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Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005

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[1] Zooplankton in the California Current had large anomalies in biomass and composition in 2005. The zone most strongly affected extended from northern California to southern British Columbia, where zooplankton biomass was low from spring through autumn, community composition showed reduced dominance by northern origin taxa, and life cycles of some species shifted to earlier in the year. Although similar anomalies have previously been observed over the entire California Current system during strong El Niño events, the 2005 zooplankton anomalies were more localized, initiated by a combination of very warm temperatures (since early 2003), plus weak and late upwelling, and low phytoplankton productivity in spring and early summer of 2005. However, the zooplankton anomalies persisted longer: through the remainder of 2005 and into 2006. **Citation:** Mackas, D. L., W. T. Peterson, M. D. Ohman, and B. E. Lavaniegos (2006), Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005, *Geophys. Res. Lett.*, 33, L22S07, doi:10.1029/2006GL027930.

1. Introduction

[2] In spring and early summer of 2005, the northern California Current System was anomalously warm [Hickey *et al.*, 2006], in part because the normal spring transition to wind-driven upwelling was delayed by 2–3 months [Schwing *et al.*, 2006; Kosro *et al.*, 2006]. Ecological consequences included reduced and late build-up of phytoplankton biomass [Thomas and Brickley, 2006] and poor reproduction and survival plus altered distributional ranges of fish and seabirds [Brodeur *et al.*, 2006; Sydeman *et al.*, 2006]. Responses by intermediate trophic levels (such as zooplankton) may have played an important role in linking these. Zooplankton monitoring programs now provide time series of zooplankton biomass and community composition in alongshore bands that span the entire California Current System (CCS, southern Canada to southern Baja California, Mexico). Zooplankton have been studied in all parts of the CCS for several decades. Examples of analyses of regional zooplankton time series include Peterson and Miller [1975], McGowan *et al.* [1998], Mackas *et al.* [2001], Rebstock

[2001, 2002], Lavaniegos and Ohman [2003], and Peterson and Schwing [2003]. This paper combines zooplankton data from all of the regional time series for a CCS-wide description and comparison of the zooplankton anomalies before and during 2005 (their intensity, qualitative character, spatial correlation scale, and their onset-timing and duration relative to anomalies of wind, currents, and water properties).

2. Data Sources and Methods

[3] Our data come from four long-term oceanographic monitoring programs in seven sub-regions of the CCS (Table 1; note the abbreviated region ID codes we will use subsequently). Collectively, these observations span 2700 km alongshore distance (>25° latitude) with a between-region spacing of 250–500 km. Despite differences in methodologies (Table 1) each provides seasonal estimates of vertically-integrated abundance/biomass of upper-ocean mesozooplankton. Within each region, data have been averaged across years to yield seasonal “zooplankton climatologies” [e.g., Mackas *et al.*, 2001; http://www.calcofi.org/data/zooplankton/6_-_seasonal_cycles.htm]. Because the zooplankton seasonal signal is large (annual biomass maximum 3–10X larger than the annual minimum), inter-annual variability is most easily studied after filtering out the average annual cycle. We report year-by-year changes in zooplankton as time series of log-scale anomalies from local climatologies. In addition to variability of total biomass, we examine changes in dominance, focusing on medium-to-large copepods of 1–4 mm size range. For regions in which 2005 species-level data are available (SC, CC, OR, SVI, NVI), we index changes in community composition and alongshore distribution by averaging species-level anomalies within four copepod groups (Table 2) with differing zoogeographic affinities: a subset of the ‘normal’ resident and dominant calanoid copepods vs. a group that usually have more southerly distribution within the CCS. Earlier studies [e.g., Peterson and Miller, 1975; Mackas *et al.*, 2001; Peterson and Keister, 2003] showed that large poleward (equatorward) distribution shifts of zooplankton and pelagic fish populations accompany anomalously warm (cold) episodes in the CCS. There is also growing evidence that differences in body size, seasonal life history, and lipid content make “southern” zooplankton less available and/or nutritious for endemic zooplankton predators [Peterson and Schwing, 2003], so anomalies of zooplankton community composition have important consequences for higher trophic level productivity.

