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COMPARISON OF LONG-TERM TRENDS OF ZOOPLANKTON FROM TWO MARINE ECOSYSTEMS ACROSS THE NORTH PACIFIC: NORTHEASTERN ASIAN MARGINAL SEA AND SOUTHERN CALIFORNIA CURRENT SYSTEM

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ABSTRACT

Long-term trends of zooplankton biomass (1968–2009) and major zooplankton taxa (1978–2009) were examined across the North Pacific in the Northeastern Asian Marginal Sea (NeAMS) and the Southern California Current System (SCC) to test for evidence of basin-scale synchrony. Zooplankton biomass showed contrasting long-term patterns in the two regions: an increasing trend (as wet mass) in the NeAMS, but a decreasing trend (as displacement volume) in the SCC. Zooplankton biomass covaried with the Pacific Decadal Oscillation in the NeAMS, but with the North Pacific Gyre Oscillation in the SCC. In the NeAMS, increasing zooplankton biomass was closely associated with increases of all major zooplankton groups (copepods, chaetognaths, euphausiids, and hyperiid amphipods). In the SCC, decreasing zooplankton biomass was caused by declining tunicates and chaetognaths. Seasonal cycles and responses to El Niño also differed between the two regions. In this cross-basin comparison, zooplankton showed differing patterns that reflect region-specific physical and biotic processes rather than synchronous responses to large-scale atmosphere-ocean forcing.

INTRODUCTION

Climate change has begun altering ecosystems on a global scale (IPCC 2013). Atmosphere-ocean interactions alter sea surface temperature, calcium carbonate saturation, dissolved oxygen concentrations, ocean circulation, nutrient supply, sea level, and other properties, leading to changes of marine ecosystems in various ways. In addition, relatively abrupt changes in marine ecosystems in response to climate variables have been reported from a number of regions (Hare and Mantua 2000; Rebstock and Kang 2003; Hunt et al. 2008; Drinkwater et al. 2009), although the mechanisms underlying these changes are under discussion (Bestelmeyer et al. 2012; DiLorenzo and Ohman 2013).

The North Pacific experiences large-scale atmosphere and ocean forcing on various timescales, including the Pacific Decadal Oscillation (PDO), the North Pacific Gyre Oscillation (NPGO), and El Niño-Southern Oscillation (ENSO; Mantua et al. 1997; Di Lorenzo et al. 2008). However, the same large-scale forcing may impact geographically separated regional ecosystems in different ways. In a comparative study of four marine ecosystems (two in the Pacific and two in the Atlantic Ocean), the four systems revealed similar patterns of variability in adjacent regions or subregions, but little similarity across the Atlantic or between high latitude regions in the Atlantic and Pacific (Drinkwater et al. 2009).

Within the North Pacific, the eastern Bering Sea and Gulf of Alaska show warming coupled with the Pacific Decadal Oscillation (PDO; Drinkwater et al. 2009) and altered marine ecosystems consistent with the timing of change of sign of the PDO (Hare and Mantua 2000; Benson and Trites 2002). On the other hand, in the southern California Current, Lavaniegos and Ohman 2007 showed that zooplankton were markedly affected by El Niño and La Niña, but apart from a long-term decline in pelagic tunicates (especially salps), these authors did not detect long-term trends in aggregated biomass in response to climate shifts (cf., McGowan et al. 2003). At the species level, Brinton and Townsend 2003 and Di Lorenzo and Ohman (2013) working with euphausiids, Keister et al. 2011 and Bi et al. 2012 with copepods, and Ohman et al. 2012 with stable *N* isotopes of selected zooplankton species have suggested zooplankton responses to PDO-related climate forcing in the North Pacific. In the western North Pacific, changes in the Oyashio Current and the Tsushima Warm Current regions have been associated with changes in ecosystem conditions (Rebstock and Kang 2003; Sakurai 2007; Kang 2008). Di Lorenzo et al. 2013 illustrate how regional forcing can differentially influence zooplankton populations in the Kuroshio-Oyashio-Extension region and the California Current System.

Contrasting with these regional ecosystem responses to regional physical forcing is the apparent basin-scale synchrony in fluctuations in biomass of some clupeoid fishes. Kawasaki 1983, Lluch-Belda et al. 1992, Schwartzlose et al. 1999, Alheit and Bakun 2010 and others have called attention to the apparent in-phase variations of geographically separated populations of small, epipe-

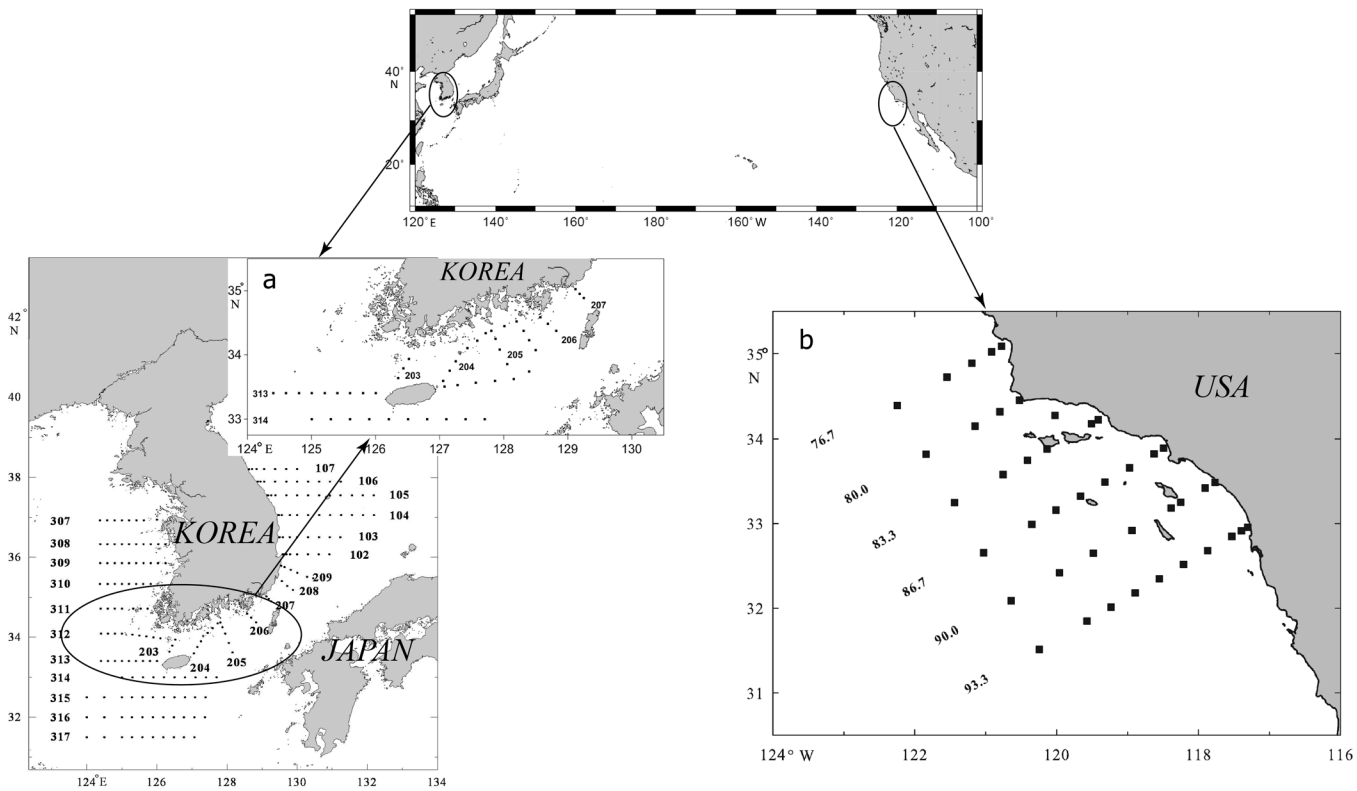

Figure 1. Research regions: the Northeastern Asian Marginal Sea (NeAMS) and the Southern California Current System (SCC), and sampling stations considered in this study: (a) NeAMS and (b) SCC.

