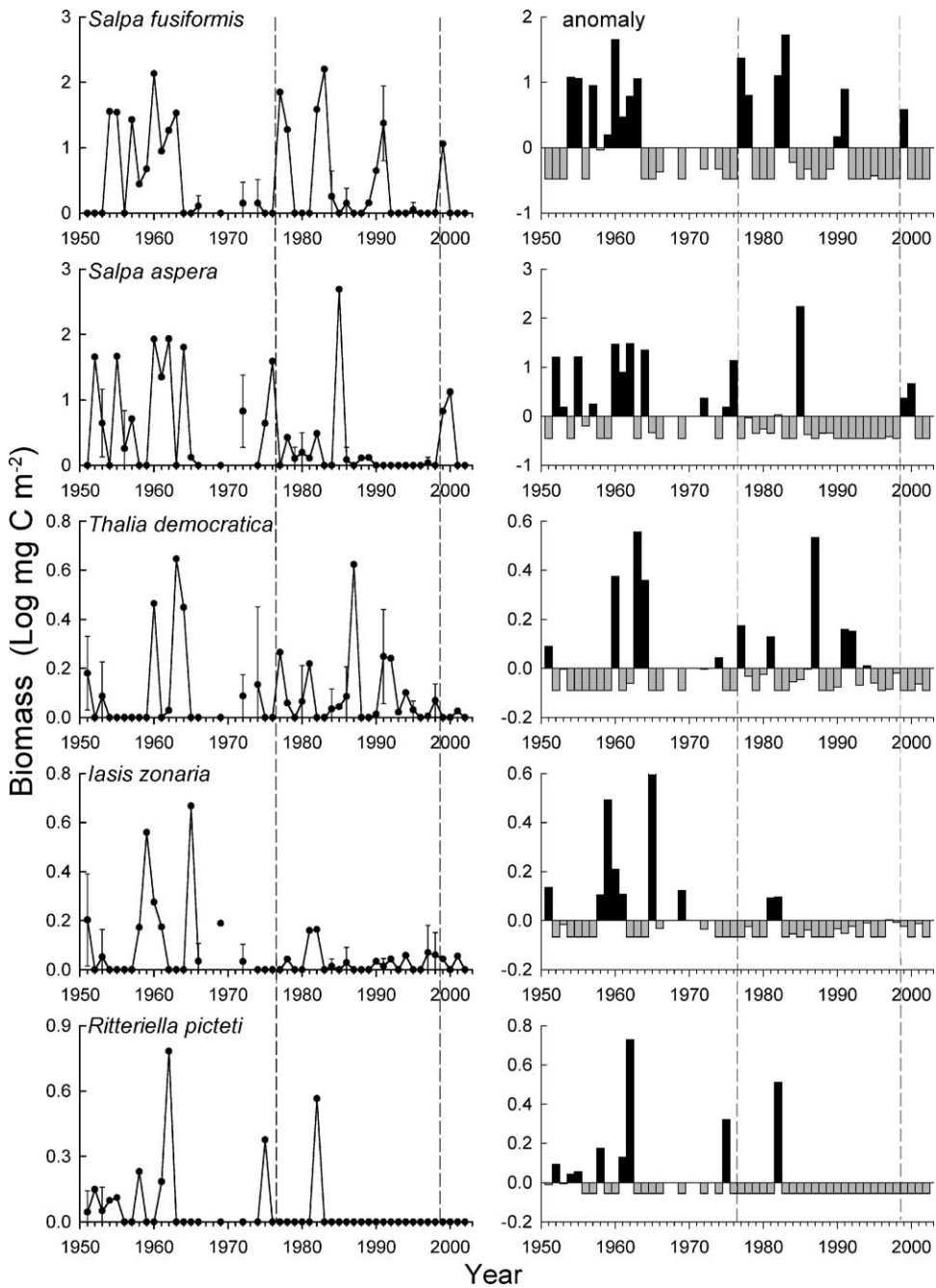


Fig. 5. Biomass, as organic carbon, of salp species observed during both cool and warm phases of the California Current. Anomalies illustrate departures from the mean from 1951 to 2002.

Pyrosomes (*Pyrosoma* spp., including *P. atlanticum* and *P. aherniosum*) were found in 21 of the 47 springtime cruises analyzed (Table 3). The few

blooms higher than 5 mg C m<sup>-2</sup> were found only in the cool-phase, prior to 1977 (Fig. 8c). Although present intermittently in the warm phase from

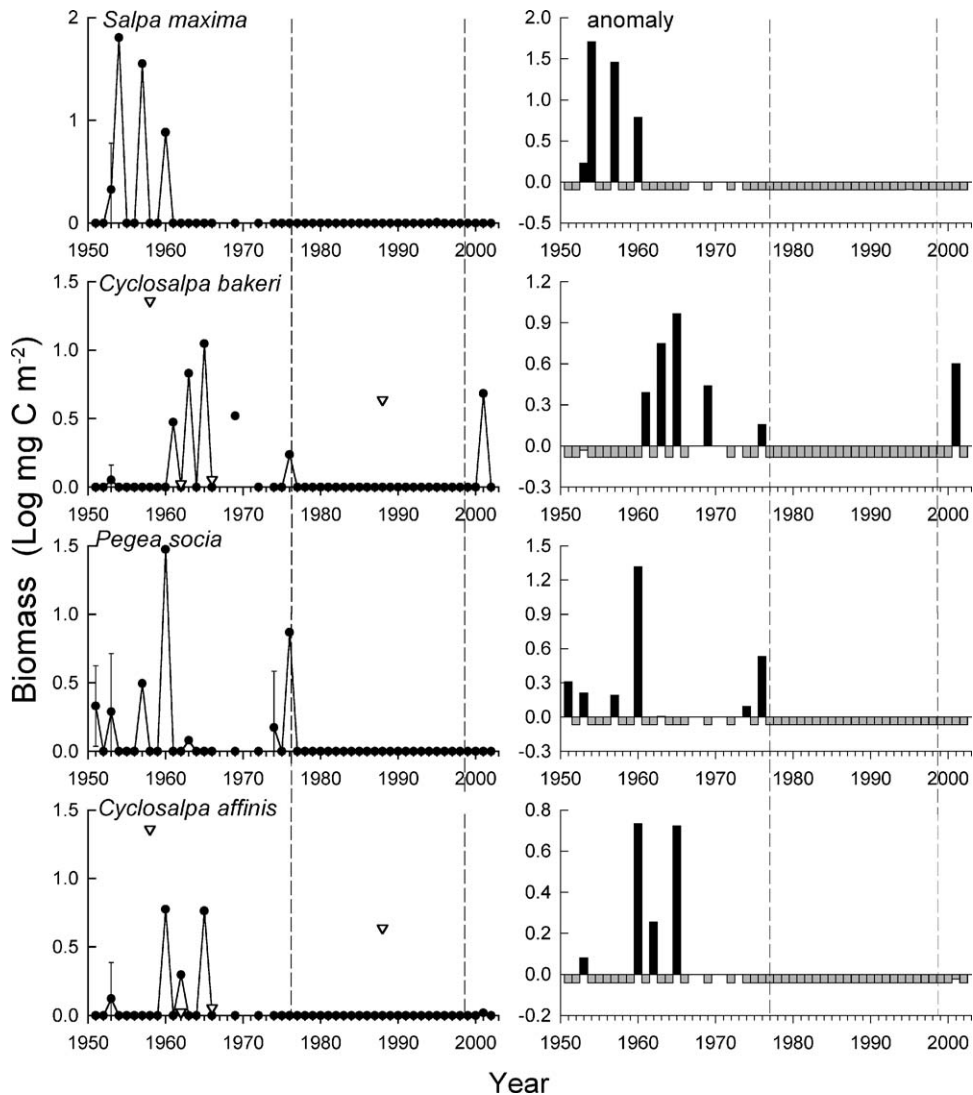


Fig. 6. Biomass, as organic carbon, of salp species that were essentially undetectable during the warm phase of the California Current. Anomalies illustrate departures from the mean from 1951 to 2002. Triangles indicate biomass of individuals of *Cyclosalpa* that could not be identified to species.

1977 to 1998, their biomass was lower during this interval ( $P < 0.05$ ) than the previous time period. In spring 2000, average biomass again increased, as seen prior to 1977.

