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Latitudinal distribution of mesozooplankton in the off-equatorial northeastern Pacific before and after the 1998/99 La Niña event

Jung-Hoon Kang [a,*], Woong-Seo Kim [b], Kyung-Il Chang [c]

[a] *Southern Coastal Environment Research Department, South Sea Institute, KORDI, 391, Jangmokmyun Koje-shi, Kyungnam 656-830, Republic of Korea*
[b] *Marine Resources Research Department, KORDI, Ansan P.O. Box 29, Seoul 425-600, Republic of Korea*
[c] *School of Earth and Environmental Sciences, Seoul National University, San 56-1, Sillim-dong, Gwanak-gu, Seoul 151-742, Republic of Korea*

Abstract

Factors affecting mesozooplankton distributions in the northeastern tropical Pacific Ocean were investigated using data obtained along a meridian line (5°–12°N, 131.5°W) in the summers of 1998, 1999, and 2003. The survey periods corresponded to a sharp transition between the 1997–1998 El Niño and 1998–1999 La Niña events, the 1999 La Niña event, and near-normal conditions after the moderate 2002–2003 El Niño in the equatorial Pacific. A strong upwelling in the divergence zone from 10.5° to 11°N caused a shoaling of the thermocline depth (∼30 m), resulting in increases in nitrate and phytoplankton chlorophyll *a* (chl-*a*) concentrations, and, in turn, mesozooplankton abundance during the La Niña in 1999. In contrast, in 1998, remnants of El Niño characteristics, deeper thermocline depth (60–150 m) and warm surface water (>28 °C), led to low concentrations of nitrate, chl-*a* and low mesozooplankton abundance, except in the convergence zone around 7°N. The thermocline depth and nitrate concentration obtained during the near-normal period in 2003 corresponded to intermediate values as compared to those obtained during El Niño and La Niña conditions.

Interannual changes in the position and strength of ecotones, such as divergence and convergence zones, affected mesozooplankton community structure and cyclopoid-to-calanoid ratios along the 131.5°W meridian line. The clustering pattern of the mesozooplankton community was mostly characterized by calanoid (mainly *Clausocalanus* sp.) and cyclopoid (mainly *Oncaea* sp.) copepods, accounting for most of the observed differences among groups during the study period. Cyclopoids and calanoids were more abundant in 1999 than in 1998 or 2003, with a sharp increase to the north, while they were less abundant to the north in 1998 and 2003. The cyclopoid-to-calanoid ratio peaked in the convergence zone in 1998 and the divergence zones in 1999 and 2003, apparently due to the strength and location of the ecotones. Principal component analysis (PCA) with environmental factors and dominant mesozooplankton groups showed that dominant groups were affected by nitrate and chl-*a* concentrations in 1998, by sigma-*t* (water density), nitrate and chl-*a* concentrations in 1999, and by sigma-*t*, salinity and chl-*a* concentration (except siphonophores) in 2003. Latitudinal distribution of thermocline depth before and after the 1998/99 La Niña event showed a distinct interannual difference. The abundance of mesozooplankton in the divergence zone in 1999 was distinctively higher than abundances found in the convergence and

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* Corresponding author. Tel.: +82 55 639 8517; fax: +82 55 639 8509.
  E-mail address: jhkang@kordi.re.kr (J.-H. Kang).

divergence zones in 1998 and 2003, which resulted from the shallow thermocline depth due to an intensified upwelling during the strong 1998–1999 La Niña event.

1. Introduction

Under normal conditions, the equatorial Pacific Ocean is characterized by an upwelling that mainly takes place between 5°N and 5°S, extending from the coast of South America to 180°W (Wyrtki, 1981). The equatorial upwelling is induced by the easterly trade winds, and upwelled water is high in macronutrients such as nitrate, phosphate, silicate, and carbon dioxide, as well as micronutrients such as iron (Coale et al., 1996). Thus, it may support a significant amount of new production each year (Chavez and Barber, 1987). Primary production and chlorophyll concentration are usually high near the equator and decrease to the north and south (Blackburn et al., 1970; Vinogradov, 1981; Barber et al., 1996). In the off-equatorial region, physical characteristics such as divergence and convergence disrupt the seasonal thermocline and allow nutrient-rich water to rise to the surface of the water column (Yang et al., 2004), resulting in latitudinal differences in chemical and biological parameters such as nutrients, chlorophyll-*a* of phytoplankton, and zooplankton (Chavez and Barber, 1987; Roman et al., 2002). Divergence and convergence zones are formed at the boundaries between the North Equatorial Current (NEC) and the North Equatorial Countercurrent (NECC), and between the NECC and the South Equatorial Current (SEC), respectively. According to mean surface circulation from surface drifters, the boundary between the SEC (NECC) and NECC (NEC) occurs approximately at 5°N (9°N) at 120°W (Kessler, 2006). Meridional section of ship-collected chlorophyll in the central Pacific, 130°–140°W shows that surface chlorophyll is the highest around equator and a subsurface chlorophyll maximum (SCM) layer with chlorophyll concentration higher than 0.2 mg m^{-3} occurs at 60–90 m depth south of 14°N (Pennington et al., 2006).

Mesozooplankton (>200 µm) is often more abundant further north and south of the equator (Vinogradov, 1981; White et al., 1995; Le Borgne et al., 2003; Gaudy et al., 2004) due to slower growth rates. The temporal evolution of plankton communities toward the north influences the latitudinal spatial patterns of mesozooplankton (Roman et al., 2002). According to results from both the US JGOFS (Joint Global Ocean Flux Study) EqPac (Equatorial Pacific) study along 140°W and the French EBENE (Etude du Broutage en Zone Equatoriale) cruise along 180°W transects, the maximum biomass of mesozooplankton (>200 µm) occurs north and south of the equator, between 1° and 5°N and between 6°S and the equator, respectively (White et al., 1995; Le Borgne et al., 2003; Gaudy et al., 2004). Moreover, mesozooplankton biomass is higher between the equator and 5°N than its biomass farther north of 5°N.

The primary source of interannual variability of physical and biogeochemical processes in the tropical Pacific Ocean is the El Niño Southern Oscillation (ENSO; Strutton and Chavez, 2000). Under normal circumstances the thermocline is deep (shallow) in the western (eastern) equatorial Pacific. During El Niño events, the thermocline shoals (deepens) in the western (central and eastern) equatorial Pacific, and the equatorial upwelling weakens with no distinct cold tongue. The flattening of the zonal thermocline gradient results from the eastward propagation of equatorially trapped Kelvin waves, followed by advection of western equatorial warm pool waters (>28 °C) into the central Pacific that are very low in nutrients (Mackey et al., 1995), especially NO$_3$. Their advection over the central region of the Pacific, combined with the cessation of upwelling, leads to nitrate deficiency, low chlorophyll concentration, and dramatically decreased phytoplankton productivity in the equatorial Pacific (Strutton and Chavez, 2000). During El Niño events, oligotrophic conditions arise from the suppression of upwelling due to the depressed thermocline, and the chlorophyll concentration becomes low (~0.05 µg L^{-1}; Chavez et al., 1999). The enhancement and expansion of the equatorial cold tongue beyond 180°W and shoaling of the thermocline characterize the central equatorial Pacific Ocean during La Niña events, resulting in enhanced primary productivity in surface waters and its westward expansion (Chavez et al., 1999).

Most zooplankton studies in relation to climate variability have focused on equatorial upwelling and the California Current regions in association with El Niño and La Niña in the Pacific Ocean (Roman et al., 1995, 2002; Roman and Gauzens, 1997; Hopcroft et al., 2002; Lavaniegos et al., 2002). However, little is known about the response of mesozooplankton to climate variability in the off-equatorial northeastern Pacific Ocean. We examined interannual variability in the latitudinal distribution of mesozooplankton based on data obtained along a meridian transect in the northeastern equatorial Pacific in July 1998, June 1999, and July 2003.