lagic planktivorous fishes. Sardine populations off the coast of California and Japan, for example, are thought to vary in-phase with one another (Lluch-Belda et al. 1992), in relation to climate forcing (Hollowed et al. 2001). If planktivorous fishes exhibit such synchrony, this leads to the question whether their zooplanktonic prey do as well. Perry et al. 2004 could not identify rigorous and statistically robust global synchronies of zooplankton from multiple sites in several ocean basins. Mackas and Beaugrand 2010 suggested, based on preliminary data, that there might be significant synchrony in decadal variations of zooplankton among regions and across ocean basins, but not globally. The more comprehensive results of Batchelder et al. 2012 suggest there may be synchronous zooplankton biomass and/or abundance fluctuations at scales up to ca. 1000–3000 km, but that the synchronous patterns observed in the sardine and anchovy are unlikely connected with lower trophic level production (e.g., zooplankton biomass/abundance). However, while Batchelder et al. 2012 presented metrics of bulk zooplankton biomass, they did not analyze variations in any of the constituent zooplankton taxa.

Here we were motivated by the result of synchrony of small clupeoid fishes like sardines across the North Pacific to address the extent to which mesozooplankton on the western and eastern sides of the North Pacific might also show common (or different) responses. We sought to conduct a comparative study between Korean coastal waters and the southern California Current System to improve our ability to understand, predict, and prepare for the expected large-scale variations in the atmosphere-ocean forcing across the North Pacific basin.

This study focuses on 1) comparing long-term and seasonal variations of zooplankton biomass and major zooplankton taxa with environmental variables from these two regions across the North Pacific, and 2) assessing the extent to which regional or basin-scale processes better account for the variations observed in the mesozooplankton.

DATA AND METHODS

Geographical Areas and Hydrographic Characteristics

The Northeastern Asian Marginal Sea, in the western Pacific, is defined as the southern region adjacent to the Korean Peninsula and the northern East China Sea (EC) between approximately 33°–35°N, 124°–130°E (fig. 1a). The Northeastern Asian Marginal Sea (NeAMS) is a representative continental shelf region less than 100 m deep and directly influenced by the Tsushima Warm Current as a branch of the Kuroshio Warm Current.

Low salinity, high turbidity water from the Yangtze River reaches the EC and gradually mixes with the Tsushima Warm Current in the NeAMS (An 1974; Hong et al. 2002). We restricted our analyses to this southern region within the larger survey region analyzed (fig. 1), because of contrasting hydrographic and plankton conditions in the southeastern Yellow Sea and southwestern East/Japan Sea (Kang et al. 2012). The Southern California Current System (SCC) is here defined as the California Current System between approximately 31°–35°N, 117°–122°W, from Point Conception to the border with Mexico (fig. 1b). The SCC includes the southward extension of the California Current proper, the Inshore Countercurrent, and the California Undercurrent (Lynn and Simpson 1987) and the seasonally formed southern California eddy (Checkley and Barth 2009). The continental shelf is narrow (<5–10 km) in most of the region. Wind-driven coastal boundary upwelling and offshore wind-stress curl upwelling are important regional physical characteristics in the SCC. The SCC is often influenced by medium-to-larger ENSO events (Ohman et al. 2012; Ohman et al. 2013).

Data

We sought similar data sets in order compare long-term changes of zooplankton in response to physical forcing in both ecosystems. Data were obtained from the Korea Oceanographic Data Center (KODC) in the NeAMS and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in the SCC.

Although the CalCOFI record extends to 1949, data analyzed were restricted to the time period since 1968 for comparability between the NeAMS and SCC regions. Temperature and salinity data at 10 m depth from 1968 to 2009 were analyzed to remove the transient effects of surface ocean-atmosphere exchange. Near-surface chlorophyll *a* data were available from 1983 in the SCC and 1995 in the NeAMS. Mesozooplankton biomass from 1968 to 2009 was examined from both regions. Total biomass was determined by wet weight in the NeAMS and by displacement volume in the SCC. The abundance of major zooplankton groups from 1978 to 2009 was obtained in the both regions but with a difference in the major zooplankton groups analyzed. Microscope enumerations of copepods, hyperiid amphipods, euphausiids and chaetognaths were available in both regions, while tunicates (here the sum of doliolids and salps) were available only in the SCC. Pelagic tunicates are a major zooplankton taxon in the SCC, but less so in the NeAMS. There were differences in collection methods of zooplankton and estimation of zooplankton biomass. Zooplankton were sampled vertically in the NeAMS with a NORPAC net (0.45 m diameter ring net with 0.33 mm mesh) from 100 m to the surface, bottom depth permitting, otherwise from near-bottom depths to the surface. In the SCC, zooplankton were sampled with a double oblique tow with a 1 m diameter ring net with 0.55 mm mesh from 140–0 m from 1951 to 1968, a 1 m diameter ring net with 0.505 mm mesh from 210–0 m from 1969–77, and a 0.71 m diameter bongo net with 0.505 mm mesh from 210–0 m depth after December 1977 (Ohman and Smith 1995).

In the NeAMS, zooplankton biomass was calculated by wet weight, following exclusion of large organisms >3 cm in size and extraction of excess water with filter paper. In the SCC the wet displacement volume was determined after removal of large (>5 mL individual biovolume) organisms. Displacement volume can give different results from carbon biomass, especially when pelagic tunicates are prevalent (Lavaniegos and Ohman 2007), but we analyze displacement volume here for comparability with the NeAMS region. To intercompare methods between the SCC and NeAMS, both wet weight and displacement volume were determined for 50 samples taken in the NeAMS region in October 2009, using the CalCOFI methodology for the latter. The resultant average density of the zooplankton was 1.25 g mL^{-1}, which is reasonable for preserved zooplankton and provides an approximate measure of comparability between methods.

Data from February, April, August, and October were used as the representative of each season in the NeAMS, while means were calculated from March–May, June–August, September–November, and December–February in the SCC. There were limited data in some months, so we used means over three months closely related to each season in the SCC. For comparison of numerical abundances of zooplankton taxa in the two regions, only spring data were used because these provide the most complete record and best interannual coverage. The spatial coverage was limited to the region described in Figure 1b and analyzed by Lavaniegos and Ohman 2007. Spring is an important time period for fish spawning in both regions.

Data Analysis

Zooplankton biomass and abundances of major zooplankton groups were $\log_{10}$ transformed. The annual mean was determined from the data averaged in each season. If there were no data in a particular season, the annual mean was not calculated. Anomalies of temperature, salinity, and zooplankton biomass from mean values for 1968–2009 were standardized by dividing by the standard deviation of the long-term mean. Anomalies of major zooplankton groups were calculated relative to the mean during 1978–2009, because taxonomic data were not available from the NeAMS for earlier years.