Total appendicularian biomass also showed great variation from year-to-year (Fig. 8d). Species were not differentiated in our analysis. Biomass did vary among the three time intervals ( $P < 0.01$ , Kruskal–Wallis). Appendicularian biomass in-

creased markedly after 1998 and has remained elevated since.

Changes in tunicate biomass were attributable not only to variable abundance but also to changes in body size. Significant changes among the three time periods (1951–76, 1977–98, and 1999–2002) were detected in average size of salp zooids (Fig. 9a,  $P < 0.05$ , Kruskal–Wallis), with smaller average sizes in the warm phase of the CCS

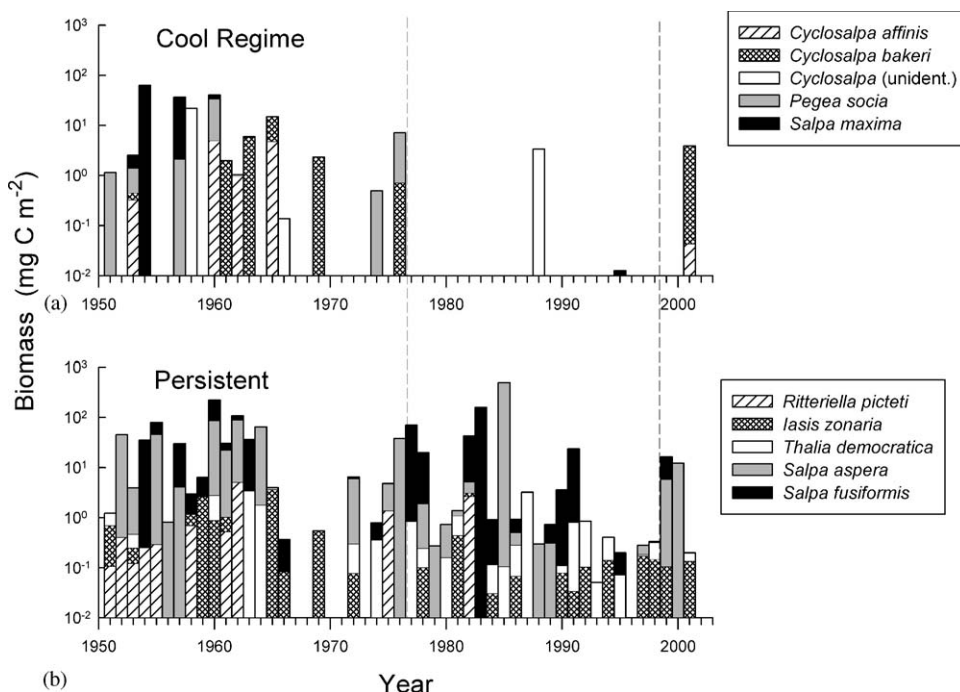


Fig. 7. Summed biomass, as organic carbon of: (a) salp species that were present primarily during the cooler phases of the California Current, and (b) salp species that were present through both cool and warm phases of the California Current. Note that the scale is logarithmic, hence the height of each shaded region is not linearly proportional to that species' relative biomass.

because the smaller body-sized species then predominated. Much of the size difference in salps is attributable to smaller zooid lengths during the early 1990s. A tendency to somewhat smaller doliolids in the warm phase was not significant (Fig. 9b,  $P > 0.10$ ). Pyrosome colony length varied significantly among time periods (Fig. 9c,  $P < 0.05$ ). The mean colony size in the earlier, cool-phase of the CCS was 3 times that of the warm period between 1977 and 1998, although no subsequent increase was detected in the samples from spring 2000. Appendicularian trunk length varied significantly among the three time periods (Fig. 9d,  $P < 0.05$ ), with body length increasing somewhat in successive time periods.

Due to the relatively large body sizes of tunicates, especially the thaliaceans, their contribution to total zooplankton biomass is likely to be significant. We found a relatively high correlation between carbon biomass of all 4 taxa of tunicates combined and total zooplankton displacement

volume (Spearman's rank = 0.50,  $P < 0.0001$ ). Considering the biomass of salps alone, variations in salp C biomass are correlated with total zooplankton displacement volume ( $r = 0.43$ ,  $P < 0.01$ ).

### 3.3. Tunicates as hosts of hyperiid amphipods

The most abundant hyperiid amphipods during this time period were, in descending order, *Primno brevidens*, *Vibilia armata*, *Paraphronima gracilis*, *Eupronoe minuta*, and *Themisto pacifica* (Fig. 10a). The rank order by C biomass was somewhat different (Fig. 10b), reflecting interspecific difference in body sizes. Temporal variability differed among the numerically dominant species (Fig. 11), but was generally of lower magnitude than temporal variability of tunicates. After 1998, the biomass of all species except *T. pacifica* became anomalously positive for varying periods of time. The summed C biomass of all hyperiids showed strong positive anomalies in 1999, 2000, and 2002

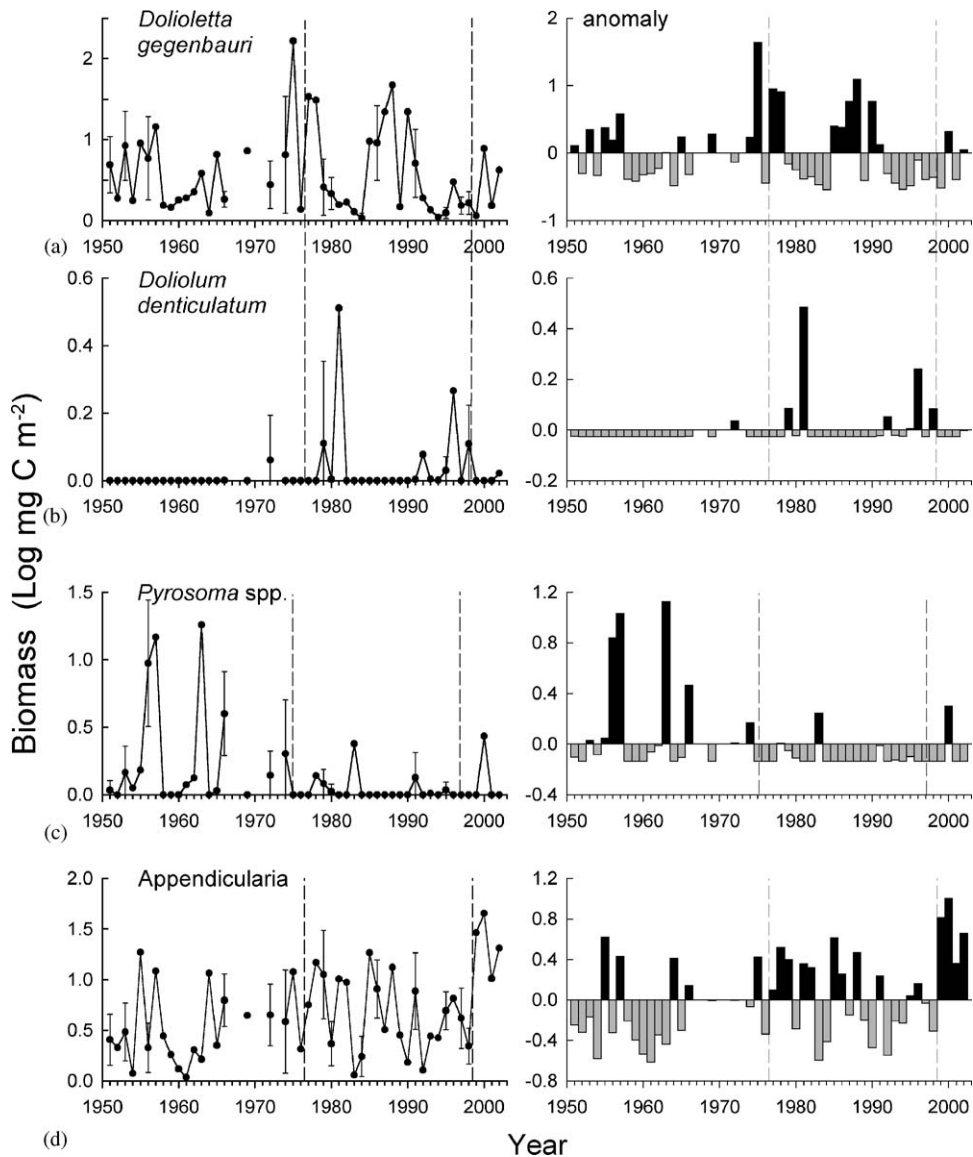


Fig. 8. Biomass, as organic carbon, of the doliolids: (a) *D. gegenbauri* and (b) *D. denticulatum*, (c) total pyrosomes, and (d) total appendicularians. Anomalies illustrate departures from the mean from 1951 to 2002.