[4] We used ordination by metric Multidimensional Scaling (MDS, ‘Manhattan’ distance metric applied to standardized vectors) to identify which years were most alike, and

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Table 1. Meta-Data Summaries for the California Current System Zooplankton Sampling Regions

Region/program	British Columbia: Vancouver Island continental margin (2 Sub-Regions)	Central Oregon	Central California: CalCOFI (2 Sub-Regions)	Baja California: IMECOCAL (Investigaciones Mexicanas de la Corriente del California) (2 Sub-Regions)
Latitude band (°N) and regional ID code	South (SVI, 48–49) North (NVI, 49.5–51.5)	‘Newport Line’, (OR, 44.5)	Southern California (SC, 30–34) Central California (CC, 35–36)	North Baja (NB, 32–30) Central Baja (CB, 25–30)
Years	1979–2005 (SVI) 1990–91 & 96–2005(NVI)	1969–73, 1983, 1990–92, 1996–2005	1977–2005 (~complete for SC, CC has many gaps)	1998–2005
Sampling frequency	4–6 surveys per year, 10–15 stations per survey	Biweekly for inner shelf (reported here), ~4 per year offshore	4 per year for SC, 2 per year for CC (‘spring’ reported here)	4 per year, ‘winter’ & ‘summer’ data reported here
Sampling method	Vertical bongo net, 0–250 m or 0–bottom+5, 0.23 mm mesh	Vertical ring net, 0–bottom, 0.20 mm	Oblique bongo net, 0–210 m, 0.50 mm	Oblique bongo net, 0–210 m, 0.50 mm
What was measured	Spatially-averaged biomass from (# m ⁻² * individual dryweight), summed within taxa and for entire sample.	Copepod biomass from (# m ⁻³ * individual C weight), summed within selected taxa and for all copepods	Biomass as spatially averaged displacement volume, Abundance as # m ⁻³ from pooled samples	Biomass as spatially averaged displacement volume, Abundance as average # m ⁻³
Time series plotted as anomalies of:	Total biomass (dryweight m ⁻²) and biomass of index species	Total copepod biomass (carbon m ⁻³) and biomass of index species	Total biomass (displacement volume) and abundance of index species	Total biomass (displacement volume) and total abundance within major taxa
Anomalies calculated as:	Log (data/1979–2001 climatology), averaged among taxa and within year, anomaly time series re-centered to zero mean for 1979–2005	Log (data/1969–2004 climatology), averaged among taxa and within year	Log (data/1977–2005 climatology), species anomalies standardized (unit standard deviation) before averaging across taxa	Log (data/1998–2005 climatology)
References for additional methodological details	<i>Mackas et al.</i> [2001, 2004]	<i>Peterson and Keister</i> [2003], <i>Peterson and Schwing</i> [2003], <i>Mackas et al.</i> [2004]	<i>Ohman and Smith</i> [1995], <i>Rebstock</i> [2002], <i>Lavniegos and</i> <i>Ohman</i> [2003], http://www.calcofi.org/data/zooplankton/zoodata.htm	<i>Jiménez-Pérez and</i> <i>Lavniegos</i> [2004], http://imecocal.cicese.mx/texto/conte.htm
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also to summarize resemblance among time series (i.e. among variables and regions). Our MDS ordinations are based solely on the zooplankton data. However, to illustrate the association between zooplankton anomalies and CCS temperature variability (described in detail by *Hickey et al.* [2006] and *Kosro et al.* [2006]), we also report 1997–2005 averages of spring season (Feb–June) CCS sea-surface temperature anomalies (25–52°N, to 2° seaward from the coast) using 1 degree grids of monthly SST anomaly (GTS temperature data relative to 1945–1989 COADS climatology) archived by the Pacific Fisheries Environmental Laboratory (<http://www.pfeg.noaa.gov/products/las.html>).

[5] Within 2005, we compare magnitudes of zooplankton anomalies between regions and between indexed variables. For zooplankton, and also for many other oceanographic

variables (see other papers in the special section), the 2005 anomalies were strongest in the mid-to-northern third of the CCS (roughly centered off central Oregon). Fortuitously, the Oregon inner shelf also had frequent zooplankton sampling (biweekly), allowing us to use monthly averages of the Oregon data to examine the within-year sequence of anomaly onset, development, and persistence.