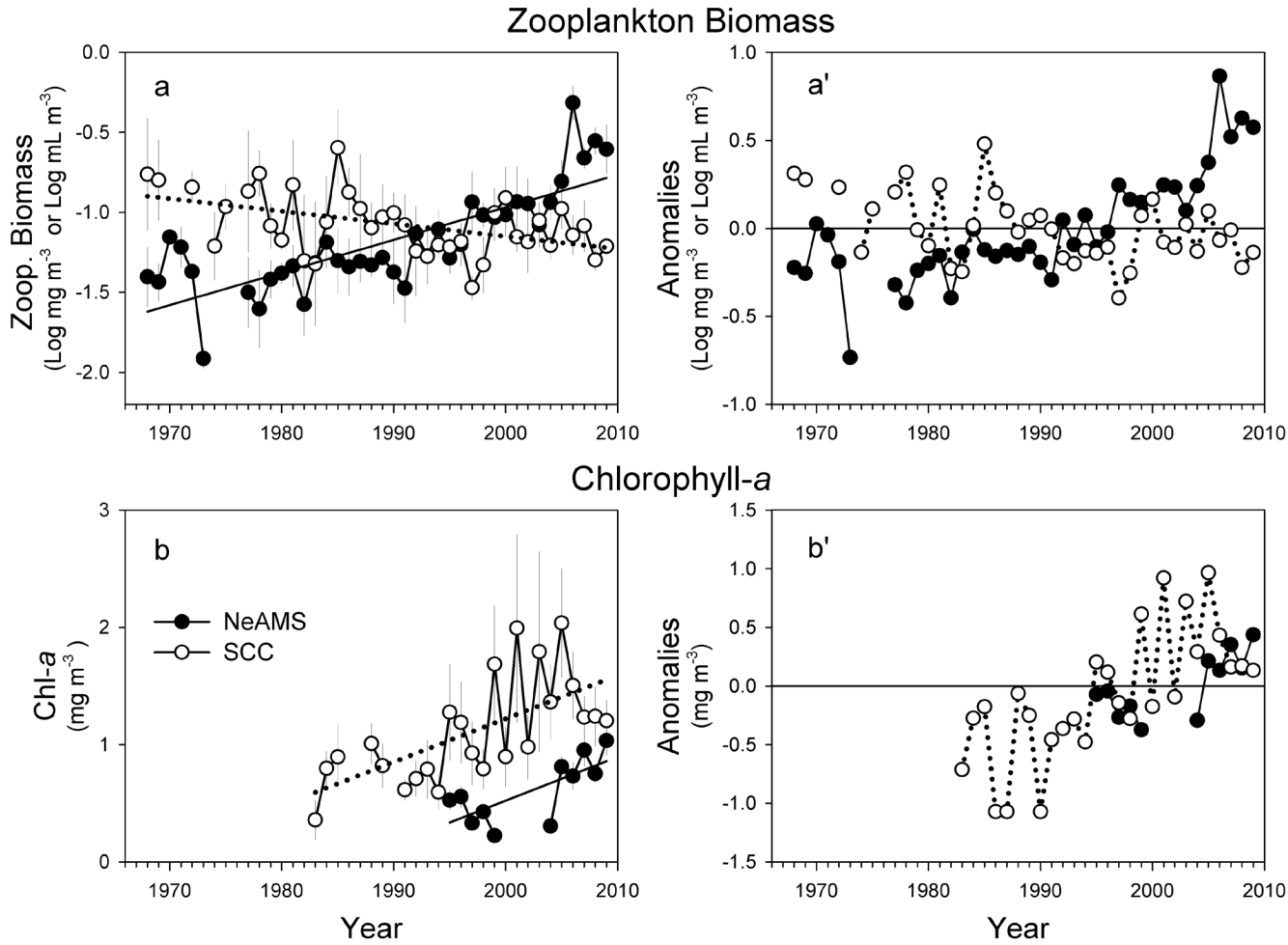

Figure 2. Time series of annual mean of $\log_{10}$-transformed zooplankton biomass and chlorophyll *a*, and their normalized anomalies in the Northeastern Asian Marginal Sea (NeAMS, filled symbols) and the Southern California Current System (SCC, open symbols). (a) Zooplankton biomass (NeAMS: $r^2 = 0.624$, SCC: $r^2 = 0.228$, $p < 0.01$), (a') normalized zooplankton biomass anomalies, (b) chlorophyll a (NeAMS: $r^2 = 0.519$, SCC: $r^2 = 0.422$, $p < 0.05$, and (b') chlorophyll *a* anomalies. Error bars in this and subsequent figures indicate 95% confidence limits.

Linear regression analyses fitted by the ordinary least squares method were carried out to analyze temporal trends. No correction was made for autocorrelation because the data are annual and essentially independent. To identify long-term trends of covarying major zooplankton groups, Principal Components Analysis was carried out with spring mean data, including tunicates in the SCC. Correlation analysis was conducted with Spearman rank correlations. We chose not to apply the Bonferroni correction for multiple testing, as this is an exceedingly conservative criterion that can increase the probability of Type II error.

RESULTS

Long-term Trends

Zooplankton biomass The time series of the annual mean of zooplankton biomass revealed an obvious contrast between the two regions (figs. 2a, a'). The NeAMS showed a significant increasing trend ($r^2 = 0.624$, $p < 0.001$), with a decreasing trend in the SCC ($r^2 = 0.228$, $p < 0.01$). In the NeAMS, zooplankton biomass increased sharply after the early 1990s compared to prior years. Zooplankton biomass was initially lower in the NeAMS than in the SCC, but this pattern reversed in the 2000s (figs. 2a, a'). In comparing biomass values, it must be recalled that the sampling and biomass determination methods were different. In the SCC, declines in annually averaged zooplankton biomass were found for the strongest El Niños (1972–73, 1982–83, 1991–92, 1997–98, 2003–04, $P < 0.05$, Mann-Whitney U test; fig. 2a') but these El Niño-related decreases reversed within one to two years. In the SCC, biomass increased abruptly in the La Niña of 1999, but thereafter continued a slow rate of decline. In the NeAMS there was no consistent response of zooplankton biomass to the strongest El Niños ($p > 0.50$). Over the entire time series, there was an inverse corre-