In the tropical Pacific, 1998 was marked by a dramatic transition from one of the strongest El Niño events in the 20th century to a strong La Niña event (Schwing et al., 2002). The multivariate ENSO index (MEI), which assesses the relative magnitude of El Niño and La Niña events based on six tropical Pacific variables (Wolter and Timlin, 1998), shows this transition (Fig. 1). The MEI dropped from an El Niño peak in spring 1998 to a minimum in late fall 1998. In early 1998, the 1997–1998 El Niño reached a secondary peak in intensity (the first having been in summer 1997). Beginning in March 1998, however, El Niño conditions in the equatorial Pacific weakened considerably. The Nino3.4 (one of El Niño indices based on the departure of spatially averaged sea surface temperature anomaly from the long-term average in a region, 5°S–5°N and 170°W–120°W) sea surface temperature (SST) anomaly sharply dropped between November 1997 and July 1998, and negative Nino3.4 SST anomalies developed in the central and eastern equatorial Pacific during May 1998 (Fig. 1). The onset and rapid decay of the 1997–1998 El Niño event (McPhaden, 1999) and biological−physical coupling in the equatorial Pacific during the event (Chavez et al., 1998) have been described. Strong La Niña conditions prevailed in fall 1998, with uplifted isopycnals suggestive of resumed equatorial upwelling, and the NECC, SEC, and equatorial undercurrent (EUC) were stronger than those in the 1997–1998 El Niño event (Johnson et al., 2000). The mature El Niño in late 1997 to early 1998 was characterized by the absence of nitrate throughout the entire euphotic zone down to 100 m, resulting in the lowest chlorophyll concentrations (0.05 μg L^{-1}) ever observed in the central equatorial Pacific (Strutton and Chavez, 2000). Rates of primary production ($\sim$0.41 g C m^{-2} d^{-1}) also dramatically decreased, to approximately half of the climatological mean (Strutton and Chavez, 2000). These conditions persisted until May 1998, and nitrate, chlorophyll, and primary productivity levels were comparable to, or in excess of, their respective climatological means by June 1998. The spatial extent of the phytoplankton bloom that followed recovery from the 1997–1998 El Niño was the largest ever observed in the equatorial Pacific (Chavez et al., 1999).

The MEI remained negative from July 1998 through 2001, representing weak to moderate La Niña conditions in the tropics. The MEI became positive in spring 2002 and peaked in December 2002−January 2003. This moderately strong event was the first El Niño since the large 1997–1998 El Niño. However, it did not evolve, or dissipate, like the canonical El Niño. A strong thermal anomaly did not fully develop on the South American coast, and the rapid decline in early 2003 contrasts with most strong El Niños, which often
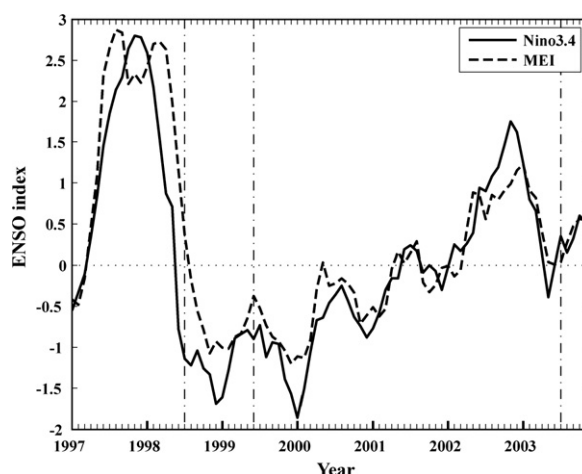

Fig. 1. Multivariate ENSO index (MEI) and Nino3.4 SST anomalies from 1997 to 2003. Three survey periods are shown with dash-dot lines.

strengthen from winter to spring. The breakdown of the weak to moderate 2002–2003 El Niño was fairly rapid, and the eastern equatorial Pacific began to cool in early spring. Since the 2002–2003 tropical El Niño, the Niño3.4 SST anomaly has been near average; the MEI remained slightly positive for the remainder of 2003.

Our surveys, conducted in the off-equatorial northeastern Pacific Ocean in July 1998, June 1999, and July 2003, corresponded to the sharp transition period between 1997–1998 El Niño and 1998–1999 La Niña events, the 1999 La Niña event, and near-normal conditions after the moderate 2002–2003 El Niño in the equatorial Pacific, respectively.

2. Materials and methods

2.1. Sampling and analysis

2.1.1. Hydrological conditions and nitrate and chlorophyll-a concentrations

Three cruises aboard the RV "ONNURI" were undertaken between 5° and 12°N, along 131.5°W, in the northeastern Pacific on 3–20 July 1998, 22 June–1 July 1999, and 10–25 July 2003 (Fig. 2). Temperature and salinity profiles were acquired with a SBE 911plus conductivity-temperature-depth (CTD) meter, binned into 1-m depths, during the three surveys. Discrete water samples were collected from nine depths (0, 10, 30, 50, 75, 100, 120, 150, and 200 m) using 10-L PVC Niskin bottles that had been previously soaked in 10% HCl, mounted on an instrumented Rosette sampler with a Seabird CTD.

For nutrient analysis, water samples taken from nine depths were filtered through 47-mm Whatman GF/F filter and then frozen in 20-mL polycarbonate scintillation vials. The filtrates were analyzed using an autoanalyzer (Alliance, EVOLUTION II) in the laboratory according to Parsons et al. (1984). Water samples (2 L) for chlorophyll-a (chl-a) determination were pre-filtered through a 300-μm mesh and then filtered through 47-mm Whatman GF/F filters under low vacuum pressure (<125 mmHg). The filters, which were kept frozen in liquid nitrogen, were extracted in 90% acetone overnight at 4 °C. Chl-a concentration was determined using a Turner Design 10-AU that was calibrated with commercial chl-a standards (Sigma), based on Parsons et al. (1984).

2.1.2. Mesozooplankton

Mesozooplankton samples were collected by vertical tows using an opening–closing net (100 cm diameter, 300-μm mesh) over the surface mixed layer at one-degree intervals. The net was lowered to the thermocline
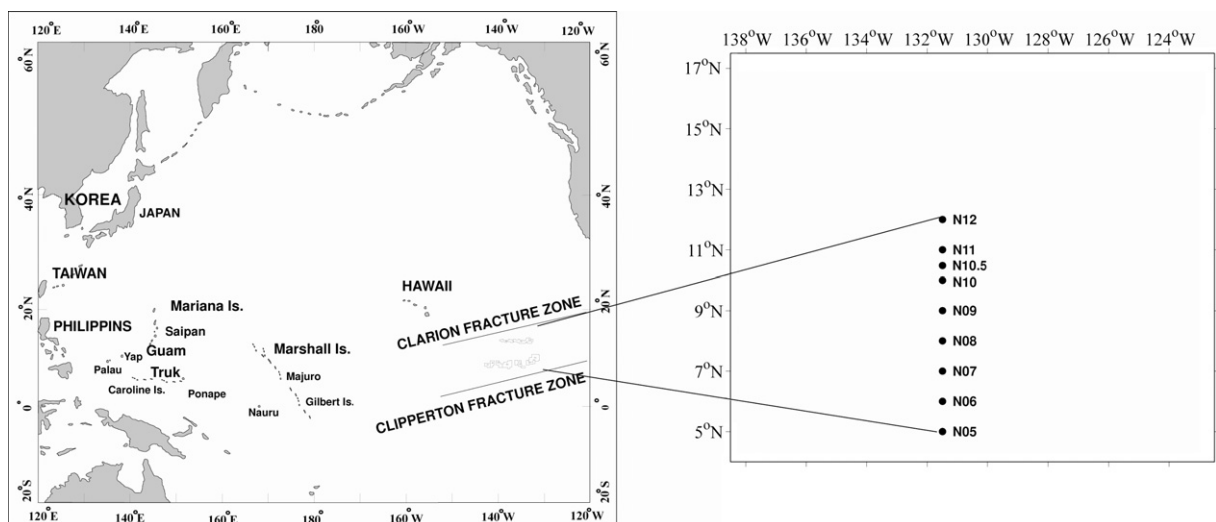