3. Results and Discussion

3.1. Interannual and Decadal Variability of Zooplankton in the CCS

[6] The CCS zooplankton time series have shown considerable alongshore similarity and synchrony over the past three decades (time series in Figure 1; matrix of pairwise

Table 2. Names and Distributional Characteristics of Taxa Included in ‘Species Group’ Anomaly Plots

Group Name	Index Species Included in Anomaly Averages	Plotted in Regions	Typical NE Pac. Distribution (Latitude Range)	Occurrence in CCS
“Northern” copepods	<i>Calanus marshallae</i> , <i>Pseudocalanus mimus</i> , <i>Acartia longiremis</i> , <i>A. hudsonica</i>	Canada (SVI, NVI) and Oregon (OR)	“Boreal”: Continental margins of northern CCS Alaska Current systems plus Bering Sea shelf, (~43–63°N)	Usual spring to summer dominants in the shelf-upper slope band of the northern CCS
“Southern” copepods	<i>Paracalanus parvus</i> , <i>Ctenocalanus vanus</i> , <i>Mesocalanus tenuicornis</i> , <i>Clausocalanus</i> spp. (<i>pergens</i> , <i>parapergens</i>)	Canada (SVI, NVI) and Oregon (OR)	“Mid-latitude”: Central CCS plus trans-Pacific in the Transition Zone and northern Central Gyre (~30–45°N)	Year-round in the central CCS, transported into the northern CCS in winter.
“Transition Zone” copepods	<i>Calanus pacificus californicus</i> , <i>Candacia bipinnata</i> , <i>Eucalanus californicus</i> , <i>Metridia</i> cf. <i>pacifica</i> (<i>lucens</i>), <i>Pleuromamma abdominalis edentata</i> , <i>P. borealis</i> , <i>Rhincalanus nasutus</i>	CalCOFI (SC & CC)	“Mid-latitude”: Similar in distribution to the above, but confined to larger taxa retained by the 0.5 mm mesh CalCOFI nets (~30–45°N)	Year-round in the central CCS, transported into the northern CCS in winter.
“Central/Equatorial” copepods	<i>Candacia aethiopica</i> , <i>Eucalanus hyalinus</i> , <i>Euchaeta media</i> , <i>E. rimana</i> , <i>Mesocalanus lighti</i> , <i>Nannocalanus minor</i> , <i>Neocalanus gracilis</i> , <i>N. robustior</i> , <i>Pareucalanus attenuatus</i> , <i>Pleuromamma abdominalis typica</i> , <i>P. gracilis</i> , <i>P. piseki</i> , <i>P. xiphias</i>	CalCOFI (SC & CC)	“Subtropical/Tropical”: southern CCS, Central Gyre, and/or the Equatorial Current (~20–30°N)	Year-round in the southern CCS (Baja), increased abundance in the central CCS in some years

correlations in supplementary¹ Table S1). From the 1970s to late 1990s, the sub-regions between 30–50°N (SC, CC, OR, and SVI) all had prolonged declines both of total biomass and of amount (abundance or biomass) of the initially resident and dominant copepod taxa (“Transition Zone” copepods in the two CalCOFI areas, “Northern” copepods off Oregon and British Columbia). Temperature anomalies and vertical density stratification trended upward over the same interval [McGowan *et al.*, 1998; Kosro *et al.*, 2006]. Zooplankton, temperature, and stratification trends reversed abruptly immediately after the 1999 La Niña event, leading to frequent positive zooplankton anomalies in the cool interval 1999–2002. The shorter time series from Baja (post-1998) and NVI (mostly post-1996) suggest weaker alongshore continuity of the biomass and ‘local resident’ anomalies at the north and south ends of the CCS. NB and CB anomalies have been positively correlated with each other (mean $r = 0.53$, range 0.0 to 0.8), but negatively with other regions (mean $r = -0.28$, range -0.8 to 0.2). NVI biomass and “Northern” copepod anomalies have been only weakly correlated with other regions. Conversely, in the central and northern CCS, anomaly sequences of taxa with southerly zoogeographic affinities (“Southern” and “Central/Equatorial” copepods) have been near mirror-images of those for total biomass and “northern/resident” taxa. The inverse pattern is clearest for OR and SVI, but is also evident off SC and NVI (Figure 1). In all regions, anomalies of southern-origin taxa were mostly positive during the mid-late 1990s and during El Niño events (1983, 1987, 1998) but negative from 1999–2002. As noted above, high abundance of southern-origin taxa is associated with El Niño events, with more prolonged warm “regimes”, and with poleward anomalies of alongshore transport. For the southern-origin taxa, between-region correlation of