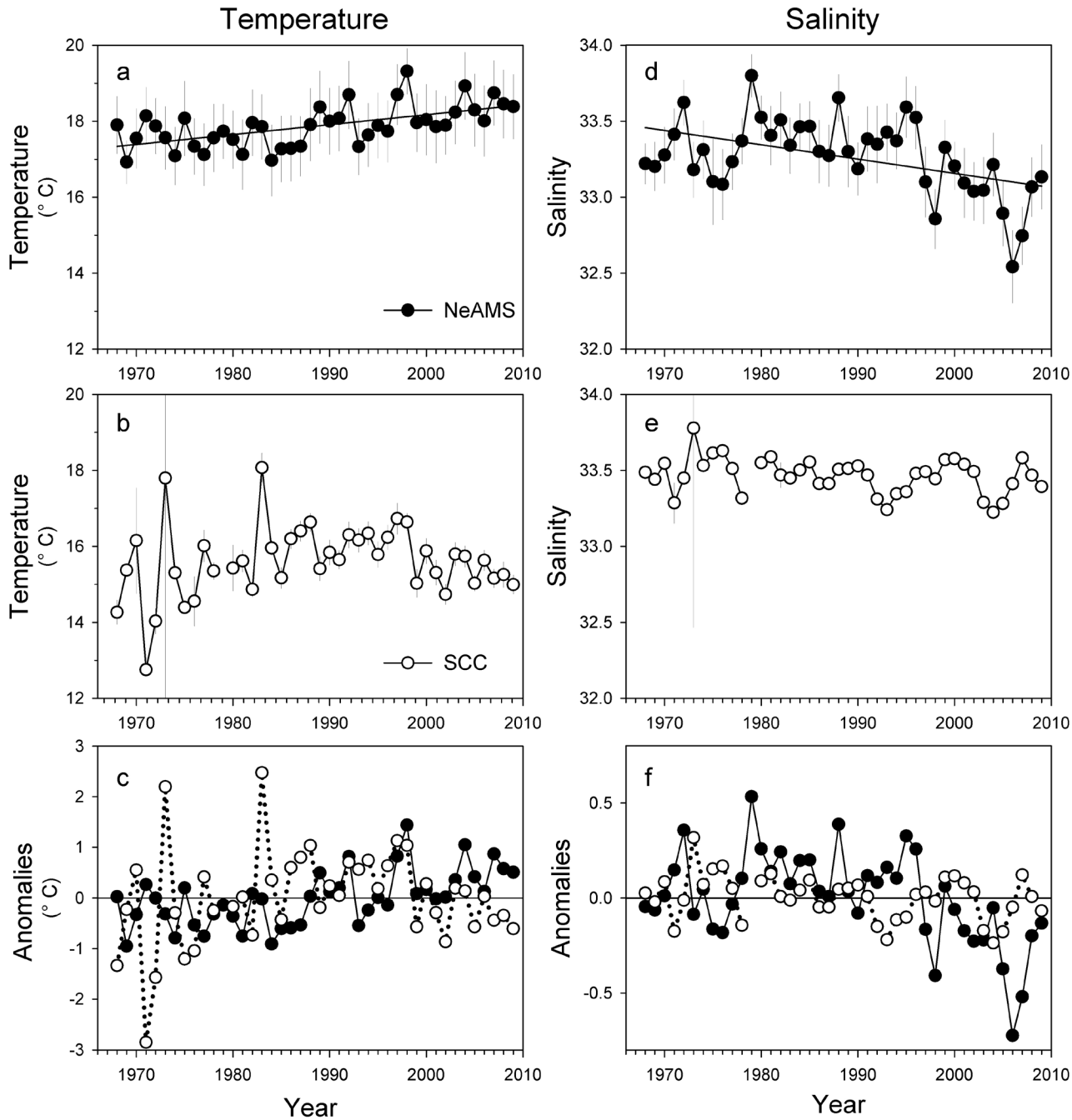

Figure 3. Time series of annual mean of temperature and salinity, and their normalized anomalies in the Northeastern Asian Marginal Sea (NeAMS, filled symbols) and the Southern California Current System (SCC, open symbols). (a) Temperature (NeAMS: $r^2 = 0.342$, $p < 0.001$), (b) Temperature (SCC: $r^2 = 0.022$, $p > 0.3$), (c) NeAMS and SCC temperature anomalies, (d) Salinity (NeAMS: $r^2 = 0.221$, $p < 0.01$), (e) Salinity (SCC: $r^2 = 0.091$, $p > 0.05$), and (f) NeAMS and SCC salinity anomalies.

lation of biomass between the two regions ($r = -0.430$, $p < 0.01$), however, once the linear trend in both regions is removed there is no remaining correlation of the residuals ($p > 0.50$).

***Chlorophyll* a** Chlorophyll *a* concentrations were consistently higher in the SCC than the NeAMS (fig. 2b). Annual mean chlorophyll *a* data were very limited for comparisons between regions, but they generally showed increasing trends in both (figs. 2b,b'; NeAMS: $r^2 = 0.519$, SCC: $r^2 = 0.422$, both $p < 0.05$). Chlorophyll *a* concentrations were uncorrelated in the two regions, both before and after removal of the linear trend ($p > 0.10$).

Temperature Mean annual temperature was usually higher in the NeAMS than in the SCC (fig. 3a,b). The long-term annual mean of temperature increased somewhat in the NeAMS (figs. 3a,c; $r^2 = 0.342$, $p < 0.001$), while no detectable trend was found in the SCC (figs. 3b,c; $r^2 = 0.022$, $p > 0.30$). Intrannual tempera-

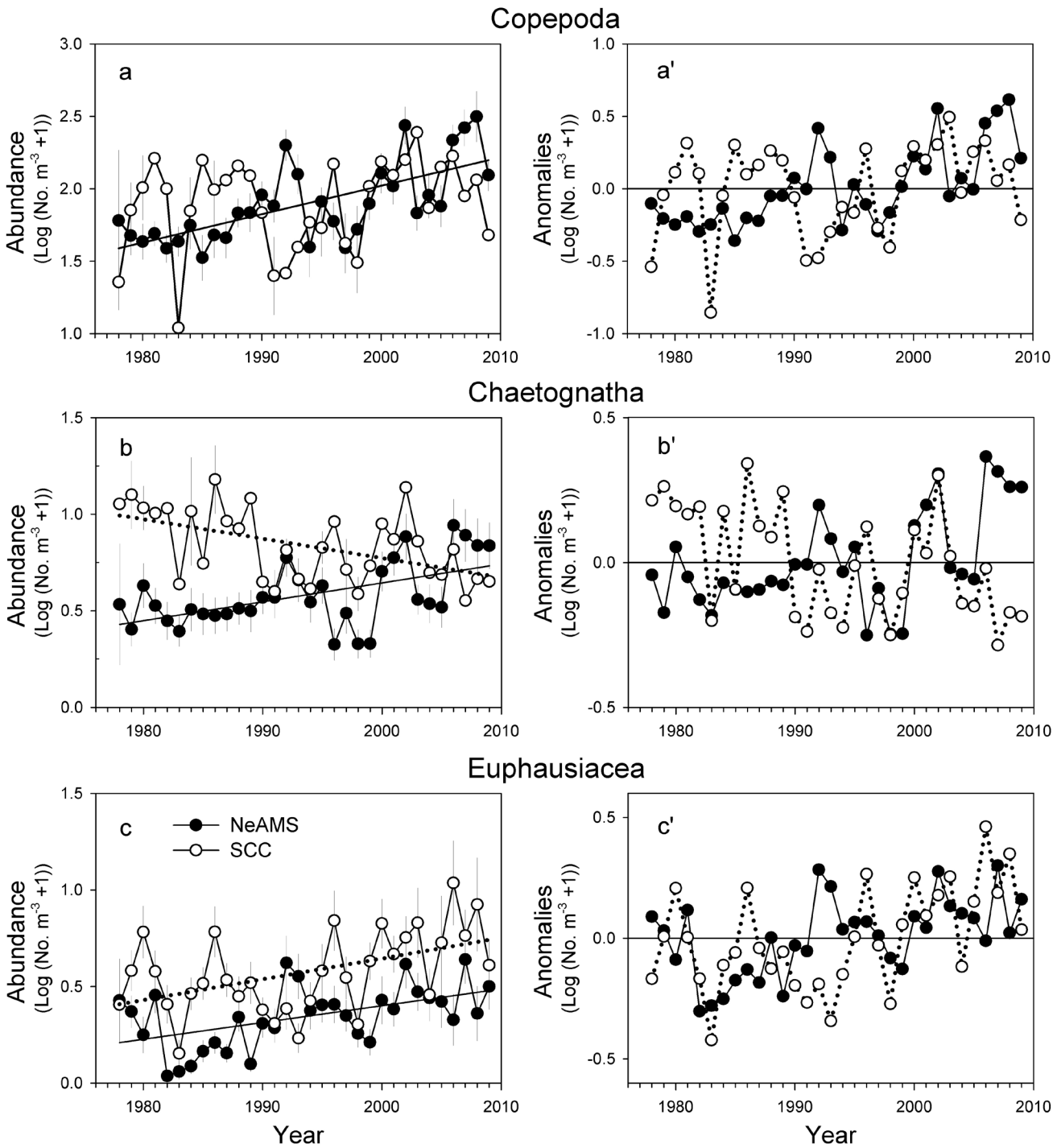

Figure 4. Time series of annual mean of $\log_{10}$-transformed abundance of zooplankton groups and their anomalies in the Northeastern Asian Marginal Sea (NeAMS, filled symbols) and the Southern California Current System (SCC, open symbols). (a) Copepoda (NeAMS: $r^2 = 0.463$, $p < 0.001$; SCC: $r^2 = 0.063$, $p > 0.10$), (a') Copepoda anomalies, (b) Chaetognatha (NeAMS: $r^2 = 0.291$, SCC: $r^2 = 0.257$, $p < 0.01$), (b') Chaetognatha anomalies, (c) Euphausiacea (NeAMS: $r^2 = 0.256$, $p < 0.01$; SCC: $r^2 = 0.230$, $p < 0.01$) and (c') Euphausiacea anomalies.

ture variability was higher in the NeAMS than in the SCC (fig. 3a,b).

Salinity Salinity was generally lower in the NeAMS than in the SCC (fig. 3d,e). Annual mean salinity revealed a significant decreasing trend in the NeAMS (figs. 3d,f; $r^2 = 0.221$, $p < 0.01$), but no significant trend in the SCC (figs. 3e,f; $r^2 = 0.091$, $p > 0.05$). Intrannual salinity variability was higher in the NeAMS than in the SCC (fig. 3d,e). Neither temperature nor salinity, nor the residual of these variables after removing the long-term trends, were correlated between the NeAMS and the SCC ($p > 0.10$).