Fig. 2. Map showing the survey stations during the 1998, 1999, and 2003 cruises along the meridian line of 131.5°W in the northeastern equatorial Pacific Ocean.

depth and towed upward at a speed of 30–50 m min^{-1}. Considering the diurnal vertical migration of zoo-plankton, all samples were taken during the local night, from 22:00 to 02:00. Mesozooplankton samples in the cod-end bucket were transferred to 1-L sampling bottles and immediately fixed to a final concentration of 5% with borax-neutralized formalin. Mesozooplankton were sorted into taxonomic groups and enumerated under a stereomicroscope (ZEISS model Stemi–2000 C). Copepods were identified to genus according to Chihara and Murano (1997). The volume filtered by the net was calculated based on the readings of a flowmeter (Hydro-Bios Model 438-115) fixed at the mouth of the net frame. Zooplankton abundance at all stations was expressed as individuals per 100 m^3.

The cyclopoid-to-calanoid ratio can be an indicator of spatial heterogeneity due to upwelling, convergence, or divergence zones where water masses with different properties meet. Cyclopoids dominate in nutrient-rich water intrusions, such as upwelling areas, because cyclopoids can reproduce more quickly than calanoids under specific environmental conditions such as high food concentration (Cowles et al., 1987; Paffenhöfer, 1993). The higher cyclopoid-to-calanoid ratio indicated the existence of newly formed high productive areas such as divergence in the northeastern Pacific (Kang et al., 2004b).

2.1.3. Data analysis

Cluster analysis was carried out on the basis of dissimilarity calculated from a Bray–Curtis similarity matrix. As a result of cluster analysis, representative species, accounting for the observed assemblage differences, were identified for different groups through the SIMPER program. The effects of physico-chemical and biological properties on spatial heterogeneity of mesozooplankton were analyzed by principal component analysis (PCA) based on correlation coefficients among parameters obtained from the sampling data. The parameters chosen for the PCA were average temperature, salinity, sigma-t (water density) and nitrate concentration, and depth integrated chl-a concentration within the surface mixed layer in 1998, 1999 and 2003. Multivariate statistical analyses were conducted using SPSS 10.0 and SIMPER (PRIMER 5.2.8) statistical software packages.

3. Results

3.1. Hydrography and chlorophyll distribution

The survey in July 1998 was conducted after the abrupt end of the strong 1997–1998 El Niño in the equatorial Pacific. Warm surface water (>28.0 °C) was found in the middle of the section (Fig. 3a). The thermocline depth defined by the 20 °C isotherm (Johnson et al., 2000) occurred at a deeper range between 86 and 132 m as compared to those in 1999 and 2003 (Fig. 4). Surface water with salinity lower than 34.0 occupied a broad area between 7° and 11°N with its lowest value (33.0) at 9°N (Fig. 3b). The low-salinity surface water was found in all surveys (Fig. 3b, h and n). A strong westward flow associated with the SEC appeared south of 6°N, and the weakened NEC was disrupted by a relatively strong eastward flow between 10° and 11°N (Fig. 3d). The nitracline depth occurred at around 100 m north of 8°N, and oligotrophic surface waters with a nitrate concentration less than 1 μM occupied the surface mixed layer (Fig. 3e). The nitracline spread and deepened to the south, between 6° and 8°N, and elevated nitrate concentrations (>1 μM) occurred in the upper 75 m above the salty southern subtropical water. The integrated chl-a concentration within the surface mixed layer (50 m) was 3.6–16.0 mg m^{-2} in 1998, the lowest value among the three surveys. The chl-a concentration in the surface layer was high south of 8°N, where nitrate concentration was elevated, and it decreased gradually as the depth of subsurface chlorophyll maximum (SCM) deepened to the north (Fig. 3f).

Vertical profiles taken in June 1999 were markedly different from those in July 1998 and reflect the 1998–1999 La Niña event. Surface temperature during the La Niña event in June 1999 was lower than 28 °C (Fig. 3g). The temperature section in June 1999 was characterized by a sharp shoaling of the 20 °C isotherm to the north, from 117 m at 5°N to 17 m at 10.5°N. The shallow low-salinity core was located in the northern part of the NECC, and upwelled southern subtropical water occupied the upper 100 m south of 7°N (Fig. 3h). Compared to the other periods, the surface low-salinity water (<34.0) was reduced. The eastward flowing NECC occupied a broad area between 5°N and 10°N, and its strength was the highest among three surveys with a peak speed greater than 50 cm s^{-1} (Fig. 3j). The NEC was weaker and reduced as compared to that in
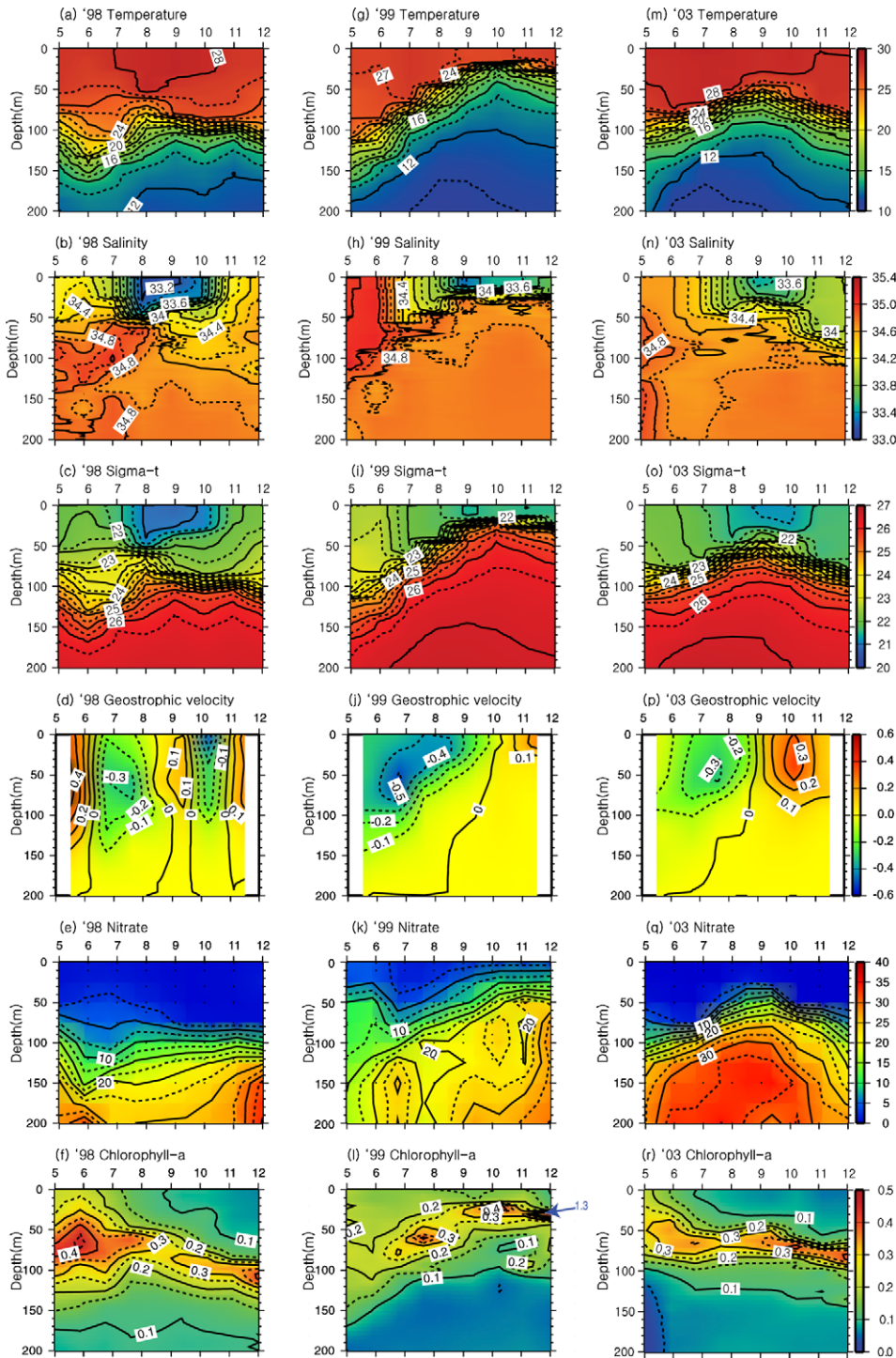
Fig. 3. Vertical profiles of: (a) temperature (°C), (b) salinity, (c) sigma-*t*, (d) geostrophic current (m s^{-1}), and (e) nitrate (μM) and (f) chlorophyll concentrations (μg l^{-1}) along the 131.5°W line from 5° to 12°N in 1998, 1999 (from g to l), and 2003 (from m to r). Contour intervals (solid lines) are 2 °C for temperature, 0.2 for salinity, 0.5 for sigma-*t*, 0.1 for geostrophic current, 5 for nitrate concentration, and 0.1 for chlorophyll concentration. Geostrophic currents are calculated relative to 200 dbar, and positive (negative) values denote westward (eastward) flows.
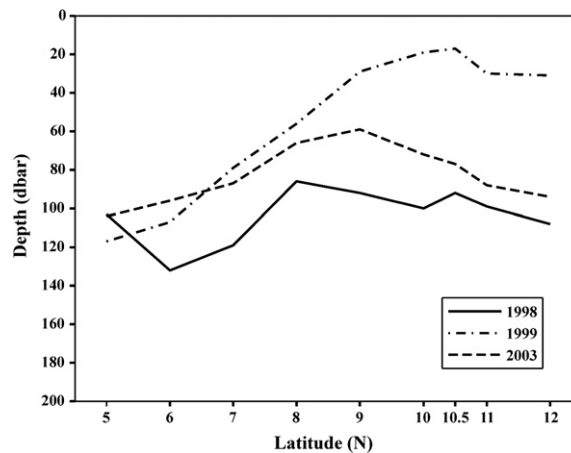
Fig. 4. Latitudinal variation in the 20 °C isothermal depth in the northeastern equatorial Pacific Ocean in 1998, 1999, and 2003.