anomalies was strong and extended to greater separation distances (max. $r = 0.87$, mean = 0.51 excluding the Baja regions and CC, where copepod species data are either absent or have large time gaps) than anomalies of local-origin taxa (max. $r = 0.66$, mean = 0.33, again excluding CC and Baja) or of total biomass (max. $r = 0.66$, mean = 0.09 excluding Baja and = -0.16 including Baja).

3.2. Similarities Among Years and Data Series

[7] Another approach to the zooplankton anomaly data shown in Figure 1 is to ask which years (across variables) and which time series (across years) are most similar. Similarity of years within the past decade (for which we have records from all regions), and their year-to-year trajectory in MDS space, are shown in Figure 2. Although temperature was not an input variable, correlation of the MDS output with SST anomalies was strong ($r = -0.77$). Zooplankton anomalies in 2005 were most like 1997 and 1998 (all warm years in much of the CCS). Conversely, the zooplankton anomalies in 2005, 1997 and 1998 were strongly dissimilar to 1999–2002 (the four coolest years). The 1999–2002 cool interval followed the strong 1999 La Niña, and was also characterized by strong upwelling and equatorward transport anomalies [Peterson and Schwing, 2003]. The 1998–1999 transition from a “warm” to a “cool” CCS was abrupt and CCS-wide. Reverse transitions from a “cool” to “warm” CCS were more gradual. The extreme zooplankton anomalies reached in 1998 had in most regions strengthened steadily since ~1990 (Figure 1). Similarly, breakdown of the post-La Niña “cool” conditions, and reversal of the 1999–2002 zooplankton anomalies may have begun as early as late 2002 or 2003 (Figures 1 and 2).

[8] Results of the parallel MDS ordination of resemblance among variables and regions are shown in supplementary Figure S1. The variables/regions that were positive on axis 1 were from the central-to-northern CCS (SC, CC

¹Auxiliary material data sets are available at <ftp://ftp.agu.org/apend/gl/2006gl027930>. Other auxiliary material files are in the HTML.