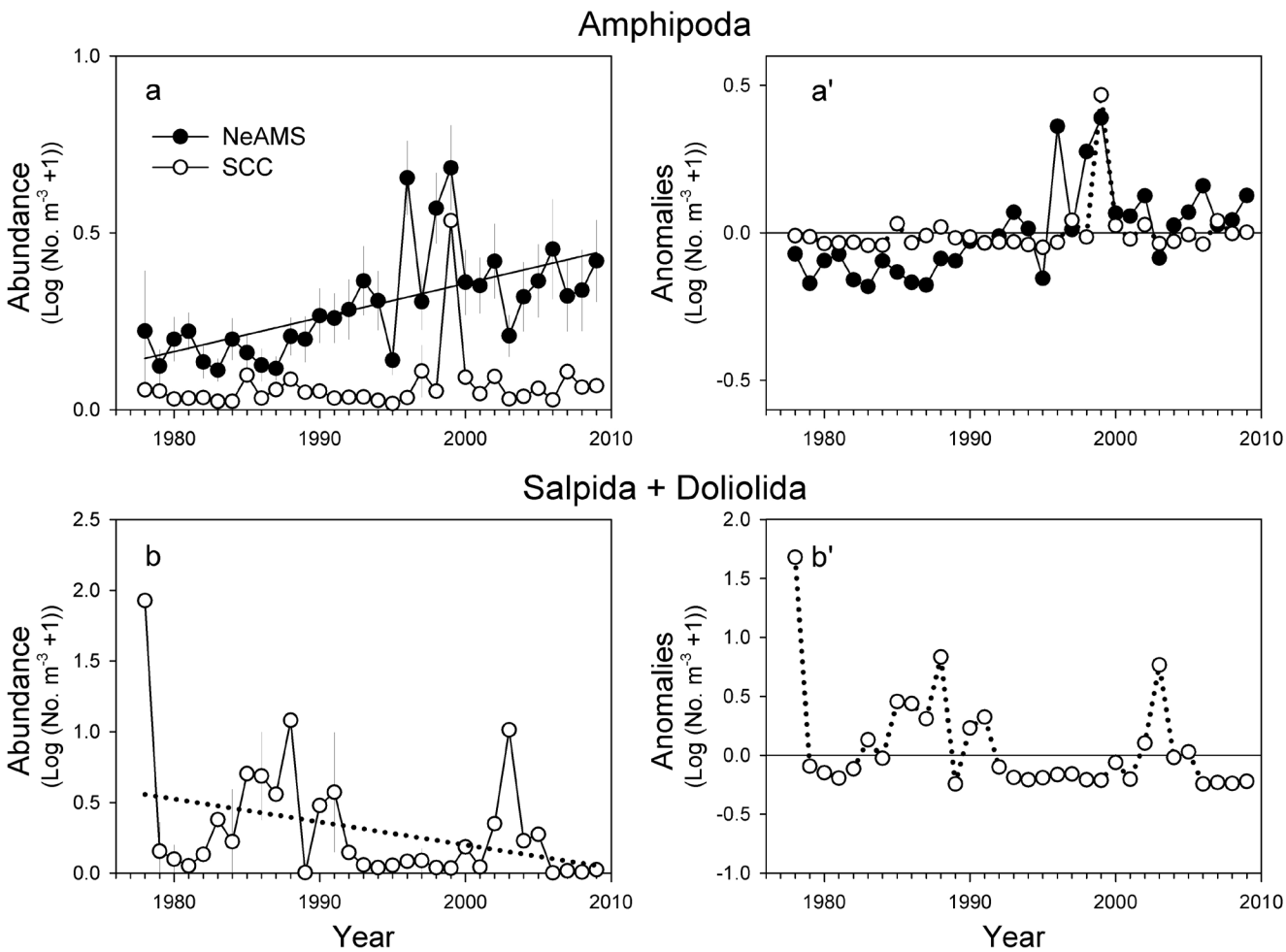

Figure 5. Time series of annual mean of $\log_{10}$-transformed abundance of zooplankton groups, and their anomalies in the Northeastern Asian Marginal Sea (NeAMS, filled symbols) and the Southern California Current System (SCC, open symbols). (a) Amphipoda (NeAMS: $r^2 = 0.372$, $p < 0.001$; SCC: $r^2 = 0.034$, $p > 0.30$), (a') Amphipoda anomalies, (b) Tunicata (SCC: $r^2 = 0.134$, $p < 0.05$) and (b') Tunicata anomalies.

Zooplankton groups The long-term mean abundance of copepods was generally similar in both regions (figs. 4a,a'). The mean abundance of copepods in spring increased from 1978 to 2009 in the NeAMS ($r^2 = 0.463$, $p < 0.001$) but not in the SCC ($r^2 = 0.063$, $p > 0.10$). Interannual variations were largely independent in both regions during 1978–97 but became somewhat more correlated after 1998 (fig. 4a').

The time series of chaetognath abundance showed contrasting trends between regions (figs. 4b,b'). Abundance increased over time in the NeAMS ($r^2 = 0.291$, $p < 0.01$), but decreased in the SCC ($r^2 = 0.257$, $p < 0.01$). Chaetognaths showed elevated abundance in 2002 in both regions, while in the SCC, a similar high abundance was found in 1986. The long-term mean of chaetognath abundance was usually higher in the SCC than the NeAMS, but approached a similar mean in both regions at the end of 2008.

The mean abundance of euphausiids was consistently higher in the SCC compared to the NeAMS and showed increasing trends in both the NeAMS ($r^2 = 0.256$, $p < 0.01$) and the SCC ($r^2 = 0.230$, $p < 0.01$, figs. 4c,c').

Hyperiid amphipods were more abundant in the NeAMS, in particular after the late 1980s compared to the long-term mean (figs. 5a,a'). They showed an increasing trend in the NeAMS ($r^2 = 0.372$, $p < 0.001$) but not in the SCC ($r^2 = 0.034$, $p > 0.30$). High positive anomalies were found in 1993, 1996, 1998–99, 2002, and 2006 in the NeAMS, and in 1999 in the SCC.

Tunicates (Doliolida+Salpida) showed a slightly decreasing trend ($r^2 = 0.134$, $p < 0.05$), and showed low abundance continuously after 1992, except around 2003 (figs. 5b,b').

None of the four taxonomic groups analyzed in both regions showed correlations between regions, either before or after removal of long-term trends ($p > 0.05$).

PCA Principal Component Analysis was used to identify dominant modes of community structure of major zooplankton groups. The 1st and 2nd principal

TABLE 1
Eigenvectors of 1st and 2nd principal components in the Northeastern Asian Marginal Sea (NeAMS) and the Southern California Current (SCC).

	TWC		SCC	
	PC 1	PC 2	PC 1	PC 2
Copepoda	**0.762**	–0.319	**0.608**	–0.065
Amphipoda	**0.680**	**0.699**	0.266	0.483
Euphausiacea	**0.816**	0.014	**0.576**	–0.329
Chaetognatha	**0.717**	–0.340	0.471	0.084
Tunicata			0.076	**0.804**
Cumulative variance	55.6%	73.2%	45.3%	70.2%

Boldface indicates values >|0.5|. Cumulative variance is the cumulative percentage of the total variance explained by PCA.

components (PC 1 and PC 2) calculated from the matrix of spring means of major zooplankton groups explained 73.2% of the total variance in the NeAMS and 70.2% in the SCC. In the NeAMS, PC 1 accounted for 55.6% of the variance, and showed a strong positive association with copepods, amphipods, euphausiids, and chaetognaths (table 1). PC 2 described 17.1% of the variance, showing a high positive relationship with amphipods. In the SCC, PC 1 accounted for 45.3% of total variance, with high positive loadings on copepods and euphausiids. PC 2 explained 24.9% of the variance, with the highest positive loading on tunicates and weaker loading on amphipods.

