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

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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 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), weak and late upwelling (in spring and early summer 2005), and low phytoplankton productivity (at both time scales). However, the zooplankton anomalies persisted longer: through the remainder of 2005 and into 2006.

INDEX TERMS: 4890, 4516, 4817, 4215

RUNNING HEAD: 2005 CCS Zooplankton Anomalies

1. Introduction

In spring and early summer of 2005, the northern California Current System was anomalously warm (Hickey et al., this issue), in part because the normal spring transition to wind-driven upwelling was delayed by 2-3 months (Schwing et al., Kosro et al., this issue). Ecological consequences included reduced and late build-up of phytoplankton biomass (Thomas and Brickley, this issue); reduced zooplankton biomass and altered community composition (this paper); and poor reproduction and survival plus altered distributional ranges of fish and seabirds (Brodeur et al., this issue; Sydeman et al., this issue).

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, and spatial correlation scale, and their onset-timing and duration relative to anomalies of wind, currents, and water properties).

2. Data Sources and Methods

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. http://www.calcofi.org/data/zooplankton/6_-_seasonal_cycles.htm; Mackas et al. 2001). Because the zooplankton seasonal signal is large (5-10X annual biomass range), interannual 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/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.

We used ordination by metric Multidimensional Scaling (MDS, 'Manhattan' distance metric applied to standardized vectors) to identify which years were most alike, and 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. and Kosro et al. this volume), 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 (relative to 1945-1989 COADS climatology) extracted from (http://www.pfeg.noaa.gov/products/PFEL/observed/GTS_surface/sfc_temp.html).

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 this issue), 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

The CCS zooplankton time series have shown considerable alongshore similarity and synchrony over the past three decades (time series in Fig. 1; matrix of pairwise correlations in supplementary table TS1). From the 1970s to late 1990s, the sub-regions between 30-50°N (SC, CC, OR, and SVI) all had prolonged declines of both total biomass and abundance/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. this volume). 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 (Fig. 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

Another approach to the zooplankton anomaly data shown in Fig 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 Fig. 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 (Fig. 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 (Figs 1-2).

Results of the parallel MDS ordination of resemblance among variables and regions are shown in supplementary figure FS1. The variables/regions that were positive on axis 1 were from the central-to-northern CCS (SC, CC 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, Fig. 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

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

Details for each region (north to south) are described below.

Northern Vancouver Island (NVI) anomalies were consistently weak for the variables plotted in Figs. 1-2. Total biomass was above average (for this time series) 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 (Mackas, Batten & Trudel, unpublished). In 2004, 2005 (and previous very warm years) large subarctic-oceanic copepods in the genus *Neocalanus* left the surface layer and commenced deep annual dormancy very early in the year. These subarctic copepods are rare further south in the CCS, but are very abundant in spring along the Vancouver Island continental slope. Off NVI, *Neocalanus* are also the primary prey for nesting Cassin’s Auklets, which had poor 2005 breeding success (Sydeman et al. this issue). NVI anomalies of euphausiids (an alternate prey for Cassin’s Auklets) were near zero to weakly positive in both 2004 and 2005.

Southern Vancouver Island (SVI) had very large 2005 anomalies of copepod species assemblages (amplitudes second only to 1998 in the 25 year time series). Preliminary results from spring 2006 indicate that these compositional anomalies have persisted. In contrast, the 2005 anomaly of total biomass was near-zero off SVI, and was 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 possible 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.

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. & Brodeur et al., this issue) suggest that large zooplankton anomalies may have extended as far south as San Francisco Bay.

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 relatively 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 euphauiids, 2005 was a very poor year off CC, but near-average in SC (for details, see Sydeman et al., this issue).

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 environmental drivers such as chlorophyll and upwelling (Thomas & Brickley, this issue) were also positive or negligible in the Baja regions.