the normal situation in 2003. The uplifted nitracline north of 7°N was concomitant with shoaling of the pycno-cline induced by upwelling during the La Niña event, resulting in high nitrate concentration in surface waters above 40 m north of 9° N (Fig. 3k). The integrated chl-*a* concentration within the surface mixed layer (50 m) was 7.1–34.6 mg m^{-2}, the highest value among three surveys. The SCM depth shoaled to the north, concurrent with an enhanced upwelling of subsurface water, and significantly high concentrations of chl-*a* (34.6 mg m^{-2}) in the upper 50 m were observed north of 8° N (Fig. 3l).

In July 2003, warm surface water (> 28.0 °C) occupied the entire surface layer, with its thickness shoaling to the north, when the Nino3.4 SST anomaly showed a slightly positive value after the moderate 2002–2003 El Niño (Fig. 3m). The meridional temperature structure indicates a shoaling of the pycnocline to the north between 5° and 9° N and deepening north of 9°N. Depth of the 20 °C isotherm ranged from 59 to 104 m, shal-lowest at 9°N and deepest at 5°N (Fig. 4). Low-salinity surface water appeared north of 8° N, and the lowest salinity (< 33.5) occurred at the boundary between the NECC and the NEC (Fig. 3n). The eastward NECC south of 9°N and the westward NEC north of 9°N had nearly the same strength, with maximum speeds of about 35 cm s^{-1} (Fig. 3p). The velocity core of the NECC occurs at 50 m depth, while the NEC is surface-intensified. High nitrate concentrations were observed from 8° to 10°N in the upper 50 m, whereas other sta-tions were characterized by oligotrophic waters (<0.01 μM) in the surface mixed layer above 50 m (Fig. 3q). The integrated chl-*a* concentration within the surface mixed layer (70 m) was 10.4–24.3 mg m^{-2}. The SCM depth deepened from south to north with two chl-*a* peaks at 6° and 9°N (Fig. 3r). The chl-*a* distribution in 2003 was similar to that in 1998, but the peak chl-*a* value (17.5 mg m^{-2}) at 9°N was different from that in 1999. The SCM depth was closer to the surface resulting in higher concentrations (>10.4 mg m^{-2}) in the sur-face mixed layer at all stations in 2003 as compared to those in 1998.

3.2. Mesozooplankton

3.2.1. Abundance and taxonomic groups of mesozooplankton

Total mesozooplankton abundance ranged from 13,146 to 110,492 individuals 100 m^{-3} in 1998, from 54,571 to 178,637 individuals 100 m^{-3} in 1999, and from 9481 to 62,487 individuals 100 m^{-3} in 2003 (Fig. 5). Mesozooplankton were abundant between 5° and 7°N in 1998, with abundance ranging from 44,229 to 110,492 individuals 100 m^{-3}. The highest abundance was observed at 7°N, slightly north of the con-vergence zone between SEC and NECC (Fig. 5). Relatively low abundance occurred between 8° and 12°N in the disrupted NEC zone (Fig. 5). In 1999, high mesozooplankton abundances (160,274−178,637 individuals 100 m^{-3}) were found between 10.5° and 11°N in the divergence zone formed between the NECC and the NEC, and eutrophic conditions occurred with a shallow nitracline. Relatively low abundance was observed between 5° and 10°N, ranging from 54,571 to 118,445 individuals 100 m^{-3}, with deep thermocline and SCM depths. In 2003, high mesozooplankton abundances, ranging from 47,573 to 62,487 individuals
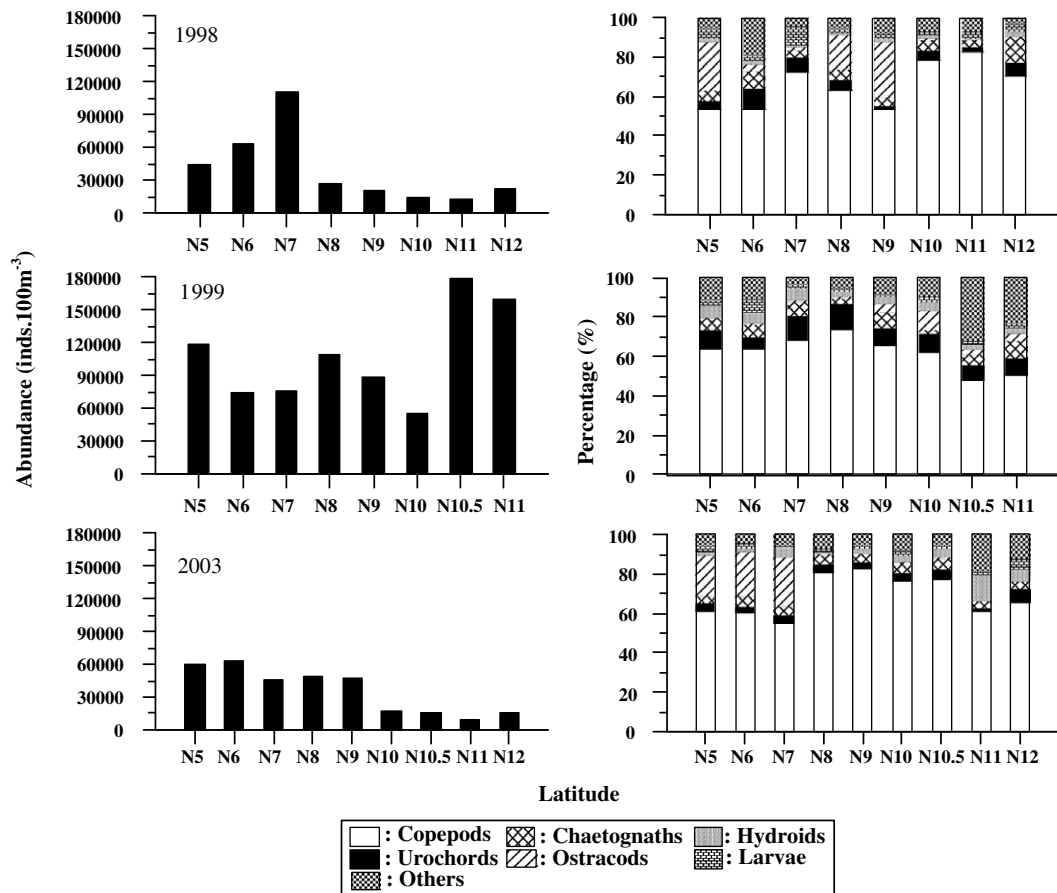
Fig. 5. Latitudinal gradients in total abundance and taxa comprising the mesozooplankton community along the meridian line of 131.5°W.