The time series of PC 1 showed a statistically significant increasing trend in the NeAMS (r^2 = 0.508, p < 0.001) with the most notable peaks in 1993 and 2002 (fig. 6a). Conversely, PC 2 decreased over time (fig. 6b , r^2 = 0.154, p < 0.05). In the SCC, there were no significant temporal trends in either PC1 or PC2 (figs. 6c,d; r^2 = 0.022 and 0.039, respectively, p > 0.10).

Seasonal Variation

It should be recalled that the availability of data necessitated rather coarse temporal resolution for these seasonal comparisons.

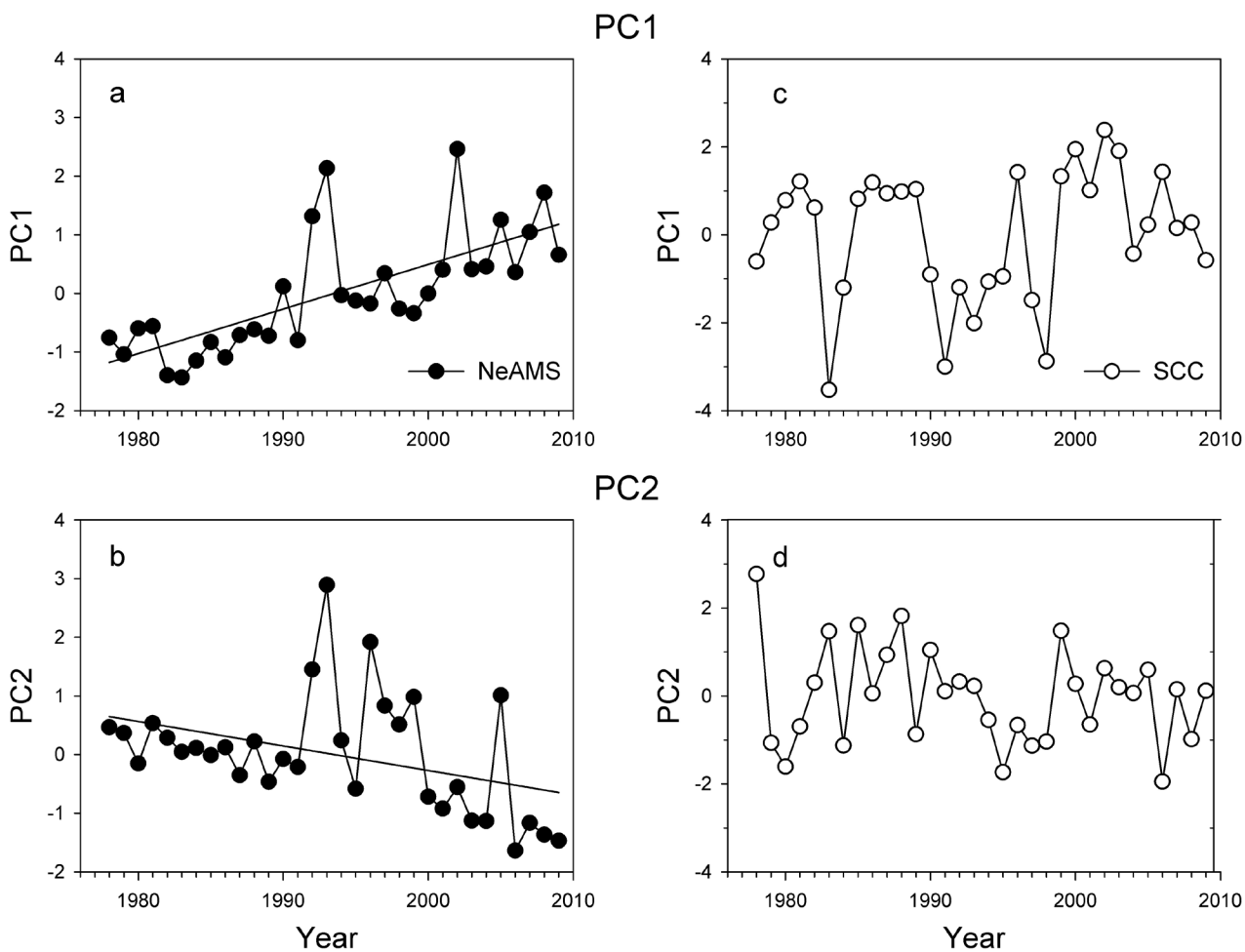

Figure 6. Time series of the 1st and 2nd principal components (PC) in the Northeastern Asian Marginal Sea (NeAMS, filled symbols) and the Southern California Current System (SCC, open symbols). (a) PC1 of NeAMS (r^2 = 0.508, p < 0.001), (b) PC2 of NeAMS (r^2 = 0.154, p < 0.05), (c) PC1 of SCC (r^2 = 0.022, p > 0.10) and (d) PC2 of SCC (r^2 = 0.039, p > 0.10).

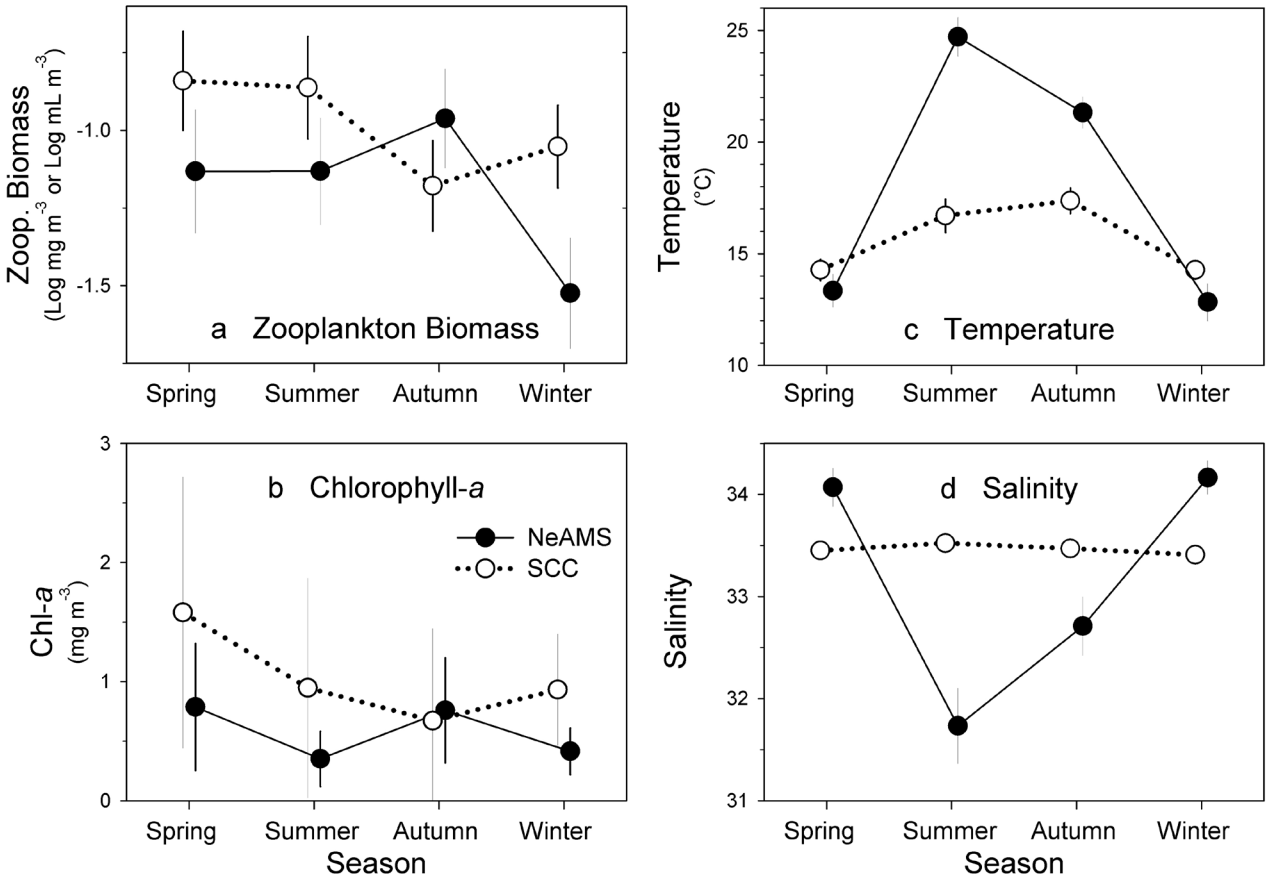

Figure 7. Seasonal variations of (a) zooplankton biomass, (b) chlorophyll *a*, (c) temperature, and (d) salinity in the Northeastern Asian Marginal Sea (NeAMS, filled symbols) and the Southern California Current System (SCC, open symbols).