3.3.2 Within-year development and persistence of the 2005 zooplankton anomalies.

When did the 2005 zooplankton anomalies start to develop, and how long did they last? Initial onset m have begun as early as 2003 (Section 3.2, Figs 1 & 2). Month-by-month plots of 2005 zooplankton biomass and compositional anomalies from central Oregon (Fig. 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 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 Fig. 3). The spring transition to low coastal sea-level and equatorward wind/currents had occurred by late May

(Kosro et al., this issue). Phytoplankton biomass then began to accumulate, and monthly average chlorophyll was high by July (Thomas and Brickley, this issue). Sea-surface temperature anomalies turned sharply negative in mid-July (Kosro et al., this issue). 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. Equally clearly, the previously-dominant "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 the cause for longer persistence of the zooplankton anomalies, but offer two possibilities:

- 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 must already be well-started by spring. Fig. 3 shows a 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 may have been able to continue reproducing in a food-rich environment, even after onset of upwelling turned that environment "cool".
- A second possibility (not mutually exclusive with the first) is competition and/or predation pressure inflicted by the southern-origin species, once they became abundant within the region. 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 mechanisms, and also document the extent of their future persistence in the northern CCS. Rebstock (2001) showed that copepod community composition off Southern California recovered relatively quickly (1-2 years) and completely following strong but brief disturbances associated with El Niño warm events.

3.5 Summary of findings and interpretations

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 abundance/biomass of “resident” northern species, greatly increased abundance/biomass of southern-origin species) resembled previous observations 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 (a conclusion shared by other papers in this issue). 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.

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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 (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, 0-250m or 0-bottom+5, 0.23 mm	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	Mackas et al. (2001, 2004)	Peterson et al. (2002), Peterson & Schwing (2003), Mackas et al. (2004)	Ohman & Smith (1995); Rebstock (2002); Lavniegos & Ohman (2003); http://www.calcofi.org/data/zooplankton/zoodata.htm	Jiménez-Pérez & Lavaniegos (2004); http://imecocal.cicese.mx/texto/conte.htm
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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	*Calanus marshallae*, *Pseudocalanus mimus*, *Acartia longiremis*, *A. hudsonica*	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	*Paracalanus parvus*, *Ctenocalanus vanus*, *Mesocalanus tenuicornis*, *Clausocalanus* spp. (*pergens*, *parapergens*)	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	*Calanus pacificus californicus*, *Candacia bipinnata*, *Eucalanus californicus*, *Metridia* cf. *pacifica* (*lucens*), *Pleuromamma abdominalis edentata*, *P. borealis*, *Rhincalanus nasutus*	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	*Candacia aethiopica*, *Eucalanus hyalinus*, *Euchaeta media*, *E. rimana*, *Mesocalanus lighti*, *Nannocalanus minor*, *Neocalanus gracilis*, *N. robustior*, *Pareucalanus attenuatus*, *Pleuromamma abdominalis typica*, *P. gracilis*, *P. piseki*, *P. xiphias*	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

Table 3. Summary comparisons of intensities of 2005 zooplankton anomalies (among-years within-region), and [among-regions within-2005]. See Table 1 for regions, Table 2 for taxonomic groups. Euphausiid comparison based in part on data in Sydeman et al. (this issue).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 to “among strongest 10% in time series” (+++, ----) and “among strongest 20%” (++, --).

Region	Total biomass	‘Northern’, ‘Transition Zone’ & ‘Total’ copepods	‘Southern’ & ‘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	(+)

Supplementary Table ts1. Matrix (lower diagonal) of pairwise product-moment correlations (*r*) among the 21 zooplankton anomaly time series (7 alongshore regions, 3 variables per region). Correlations are calculated only from the years with overlapping coverage. Degrees of freedom vary from 15-20 (for comparisons among the longest and most complete series: CalCOFI Southern California, Southern Vancouver Island, Oregon) down to 4-8 (for comparisons among the shorter and gappier series: CalCOFI Central California, Northern Vancouver Island, and Northern and Central Baja).