100 m^{-3}, were found south of 9°N in the NECC region, whereas low abundances (ranging from 9481 to 17,518 individuals 100 m^{-3}) was found north of 9°N in the NEC region (Fig. 5).

Most of the mesozooplankton community was composed of copepods in the surface mixed layer during the study period (Fig. 5). Copepods accounted for 53.6–82.6% (average = 65.9%) of the total zooplankton community in 1998, 47.9–73.1% (61.8%) in 1999, and 55.5–82.2% (69.0%) in 2003 (Fig. 5). The next largest group was ostracods, followed by urochordates (appendicularians and salps) and chaetognaths. Ostracods constituted 0–28.0% (average = 9.5%) of the mesozooplankton community in 1998, 0.3–9.2% (2.7%) in 1999, and 0–24.9% (7.4%) in 2003 (Fig. 5). The percent contribution of ostracods to the mesozooplankton community was greater at lower latitudes (5°–9°N) in 1998 and 2003, while a higher percentage of ostracods occurred at higher latitudes (10°–11°N) in 1999 (Fig. 5).

Urochordates and chaetognaths, although less abundant than copepods, showed a stable contribution to the mesozooplankton community. Urochordates accounted for 1.7–10.0% (average = 5.4%) of the mesozooplankton community in 1998, 6.3–11.6% (9.4%) in 1999, and 2.5–7.3% (4.4%) in 2003 (Fig. 5). Chaetognaths constituted 3.7–13.1% (average = 6.4%) of the mesozooplankton community in 1998, 2.3–8.6% (6.0%) in 1999, and 3.4–5.4% (4.5%) in 2003 (Fig. 5). The gelatinous plankton contributed more to the mesozooplankton community at all stations in 1999 than in 1998 and 2003.

3.2.2. Temporal and latitudinal variations of major taxonomic groups

Interannual variation in abundance within the study area was substantial for copepods, appendicularians, salps, siphonophores, chaetognaths, and radiolarians, as can be seen from the distinctive peaks of those

groups in 1998, 1999, and 2003 (Table 1). The latitudinal distribution of the groups also varied during the study periods. Abundances of copepods, radiolarians, chaetognaths, appendicularians, and salps decreased from south to north in 1998 and 2003, while in 1999 their abundance increased to the north and peaked at 10.5° and 11°N (Fig. 6). Larvae and other groups also had opposite latitudinal distributions in 1998/2003 and 1999, even though they had no significant interannual variation in average abundance. Immature copepods peaked at 7°N in 1998, corresponding to the convergence zone, and at 10.5°N in 1999 and 9°N in 2003, in the divergence zones. The abundance of siphonophores in 1999 was higher than that in 1998 and 2003, however, its decreasing pattern to the north was identical in 1998, 1999 and 2003 (Fig. 6).

3.2.3. Cluster analysis

Three different groups were identified based on a Bray–Curtis similarity index of 65% (Fig. 7). The groups were coincident with each survey period: 1998 (Group A), 1999 (Group B), and 2003 (Group C). Within each group, the stations were sub-divided into two or three clusters in latitudinal order based on an index of 75%. The sub-divided clusters were in accordance with the convergence and divergence zones, which correspond to the boundaries between the SEC and NECC and between NECC and NEC, respectively. The stations in Group A and C were sub-divided into three clusters, whereas those in Group B were sub-divided into two clusters.

Group A consisted of two classes, stations south of the convergence zone (A-1) and those north of convergence zone (A-2 and A-3). The A-2 stations were located on the boundary between NEC and NECC with current speed less than 30 cm s^{-1} (Fig. 7).

Group B consisted of two clusters, B-1 and B-2. Cluster B-1 corresponded to the southernmost stations, between 5° and 7°N, located in the strong NEC region. Cluster B-2 occurred in the upwelling zone (Fig. 7).

Group C was sub-divided into two classes, stations south of the divergence zone (C-1) corresponding to NECC, and stations north of the divergence zone (C-2 and C-3). The C-2 class was located in the NEC region with current speed of 30 cm s^{-1}, and the C-3 class was in the NEC region with weak current speed (5 cm s^{-1}; Fig. 7).

Analysis of similarity (SIMPER) was carried out to determine the species responsible for similarities within and dissimilarities between groups. The abundances of the 19 taxa that contributed $\geqslant 3\%$ to within-group similarity or between-group dissimilarity for at least one of the groups are shown in Table 2. Average within-group similarity ranged from 51% to 67%. All taxa listed in Table 2 collectively account for between 72% and 85% of within-group similarity. The between-group dissimilarity ranges from 40% to 66%. There was a similar taxonomic composition for all groups in 1998, 1999, and 2003. Copepods such as *Oncaea* sp. and *Clausocalanus* sp. were abundant and widely distributed; hence, they affected all three groups (A–C; Table 2).

