Multi-decadal variations in calcareous holozooplankton in the California Current System: Thecosome pteropods, heteropods, and foraminifera

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[1]   We examine long-term (1951–2008) variability of three major taxa of calcareous holozooplankton (aragonite-secreting thecosome pteropods and heteropods, and calcite-secreting large planktonic foraminifera) in light of recent interest in the impingement of waters undersaturated with respect to aragonite onto continental shelf depths in the California Current System. We assess interannual variability in springtime abundances of zooplankton sampled in the epipelagic layer, using CalCOFI (California Cooperative Oceanic Fisheries Investigations) zooplankton samples from two regions: Southern California (SC) and Central California (CC). Thecosome pteropods show no evidence of recent declines in abundance in SC or CC waters. In SC, sampling was sufficient to conclude that heteropods and large foraminifera also show no evidence of declines in abundance in recent years. These results do not preclude as-yet undetected changes in vertical distributions or shell morphology, and underscore the importance of sustained in situ measurement programs in order to detect and understand changes to pelagic ecosystems. **Citation:** Ohman, M. D., B. E. Lavaniegos, and A. W. Townsend (2009), Multi-decadal variations in calcareous holozooplankton in the California Current System: Thecosome pteropods, heteropods, and foraminifera, *Geophys. Res. Lett.*, *36*, L18608, doi:10.1029/2009GL039901.

1. Introduction

[2]   Recent results have shown that waters undersaturated with respect to aragonite penetrated into relatively shallow depths over a broad geographic area in the California Current upwelling domain in May-June 2007 [*Feely et al.*, 2008]. Feely et al. attributed the shoaling of high CO_2, low pH waters to the ocean's uptake of anthropogenically-enriched CO_2 from the atmosphere. While normal upwelling brings waters elevated in CO_2 toward the surface, increased pCO_2 in source waters for upwelling due to anthropogenic augmentation of atmospheric CO_2 [*Keeling et al.*, 1995] apparently has caused shoaling of the depth where aragonite dissolution would be favored. Waters undersaturated with respect to aragonite now penetrate onto shallow continental shelf depths off the U.S. west coast and even outcrop the surface [*Feely et al.*, 2008]. Shoaling of undersaturated waters has significant implications for the ability of some marine organisms to successfully secrete calcium carbonate shells [*Orr et al.*, 2005; *Fabry et al.*, 2008].

[3]   Other results suggest that the rate of upwelling in the California Current System (CCS) has intensified in recent decades. *Bakun* [1990] first proposed this trend from analysis of atmospheric pressure gradients over relatively large spatial scales (3° grids). The result was confirmed by *Schwing and Mendelssohn* [1997] and intensified upwelling has also been identified elsewhere [*Bakun*, 1990; *McGregor et al.*, 2007]. *Rykaczewski and Checkley* [2008] differentiated two different upwelling domains in the CCS: the coastal boundary upwelling zone, which is located close to the coastline, and the wind stress curl upwelling domain, located further offshore. Rykaczewski and Checkley suggest that over the past several decades there has been a progressive increase in the vertical transport of upwelled waters in the curl-driven upwelling domain, but not the coastal boundary domain.

[4]   These results together suggest that recent changes in upper ocean chemistry in the CCS may have occurred because of two factors: both increased flux of anthropogenic CO_2 into the ocean as well as an increased rate at which the pCO_2-enriched subsurface waters are delivered to the ocean's surface through stronger upwelling, particularly in the wind stress curl domain. Both imply a possible reduction in habitat favorable for calcareous holozooplankton in epipelagic waters of the CCS. Here we seek to determine whether major taxa of calcareous holozooplankton (aragonite-secreting thecosome pteropods and heteropods, and calcite-secreting planktonic foraminifera) show evidence of recent declines in abundance.

[5]   The pteropods include the Thecosomata and Gymnosomata, the latter lacking shells as adults. Among thecosomes, Euthecosomata all bear calcium carbonate shells as adults, but the Pseudothecosomata includes one genus (*Peraclis*) that bears a true shell and several families that have a thin, noncalcareous pseudoconch [*Lalli and Gilmer*, 1989]. However, all Thecosomata and Gymnosomata produce shell-bearing veliger larvae and are therefore potentially affected by the aragonite saturation state in the seawater in which they grow. Similarly, heteropods of the family Pterotracheidae that lack shells as adults, as well as the adult shell-bearing families Atlantidae and Carinariidae, develop through a shelled veliger stage [*Lalli and Gilmer*, 1989].