(Fig. 12), although there was no significant relation of hyperiid biomass variability to the three temporal periods discussed above ( $P > 0.10$ , Kruskal–Wallis).

The association of hyperiids with all of the above potential tunicate hosts was tested using Spearman's rank correlation analysis. Positive correlations ( $P < 0.01$ ) were observed between

*Paraphronima gracilis* and *Themisto pacifica* and the host *S. aspera*, as well as between *Primno brevidens* and *Themisto pacifica* and the host *D. gegenbauri*. These correlations would not be significant if corrected for multiple comparisons by the Bonferroni criterion. Total hyperiid C biomass was not correlated with total C biomass of any of the four major taxa of tunicates considered

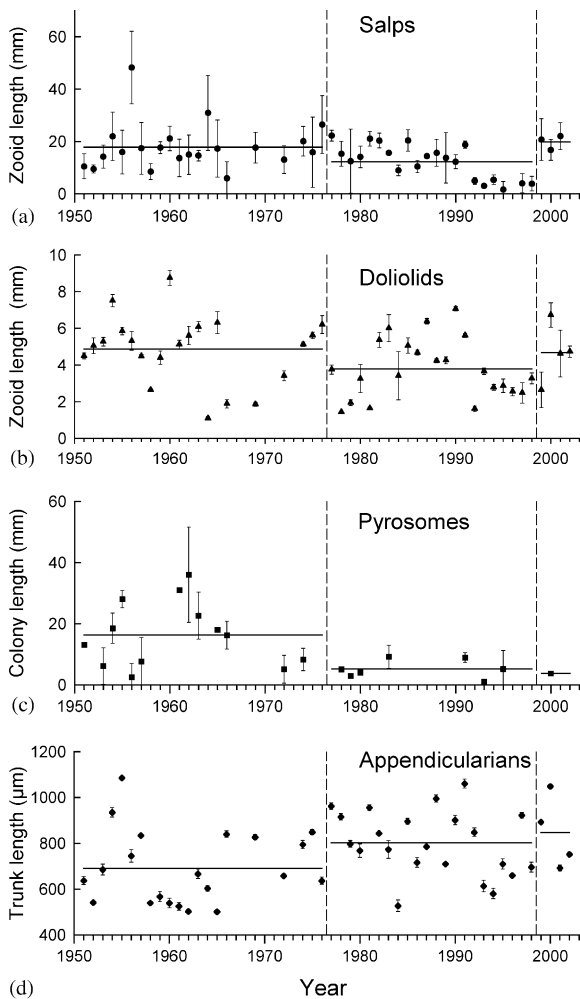


Fig. 9. Variations in body size of: (a) salps, (b) doliolids, (c) pyrosomes, and (d) appendicularians (mean  $\pm$  standard deviation). Continuous lines indicate mean values from 1951–76, 1977–98, and 1999–2002.

separately or with biomass of all tunicates combined ( $P > 0.05$ ).

### 3.4. Relationships with environmental variables

The usefulness of multiple regression in explaining the long-term variability of zooplankton differed according to the taxon considered. Total zooplankton displacement volume was reasonably well described by a general linear regression model, which accounted for 42.1% of the observed

variance, but only a single independent variable was selected. Anomalies from mean zooplankton displacement volume were negatively related to anomalies in temperature at 10 m ( $P < 0.01$ , corrected for serial correlation according to Dutilleul, 1993). Temperature stratification, the upwelling index, and all other local and remote variables in Table 2 made no significant additional contribution to explaining the variance in total zooplankton displacement volume. Multiple regression equations for the other dependent variables (persistent salps, cool regime salps, doliolids, pyrosomes, and appendicularians) all explained little or none of the variance ( $r^2 = 0.0, 0.0, 0.0, 0.07, \text{ and } 0.207$ , respectively), and thus are not discussed further here. Substitution of the Northern Oscillation Index (NOI, Schwing et al., 2002b) for the Southern Oscillation Index made no difference in the regression relationships.

## 4. Discussion

Assemblages of California Current pelagic tunicates, and particularly salps and doliolids, show variability on a time scale of 20–25 years that is coincident with low-frequency perturbations in the physical environment. The most pronounced pattern we observe is the rearrangement of species of salps and doliolids at the time of the 1976–77 warming in the Northeast Pacific. No such change is apparent in total zooplankton biomass. The subsequent abrupt cooling of the Northeast Pacific that began in late 1998 may have resulted in reciprocal changes in the relative abundance of the two dominant doliolid species and in some species of salps. The composition of tunicate assemblages after 1998 bears greater resemblance to the pre-1977 cool conditions than to the intervening warm period from 1977 to 1998, although a longer record is clearly needed to ascertain the persistence of this assemblage.

The observed warming of the water column per se is not likely to have much influence on the growth and survival of different zooplankton taxa. If the average  $Q_{10}$  were 2.0, an increase in mean temperature of 1°C (cf. Roemmich, 1992, also Fig. 2 above) would be expected to lead to only a

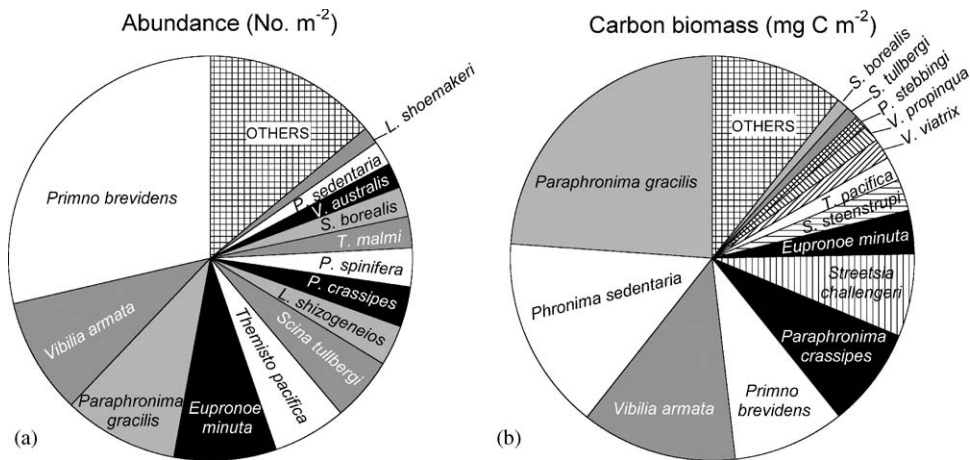


Fig. 10. Proportional contribution of the dominant hyperiid species by (a) abundance and (b) carbon biomass, averaged over 1951–2002. Proportions are based on antilogged means.

10% change in physiological rate processes. Moreover, many zooplankton migrate vertically through a thermocline on a daily basis and therefore experience diel temperature changes that greatly exceed the magnitude of long-term increase. Rather, it is the altered ocean circulation and vertical stratification associated with this warming that is likely to have significant consequences for the zooplankton fauna and for pelagic food web structure.

We are not able to ascertain directly whether volume transports changed significantly at the time of the 1976–77 ecosystem shift, because of the 3-year interval between CalCOFI cruises in the 1970s. Discerning long-term trends in volume transport is also difficult because of considerable cruise-to-cruise variability. Part of this variability may be contributed by lateral meandering of the core of the California Current to stations offshore of station 80, where our calculations stopped (D. Roemmich, pers. comm.). Nevertheless, we did detect a change in alongshore volume transport from anomalously northward during the 1997–98 El Niño to anomalously southward beginning in late 1998. This transport change is consistent with coincident cooler SIO pier temperatures, somewhat weaker vertical stratification, and anomalously low sea-level height, all of which suggest increased flow of higher-latitude waters into our sector of the California Current following El Niño.

The biogeographic distributions of the pelagic tunicates are helpful in interpreting the long-term changes we detected. The Southern California Bight together with the ocean immediately offshore is a boundary region where the southern limits of some northern/transition zone species overlap with the northern limits of some southern and subtropical zooplankton species. Hence, the admixture of zooplankton observed at any one time can sometimes provide a relatively sensitive indicator of the source water flowing into the region.