Zooplankton biomass Zooplankton biomass showed different seasonal cycles with different peaks in the two regions (fig. 7a). A small seasonal peak occurred in autumn in the NeAMS, while the maximum occurred in spring–summer in the SCC. The lowest zooplankton biomass was found in winter in the NeAMS and in autumn in the SCC.

***Chlorophyll* a** The seasonal peak of chlorophyll *a* appeared in autumn and, to a lesser extent, in spring in the NeAMS, while values peaked in spring in the SCC (fig. 7b). The lowest value was found in summer in the NeAMS, but in autumn in the SCC.

Temperature There was a substantial seasonal difference in mean temperature in the NeAMS, with a smaller range in the SCC (fig. 7c). The SCC showed similar temperatures between summer and autumn, and spring and winter differed less than 1°C. In contrast, the NeAMS exhibited high differences between spring and summer (11.3°C), and autumn and winter (8.5°C). Seasonal peaks were found in the summer in the NeAMS and in the autumn in the SCC.

Salinity Salinities were similar in winter and spring in the NeAMS , but appreciably lower in summer and autumn (fig. 7d). The SCC showed no detectable seasonal differences.

Correlation Between Environmental Variables and Zooplankton

Northeast Asian Marginal Sea (NeAMS) Total zooplankton biomass exhibited a significant positive correlation with three major zooplankton groups: copepods, chaetognaths, and euphausiids ($p < 0.05$, table 2). Of the environmental variables, biomass showed a significant negative correlation with the PDO and positive correlation with temperature ($p < 0.05$).

Copepods were closely positively related with chaetognaths and euphausiids ($p < 0.05$). They were negatively correlated with the PDO as the representative oceanic variable in the North Pacific ($p < 0.05$). Amphipods showed no significant relation with environmental variables, but covaried with euphausiids ($p < 0.05$). Chaetognaths were significantly related to copepods ($p < 0.05$). Similar to amphipods, euphausiids had no significant relations with any of the physical variables, while they were associated with other zooplankton groups.

TABLE 2
Correlations (bold values $p < 0.05$) among environmental variables and zooplankton in spring in the Northeastern Asian Marginal Sea (NeAMS).

	Zooplankton biomass	Temperature	Salinity	NPGO	PDO	Copepoda	Amphipoda	Chaetognatha
Temperature	**0.545**							
Salinity	–0.337	0.081						
NPGO	0.066	0.052	**–0.504**					
PDO	**–0.397**	–0.275	0.252	**–0.405**				
Copepoda	**0.430**	0.182	–0.340	0.255	**–0.374**			
Amphipoda	0.332	0.276	0.127	–0.170	0.070	0.322		
Chaetognatha	**0.634**	0.237	–0.347	0.268	–0.209	**0.407**	0.320	
Euphausiacea	**0.425**	0.241	–0.138	–0.119	–0.150	**0.516**	**0.438**	**0.428**

TABLE 3
Correlations (bold values $p < 0.05$) among environmental variables and zooplankton in spring in the Southern California Current System (SCC).

	Zooplankton biomass	Temperature	Salinity	NPGO	PDO	Chl. *a*	Copepoda	Amphipoda	Chaetognatha	Euphausiacea
Temperature	0.063									
Salinity	**0.346**	–0.261								
NPGO	**0.341**	–0.222	**0.345**							
PDO	0.142	**0.643**	–0.332	–0.212						
Chl. *a*	–0.030	**–0.499**	0.039	0.0005	–0.054					
Copepoda	**0.424**	**–0.422**	**0.410**	**0.342**	–0.060	**0.415**				
Amphipoda	0.124	**–0.447**	**0.484**	0.277	**–0.416**	0.105	0.162			
Chaetognatha	**0.698**	0.252	0.091	0.108	0.177	0.023	**0.406**	–0.081		
Euphausiacea	0.243	**–0.491**	0.277	0.123	–0.123	**0.418**	**0.694**	0.143	0.320	
Tunicata	**0.444**	0.264	–0.172	–0.004	**0.356**	–0.085	–0.032	0.008	0.251	–0.267

Southern California Current (SCC) Zooplankton biomass was significantly correlated with the NPGO and salinity ($p < 0.05$, table 3), but there no relationships were found with temperature and the PDO. Of the biotic variables, copepods, chaetognaths, and tunicates showed significant correlations with zooplankton biomass ($p < 0.05$). In contrast to zooplankton biomass, chlorophyll *a* was inversely associated with temperature among environmental variables, and positively associated with copepods and euphausiids among biotic components ($p < 0.05$).

From the major zooplankton groups, copepods were significantly related with chaetognaths and, especially, with euphausiids (r^2=0.694, $p < 0.05$). In addition, copepods were inversely related to temperature and positively related to salinity and the NPGO. Conversely, amphipods did not show any significant relationships with the other zooplankton groups examined in this study. However, they showed significant negative relations with temperature and the PDO, and a positive relation with salinity. Chaetognaths exhibited no identifiable correlations with environmental variables, but they were significantly related to copepods ($p < 0.05$). Euphausiids were negatively related with temperature ($p < 0.05$). Tunicates showed no detectable relations with other zooplankton groups. In terms of the environmental variables, they showed a significant positive relationship with the PDO.

DISCUSSION

Contrasting Long-term Changes in Zooplankton Biomass and Major Taxa

Zooplankton biomass in two regions on opposite sides of the North Pacific basin revealed contrasting responses to atmosphere-oceanic forcing and no evidence of in-phase fluctuations over the 40 year period analyzed here. Zooplankton biomass showed an increasing long-term trend in the Northeastern Asian Marginal Sea (NeAMS), with interannual variability related to the PDO, while a decreasing trend was evident in the Southern California Current (SCC), where interannual variability is related to the NPGO. Despite the presence of basin-scale forcing that influences both ecosystems, there were pronounced differences in regional expression of this climate forcing.

Di Lorenzo et al. 2013 illustrate that region-specific transport processes associated with large-scale forcing may influence zooplankton on eastern and western sides of the North Pacific differently. The present results are also in accord with the broader comparisons among many zooplankton time series from diverse ocean regions reported by Batchelder et al. 2012. Those authors reported that zooplankton biomass/abundance have 50% decorrelation length scales of ca. 700–1400 km and scales of significant coherence that extend to separation dis-

tances of ca. 3000 km, although only biomass time series were available for Pacific sites. For comparison, the distance between our two study sites is approximately 9,500 km. Batchelder et al. 2012 also observed low correlations between biomass fluctuations in different sites within the California Current System and sites in the Kuroshio-Transition-Oyashio region off Japan. Our results extend those findings for direct comparison between the SCC and NeAMS, and for key higher taxa of zooplankton taxa (rather than total biomass alone).