[6]   In order to measure changes in the ocean it is imperative to have a documentary record of sufficient duration to characterize long-term ecosystem variability. The California Current System is one of the few ocean regions where a multi-decadal interdisciplinary measurement program exists, thanks to the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program [*Ohman and Venrick*, 2003]. Previous results based on CalCOFI samples through 2005 suggest no secular changes

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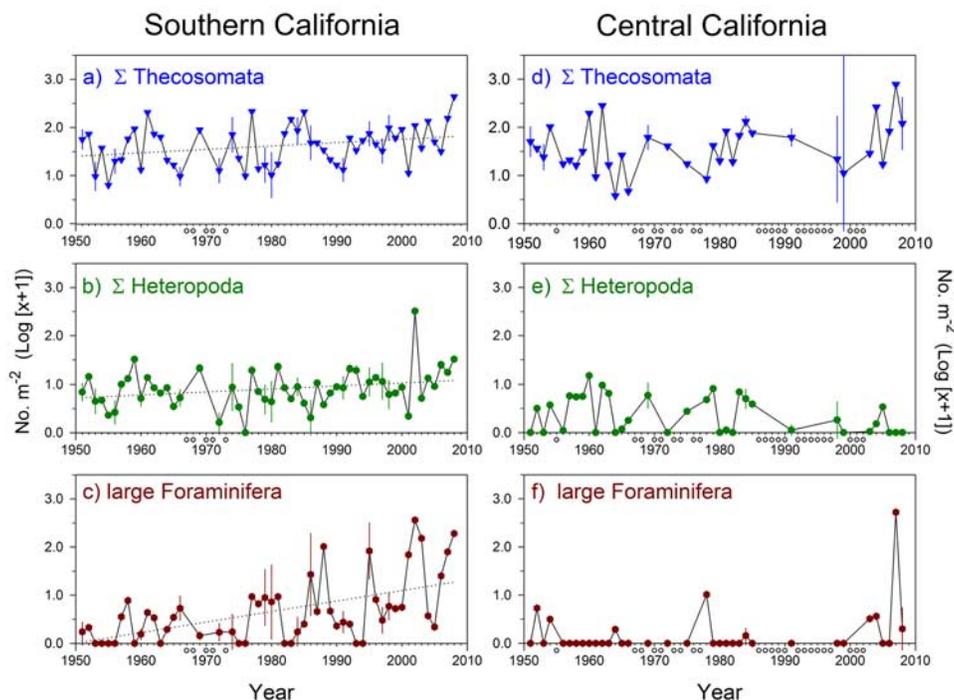
Figure 1. Interannual variation in springtime abundance of 3 taxa of calcareous holozooplankton: (a, d) total Thecosomata, (b, e) total Heteropoda and (c, f) large planktonic foraminifera in Southern California and Central California, from 1951–2008. Circles below the abscissa indicate years of no samples; 95% C.L. shown in years when individual stations were analyzed. All other years were pooled samples (see Methods). Significant ($p < 0.05$) linear regressions indicated by dotted lines (Thecosomata: $Y = 0.0070X - 12.34$, Heteropoda: $Y = 0.0063X - 11.47$, Foraminifera: $Y = 0.0218X - 42.58$).

in carbon biomass of thecosome or gymnosome pteropods [*Lavaniegos and Ohman*, 2007, supplementary material], but these results do not extend to the more recent time period when undersaturated waters have impinged into shallow waters, nor do they address heteropods or planktonic foraminifera, or constituent genera. To test for recent changes in abundance of calcareous holozooplankton we analyzed CalCOFI zooplankton samples from two regions: off Southern California, which overlaps the location of the California Current Ecosystem-Long Term Ecological Research site, and off Central California.

2. Methods

[7] Sampling: Samples selected were from springtime CalCOFI cruises (usually April; range March-May), the onset of the primary upwelling season and also the time of year best represented in the CalCOFI time series. However, there were unsampled springs in several years, especially in Central California. Zooplankton were sampled with a 0.5-mm mesh net (1-m ring net from 1951–1977, 0.71-m bongo net from 1978 to present; see *Ohman and Smith* [1995]) with calibrated flowmeters, fished obliquely from 140–0 m from 1951–1968 and 210–0 m from 1969–present. Net changes had no detectable effect on abundance or size distributions of pteropods or heteropods; foraminifera were not analyzed [*Ohman and Lavaniegos*, 2002]. Samples from Southern California (SC) were from CalCOFI lines 80 through 93, from the shore through station 70, and those from Central California (CC) were from CalCOFI

lines 60–70, from shore through station 90 (see Figure S1).[1] Typically 400–800 m^3 of seawater were filtered for each sample. Only nighttime samples were analyzed, except for 2008 in CC when 4 daytime samples were included. Samples from shallow waters (< 100 m) were excluded from analysis. Samples were fixed in 1.8% formaldehyde-seawater buffered with saturated sodium borate.