The larger-scale biogeography of salps and doliolids in the Pacific has not been summarized in detail outside the CalCOFI region (Bernier, 1967). Van Soest (1998) makes only generalized comments about geographic distributions. We therefore compiled records from existing primary literature (see Fig. 13 legend). We found that California Current salps tend to show latitudinal range limits that cluster into two groups (Fig. 13). Of the first five species (*S. maxima*, *P. socia*, *C. bakeri*, *C. affinis*, and *R. picteti*), all or most Northeast Pacific records of occurrence are clustered in mid-latitudes (Fig. 13). A limited number of records of *P. socia* (sometimes confounded with *P. confoederata*) and *C. bakeri* exist for latitudes south of 20°N. The remaining four species (*T. democratica*, *I. zonaria*, *S. fusiformis* and *S. aspera*; the latter two species were not differ-



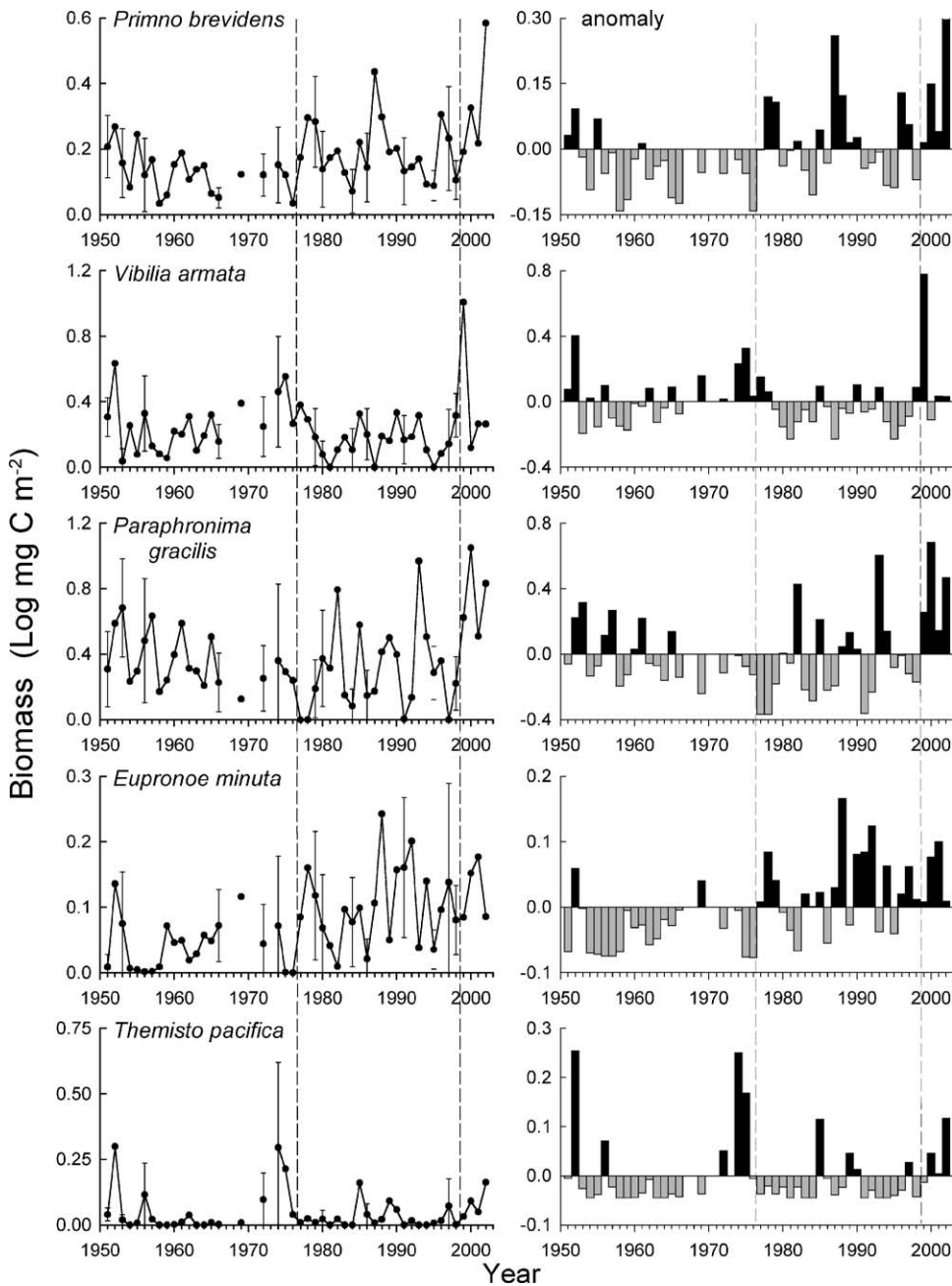


Fig. 11. Biomass, as organic carbon, of the five numerically dominant hyperiid amphipods. Anomalies illustrate departures from the mean from 1951 to 2002.

entiated in the early literature) have much broader latitudinal ranges and are known from the equator to 40–60°N latitude in the NE Pacific. These two

groups correspond nearly exactly with the two groups of salps noted above (i.e., cool regime and persistent species). The one exception is *R. picteti*,

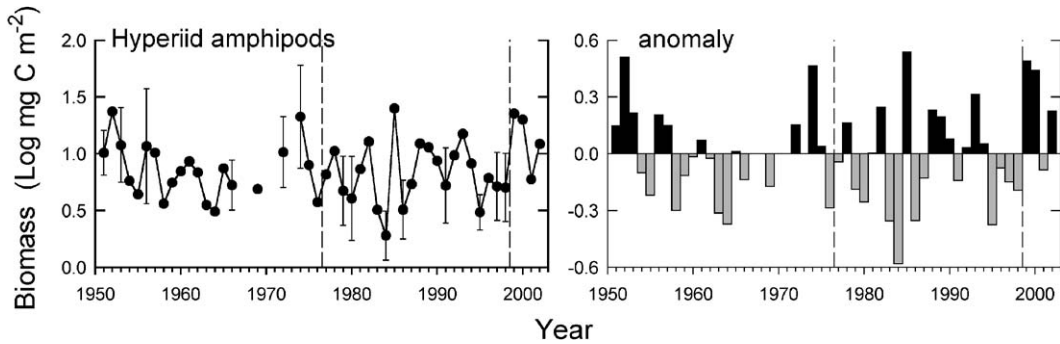


Fig. 12. Biomass, as organic carbon, of total hyperiid amphipods. Anomalies illustrate departures from the mean from 1951 to 2002.

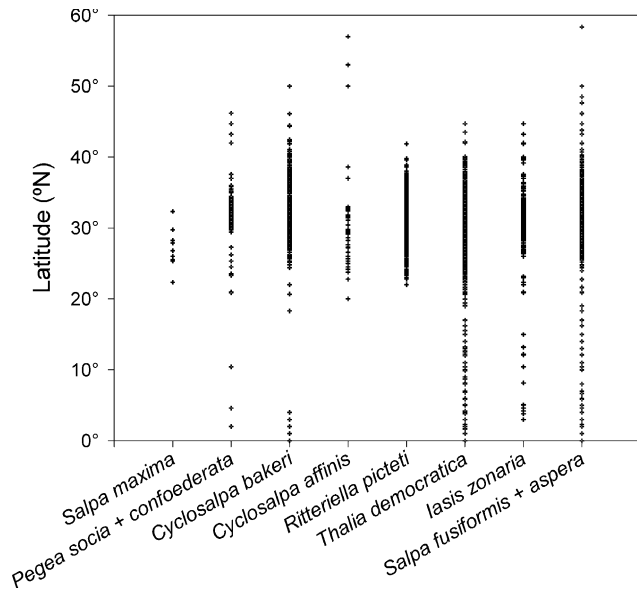


Fig. 13. Reported latitudinal ranges in the northeast Pacific (here defined as extending from the equator to 60°N, from the international dateline to the American continent) of the principal salp species in the present study. Distributional ranges were compiled from examination of records at 737 stations reported by Berner (1967), Bruland and Silver (1981), Chamisso (1819), Herdman (1888), Hubbard and Percy (1971), Madin (1974), Metcalf (1918), Miller et al. (1988), Parsons and Lalli (1988), Purcell and Madin (1991), Ritter (1905), Ritter and Byxbee (1905), Ritter and Johnson (1911), Silver and Bruland (1981), Tokioka (1960) and Yount (1958). *S. fusiformis* and *S. aspera* were not differentiated in the earlier literature, nor were *P. socia* and *P. confoederata*.

which we grouped with the persistent species, although it was found in our region in only one year (1982) after 1976. The biogeographic distributions imply that the cool regime species will be introduced into our region primarily from middle-higher latitude environments while the persistent species may be seeded into our region either from equatorial or subtropical latitudes or

from middle-high latitudes. Hence, persistence of the latter group during the warm regime of 1977–98 suggests enhanced transport from more southerly waters into our sampling region during that period. Much of the interdecadal variability in salp abundance that we observe may be affected by interdecadal variability in alongshore transport, although the calculated transports themselves may

not be sufficiently well resolved temporally to test this assertion, as noted above.