Within the California Current System, Mackas et al. 2006 found different responses of both zooplankton biomass and key species groupings to an extreme year of delayed upwelling in the far northern and southern sectors of the California Current System (CCS), separated by ca. 2,250 km. However, on the scale of separation of the southern and central California sectors of the CCS (ca. 400 km), much of the variability in zooplankton higher taxa (Lavaniegos and Ohman 2007) and zooplankton stable *N* isotope content (Ohman et al. 2012) is shared between regions. Of the three seas surrounding the Korean peninsula, the East/Japan and East China Seas showed similar time series of some zooplankton taxa, while the Yellow Sea differed (Rebstock and Kang 2003).

Therefore we do not find evidence from either total zooplankton biomass or abundance of major taxa that could account for the correlated fluctuations of clupeoid fishes across the North Pacific (e.g., Lluch-Belda et al. 1992). Although our study site in the NeAMS is displaced somewhat westward of the locations of catch of Japanese sardine during times of low sardine abundance, during times of high abundance the regions of primary sardine catch overlap our study location off the southern Korean peninsula (Lluch-Belda et al. 1989). Our study site off southern California is a primary site of sardine spawning in the California Current System.

The NeAMS In the NeAMS, increased temperature in winter creates early phytoplankton blooms and extends the duration of the phytoplankton outbreak in the East/Japan Sea (Chiba and Saino 2002). Lower salinity indicates elevated river discharge and accompanying dissolved nutrients (Hong et al. 2002) in the East China Sea. Consequently, warmer and less saline waters enhance the production of phytoplankton, thus fostering increased zooplankton biomass. The limited data available suggest chlorophyll *a* increased somewhat in recent years. In addition to total zooplankton biomass, all four major zooplankton taxa increased in abundance, and their correlated responses were corroborated by the consistent high positive loadings of all four taxa on PC 1. Thus, in the NeAMS, zooplankton biomass appears to be controlled from the bottom-up, and closely linked with physical forcing.

The NeAMS is a marginal sea exposed to two dominant currents, the Tsushima Warm Current as a branch of the Kuroshio Warm Current. Plankton variations of the NeAMS are closely related to fluctuations of these currents (An 1974; Hong and Cho 1983). Anomalously high zooplankton biomass can be caused by strong intrusions of the Tsushima Warm Current (Kang and Rebstock 2004). The PDO is closely correlated with characteristic pressure, wind, temperature and precipitation patterns in the North Pacific (Latif and Barnett 1994; Zhang et al. 1997; Mantua et al. 1997). Thus, the PDO is also indirectly or directly connected to the Tsushima Warm Currents, and precipitation. Density stratification is also an important physical variable related to production of phytoplankton and zooplankton in the NeAMS (Chiba and Saino 2002; Chiba et al. 2008; Kim et al. 2007).

The SCC In the SCC there were no detectable long-term linear trends in temperature and salinity over the duration of the data analyzed here, even though zooplankton biomass showed a decreasing trend. Lavaniegos and Ohman 2007, who analyzed a longer record from 1951–2005, noted that zooplankton biomass expressed as displacement volume declined because of a long-term decrease in contribution of pelagic tunicates. The decline in displacement volume was not detectable as a change in carbon biomass because of the disproportionate contribution that large, gelatinous tunicates make to displacement volume without corresponding contributions to C biomass (Lavaniegos and Ohman 2007). In that study, the decline in pelagic tunicates was accompanied by a long-term increase in water column stratification, and the species of salps that declined tended to be those introduced into the region from higher latitudes (Lavaniegos and Ohman 2003; 2007). In the present study, both tunicates and chaetognaths showed a long-term declining trend over the shorter period from 1978–2008. The decline in these taxa appears to be dominated by the decreasing contribution of large biovolume zooplankton, in particular salps, although the more recent spring of 2012 was again a period of high salp biomass (Smith et al. 2014).

The relationship between zooplankton displacement volume and the NPGO is evidence that interannual variations in this metric of zooplankton biomass are associated with upwelling in the SCC. The NPGO is related to wind-driven upwelling and horizontal advection, and is related to fluctuations of salinity and nutrients (Di Lorenzo et al. 2008; 2013). Variations in nutrients influence phytoplankton production and then appear to connect to higher trophic levels. Therefore, fluctuations of zooplankton biomass are affected by fluctuations of phytoplankton under the influence of the NPGO.

The correlations observed with copepods suggest they are related to variations in upwelling. Analyses

of fish populations and chlorophyll-*a* calculated with satellite data also suggest that the CalCOFI region is under bottom-up forcing (Ware and Thomson 2005; Rykaczewski and Checkley 2008). Euphausiids were also significantly correlated with chlorophyll *a* and inversely related to temperature.

Amphipods showed significant relations with the PDO, as well as temperature and salinity. Most species of hyperiid amphipods are known to be parasitoids on gelatinous zooplankton hosts (Madin and Harbison 1977; Lavaniegos and Ohman 1999). However, we did not find a relationship between total hyperiids and total tunicates, even though the latter include important host taxa. In contrast, Lavaniegos and Ohman 2007 found significant correlations between total biomass of hyperiids and medusae, salps, doliolids, and physonect+cystonect siphonophores. The differences in findings may be attributed to the longer data record and larger sample sizes in the Lavaniegos and Ohman 2007 study, and to the treatment of salps and doliolids together as tunicates in the present study.

Chaetognaths showed a significant relationship only with copepods in this study. Chaetognaths are known as carnivores mainly feeding largely on planktonic copepods (Feigenbaum and Maris 1984). Thus, the relation between copepods and chaetognaths suggests a prey-predator relationship.

Variability in Zooplankton Biomass Response to El Niños

The SCC, in particular, shows interannual variability in physical processes associated with specific El Niño events (Lavaniegos et al. 2002; Todd et al. 2011). In the present study, annually averaged zooplankton biomass decreased in strong El Niño events in the SCC, apparently via reduced upwelling and phytoplankton production (Kahru and Mitchell 2000), supplemented by advection of lower biomass subtropical waters in some events (Lavaniegos and Ohman 2007). In the NeAMS, Kang and Rebstock 2004 reported anomalously high zooplankton biomass in 1997 caused by the increase of thaliaceans, especially the warm-water species *Doliolum nationalis*, transported by the Tsushima Warm Current. The present results suggest no consistent response across all El Niño events in the NeAMS.

Contrasting Seasonal Cycles

In the NeAMS, the discharge of freshwater from rivers is the most important nutrient source (Hong et al. 2002). Low salinities in summer and autumn, due to heavy rainfall, are associated with the supply of nutrients into the sea. Consequently, phytoplankton increase, and then zooplankton increase. On the other hand, the zooplankton peak was found in spring in the SCC. The SCC in the southern region of the California Current System is a major region of coastal upwelling, which is closely related to plankton production. The spring peak of zooplankton biomass arises from the main seasonal forcing of coastal and curl-driven upwelling.

Therefore, seasonal variation in zooplankton biomass in the SCC is associated with variations in coastal upwelling, together with regional circulation, while biomass in the NeAMS is linked with large scale currents and river discharge. Biotic and abiotic seasonal cycles are related to different physical processes in the two regions.

Conclusions

The NeAMS and the SCC experience different regional physical and biotic forcing even though they are exposed to the same large-scale climate forcing. The regionally important physical forcing includes river discharge and large-scale currents in the NeAMS, in contrast to upwelling and large-scale currents in the SCC. The dominant regional physical characteristics associated with variations in total zooplankton biomass are the PDO in the NeAMS and the NPGO in the SCC. There were long-term biomass trends of contrasting signs in the two regions. Zooplankton biomass responses to seasonal cycles showed opposite patterns between the two regions, and El Niño's have a depressive effect on zooplankton biomass in the SCC, but less consistent effects in the NeAMS.

There is no evidence for correlated fluctuations of zooplankton that would account for the coherent variability in clupeoid fishes between the eastern and western North Pacific. More detailed process studies that focus at the species level, rather than aggregated higher taxa of zooplankton, are needed to understand the differential responses of zooplankton between these ocean provinces.

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