3.2.4. Relationship between mesozooplankton groups and environmental factors

In 1998, the first principal component (Z_1), which explained 38.0% of the total variation in mesozooplankton abundance, had high positive factor loadings for nitrate (0.54) and chl-*a* (0.28), and low positive factor

Table 1
Interannual differences in average abundances (individuals per 100 m^3) of the mesozooplankton taxa

| Taxon	1998	1999	2003	*F*	*p*
Calanoid copepods	13,915	37,002	14,350	14.75	<0.01
Cyclopoid copepods	9534	22,717	6926	6.78	<0.01
Immature copepods	2005	4270	3327	2.29	>0.05
Ostracods	3194	2524	4096	0.26	>0.05
Chaetognaths	2433	6692	1599	9.48	<0.01
Siphonophores	376	4265	988	39.3	<0.01
Appendicularians	2288	8594	989	19.16	<0.01
Salps	326	1342	556	6.01	<0.01
Radiolarians	2071	16,346	1272	4.59	0.05
Larvae	2263	2669	904	1.47	>0.05
Others	1139	1047	1017	0.08	>0.05
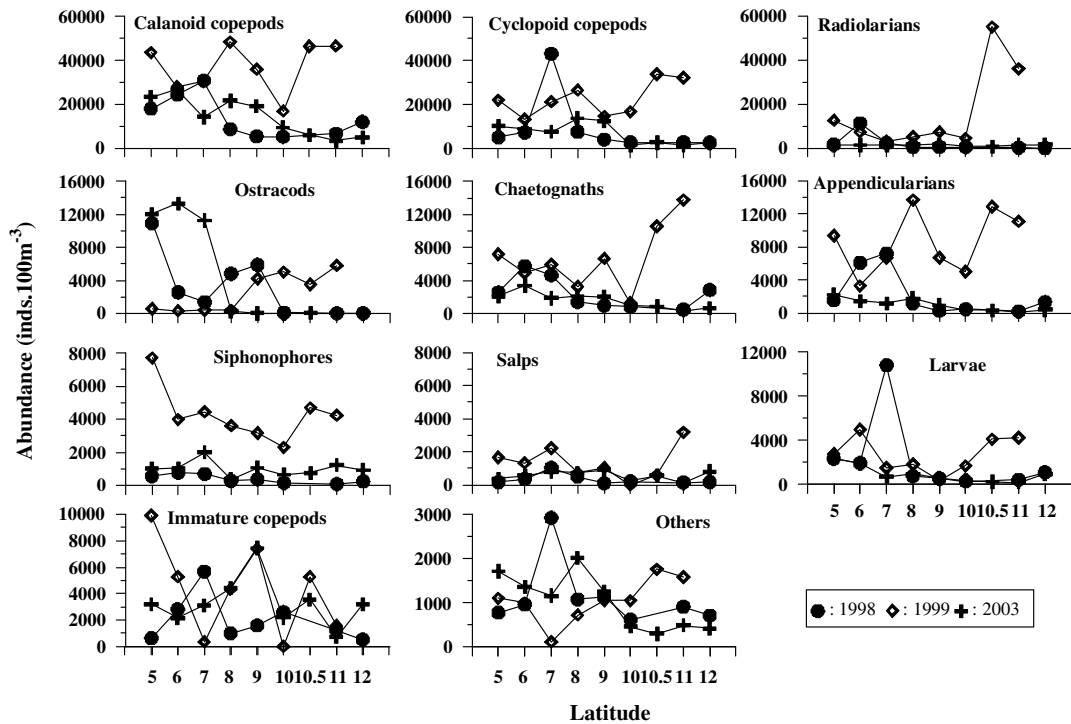
Fig. 6. Interannual differences in the latitudinal distribution of major mesozooplankton groups in the surface mixed layer.
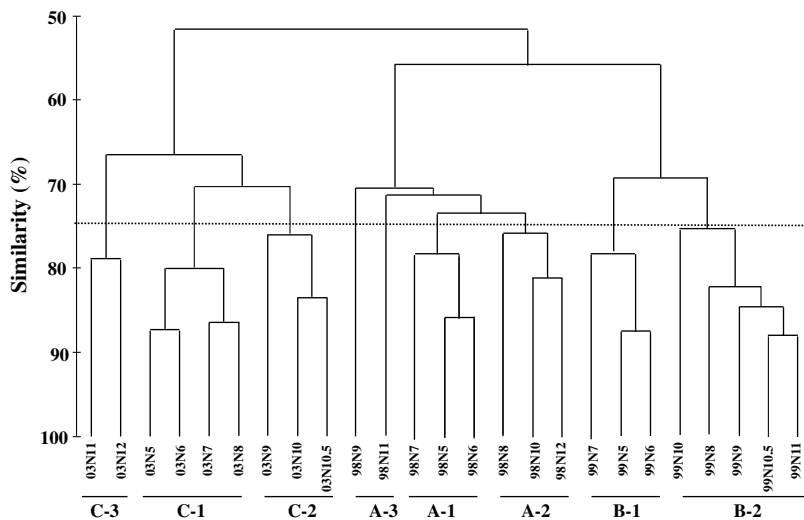

Fig. 7. Dendrogram showing clustered groups based on the Bray–Curtis index of mesozooplankton abundance.

loadings for temperature, salinity, and sigma-t (less than 0.03). Eigenvalues for most mesozooplankton groups exceeded 0.5. The second principal component (Z_2), which explained 30.4% of the total variation, showed high positive factor loadings for nitrate (0.76) and chl-a (0.87), low positive factor loadings for salinity and sigma-t, and a negative factor loading for temperature. In mesozooplankton groups, the positive factor loading was high for all groups except cyclopoids, with a low positive factor loading (0.17). A scatter diagram of Z_1 and Z_2 factor loading distributions indicates most mesozooplankton groups were associated with nitrate and chl-a (Fig. 8).

Table 2
Species in the surface mixed layer during the study period, listed in decreasing order of importance for discriminating among groups on the basis of similarity percentage

| Rank	A group (1998)		B group (1999)		C group (2003)	
	Taxon	Abund. (%)	Taxon	Abund. (%)	Taxon	Abund. (%)
1	*Clausocalanus* sp.	6507 (20.5)	*Oncaea* sp.	12,424 (12.8)	*Clausocalanus* sp.	2896 (9.7)
2	*Oncaea* sp.	4270 (10.9)	*Clausocalanus* sp.	8693 (10.8)	*Oncaea* sp.	3355 (9.2)
3	Chaetognaths	2433 (7.4)	Appendicularians	8593 (9.8)	*Paracalanus* sp.	2498 (8.5)
4	*Calanus* sp.	1865 (6.7)	Radiolarians	16,346 (9.8)	*Oithona* sp.	2416 (7.4)
5	*Euchaeta* sp.	1198 (5.9)	*Oithona* sp.	6088 (7.9)	*Euchaeta* copepodite	1624 (6.9)
6	*Oithona* sp.	1108 (5.9)	Chaetognaths	6692 (6.6)	Radiolarians	1232 (6.4)
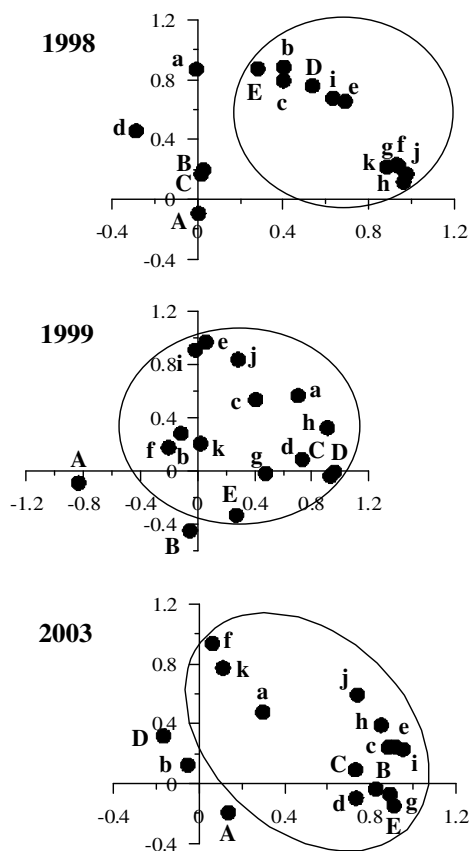
Fig. 8. Factor loading results for the first and second principal components in the surface mixed layer in the eastern equatorial Pacific Ocean (A, temperature; B, salinity; C, sigma-t; D, nitrate; E, chl-a; a, Radiolarians; b, Siphonophores; c, Chaetognaths; d, Ostracods; e, Appendicularians; f, Salps; g, larvae; h, others; i, Calanoids; j, Cyclopoids; k, immature copepods).