Another contrast between the two groups of salps is that the persistent species are, for the most part, thought to undergo diel vertical migration (DVM) while the cool regime species are not known to migrate vertically. Evidence on this point is incomplete and derives primarily from observations in the Atlantic, which may or may not be representative of salp vertical distributions in the Pacific. However, our persistent species *S. aspera*, *S. fusiformis*, *I. zonaria*, as well as *Ritteriella retracta* (a congener of our *R. picteti*), all have been reported to appear in surface waters more frequently at night off Bermuda (Madin et al., 1996) or off the US Atlantic coast (Wiebe et al., 1979). Conversely, our cool regime species *C. affinis* and *P. socia* appear not to migrate near Bermuda (Madin et al., 1996), and *C. bakeri* shows only shallow vertical migrations in the upper 60 m in the subarctic Pacific (Purcell and Madin, 1991). The vertical distribution of *S. maxima* is not clear.

The only clear exception to the association of long-term variability with DVM is *T. democratica*, another of our persistent species, which is not known to migrate vertically, at least in the Western Mediterranean (Andersen et al., 1998) or on Agulhas Bank (Gibbons, 1997). In general, salp species that spend half the day below the surface mixed layer may be less subject to horizontal advection out of the region, if vertical currents are strongly sheared. In addition, species that undergo DVM may have inherently greater tolerances for changing thermal and other conditions in the surface mixed layer, permitting them to persist through a range of different environmental circumstances.

Geographic distributions are an important component of the temporal variability of the two primary doliolids. *D. gegenbauri* is a cool water California Current or subarctic species (Berner, 1960) that is introduced into this sector of the California Current from the north (Fig. 14a, reproduced from Berner, 1960). Conversely,

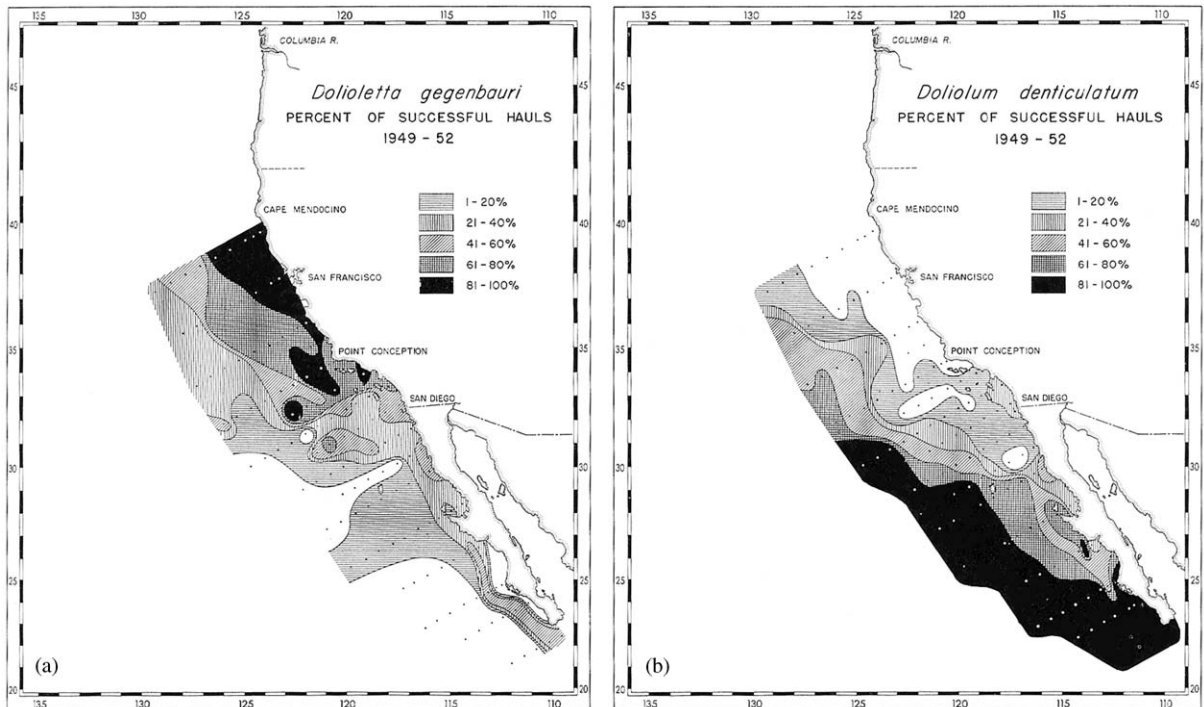


Fig. 14. Geographic distributions of the doliolids: (a) *D. gegenbauri* and (b) *D. denticulatum* (reproduced from Berner, 1960). Shading indicates the percentage of net hauls in which each species was found in CalCOFI samples, between 1949 and 1952.

*D. denticulatum* is a subtropical or central water mass species that is introduced into the California Current from more southerly or perhaps westerly waters (Fig. 14b, also Berner and Reid, 1961; Blackburn, 1979). The subtropical affinity of *D. denticulatum*, and its intermittent occurrence during the warm regime between 1977 and 1998, but rarely before or after, is consistent with anomalous transport of subtropical water into the region, as inferred from the salps. The persistence of the more northerly *D. gegenbauri* during 1977–98, when several cool-water affiliated salps did not occur, suggests that this sub-assembly of salps and *D. gegenbauri* have rather different geographic microdistributions and environmental optima.

As we have not identified the appendicularians or pyrosomes to species, and thus their biogeographic distributions are not resolved, we are not able to infer circulation changes from these taxa. However, the work of Brinton and Townsend (2003) concerning long-term variations in California Current euphausiids suggests that the warm regime from 1977 to 1998 was also a time of anomalously high abundance of subtropical euphausiids (notably *Nyctiphanes simplex* and *Euphausia eximia*, and to some extent *Euphausia gibboides* and *E. recurva*) in the Southern California domain. This pattern changed and the abundances of all four warm-water euphausiid species decreased after 1998.

Our working hypothesis to explain the long-term variability that we observe in salp and doliolid abundances therefore begins with altered transport that “seeds” organisms from different source regions into the Southern California region of the California Current. As we do not see evidence of anomalous transport sustained for two decades, we infer that the altered conditions in the water column then become more favorable to the organisms seeded into the region, such that populations can become self-sustaining in situ and do not require continued reintroduction of propagules to support population growth. A change to warmer, more stratified ocean conditions may favor the growth, development, and survival of subtropical taxa if the food and/or predator conditions become more appropriate. Increased

vertical stratification of temperature (and density), such as we observed during 1977–98, is thought to result in reduced vertical supply of inorganic nutrients limiting phytoplankton growth (Roemmich and McGowan, 1995a). If a shift in primary producers from microplankton to picoplankton followed such a change in nutrient supply, such floristic changes might then enable some microphagous subtropical tunicates to grow, survive, and predominate. Reciprocal changes would be expected at transitions to cooler, less stratified conditions. Pelagic tunicates that routinely undergo large amplitude vertical migrations may be less influenced by such alterations to the mixed layer environment.

We do not have a sufficiently long record of phytoplankton biomass or compositional changes in phytoplankton assemblages to directly test their relations to the observed changes in pelagic tunicates. Regular chlorophyll measurements on CalCOFI cruises began in 1984 and systematic phytoplankton floristic studies started more recently (Venrick, 2002). However, we note that the abrupt increase in total zooplankton biomass observed in 1999 was associated with increases in primary production rates and chlorophyll standing stocks (Chavez et al., 1999; Hayward et al., 1999; Bograd et al., 2000).