[8] Enumeration: Samples within a cruise were usually pooled for enumeration, except for 17 cruises in Southern California (SC) and 8 cruises in Central California (CC), where samples were analyzed individually by station in order to assess spatial variability. Samples representing, on average, 13 stations from SC (range: 7–32) and 8 stations from CC (range: 2–23) were enumerated per cruise. For pooling, a volume of each sample corresponding to 50 m^3 of seawater filtered was removed and combined for each cruise [*Rebstock*, 2001; *Lavaniegos and Ohman*, 2007]. At least 20% of each pooled sample and 1/8 of nonpooled samples was analyzed by microscopy. Tests for linear trends as a function of time were carried out using the Ordinary Least Squares method. No correction was made for serial autocorrelation because the data points are separated by a year and should be statistically independent for short-lived organisms.

[9] Thecosome pteropods were identified from two families of Euthecosomata (Limacinidae: *Limacina* spp.; Cavoliniidae: *Clio pyramidata*, *Clio* spp., *Cavolinia* spp., plus others) and three families of Pseudothecosomata
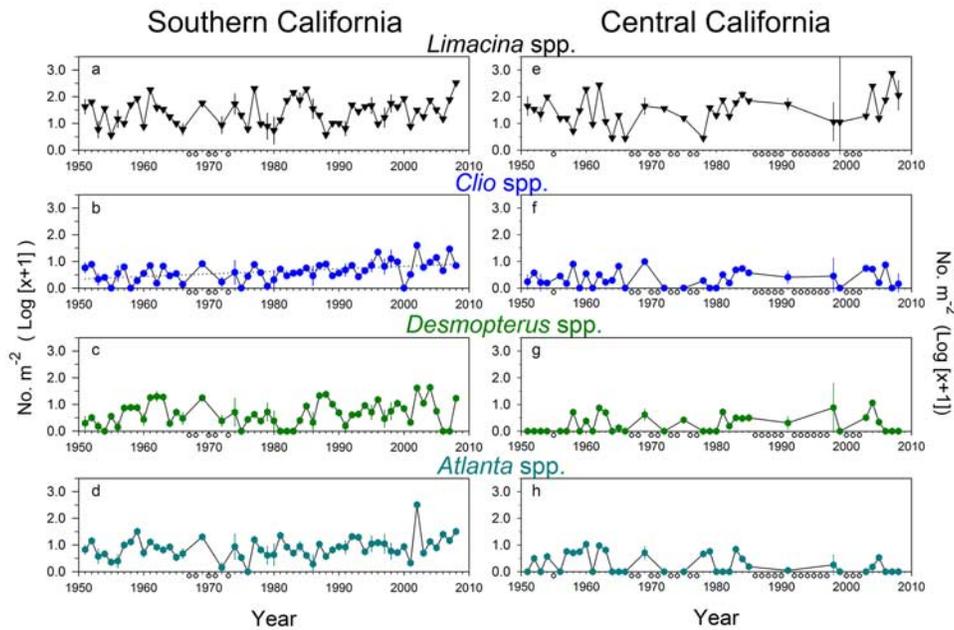
Figure 2. Interannual variation in springtime abundance of the two numerically dominant genera of Euthecosome pteropods, (a, e) *Limacina* spp. and (b, f) *Clio* spp., the dominant genus of Pseudothecosome pteropods, (c, g) *Desmopterus* spp, and dominant genus of Heteropoda, (d, h) *Atlanta* spp., in Southern California and Central California, from 1951–2008. Significant (p<0.05) linear regression indicated by dotted lines (*Clio* spp., Southern CA: Y=0.0095X − 18.20).

(Desmopteridae: *Desmopterus pacificus, Desmopterus* spp.; Cymbuliidae: *Corolla spectabilis, Corolla* spp., *Cymbulia peroni*; Peraclididae and others). Gymnosome pteropods were much less abundant than thecosomes [*Lavaniegos and Ohman*, 2007] and are not discussed here. Heteropods were typically identified to genus or species (*Atlanta* spp., *Cardiapoda richardi, Carinaria cristata, Carinaria japonica, Carinaria* spp., *Firoloida desmaresti, Pterotrachea coronata, Pterotrachea scutula, Pterotrachea* spp., and others). Large foraminifera were counted collectively and not identified to species. The coarse net mesh excluded most of the foram population and is suitable only for the very largest foram individuals. All abundances are expressed as numbers integrated vertically under 1 m^2 of sea surface.