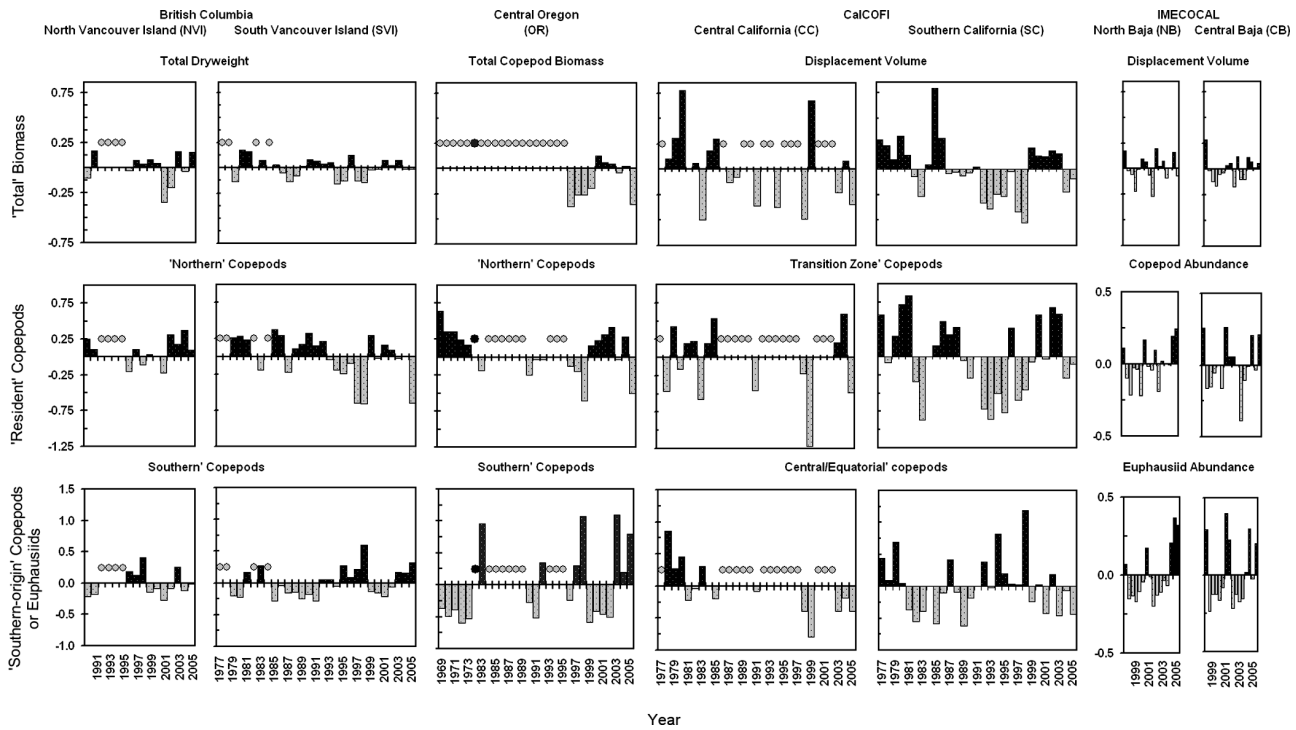


Figure 1. Zooplankton anomaly time series (log scale) from 7 regions spanning the California Current system (Table 1 for locations and sampling/analysis methodologies). Anomalies are annual except for the Baja California regions (semi-annual). Each region has three plots: summed biomass (displacement volume, dryweight, or carbon weight), plus two taxonomic components of the local communities: ‘local’ vs. ‘southern-origin’ copepods (5 northern regions) or ‘copepod abundance’ vs. ‘euphausiid abundance’ (2 Baja regions). Circles indicate years without data. Time axes are continuous except for Oregon (where the dark circle marks a 9 year gap). Earlier comparison between OR and SVI time series [Mackas *et al.*, 2004] suggests that unobserved OR anomalies 1977–1982 were probably similar to those plotted for 1969–1972.

and OR biomass; SC, CC, OR and SVI ‘Northern’/‘Transition Zone’ copepods) and shared negative anomalies in 2005 and the mid-late 1990s, positive anomalies in much of the 1970s, 80s, and ~1999–2003. Variables/regions that were strongly negative on axis 1 (one cluster made up of OR, SVI and NVI “Southern copepods”, a second cluster containing the Baja time series) were all negatively correlated with the above; although the two clusters were separated along MDS axis 2 (probably due to very differing anomalies in 2002, Figure 1). Variables near the midpoint of axis (SVI and NVI biomass, plus SC and CC ‘Central/Equatorial’ copepods) had weak anomalies and/or between-region correlations that varied over time.

3.3. CCS Zooplankton in 2005

3.3.1. Comparisons Among Regions and With Other Years

[9] Table 3 summarizes the within- and between-region comparisons of the 2005 anomalies.

[10] Northern Vancouver Island (NVI) anomalies were consistently weak. Total biomass was above average but the anomaly was small on log scale. “Northern” and “southern” copepod anomalies were near zero. However, seasonal timing of peak copepod biomass was anomalously early, both off NVI and SVI and further north and seaward into the Alaska Gyre (D. L. Mackas *et al.*, Effects on zooplankton of a warmer ocean: recent evidence from the northeast Pacific, submitted to *Progress in Oceanography*, 2006). In 2004, 2005 (and previous warm years) large subarctic-

oceanic copepods in the genus *Neocalanus* left the surface layer and commenced deep annual dormancy early in the year. These subarctic copepods are rare further south in the CCS, but are abundant in spring along the NVI and SVI continental slope. Off NVI, *Neocalanus* are also the primary prey for nesting Cassin’s Auklets, which had poor 2005 breeding success [Sydeman *et al.*, 2006]. NVI anomalies of