The importance of southward transport in the CCS in controlling interannual variations in overall zooplankton biomass was emphasized by Chelton et al. (1982). Roesler and Chelton (1987) subsequently analyzed regional variations within the CCS and found that zooplankton displacement volume variations were more strongly associated with advection in the northern sector of the CCS and less strongly so in the Southern California domain. The results of our multiple regression analysis confirm that springtime zooplankton biomass variability is related to variations in 10 m temperature, but not to changes in upwelling and other indices. Several authors, dating back to Reid et al. (1958), have found an inverse relationship between zooplankton displacement and temperature on various spatial scales in the California Current, although the causal mechanisms invoked differ. The relatively high fraction of variability explained in total zooplankton biomass contrasts

with the poor explanatory power of our multiple linear regressions for interannual variability in salps, doliolids, pyrosomes, and appendicularians. Part of the inadequacy of multiple regression for individual tunicate taxa stems from the mismatch between the rapid population response capability of the tunicates and our temporally/spatially averaged measures of the environment. Moreover, population growth of these organisms is likely to be a nonlinear function of environmental properties, while we employed a linear technique. Finally, the highly patchy dispersion pattern of many pelagic tunicates, especially salps, introduces considerable uncertainty into the biomass measures that were used in the regression equations.

The possible impact of predators on tunicates was restricted in the present study to hyperiid amphipods, but there is evidence of other pelagic organisms preying on tunicates (Harbison, 1998). The association of hyperiids with gelatinous plankton is well known (Laval, 1980). Lavaniegos and Ohman (1999) found correlations between some hyperiid species and different groups of gelatinous hosts in the Southern California region, based on data from 12 CalCOFI cruises during the period 1951–97. In the present study treating 47 spring cruises (1951–2002) it must be noted that the modest correlations between hyperiid amphipods and tunicates is due in part to the loss of spatial information on host-parasitoid associations by pooling samples within a cruise. Moreover, some hyperiids are associated with more than one type of host (Lavaniegos and Ohman, 1999), suggesting the possibility of switching according to host availability.

The correlation of summed tunicate C biomass with total zooplankton displacement volume suggests that much of the 70% decline in zooplankton displacement volume between 1951–57 and 1987–93 reported by Roemmich and McGowan (1995b) is attributable to changes in the biomass of pelagic tunicates. Indeed, the change in tunicate C biomass between these same time periods is an average decline of 75% (based on antilogged values), which could account for the previously documented change in total biomass. Neither the biomass of copepods (calculations from data in Rebstock, 2002) nor that of

euphausiids (Brinton and Townsend, 2003) exhibits such a trend. This result underscores the importance of resolving changes in different taxa within the zooplankton, as it is quite clear that co-occurring organisms can show markedly different responses to the same environmental forcing. In studies associated with higher trophic levels, temporal variations in particular taxa with strong links (*sensu* Runge, 1988) to fish populations and other consumers will be a more useful focus of research than aggregated zooplankton biomass alone. Similarly, understanding the processes structuring pelagic assemblages requires attention to the differences among taxa with a spectrum of life history traits and different biogeographic affinities.

Studies of CalCOFI copepods have revealed that calanoid copepod species composition shows transient disruptions at the time of El Niños, but the proportional composition of species remains relatively stable on a time scale of 50 years (Rebstock, 2001). Absolute abundances of copepods, however, can change in response to low-frequency changes in the California Current (Rebstock, 2002). Brinton and Townsend (2003) show that abundances of subtropical euphausiids shifted in both 1976–77 and 1998–99. The nitrogen stable isotope content of copepods and chaetognaths off Central California suggest that there were large (and reversible) changes in zooplankton  $^{15}\text{N}$  in response to El Niño events, but relatively small multi-decadal changes in zooplankton  $^{15}\text{N}$  content (Rau et al., 2003).

Increasingly, the importance of pelagic tunicates in marine food webs is being recognized (Andersen, 1998). The capacity of these large microphages to swarm can permit them to control phytoplankton blooms (Fortier et al., 1994) and to increase the transfer of biogenic carbon to the bottom through their fast-sinking, resistant, fecal pellets. Wiebe et al. (1979) estimated that mortality and fecal pellet production of *S. aspera* in the northwest Atlantic could contribute substantially to the carbon requirements of the deep-sea benthic fauna. Smith and Kaufmann (1999), also Smith et al. (2001), documented a trend between 1989 and 1996 toward a decreased flux of particulate organic carbon to the deep-sea benthos underlying

the California Current. As that interval was a time period of generally declining biomass of salps and doliolids, variations in these tunicates could have contributed significantly to a long-term change in particulate flux extending to the deep sea.

There are few truly long-term records of abundance of pelagic tunicates from any sector of the ocean. In the Western Mediterranean, temporal fluctuations of salps were documented by Ménard et al. (1994) for the period 1967–90. They sampled one station weekly and focused on seasonal changes, attributing the occurrence of salp blooms to breakdown of water column thermal stratification by winds. Fraser (1949) reported on salp and doliolid fluctuations in Scottish waters between 1920 and 1939 and suggested that interannual variations in abundance were related to the influx of relatively warm North Atlantic water into the North Sea. Long-term studies of plankton variations in the North Atlantic have generally focused on smaller organisms such as copepods (Beaugrand et al., 2002) rather than tunicates other than appendicularians, because the 1.27 cm<sup>2</sup> mouth opening of the Continuous Plankton Recorder is not appropriate for quantitative sampling of larger organisms (Clark et al., 2001; but see Roskell, 1983). In the Southern Ocean, interannual variations in salp abundance have been related inversely to variations in both sea ice cover and krill recruitment (Loeb et al., 1997, Nicol et al., 2000).

Our analyses address interannual and longer-term variations in springtime abundance, but do not resolve seasonal or higher-frequency variability, or spatial patterns. Pelagic tunicates, and especially salps, doliolids, and appendicularians, can have very short generation times under optimal conditions for growth (Alldredge and Madin 1982; Madin and Deibel, 1998), hence it is certain that we have aliased changes in population size and population structure on time scales shorter than the annual. It is also possible that an apparent absence or reduction in abundance in springtime is not indicative of abundance patterns at other times of year. Mackas et al. (1998) have documented that seasonal timing of ascent of zooplankton into subarctic Pacific surface waters can shift by 2 months over a period of 2½ decades.

Our work in progress may resolve the issue of shifts in seasonal timing in this region. Furthermore, an absence of animals in our samples does not imply that the animals were not present in the ocean, but only that they were not detectable in ca. 15 plankton tows over a defined geographic area. Irrespective of these caveats, the consistent CalCOFI sampling at multiple stations over a sizable sector of the California Current enables us to analyze lower frequency changes in a way that is possible in few other regions of the world ocean. Documentation of interannual and interdecadal changes in springtime patterns, even if confined to this time of year, reflect significant perturbations to epipelagic food webs.

Detecting low-frequency variability in the ocean is impossible in the absence of sustained, long-term measurements. The CalCOFI program is a singular biological oceanographic measurement program in the Northeast Pacific that permits the reliable detection of such multi-decadal ecological shifts. In light of the implications of long-term ecosystem shifts for resource management (Scheffer et al., 2001), it is of pivotal importance to sustain observational programs of pelagic assemblages and to begin to build our knowledge gained into prognostic models of marine ecosystems.