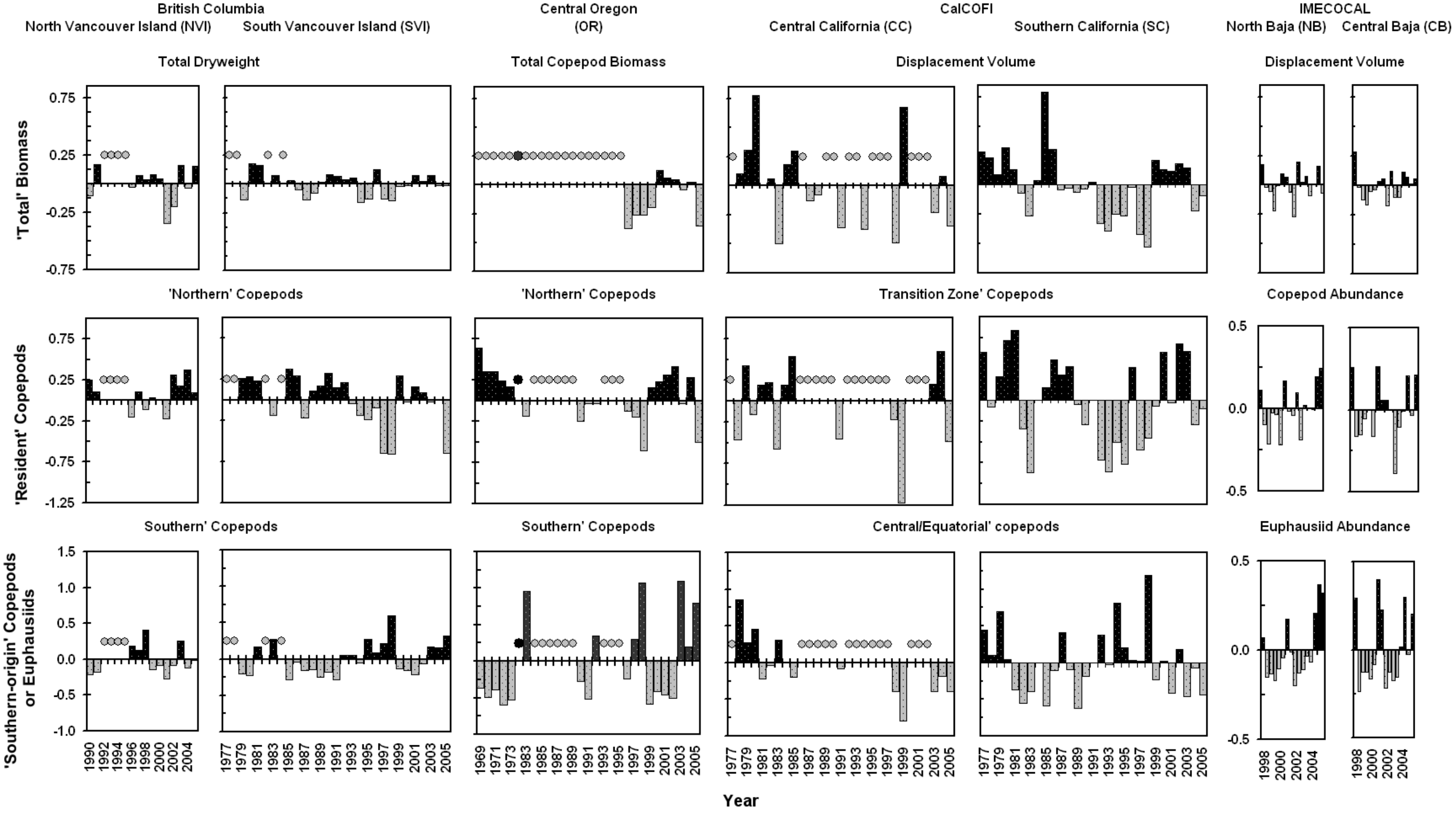
Region-variable-(ID code)	CBb	CBc	CBe	NBb	NBc	Nbe	SCb	SCtzc	SCcec	CCb	CCtzc	CCcec	ORb	ORnc	ORsc	SVIb	SVInc	SVIsc	NVIb	NVInc	NVIsc
Central Baja displacement volume (CBb)	1																				
Central Baja copepod abundance (CBc)	0.77	1																			
Central Baja euphausiid abundance (CBe)	0.68	0.81	1																		
Northern Baja displacement volume (NBb)	0.48	0.03	0.13	1																	
Northern Baja copepod abundance (NBc)	0.56	0.71	0.59	0.29	1																
Northern Baja euphausiid abundance (NBe)	0.48	0.54	0.66	0.36	0.83	1															
Southern California displacement volume (SCb)	-0.85	-0.42	-0.38	-0.48	-0.32	-0.34	1														
Southern California Transition Zone copepods (SCtzc)	-0.63	-0.56	-0.65	0.03	-0.36	-0.44	0.71	1													
Southern California Central/Equatorial copepods (SCcec)	0.53	0.17	-0.11	0.31	-0.11	-0.32	-0.37	-0.11	1												
Central California displacement volume (CCb)	-0.64	-0.24	-0.32	-0.99	-0.57	-0.48	0.66	0.48	-0.21	1											
Central California Transition Zone copepods (CCtzc)	0.5	0.13	0.43	0.44	0.06	0.17	0.17	0.3	-0.02	0.05	1										
Central California Central/Equatorial copepods (CCcec)	0.72	0.43	0.68	0.57	0.41	0.48	0.12	-0.01	0.16	0.11	0.11	1									