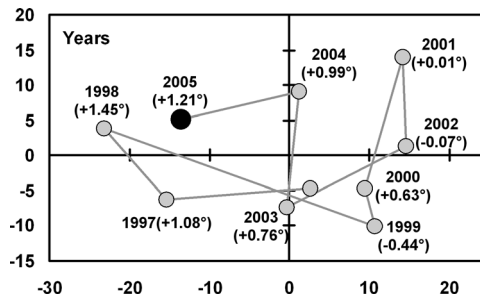


Figure 2. MDS ordination of the 1996–2005 zooplankton anomaly time series, showing relative similarity among years (data points), and the year-to-year trajectory in the ordination space. Data point labels also show spring season (Feb–June) temperature anomalies. Zooplankton anomalies in 2005 were most ‘similar’ to those in warm years 1997 and 1998, and most ‘different’ from those in the cool years 1999–2002. Zooplankton anomalies (and temperatures) in 1996, 2003 and 2004 were transitional between these extremes.

Table 3. Summary Comparisons of Intensities of 2005 Zooplankton Anomalies, Both Among-Years Within-Region, and Among-Regions Within-2005^a

Region	Total Biomass	'Northern', 'Transition Zone' and 'Total' Copepods	'Southern' and 'Central/Equatorial' Copepods	Euphausiids
Canada (NVI) ^a	(+) [~0 to +]	(~0) [~0]	(~0) [~0]	(~0 to +)
Canada (SVI)	(- to ~0) [~0]	(---) [---]	(+++) [++]	(- to --?)
Central Oregon	(---) [---]	(---) [---]	(++) [+++]	(?)
CalCOFI (CC)	(-) [---]	(-) [-?]	(-) [-?]	(--) [---?]
CalCOFI (SC)	(-) [-]	(-) [-?]	(-) [---?]	(~0)
IMECOCAL (Northern Baja)	(- to ~0)	(+) [NC]	NC	(++)
IMECOCAL (Southern Baja)	(~0 to +)	(+) [NC]	NC	(+)

^aAnomaly magnitude comparisons among-years within-region are indicated by symbols in parentheses, and among-regions within-2005 are indicated by symbols in brackets. See Table 1 for regions, Table 2 for taxonomic groups. Euphausiid comparison based in part on data in *Sydeman et al.* [2006]. Positive-to-strongly positive anomalies indicated qualitatively by "+" to "+++", near-average by "~0", negative-to-strongly negative by "-" to "---", uncertain/impossible comparison by "?/NC". For the among-years comparison, classification thresholds correspond quantitatively to "among strongest 10% in time series" (+++, ---) and "among strongest 20%" (++, --).

euphausiids (an alternate prey for Cassin's Auklets) were near zero to weakly positive in both 2004 and 2005.

[11] Southern Vancouver Island (SVI) had large 2005 anomalies of copepod species assemblages (amplitudes second only to 1998 out of 25 years). Preliminary results indicate that these compositional anomalies persisted into spring 2006. In contrast, the 2005 anomaly of total biomass was near-zero off SVI; much weaker than local negative anomalies during the mid-late 1990s, or OR, CC and SC biomass anomalies during both the 1990s and 2005. Our interpretation is that both SVI and NVI remained productive in 2005 for some kinds of zooplankton, but that advection and temperature preference caused shifts in community structure, while phenologic changes altered the timing of peak abundance. One explanation for a weak biomass response is that, compared to the remainder of the CCS, annual nutrient supply off Vancouver Island is provided less by Ekman upwelling, and more by topographic/estuarine/tidal interactions.