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## References

- Allredge, A.L., Madin, L.P., 1982. Pelagic tunicates: unique herbivores in the marine plankton. *BioScience* 32, 655–663.
- Andersen, V., 1998. Salp and pyrosomid blooms and their importance in biogeochemical cycles. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 125–137.
- 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.
- Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189, 117–123.
- Andersen, V., François, F., Sardou, J., Picheral, M., Scotto, M., Nival, P., 1998. Vertical distributions of macroplankton and micronekton in the Ligurian and Tyrrhenian Seas (northwestern Mediterranean). *Oceanologica Acta* 21, 655–676.
- Batchelder, H.P., Barth, J.A., Kosro, P.M., Strub, P.T., Brodeur, R.D., Peterson, W.T., Tynan, C.T., Ohman, M.D., Botsford, L.W., Powell, T.M., Schwing, F.B., Ainley, D.G., Mackas, D.L., Hickey, B.M., Ramp, S.R., 2002. The GLOBEC northeast Pacific California Current System program. *Oceanography* 15, 36–47.
- Beamish, R.J., Neville, C.E., Cass, A.J., 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Canadian Journal of Fisheries and Aquatic Science* 54, 543–554.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694.
- Berner, L.D., 1960. Unusual features in the distribution of pelagic tunicates in 1957 and 1958. *California Cooperative Oceanic Fisheries Investigations Reports* 9, 247–253.
- Berner, L.D., 1967. *Distributional Atlas of Thaliacea in the California Current region*. California Cooperative Oceanic Fisheries Investigations Atlas 8, 1–322.
- Berner, L.D., Reid Jr., J.L., 1961. On the response to changing temperature of the temperature-limited plankter *Doliolum denticulatum* Quoy and Gaimard 1835. *Limnology and Oceanography* 6, 205–215.
- Blackburn, M., 1979. Thaliacea of the California Current region: relations to temperature, chlorophyll, currents, and upwelling. *California Cooperative Oceanic Fisheries Investigations Reports* 20, 184–214.
- Bograd, S.J., DiGiacomo, P.M., Durazo, R., Hayward, T.L., Hyrenbach, K.D., Lynn, R.J., Mantyla, A.W., Schwing, F.B., Sydeman, W.J., Baumgartner, T., Lavaniegos, B., Moore, C.S., 2000. The state of the California Current, 1999–2000: forward to a new regime? *California Cooperative Oceanic Fisheries Investigations Reports* 41, 26–52.
- 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*, this issue (doi: 10.1016/S0967-0645(03)00126-7).
- Brodeur, R.D., Frost, B.W., Hare, S.R., Francis, R.C., Ingraham Jr., J.I., 1996. Interannual variations in zooplankton biomass in the Gulf of Alaska, and covariation with California Current zooplankton biomass. *California Cooperative Oceanic Fisheries Investigations Reports* 37, 80–99.
- Brodeur, R.D., Sugisaki, H., Hunt, G.L., 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* 233, 89–103.
- Bruland, K.W., Silver, M.W., 1981. Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). *Marine Biology* 63, 295–300.
- Brusca, G.J., 1981. Annotated keys to the Hyperieida (Crustacea: Amphipoda) of North American coastal waters. Allan Hancock Foundation, Technical Report 5, 1–76.
- Chamisso, A., 1819. De animalibus quibusdam e classe Vermium Linnaeana in circumnavigatione terrae: auspicante Comite N. Romanzoff duce Ottone de Kotzebue, annis 1815. 1816. 1817. 1818. peracta/observatis Adelbertus de Chamisso. *Fasciculus primus, De Salpa*, printed by Berolini.
- Chavez, F.P., Strutton, P.G., Friederich, G.E., Feely, R.A., Feldman, G.C., Foley, D.G., McPhaden, M.J., 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. *Science* 286, 2126–2131.
- Chelton, D.B., Davis, R.E., 1982. Monthly mean sea level variability along the west coast of North America. *Journal of Physical Oceanography* 12, 757–784.
- 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.
- Clark, R.A., Frid, C.L.J., Batten, S., 2001. A critical comparison of two long-term zooplankton time series from the central-west North Sea. *Journal of Plankton Research* 23, 27–39.
- De Decker, A., 1973. Agulhas Bank plankton. In: Zeitzschel, B. (Ed.), *The Biology of the Indian Ocean*. Springer, New York, pp. 189–219.
- Deibel, D., 1982. Laboratory determined mortality, fecundity and growth rates of *Thalia democratica* Forskal and *Doliolletta gegenbauri* Uljanin (Tunicata, Thaliacea). *Journal of Plankton Research* 4, 143–153.
- Drits, A.V., Arashkevich, E.G., Semenova, T.N., 1992. *Pyrosoma atlanticum* (Tunicata, Thaliacea)—Grazing impact on phytoplankton standing stock and role in organic carbon flux. *Journal of Plankton Research* 14, 799–809.
- Dutilleul, P., 1993. Modifying the *t* test for assessing the correlation between two spatial processes. *Biometrics* 49, 305–312.

- Ebbesmeyer, C.C., Cayan, D.R., McLain, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1991. 1976 Step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. In: Proceedings of the Seventh Annual Pacific Climate Workshop, California. Department of Water Resources, Interagency Ecology Studies. Program Technical Report 26, pp. 115–126.
- 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.
- Fortier, L., Lefevre, J., Legendre, L., 1994. Export of biogenic carbon to fish and to the deep-ocean. The role of large planktonic microphages. Journal of Plankton Research 16, 809–839.
- Foxton, P., 1961. *Salpa fusiformis* Cuvier and related species. Discovery Reports 32, 1–32.
- Fraser, J.H., 1947. Thaliacea II. Family Doliolidae. Conseil International pour l'exploration de la Mer. Zooplankton Sheet 10, 1–4.
- Fraser, J.H., 1949. The distribution of Thaliacea (Salps and Doliolids) in Scottish waters, 1920–1939. Scottish Home Department, Fisheries Division Scientific Investigations 1, 1–44.
- Fraser, J.H., 1961. The oceanic and bathypelagic plankton of the North-East Atlantic. Marine Research 4, 1–48.
- Fraser, J.H., 1981. British Pelagic Tunicates. Cambridge University Press, Melbourne, pp. 1–57.
- Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series 134, 111–118.
- Gibbons, M.J., 1997. Vertical distribution and feeding of *Thalia democratica* on the Agulhas Bank during March 1994. Journal of the Marine Biological Association of the United Kingdom 77, 493–505.
- Gibson, D.M., Paffenhöfer, G.A., 2000. Feeding and growth rates of the doliolid *Doliolletta gegenbauri* Uljanin (Tunicata, Thaliacea). Journal of Plankton Research 22, 1485–1500.
- Godeaux, J., 1998. The relationships and systematic of the Thaliacea, with keys for identification. In: Bone, Q. (Ed.), The Biology of Pelagic Tunicates. Oxford University Press, Oxford, pp. 273–294.
- Gorsky, G., Fenaux, R., 1998. The role of Appendicularia in marine food webs. In: Bone, Q. (Ed.), The Biology of Pelagic Tunicates. Oxford University Press, Oxford, pp. 161–169.
- Gorsky, G., Dallot, S., Sardou, J., Fenaux, R., Carré, C., Palazzoli, I., 1988. C and N composition of some north-western Mediterranean zooplankton and micronekton species. Journal of Experimental Marine Biology and Ecology 124, 133–144.
- Graham, N.E., 1994. Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: observations and model results. Climate Dynamics 10, 135–162.
- 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.
- Hayward, T.L., Baumgartner, T.R., Checkley, D.M., Durazo, R., Gaxiola-Castro, G., Hyrenbach, K.D., Mantyla, A.W., Mullin, M.M., Murphree, T., Schwing, F.B., Smith, P.E., Tegner, M., 1999. The state of the California Current, 1998–1999: transition to cool water conditions. California Cooperative Oceanic Fisheries Investigations Reports 40, 29–62.
- Herdman, W.A., 1888. Report upon the Tunicata collected during the voyage of H.M.S. Challenger, during the years 1873–76. Zoology Challenger Expedition 27(77), 1–63; Lams. I–XI.
- 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.
- Hollowed, A.B., Wooster, W.S., 1992. Variability of winter ocean conditions and strong year classes of Northeast Pacific groundfish. ICES Marine Science Symposia 195, 433–444.
- Hopcroft, R.R., Roff, J.C., 1995. Zooplankton growth rates—extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. Journal of Plankton Research 17, 205–220.
- Hubbard Jr., L.T., Percy, W.G., 1971. Geographic distribution and relative abundance of Salpidae off the Oregon coast. Journal Fisheries Research Board of Canada 28, 1831–1836.
- 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 Oceanographical 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.
- Issacs, J.D., 1976. Some ideas and frustrations about fishery science. California Cooperative Oceanic Fisheries Investigations Reports 18, 34–43.
- Kremer, P., Madin, L.P., 1992. Particle retention efficiency of salps. Journal of Plankton Research 14, 1009–1015.
- Latif, M., Barnett, T.P., 1994. Causes of decadal climate variability over the North Pacific and North America. Science 266, 634–637.
- Laval, P., 1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. Oceanography and Marine Biology Annual Review 18, 11–56.
- Lavaniegos, B.E., Ohman, M.D., 1999. Hyperiid amphipods as indicators of climate change in the California Current. In: Schram, F.R., von Vaupel Klein, J.C. (Eds.), Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998, Vol. I. Brill, Leiden, pp. 489–509.
- Lavaniegos, B.E., Gómez-Gutiérrez, J., Lara-Lara, J.R., Hernández-Vázquez, S., 1998. Long-term changes of