Oregon total copepod biomass (ORb)	-0.16	-0.08	-0.05	-0.11	-0.46	-0.45	0.47	0.43	-0.18	0.28	0.66	0.37	1								
Oregon Northern copepods (ORnc)	-0.39	-0.03	-0.07	-0.59	-0.41	-0.47	0.64	0.46	-0.3	0.68	0.16	-0.06	0.8	1							
Oregon Southern copepods (ORsc)	0.36	-0.18	0.03	0.67	0.28	0.39	-0.61	-0.4	0.15	-0.65	0.4	0.28	-0.38	-0.65	1						
Southern Vancouver Island dryweight biomass (SVIb)	-0.48	-0.19	0.04	-0.19	0.01	0.01	0.36	0.33	-0.58	0.28	-0.03	0.29	0.09	0.27	-0.28	1					
Southern Vancouver Island Northern copepods (SVInc)	-0.61	-0.25	-0.16	-0.72	-0.57	-0.58	0.67	0.42	-0.34	0.73	0.23	0.22	0.61	0.66	-0.64	0.46	1				
Southern Vancouver Island Southern copepods (SVIsc)	0.58	0.08	0.06	0.55	0.35	0.34	-0.63	-0.41	0.27	-0.56	-0.09	-0.28	-0.6	-0.67	0.87	-0.18	-0.75	1			
Northern Vancouver Island dryweight biomass (NVIb)	-0.29	-0.62	-0.49	0.2	-0.18	0.13	-0.19	-0.06	0.01	-0.32	-0.37	0.02	-0.47	-0.5	0.45	-0.25	-0.37	0.33	1		
Northern Vancouver Island Northern copepods (NVInc)	-0.13	-0.19	-0.38	-0.3	-0.07	-0.11	0.05	0.02	-0.17	0.21	0.66	0.44	0.34	0.22	0.05	-0.12	0.19	-0.07	0.16	1	
Northern Vancouver Island Southern copepods (NVIsc)	0.21	-0.39	-0.33	0.6	-0.09	-0.1	-0.54	-0.04	0.57	-0.52	0.27	-0.1	-0.54	-0.59	0.76	-0.31	-0.68	0.83	0.43	-0.24	1