3. Results

[10] In Southern California (SC) waters, springtime abundances of all three major taxa (thecosome pteropods, heteropods, and large planktonic foraminifera) showed considerable interannual variability but no evidence of a recent decline (Figures 1a, 1b, and 1c). The three most recent springs (2006–2008) showed relatively high abundances of all three taxa. A test for a linear trend over the entire time series showed a positive trend in abundance of thecosomes (p < 0.05, test of departure of slope from 0), heteropods (p < 0.05), and large forams (p < 0.0001).

[11] We also evaluated changes in the most abundant genera comprising the shell-bearing Euthecosomata (*Limacina* spp. and *Clio* spp., Figures 2a and 2b), Pseudothecosomata (*Desmopterus* spp., Figure 2c), and Heteropoda (*Atlanta* spp., Figure 2d). Again, there was no evidence of a decline in abundance in recent years in SC (Figures 2a–2d). Although *Desmopterus* spp. was not detected in spring 2006 or 2007, it was in 2008 and, furthermore, as many as 3 successive

springs of undetectable abundance occurred previously in the early 1980's. There was no significant trend with time (p> 0.05) in any of these taxa except for *Clio* spp. (p < 0.001).

[12] In Central California (CC) waters, total thecosomes showed no long-term trend (p > 0.05) and abundances in the three most recent springs were above the long-term mean (Figure 1d). The time series of total heteropods and large foraminifera in CC often showed undetectable abundances. No trends in abundance of total heteropods or large foraminifera were detected, either for aggregated taxa (Figures 1d, 1e, and 1f) or individual dominant genera (Figures 2e, 2f, 2g, and 2h, p > 0.05), but the significance of this result is uncertain because of unsampled years and a high incidence of zeroes. Zeroes occurred in 11 years (heteropods) or 26 years (forams) out of a total of 35 springs sampled in CC. Heteropods and large forams were almost certainly present, but too rare or patchy to be recorded by our sampling/subsampling methods. Low abundances of the Euthecosome *Clio* spp. and the Pseudothecosome *Desmopterus* spp. were recorded in 2008 (Figures 2f and 2g), although for both genera negligible abundances had previously occurred multiple times, including in 2–3 successive years, suggesting that it is not possible to infer any changes at this time.

[13] None of the calcareous zooplankton groups showed significant differences (p > 0.05, Mann-Whitney U test) in comparisons between ENSO (El Niño-Southern Oscillation, defined for mid-latitudes as by *Lavaniegos and Ohman* [2007]) and non-ENSO years, whether aggregated into the three higher taxa or treated as individual dominant genera.

4. Discussion

[14] Our results over nearly 60 years show that the major taxa of calcareous holozooplankton (thecosome pteropods,

heteropods, and large planktonic foraminifera) exhibit no evidence of a recent decline in abundance in Southern California waters of the California Current System (CCS) through Spring, 2008. This conclusion applies equally to the thecosome pteropods in Central California waters. The rarer occurrence of heteropods and large foraminifera in Central California waters, combined with the relatively large number of unsampled springs (especially in the late 1980's–early 1990's) makes any inference of a change in abundance of these latter two taxa in Central California waters uncertain at this time.

[15] Because thecosome pteropods and heteropods secrete aragonitic shells, they would be expected to show greater sensitivity to shoaling of the aragonite saturation horizon than foraminifera, which secrete calcitic tests. However, our results illustrate that average population densities of thecosomes have not yet been affected by the shoaling of the aragonite saturation horizon described by *Feely et al.* [2008]. The abundance of heteropods in Southern California waters, dominated by *Atlanta* spp., has similarly not been affected. Our Southern California region includes the location of transect 10 of Feely et al., where undersaturated waters reached depths as shallow as 40 m, and our Central California region includes their transect 8, where undersaturated waters were somewhat deeper. It is important to continue to document changes in areal extent of undersaturated waters, as well as the response of the planktonic biota.