[12] Off central Oregon, the 2005 zooplankton response was overall the strongest that we observed, with very large 2005 anomalies for all three zooplankton indices in comparison both to other years and to other regions. Negative anomalies of total and "Northern" copepod biomass were the second strongest in the Oregon time series (exceeded by 1998 for "Northern" copepods, and by 1996 for total biomass). The positive anomaly of the "Southern" copepods matched the previous extreme years (1983, 1998, and 2003). Spatial comparisons show that the Oregon anomaly amplitudes equaled or exceeded the corresponding anomalies from SVI, CC and SC. However, predator responses [*Sydeman et al.*, 2006; *Brodeur et al.*, 2006] suggest that large zooplankton anomalies extended as far south as San Francisco Bay.

[13] Zooplankton anomalies in the two CalCOFI regions (CC and SC) were similar to each other, but differed from Oregon and Canada in the responses by southern-origin taxa. Off California, 2005 anomalies of all three zooplankton indices were negative. Biomass anomalies were large in

comparison to other regions, but weaker than CalCOFI anomalies from the mid-late 1990s. Amplitudes of the CalCOFI compositional anomalies cannot be directly compared to non-CalCOFI regions because of a differing processing method. However, the sign match of resident/northern and southern-origin assemblages (anomalies of both "Transition Zone" and "Central/Equatorial" copepods were negative in 2005) contrasts with the entire OR and SVI time series, and also with earlier years in the CalCOFI regions. In 2005, the environment off southern and central California regions was moderately (but not extremely) poor for both northern- and southern-origin copepods, and the primary response mode was depletion of all copepod taxa rather than displacement of northern by southern species. For euphausiids, 2005 was a very poor year off CC, but near-average in SC (for details, see *Sydeman et al.* [2006]).

[14] Anomalies from northern and central Baja were of opposite sign from all other regions: positive for total biomass, copepod abundance, and euphausiid abundance. Most other major taxonomic groups (not shown) also had positive anomalies in 2005 (ostracods, chaetognaths, siphonophores, pteropods), but 2005 anomalies were negative for planktonic tunicates, their hyperiid amphipod parasites/predators, and also for larval fish. Our interpretation is that although 2005 was unfavorable for copepods and euphausiids in much of the CCS, this did not extend south to Mexican waters. 2005 spring-summer anomalies of chlorophyll and upwelling [*Thomas and Brickley*, 2006] were also positive or negligible in the Baja regions.

3.3.2. Within-Year Development and Persistence of the 2005 Zooplankton Anomalies

[15] When did the 2005 zooplankton anomalies start to develop, and how long did they last? Initial onset may have begun as early as 2003 (Section 3.2 and Figures 1 and 2). Month-by-month plots of 2005 zooplankton biomass and compositional anomalies from central Oregon (Figure 3) show that the signs of the compositional anomalies were already fixed by the start of 2005, when January-March total biomass was near the (low) seasonal norm. In late

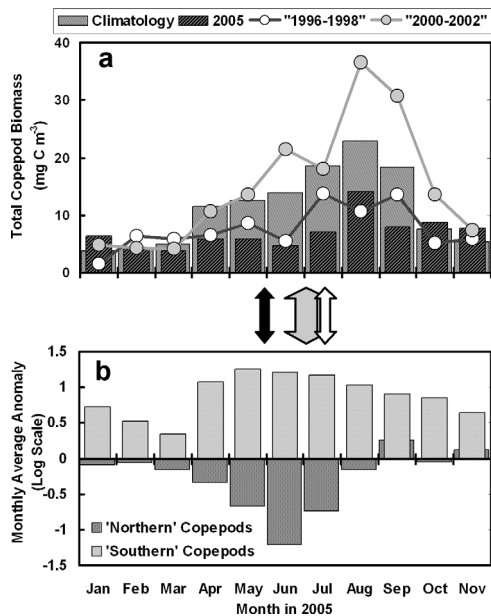


Figure 3. Monthly development of the 2005 zooplankton anomalies on the Oregon inner shelf. (a) Monthly average total copepod biomass in 2005 vs. 1996–2005 climatology, averages of 1996–1998 (other warm years), and 2000–2002 (cool years). (b) Log-scale monthly abundance anomalies in 2005 averaged within “Northern” vs. “Southern” copepod species groups. Filled arrows between panels show dates when environmental conditions reversed sign off Oregon in 2005: black = spring transition to upwelling (drop in coastal sea level, equatorward wind stress), white = transition to negative SST anomaly, grey = transition to positive chlorophyll anomaly, coast to 100 km offshore.