- zooplankton volumes in the California Current System. The Baja California region. Marine Ecology Progress Series 169, 55–64.
- 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.
- Mackas, D.L., Goldblatt, R., Lewis, A.G., 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Canadian Journal of Fisheries and Aquatic Science* 55, 1878–1893.
- Madin, L.P., 1974. Field studies on the biology of salps (Tunicata: Thaliacea). Ph.D. Thesis, University of California, Davis, pp. 1–204.
- 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., 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., Cetta, C.M., McAlister, V.L., 1981. Elemental and biochemical composition of salps (Tunicata, Thaliacea). *Marine Biology* 63, 217–226.
- Madin, L.P., Kremer, P., Hacker, S., 1996. Distribution and vertical migration of salps (Tunicata, Thaliacea) near Bermuda. *Journal of Plankton Research* 18, 747–755.
- 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.
- Ménard, F., Dallot, S., Thomas, G., Braconnot, J.C., 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. *Marine Ecology Progress Series* 104, 139–152.
- Metcalf, M.M., 1918. The Salpidae: a taxonomic study. *United States National Museum Bulletin* 100 (2(Part 2)), 5–193.
- Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. *Deep-Sea Research II* 35, 473–490.
- Miller, A.J., Cayan, D.R., Barnett, T.P., Graham, N.E., Oberhuber, J.M., 1994. The 1976–77 climate shift of the Pacific Ocean. *Oceanography* 7, 21–26.
- Miller, C.B., SUPER group., 1988. Lower trophic level production dynamics in the oceanic subarctic Pacific Ocean. *Bulletin of the Ocean Research Institute, University of Tokyo*, 26, pp. 1–28.
- Moser, H.G., Charter, R.L., Smith, P.E., Ambrose, D.A., Watson, W., Charter, S.R., Sandknop, E.M., 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951–1998. *California Cooperative Oceanic Fisheries Investigations Atlas* 34, 1–166.
- Mullin, M.M., 1986. Spatial and temporal scales and patterns. In: Eppley, R.W. (Ed.), *Plankton Dynamics of the Southern California Bight*. Lecture Notes on Coastal and Estuarine Studies, Vol. 15. Springer, New York, pp. 216–273.
- Nicol, S., Pauly, T., Bindoff, N.L., Wright, S., Thiele, D., Hosie, G.W., Strutton, P.G., Woehler, E., 2000. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* 406, 504–507.
- 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, pp. 153–158.
- Ohman, M.D., Lavaniegos, B.E., 2002. Comparative zooplankton sampling efficiency of a ring net and bongo net with comments on pooling of subsamples. *California Cooperative Oceanic Fisheries Investigations Reports* 43, 162–173.
- Parsons, T.R., Lalli, C.M., 1988. Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. 1988. *Oceanography and Marine Biology Annual Review* 26, 317–359.
- Purcell, J.E., Madin, L.P., 1991. Diel patterns of migration, feeding, and spawning by salps in the subarctic Pacific. *Marine Ecology Progress Series* 73, 211–217.
- 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*, this issue (doi: 10.1016/S0967-0645(03)00128-0).
- 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.
- Reid, J.L. Jr., Roden, G.I., Wyllie, J.G., 1958. Studies of the California Current System, 1 July 1956 to 1 January 1958. *California Cooperative Oceanic Fisheries Investigations Reports* 6, 28–57.
- Reid, P.C., Beaugrand, G., 2002. Interregional biological responses in the North Atlantic to hydrometeorological forcing. In: Sherman, K., Skjoldal, H.R. (Eds.), *Large Marine Ecosystems of the North Atlantic*. Changing States and Sustainability. Elsevier, Amsterdam, pp. 27–48.
- Ritter, W.E., 1905. Contributions from the laboratory of the Marine Biological Association of San Diego. III. The pelagic Tunicata of the San Diego region excepting the Larvacea. *University of California Publications in Zoology* 2, 51–112.
- Ritter, W.E., Byxbee, E.S., 1905. Reports on the scientific results of the expedition to the tropical Pacific in the Albatross. VIII. The pelagic Tunicata. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 26, 195–214.
- Ritter, W.E., Johnson, M.E., 1911. The growth and differentiation of the chain of *Cyclosalpa affinis* Chamisso. *Journal of Morphology* 22, 395–453.
- Roemmich, D., 1992. Ocean warming and sea level rise along the southwest US coast. *Science* 257, 373–375.
- Roemmich, D., McGowan, J.A., 1995a. Climatic warming and the decline of zooplankton in the California Current. *Science* 267, 1324–1326.

- Roemmich, D., McGowan, J.A., 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.
- Roskell, J., 1983. Thaliacea in continuous plankton records during 1983. *Annals of Biology* 41, 77–79.
- Rudnick, D.L., Davis, R.E., 2003. Red noise and regime shifts. *Deep-Sea Research I* 50, 691–699.
- Runge, J.A., 1988. Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. *Hydrobiologia* 167/168, 61–71.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Schwing, F., Moore, C., 2000. A year without summer for California, or a harbinger of a climate shift? *EOS, Transactions, American Geophysical Union* 81, 301–305.
- Schwing, F.B., Bograd, S.J., Collins, C.A., Gaxiola-Castro, G., García, J., Goericke, R., Gómez-Valdéz, J., Huyer, A., Hyrenbach, K.D., Kosro, P.M., Lavaniegos, B.E., Lynn, R.J., Mantyla, A.W., Ohman, M.D., Peterson, W.T., Smith, R.L., Sydeman, W.J., Venrick, E., Wheeler, P.A., 2002a. The state of the California Current, 2001–2002: Will the CCS keep its cool, or is El Niño looming? *California Cooperative Oceanic Fisheries Investigations Reports* 43, 31–68.
- Schwing, F.B., Murphree, T., Green, P.M., 2002b. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. *Progress in Oceanography* 53, 115–139.
- Sette, O.E., Isaacs, J.D.(Eds.), 1960. Symposium on “The changing Pacific Ocean in 1957 and 1958”. *California Cooperative Oceanic Fisheries Investigations Reports* 7, pp. 13–217.
- Silver, M.W., 1975. The habitat of *Salpa fusiformis* in the California Current as defined by indicator assemblages. *Limnology and Oceanography* 20, 230–237.
- Silver, M.W., Bruland, K.W., 1981. Differential feeding on fecal pellet composition of salps and pteropods, and the possible origin of the deep-water flora and olive-green “cells”. *Marine Biology* 62, 263–273.
- Smith, K.L., Kaufmann, R.S., 1999. Long-term discrepancy between food supply and demand in the deep eastern North Pacific. *Science* 284, 1174–1177.
- Smith, K.L., Kaufmann, R.S., Baldwin, R.J., Carlucci, A.F., 2001. Pelagic-benthic coupling in the abyssal eastern North Pacific: an 8-year time-series study of food supply and demand. *Limnology and Oceanography* 46, 543–556.
- Smith, P.E., Richardson, S.L., 1977. Standard techniques for pelagic fish egg and larva surveys. *FAO Fisheries Technical Paper* 175, pp. 1–100.
- Tokioka, T., 1960. Studies on the distribution of appendicularians and some thaliaceans of the North Pacific, with some morphological notes. *Publications of the Seto Marine Biological Laboratory* 8, 351–443.
- Trenberth, K.E., Hurrell, J.W., 1994. Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics* 9, 303–319.
- van Soest, R.W.M., 1998. The cladistic biogeography of salps and pyrosomas. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 231–249.
- Venrick, E.L., 2002. Floral patterns in the California Current System off Southern California: 1990–1996. *Journal of Marine Research* 60, 171–189.
- Venrick, E.L., McGowan, J.A., Cayan, D.R., Hayward, T.L., 1987. Climate and chlorophyll a: Long-term trends in the central North Pacific Ocean. *Science* 238, 70–72.
- Vinogradov, M.E., Volkov, A.F., Semenova, T.N., 1996. *Hyperiid Amphipods (Amphipoda, Hyperiidea) of the World Oceans*. Science Publishers, Lebanon, pp. 1–632.
- Wiebe, P.H., Madin, L.P., Haury, L.R., Harbison, G.R., Philbin, L.M., 1979. Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to deep-sea. *Marine Biology* 53, 249–255.
- Yount, J.L., 1954. The taxonomy of the Salpidae (Tunicata) of the Central Pacific Ocean. *Pacific Science* 8, 276–330.
- Yount, J.L., 1958. Distribution and ecologic aspects of Central Pacific Salpidae (Tunicata). *Pacific Science* 12, 111–130.