[16] We do not have historical measurements of pH concurrent with our zooplankton samples, however we did not seek to address the interannual covariability of these two variables. Rather, we addressed whether recent changes in aragonite saturation horizons documented by others have had a measureable effect on recent measures of abundance of calcareous holozooplankton, evaluated in the context of variability of these organisms within the past 6 decades. Similarly, we do not attempt to explain interannual variability in abundances with respect to a variety of possible causes (including predator-prey relationships, food availability, ocean circulation, etc.), as this would require much more detailed information than is available. We note, however, that extremes of the ENSO cycle do not seem to be related to abundance variations of the organisms studied here. Also, the suggestion of a positive abundance trend of the three major calcareous zooplankton taxa in recent years in Southern California is consistent with other results indicating increases in chlorophyll *a* concentration [*Rykaczewski and Checkley*, 2008] and decreases in optical transparency [*Aksnes and Ohman*, 2009], together with a slight (but non-significant) tendency to increased carbon biomass of total mesozooplankton [*Lavaniegos and Ohman*, 2007]. Such changes in transparency and chlorophyll *a* are likely associated with an increase in particulate food supply to the mucous-net feeding thecosome pteropods and the carnivorous heteropods, perhaps linked with the increase in wind stress curl upwelling documented by *Rykaczewski and Checkley* [2008].

[17] The sample pooling procedure employed here for most cruises permitted analysis of a large number of cruises over time. However, our previous results have shown that sample pooling is not satisfactory for quantitative estimates of abundance of rare taxa [*Ohman and Lavaniegos*, 2002], whose occurrence in aliquots drawn from a pooled sample is subject to random error. Organisms from a minimum of $70–170$ m^3 of seawater were represented in our counts, considering the pooling and aliquoting procedure. This volume is sufficient for the more abundant taxa, but appears to be insufficient and less reliable for rarer forms.

[18] For planktonic foraminifera, the 0.5 mm net mesh size excluded most of the epipelagic taxa [*Field*, 2004] and our results do not bear on changes in abundance of the predominant, smaller foram taxa, which are more likely to show dissolution. The largest epipelagic forams in the Southern California Current region are principally subtropical/tropical species [*Field et al.*, 2006]. The relatively abrupt increase in large foraminifera that we observed in 1977, to levels not recorded in the previous 26 years, is consistent with a large-scale warming in the NE Pacific and concurrent changes in a variety of ecosystem properties in the NE Pacific [e.g., *Miller et al.*, 1994; *Ohman and Venrick*, 2003]. The average springtime foram abundance in Southern California waters after 1976 was significantly higher than in previous decades (p < 0.001, Mann-Whitney U test), suggesting that the temporal changes in abundance may not be linear. This increased abundance of large forams in the water column parallels the increased fluxes of larger subtropical/tropical foraminifera to sediments of the Santa Barbara Basin recorded by *Field et al.* [2006], and is consistent with their analysis of a warming trend in the NE Pacific. The lower abundance of large forams in CC than SC waters is also consistent with a more southerly origin of these taxa.

[19] Few other records are available to assess multi-decadal variations in calcareous zooplankton in major ocean ecosystems. Continuous Plankton Recorder samples from the North Atlantic have been analyzed for trends in jellyfish (estimated as the frequency of occurrence of nematocysts) in relation to pH, as Scyphozoan and some Hydrozoan medusae bear statoliths [*Richardson and Gibbons*, 2008]. Contrary to *Attrill et al.* [2007], *Richardson and Gibbons* [2008] detected no relationship between jellyfish and pH.

[20] The lack of evidence of recent decline in average springtime abundance of calcareous holozooplankton in the California Current System does not preclude other changes in these organisms. First, while our sampling was done at or near the peak of the upwelling season [*Aksnes et al.*, 2007], upwelling is variable in time and space and our sampling may not have coincided with times or locations of the most intense upwelling events. Second, horizontal spatial distributions could be modified on a very local scale, smaller than the spatial domains averaged in our analysis. Third, changes in vertical distributions [cf. *Hunt et al.*, 2008] would not be resolved here because sampling was conducted with oblique plankton tows that integrated epipelagic strata. Fourth, we did not examine changes in ultrastructure of mollusk shells and foram tests, and changes in shell morphology [*Orr et al.*, 2005; *Fabry et al.*, 2008] could have occurred without affecting numerical abundance.

[21] Despite these caveats, our results are based on quantitative systematic sampling across the epipelagic zone in two sectors of a major eastern boundary current ecosystem, over nearly 60 years. This historical context is essential in order to understand the range of ecosystem variability and provide a benchmark against which to measure change. The results indicate that significant recent perturbations to

the aragonite saturation state in the California Current System have not yet had measureable effects on average calcareous zooplankton abundances in springtime as we have sampled them. We fully expect changes in upper ocean chemistry to continue and a threshold to be reached where the abundance of calcareous holozooplankton is measurably affected. Our ability to detect future changes in marine ecosystems, whether related to ocean pH or other factors, is directly linked to a sustained commitment to in situ ocean measurement programs.

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