March or April, all zooplankton anomalies began to strengthen rapidly, and continued to intensify through June. From April onward, 2005 was well below the climatology, even further below the “cool” years 2000–2002, and often below the “warm” years 1996–1998. Low biomass persisted until October, negative anomalies of “Northern” copepods persisted until September, and positive anomalies of “Southern” copepods to the end of 2005 and on into 2006. In contrast, most 2005 atmospheric and oceanographic environmental anomalies ended earlier (arrows in Figure 3). The spring transition to low coastal sea-level and equatorward wind/currents had occurred by late May [Kosro *et al.*, 2006]. Phytoplankton biomass then began to accumulate, and monthly average chlorophyll was high by July [Thomas and Brickley, 2006]. Sea-surface temperature anomalies turned sharply negative in mid-July [Kosro *et al.*, 2006]. Clearly, many of the wind-forced environmental characteristics of the Oregon upwelling system (upper layer temperature, Ekman transport, phytoplankton biomass and productivity) had returned to near-average by mid summer. However, “Northern” copepods were unable to match this return to normal levels off Oregon (nor off southern Vancouver Island), and the “Southern” copepods were not dislodged from the Oregon shelf (nor from the Vancouver Island shelf). We do not as yet know why the zooplankton anomalies persisted longer, but offer two possibilities:

[16] 1. Populations of resident/northern species are constrained by evolved seasonal life history strategies. If they are to have large populations in summer through autumn, reproduction and growth must be strong in spring. Figure 3 shows partial recovery of the “northern” taxa in July and August, but their absolute amount (exaggerated on a logarithmic scale) contributed relatively little total biomass. In contrast, many of the “southern”-origin (warm water) taxa have less seasonal and more opportunistic life history and reproductive strategies. Once established, they continued reproducing in a food-rich environment, even after onset of upwelling turned that environment “cool”.

[17] 2. A second possibility (not mutually exclusive) is competition and/or predation pressure inflicted by the southern-origin species, once they became abundant. Interference with post-disturbance recruitment of later-arrivals by successful initial colonists has been hypothesized in many terrestrial and benthic systems [e.g., Connell, 1978; Yu and Wilson, 2001], but the mechanism often involves competition for space in addition to competition for food resources and predator avoidance. Results from 2006 and subsequent years will help discriminate among these mechanisms, and also document the extent of future persistence in the northern CCS. *Rebstock* [2001] showed that copepod community composition off Southern California recovers relatively quickly (1–2 years) following strong but brief disturbances associated with El Niño warm events.

3.4. Summary of Findings and Interpretations

[18] Significant zooplankton anomalies were observed in 2005 in much of the CCS, but were most intense off central Oregon, and gradually weakened and changed character both poleward and equatorward. Off Oregon and southern British Columbia, the zooplankton response (reduced total biomass, greatly reduced biomass of “resident” northern species, greatly increased abundance and biomass of southern-origin species) resembled responses during strong El Niño events, but local details and between-region comparisons suggest forcing in 2005 was primarily by regional weather patterns rather than by coast-wide or basin-scale physical anomalies. Zooplankton anomalies persisted two-to-many months longer than the 2005 environmental anomalies of wind, water properties, and phytoplankton productivity, suggesting significant inertia of zooplankton anomalies once they have become established. Further persistence is as yet unknown, but is an important issue because of the potential consequences of sustained zooplankton anomalies for higher trophic level populations.

[19] **Acknowledgments.** We thank the sea-going personnel who collected CCS zooplankton samples over many decades and the zooplankton ID specialists (most recently, Moira Galbraith Ginger Rebstock, and Connie Fey) who turn these samples into ecological data. Funding sources include Fisheries and Oceans Canada; CONACYT (47044); the USGLOBEC NE Pacific program; the NSF LTER program; NOAA NMFS; California Fish and Game; and the Bonneville Power Authority. This is contribution 327 of USGLOBEC and a contribution of the CCE LTER site and SIO Pelagic Invertebrates Collection.

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