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

Bertha E. Lavaniegos [a,b], Mark D. Ohman [b,*]

[a] *Departamento de Oceanografía Biológica, Centro de Investigación Científica y Educación Superior de Ensenada, km 107 Carretera Tijuana-Ensenada, Apdo. Postal 360, 22800 Ensenada, Baja California, Mexico*
[b] *Integrative Oceanography Division, Scripps Institution of Oceanography, University of California, 9500 Gilman Dr., San Diego, La Jolla, CA 92093-0218, USA*

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Abstract

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

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

* Corresponding author. Tel.: +1 858 534 2754; fax: +1 858 822 0562.
E-mail addresses: berlav@cicese.mx (B.E. Lavaniegos), mohman@ucsd.edu (M.D. Ohman).

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1. Introduction

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

This need for adequate characterization of the biotic properties of ocean ecosystems focuses attention on the very limited number of research programs that have sufficient continuity to address ecological responses on time scales of several decades. In the Northeast Pacific the program that stands out in this regard is CalCOFI (the *California Cooperative Oceanic Fisheries Investigations*). Since 1949, CalCOFI cruises have been conducted in the CCS, providing a rich empirical foundation for understanding biotic changes on a multi-decadal scale. An important component of CalCOFI is the simultaneous resolution of spatial and temporal changes in the ecosystem, together with high quality physical and chemical measurements. Unlike measurement programs that focus on one location or a limited number of geographic points in space, CalCOFI samples a broader geographic area. Although the coverage of cruises has changed considerably over time (e.g., Hewitt, 1988), even in years of minimal spatial coverage CalCOFI has sampled a minimum of 66 stations over ca. 200,000 km^2 of ocean surface. Other significant programs in the Northeast Pacific are reported in Mackas et al. (2006).

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

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