In 1999, the first principal component (Z_1), which explained 30.9% of the total mesozooplankton variation, showed high positive factor loadings for sigma-t (0.93), nitrate (0.96), and chl-a (0.27), and negative factor loadings for temperature and salinity. Most dominant groups of mesozooplankton had low positive or negative factor loadings, whereas less abundant groups such as siphonophores and salps had negative factor loadings. The second principal component (Z_2), which explained 22.9% of the total variation, had negative factor loadings for temperature, salinity, sigma-t, nitrate, and chl-a. The factor loading was positive for most mesozooplankton groups except larvae. A scatter diagram of Z_1 and Z_2 factor loading distributions indicates that all groups were associated with sigma-t, nitrate, and chl-a (Fig. 8).
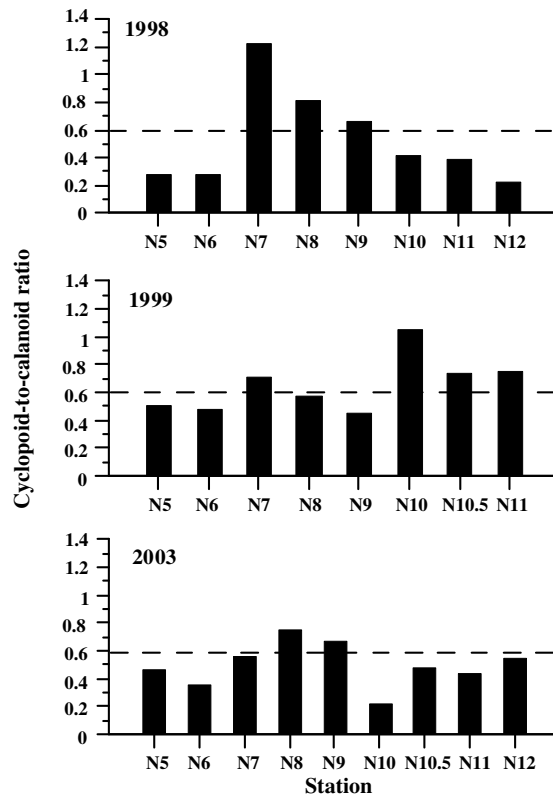
Fig. 9. Average ratio of cyclopoid-to-calanoid in the surface mixed layer along the meridian line of 131.5°W in the northeastern equatorial Pacific Ocean.

In 2003, the first principal component (Z_1), which explained 45.9% of the total mesozooplankton variation, showed high positive factor loadings for chl-a (0.91), salinity (0.83), and sigma-t (0.73). Temperature had a low positive factor and nitrate had a negative factor. Eigenvalues of most mesozooplankton groups were larger than 0.5 except for siphonophores, salps, and immature copepods. The second principal component (Z_2) accounted for 16.2% of the total variation and showed low positive factor loadings for sigma-t and nitrate, and negative factor loadings for temperature, salinity, and chl-a. The mesozooplankton groups showed high positive factor loadings for salps (0.94), immature copepods (0.77), and cyclopoids (0.59), while the positive factor loading was very low for other groups. Ostracods and larvae had negative factor loadings. Most groups were associated with sigma-t, salinity, and chl-a, except siphonophores, according to a scatter diagram of Z_1 and Z_2 factor loading distributions (Fig. 8).

3.2.5. Cyclopoid-to-calanoid ratio

The average ratio of cyclopoid-to-calanoid in the surface mixed layer was higher in 1999 than in 1998 or 2003 (Fig. 9). The average ratios were 0.54, 0.66, and 0.49 in 1998, 1999, and 2003, respectively. The ratio peaked at 7°N, corresponding to the convergence zone, in 1998. The peak ratios, however, were found around 10.5°N in 1999 and around 9°N in 2003, corresponding to the divergence zone between the NECC and NEC, and were associated with different upwelling intensity. The average ratio was highest, exceeding 1, at 7°N in 1998 and 10°N in 1999, while the highest value occurred at 8°N in 2003 and was less than 1 (Fig. 9).

4. Discussion

In a marine environment, an ecological boundary, or ecotone, generally stems from new or consistent encounters between water masses with opposite characteristics (Cowles et al., 1987; Pakhomov and

Perissinotto, 1997; Roman et al., 2002; Kang et al., 2004a). Here, different locations and magnitudes of ecotones observed within the study area coincided with latitudinal heterogeneity in physico-chemical properties, chl-*a* concentration, and mesozooplankton abundance during the study periods.

In general, latitudinal gradients in phytoplankton biomass and functional responses of mesozooplankton are greatly influenced by upwelled nutrients from subsurface waters in the equatorial upwelling area (White et al., 1995; Roman et al., 2002). High concentration of phytoplankton was observed near the equator, and high zooplankton biomass was found further north due to the uncoupling of zooplankton and phytoplankton growth (Blackburn et al., 1970; Vinogradov, 1981; White et al., 1995; Roman et al., 2002).

In the off-equatorial northeastern Pacific, surface chl-*a* concentration was high between 5°–7°N and low north of 8°N in 1998, when the thermocline was relatively deep. Nitrate concentration above the thermocline depth showed a similar pattern, ranging between 1.1 and 1.8 μM from 5° to 7°N and between 0.4 and 0.9 μM from 8° to 12°N. Mesozooplankton abundance was also relatively higher between 5° and 7°N than the abundance between 8° and 12°N in 1998. This pattern coincided with the latitudinal distribution of zooplankton biomass between 12°N and 12°S along 140°W during the EqPac survey and from 7°N to 8°S along 180°W during the EBENE survey (Roman et al., 2002; Gaudy et al., 2004). The abundance of herbivorous zooplankton and larvae peaked at 7°N, near the convergence zone formed between the SEC and NECC (Fig. 6). The peaks, however, were not observed at the same latitude along 140°W or 180°W when El Niño conditions prevailed (Roman et al., 2002; Le Borgne et al., 2003). Most stations in 1998 were characterized by low abundance of mesozooplankton and deep thermocline as compared to those in 1999 and 2003, except for the high abundance of mesozooplankton at the convergence zone. The survey period (July 1998) corresponded to a sharp transition between the 1997–1998 El Niño and 1998–1999 La Niña (Schwing et al., 2002), but El Niño conditions seemed to still influence the study area in July 1998 considering high surface temperature (>28 °C) and the deep thermocline. During this period, remnants of the El Niño warm water pool lingered to the north and south of the equator (Bell et al., 1999).

During a mature La Niña condition in summer 1999, the depth of the 20 °C isotherm, representing the thermocline depth, sharply shoaled to the north, and was shallower than 20 m between 9° and 10.5°N in association with strong upwelling. The depth of the nitracline and SCM were also drastically raised between these latitudes, resulting in higher chl-*a* concentrations at higher latitudes than those at lower latitudes. The peak chl-*a* concentration occurred north of 9°N, in association with the strong upwelling at the boundary between the strong eastward NECC and relatively weak NEC (Fig. 3). The NECC strengthened and shifted farther to the north during this period. Due to the supply of nutrients into surface waters, the increased phytoplankton biomass led to an increase in the abundance of herbivorous and carnivorous zooplankton (Vinogradov, 1981; White et al., 1995; Roman et al., 2002). The upwelling-related increase in chl-*a* concentration in surface waters affected the latitudinal distribution of mesozooplankton over the entire study area, with the peak abundance north of 10°N.

When near-normal conditions prevailed in the study area during summer 2003, after the moderate 2002–2003 El Niño, a relatively weaker divergence zone was found between NECC and NEC around 9°N, as compared to that in summer 1999. The northward extension of upwelled nutrients from the equator and their effects on the increase of phytoplankton to mesozooplankton was likely limited to latitudes south of 9°N. However, relatively low chl-*a* concentrations and mesozooplankton abundance were observed north of 9°N in summer 2003.