Figure 1. Time series of log-scale zooplankton anomalies from seven 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 different components of the local zooplankton communities: either ‘local’ vs. ‘southern-origin’ copepods (the 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-filled circle marks a 9 year gap. An 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.

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.

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.

Supplementary figure FS1. MDS ordination of the 1977-2005 zooplankton anomaly time series, showing relative similarity/dissimilarity of regions and variables. Series close together in the plots have similar anomaly patterns; series at opposing poles are negatively correlated. Colors code for location (red = south, blue = north); shapes code for variable type (triangles = total biomass, circles = resident/northern-origin copepods; diamonds = southern-origin copepods, squares = euphausiids. All points are in the same ordination space, but total biomass (top panel) and species groups (bottom panel, see Table 2 for makeup) are plotted separately for clarity. Total biomass and resident/northern copepods covary positively off California, Oregon and Southern Vancouver Island, but negatively with southern-origin copepods and with all of the Baja California time series.


British Columbia
North Vancouver Island (NVI)
South Vancouver Island (SVI)
Central Oregon
(OR)
CalCOFI
Central California (CC)
Southern California (SC)
IMECOCAL
North Baja (NB)
Central Baja (CB)
Total Dryweight
Total Copepod Biomass
Displacement Volume
Displacement Volume
'Total' Biomass
0.75
0.25
-0.25
-0.75
'Northern' Copepods
'Northern' Copepods
Transition Zone' Copepods
Copepod Abundance
'Resident' Copepods
0.75
0.25
-0.25
-0.75
-1.25
0.5
0.0
-0.5
Southern' Copepods
Southern' Copepods
Central/Equatorial' copepods
Euphausiid Abundance
'Southern-origin' Copepods or Euphausiids
1.5
1.0
0.5
0.0
-0.5
-1.0
0.5
0.0
-0.5
1990
1992
1994
1996
1998
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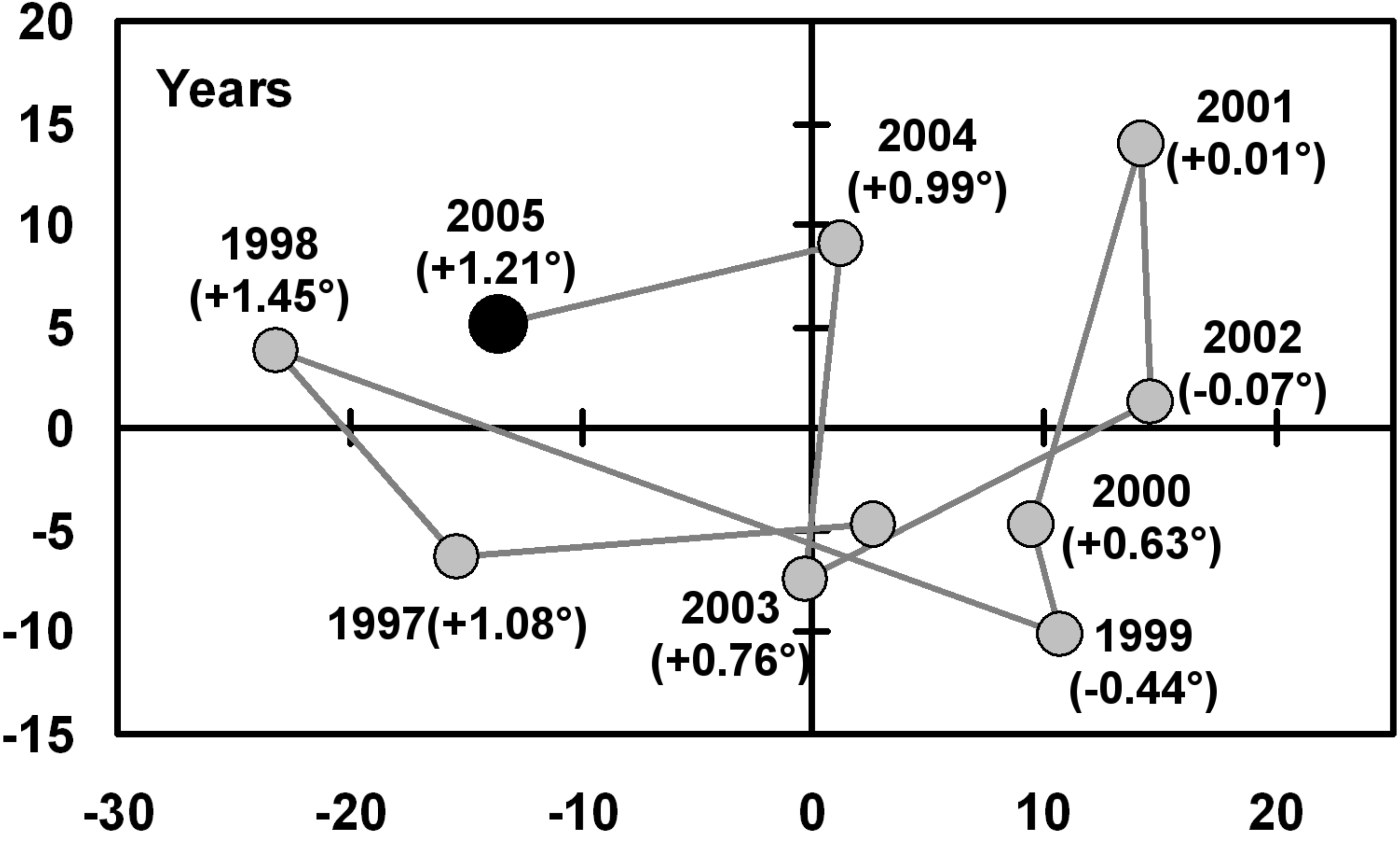
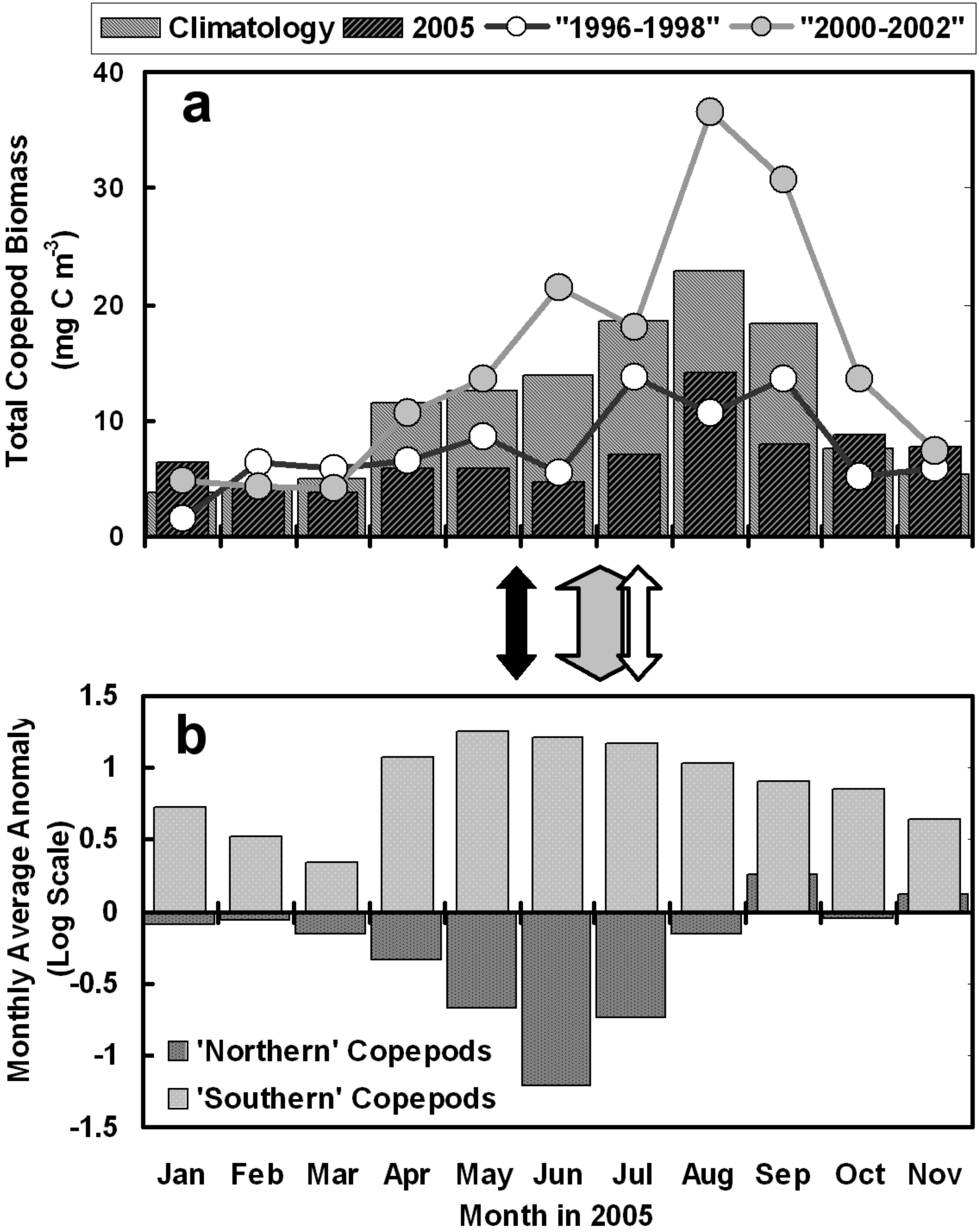
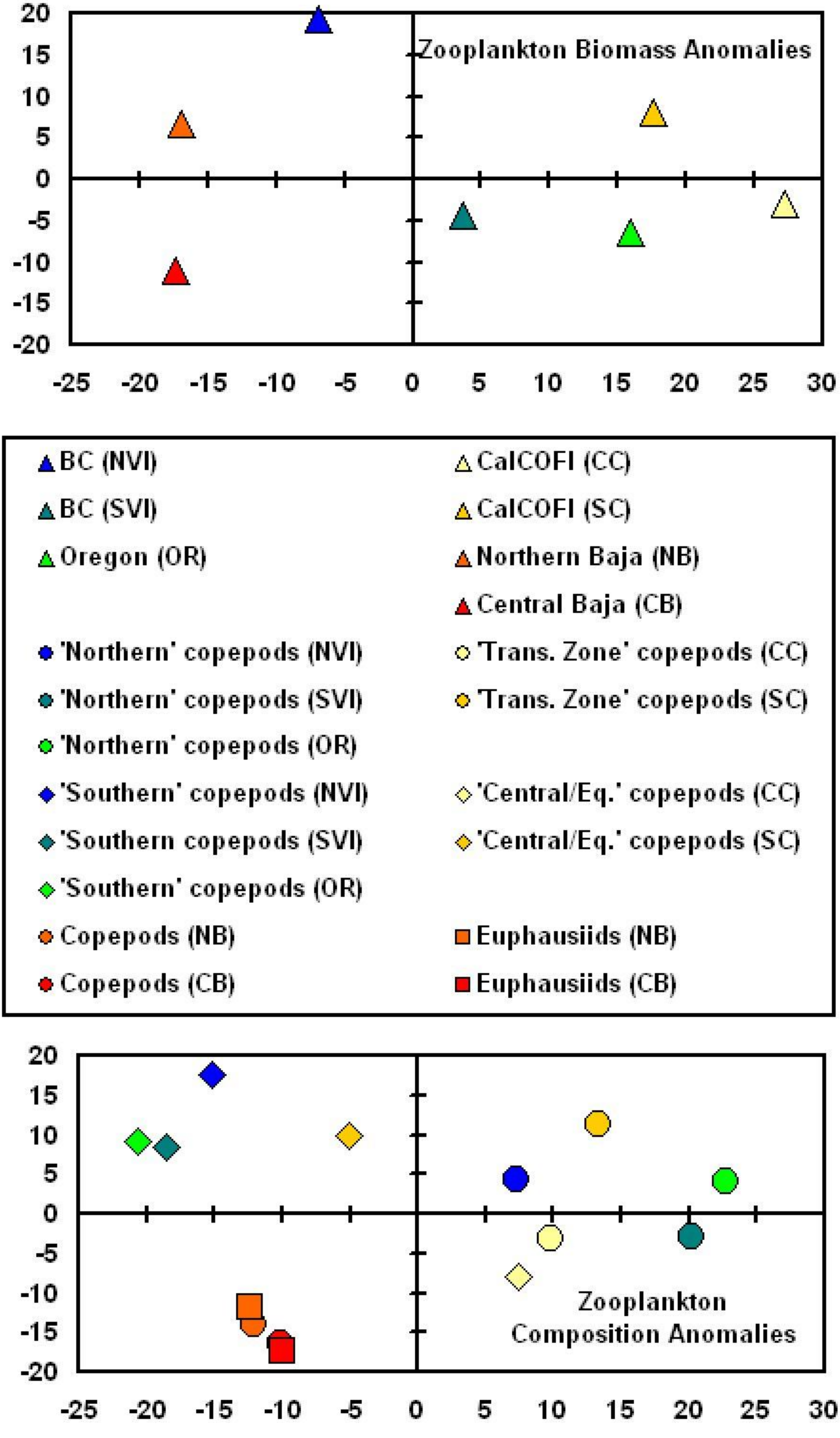
2004
Year



Years
2001 (+0.01°)
2004 (+0.99°)
2005 (+1.21°)
1998 (+1.45°)
2002 (-0.07°)
2000 (+0.63°)
1997(+1.08°)
2003 (+0.76°)
1999 (-0.44°)
20
15
10
5
0
-5
-10
-15
-30
-20
-10
0
10
20


Climatology
2005
"1996-1998"
"2000-2002"
a
Total Copepod Biomass (mg C m^{-3})
0
10
20
30
40
b
Monthly Average Anomaly (Log Scale)
1.5
1
0.5
0
-0.5
-1
-1.5
'Northern' Copepods
'Southern' Copepods
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month in 2005


Zooplankton Biomass Anomalies
20
15
10
5
0
-5
-10
-15
-20
-25
-20
-15
-10
-5
0
5
10
15
20
25
30
▲BC (NVI)
▲BC (SVI)
▲Oregon (OR)
△CalCOFI (CC)
▲CalCOFI (SC)
▲Northern Baja (NB)
▲Central Baja (CB)
● 'Northern' copepods (NVI)
● 'Northern' copepods (SVI)
● 'Northern' copepods (OR)
◆ 'Southern' copepods (NVI)
◆ 'Southern copepods (SVI)
◆ 'Southern' copepods (OR)
● Copepods (NB)
● Copepods (CB)
○ 'Trans. Zone' copepods (CC)
● 'Trans. Zone' copepods (SC)
◇ 'Central/Eq.' copepods (CC)
◆ 'Central/Eq.' copepods (SC)
■ Euphausiids (NB)
■ Euphausiids (CB)
Zooplankton Composition Anomalies
20
15
10
5
0
-5
-10
-15
-20
-25
-20
-15
-10
-5
0
5
10
15
20
25
30