Seasonal and interannual variations in equatorial upwelling affect the position and strength of currents in the equatorial waters (Blackburn et al., 1970; Dessier and Donguy, 1985; Bidigare and Ondrusek, 1996; Whitney et al., 1998). In the off-equatorial Pacific area, ecotone composition and the strength of upwelling in relation to the El Niño, La Niña, and near-normal conditions appear to have influence on the latitudinal distribution of chl-*a* concentration and mesozooplankton abundance in summers 1998, 1999 and 2003. Hydrographic and biogeochemical properties were investigated at the Korea Deep-Sea Environmental Study Long-term Monitoring Station (KOMO; 10.5°N, 131.5°W) once a year during 1995–2002 (Son et al., 2004). The results show that the mesozooplankton in the study area is likely to respond to long-term changes in off-equatorial oceanic currents. A deep thermocline (100–120 m) with a thick surface mixed layer (∼100 m) and a low integrated nitrate concentration (2.0 gN m^{-2}) were recorded during El Niño periods, whereas a shallow thermocline (20–45 m) and thin surface mixed layer (∼20 m) with a high integrated nitrate concentration (23.1 gN

m^{-2}) were recorded in July 1999 (Son et al., 2004). The thermocline depth and nitrate concentration obtained during the near-normal period in 2003 correspond to intermediate values as compared to those obtained during El Niño and La Niña conditions.

Representative peaks of chl-*a* concentration and mesozooplankton abundance in surface waters coincided with different ecotone strengths related to the convergence and divergence zones along the meridian line. Factor analysis showed that nitrate and chl-*a* concentrations influence most mesozooplankton groups (Fig. 8). In oligotrophic waters, temporal evolution might be influenced by the size ratio between planktonic predators and their prey (Hansen et al., 1994). The equatorial Pacific zooplankton are primarily omnivores (Zhang et al., 1995; Roman and Gauzens, 1997); thus, correlation of most mesozooplankton groups with chl-*a* concentration is likely the result of an overall increase of other trophic groups consumed by zooplankton, coincident with increases in chl-*a* concentration (Roman et al., 2002).

High abundance of mesozooplankton observed around the convergence and divergence zones could also result from new production, promoting an increase of larger phytoplankton (i.e., diatoms) that can be directly grazed by copepods (Roman and Gauzens, 1997). Diatoms such as *Pseudonitzschia* sp. and *Lioloma* sp. were most abundant around 10°N in the divergence zone in 1999 (MOMAF, 2003). A high production ratio (zooplankton production/primary production) occurred near the convergence zones at 5°N and 7°N along 140°W, concurrent with high stocks of zooplankton (Roman et al., 2002). The positions and strength of convergence (1998) and divergence (1999 and 2003) zones are likely associated with high concentrations of chl-*a* and abundance of most mesozooplankton groups, resulting in an interannual variation in their latitudinal distribution in surface waters. Siphonophores, however, did not follow the pattern of high abundance at high latitudes in 1999 and low latitudes in 1998, but showed higher abundances at all stations in 1999 as compared to those in other years. The respective responses of each mesozooplankton group to the physical characteristics likely affected the clustered grouping of the mesozooplankton community in the surface waters (Fig. 6). *Clausocalanus* sp. and *Oncaea* sp. numerically dominated the discrimination between groups in 1998, 1999, and 2003. The smaller-bodied taxa such as clausocalanids appear to be less influenced by either warm or cold events (Hopcroft et al., 2002). However, *Oncaea* sp., which was abundant in surface waters during the strong upwelling event in 1999, showed higher abundance concomitant with increased primary production and lowered temperature (Nakata et al., 2004), like omnivores in field observations (Paffenhöfer, 1993). Doubling of the abundance of *Oncaea* spp. occurred after an event of mixing with nutrient-rich water (Cowles et al., 1987), which is likely associated with preying on larvae or immature copepods of other species. *Oncaea* sp. dominated mostly in the lower layer (from thermocline depth to 200 m) in the same study area (Kang, 2004), which corresponds to the observed high abundance in the deep mixed layer in a temperature range of 17–20 °C (Paffenhöfer, 1993). This indicates that the copepods, which are positively correlated with the upwelling index (Hopcroft et al., 2002), were upwelled from subsurface layers at higher latitudes in 1999.

A higher ratio of cyclopoid-to-calanoid indicates that the abundance of cyclopoid copepods is affected by not only large-scale upwelling but also small-scale divergence (Fig. 9). Cyclopoid copepods dominate increases of zooplankton abundances in enclosed water columns following nutrient enrichment (Harris et al., 1982) and in warm core rings enriched with nutrients (Roman et al., 1985). This trend reflects the latitudinal gradients of cyclopoid-to-calanoid ratios in response to the various ecotones during our study. The greater ratio in 1999 than in other years further suggests that the strength of upwelling in 1999 was larger than that in other periods. In contrast, cyclopoids were more abundant during the 1992 El Niño, with an average sea surface temperature of 28.7 °C and thermocline depressed to 20–40 m at the equator at 140°W (Roman et al., 1995). Cyclopoids may have dominated due to their tendency toward sit-and-wait predation, reducing their swimming activity and respiratory demand (Roman et al., 1995). However, this conservation of energy is mainly supported by lower respiration measurements from the cyclopoid copepod *Oithona* (Lampitt and Gamble, 1982), which is not consistent with our finding of communities dominated by *Oncaea* sp.

In addition to the *Oncaea* sp., ostracods and radiolarians might be affected by ecotones, considering their higher abundance at lower latitudes in 1998 and 2003 and at higher latitudes in 1999. The highest standing stocks of radiolarians are found in the convergence and divergence zones along 12°S and 12°N at 140°W (Welling et al., 1996). This pattern is also found in our study area, consistent with the species percentage of group B-2 in 1999 (Table 2, Fig. 7).

Calanoid and cyclopoid copepods as the dominant groups, salps and appendicularians also showed inter-annual latitudinal distributions related to chl-*a* concentrations associated with ecotones (Fig. 8). Salp abundance could increase due to their ability to remove minute particles at high filtration rates (Lavaniegos et al., 2002), and appendicularians prefer nanoplankton and picoplankton as prey (Scheinberg et al., 2005). Therefore, high abundances of copepods, salps, and appendicularians in the convergence and divergence zones suggest that phytoplankton should consist of diatoms and smaller-sized phytoplankton in response to the ecotones along the meridian line during the study periods.

In summary, meridional distribution pattern of mesozooplankton between 5° and 12°N along 131.5°W was characterized by ecotones formed at the boundaries between currents moving in different directions such as SEC, NECC and NEC. The enhanced concentration and abundance of chl-*a* and mesozooplankton were found in the convergence zone in 1998, while those were observed in the divergence zones in 1999 and 2003. However, the enhanced abundances of mesozooplankton in the divergence zone in 1999 ranged distinctively higher than those in the convergence and divergence zones in 1998 and 2003, which was coincident with shallow thermocline depth due to an intensified upwelling during the La Niña period. During the study periods, the peaks of mesozooplankton abundance were caused by the bottom-up regulation from introduced nitrate into surface waters via phytoplankton to mesozooplankton. *Oncaea* sp. dominant cyclopoid copepods constituted mostly the peaks of mesozooplankton abundances. The cyclopoid-to-calanoid ratio, which showed different magnitude of peaks in the convergence zone in 1998 and divergence zones in 1999 and 2003, suggested that the ratio could indicate existence and characteristics of ecotones found between 5° and 12°N along 131.5°W during the study periods. The ecotones were associated with the different strengths of upwelling observed in sharp transition period between 1997–1998 El Niño and 1998–1999 La Niña events, the 1999 La Niña event, and the near-normal condition after the moderate 2002–2003 El Niño.

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