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East–west comparison of the zooplankton community in the subarctic Pacific during summers of 2003–2006

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The subarctic Pacific is known to have east–west gradients in the oceanic environment and phytoplankton community. The western subarctic Pacific is characterized by low temperature and high chlorophyll *a* (Chl *a*) while the eastern region by high temperature and low Chl *a*. Although there is little information on the differences in the zooplankton community between the eastern and western subarctic Pacific, the gradients in the oceanographic environment and phytoplankton community may markedly affect the zooplankton community in this region. The aim of this study is to clarify east–west differences in the subarctic Pacific zooplankton community. Zooplankton were sampled at stations along the 165°E line (western subarctic Pacific from 41°30′N to 49°30′N) and 165°W line (eastern subarctic Pacific from 39°N to 53°30′N) using 335 and 100 µm mesh size Twin NORPAC net during the summers of 2003–2006. East–west differences in the zooplankton community were characterized as: (i) greater total zooplankton abundance in the west and (ii) larger body size of calanoid copepods of the same copepodid stage in the west. Differences in east–west zooplankton abundances are attributed to differences in the magnitude of primary production (high in the west) and the size of primary producers (large in the west). Larger body sizes of calanoid copepods in the west are attributed to the lower temperature. Thus, differences in zooplankton abundance and body size are concluded to be due to east–west gradients in the oceanographic environment and phytoplankton community.

KEYWORDS: subarctic Pacific; east–west comparison; zooplankton; calanoid copepods

INTRODUCTION

The subarctic Pacific is bounded by the Aleutian Islands in the north and in the south by the subarctic boundary [34‰ (=PSU) isohaline line vertically stretched in the surface layer, located at ca. 42°N: Favorite *et al.*, 1976; Anma *et al.*, 1990], North America in the east and Kuril Islands and Hokkaido, Japan, in the west. This area can be divided into two regions, the western subarctic Pacific, Western Subarctic Gyre as its center, and the eastern subarctic Pacific, Alaskan Gyre

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as its center (Longhurst, 2007). The deep water in this region is characterized by high nutrient concentrations since the region is located at the end of the global deep-water circulation (Harrison *et al.*, 2004). Therefore, all trophic levels from primary producer through higher trophic levels in this region are highly productive (Pearcy *et al.*, 1996). However, the biological community is not constant throughout the subarctic Pacific and differences between east and west have recently received much attention (Frost and Kishi, 1999).

The subarctic Pacific is a high nutrient and low chlorophyll (HNLC) area, and the oceanographic environments in the eastern and the western regions have different features (Harrison *et al.*, 1999). Environmental parameters in the western subarctic Pacific are characterized by high nutrient concentrations and a low temperature. This is caused by the nutrient-rich Eastern Kamchatka Current, originated from the Bering Sea Gyre and cold intermediate water from the Okhtotsk Sea diffusing through Kuril Island channels (Aramaki *et al.*, 2001). In the eastern subarctic Pacific, environmental parameters are characterized by low nutrient concentrations and a high temperature. This is due to the effects of the low-nutrient and high-temperature Alaska Current and Alaskan Stream in this region (Whitney *et al.*, 1999).

These east–west differences in oceanographic environment influence the phytoplankton community. In the Oyashio region (western subarctic Pacific), large phytoplankton blooms occur during spring, and the phytoplankton biomass shows large seasonal variability (Banse and English, 1999). In the Western Subarctic Gyre and Alaskan Gyre, phytoplankton blooms of small-sized species occur during summer to autumn, and the biomass remains low throughout the year (Banse and English, 1999; Tadokoro, 2000). Comparing chlorophyll *a* (Chl *a*) standing stock between the Alaskan Gyre (east) and Western Subarctic Gyre (west) in the subarctic Pacific during spring, Shiomoto and Hashimoto (Shiomoto and Hashimoto, 2000) reported that the standing stock in the western region was higher than that in the east. Phytoplankton size is also larger in the west than in the east within the same latitudes during spring, and thus the Chl *a* standing stock is higher in the west (Hashimoto and Shiomoto, 2000), and primary production is known to be greater in the west than in the east (Shiomoto and Asami, 1999). Greater primary productivity in the west leads to the POC flux being higher in the west than in the east (Kawakami *et al.*, 2010). Recent multi-sensor satellite data (Goes *et al.*, 2004) have also revealed higher Chl *a* and primary production in the west than in the east.

HNLC in the subarctic Pacific is attributed to the low iron concentration (Martin and Fitzwater, 1988). Iron is an important trace element for phytoplankton to perform photosynthesis and uptake of nitrate (Raven *et al.*, 1999). In the western subarctic Pacific, iron transported from the Asian continent by westerly winds (Duce and Tindale, 1991), diffusion of iron-rich Okhotsk Sea Intermediate Water (Nishioka *et al.*, 2007) and Eastern Kamchatka Current flowing southward adjacent to the Kamchatka Peninsula (Tadokoro, 2000) lead to high iron concentrations. In the eastern subarctic Pacific, iron input and supply are almost negligible (Harrison *et al.*, 1999). Compared with the same latitudes, the iron concentration is consistently higher in the west than in the east (Takata *et al.*, 2006; Kitayama *et al.*, 2009) and is the primary cause of the east–west differences in phytoplankton community (Suzuki *et al.*, 2002). The east–west difference in iron concentration also affects the food web structure. In the iron-limited eastern subarctic Pacific, phytoplankton utilize ammonium rather than nitrate, and microzooplankton, such as ciliates, graze on these small-sized phytoplankton species (Miller *et al.*, 1991). In an area where small-sized phytoplankton are dominant, microzooplankton are abundant and the microbial loop is the major pathway of the pelagic ecosystem.

Mesozooplankton function as a vital link between the microplankton community and higher trophic levels in marine ecosystems. Among the mesozooplankton communities of the subarctic Pacific, large calanoid copepods are abundant in the zooplankton biomass (Vinogradov, 1970). In the subarctic Pacific, the species composition of the mesozooplankton is similar throughout east and west (Mackas and Tsuda, 1999), and the wet biomass of copepods from the surface to deep water apparently does not vary between east and west (Nishikawa *et al.*, 2001). As the life histories of the major calanoid copepods have been gradually clarified, differences in their life spans have been better understood. Species with identical life spans in the east and the west (*Neocalanus cristatus*: Kobari and Ikeda, 1999, *Neocalanus plumchrus*: Kobari and Ikeda, 2001a), and species with a longer life span in the east (*Eucalanus bungii*: Tsuda *et al.*, 2004; Shoden *et al.*, 2005) and with a longer life span in the west (*Neocalanus flemingeri*: Tsuda *et al.*, 1999; Kobari and Ikeda, 2001b) have been reported. The life history pattern of calanoid copepods also varies among regions (Mackas and Tsuda, 1999; Batten *et al.*, 2006). In addition to the east–west differences, the life history timing of *N. plumchrus* is different between north and south, with the higher temperature in the south being considered to accelerate their development rate (Batten *et al.*, 2003).

Body size of zooplankton, especially copepods, also varies between the eastern and western subarctic Pacific. Comparing the body length between the east and the west, the calanoid copepod *E. bungii* is larger in the west than in the east (Shoden *et al*., 2005). *Neocalanus flemingeri* is also larger in the west than the east (Tsuda *et al*., 1999, 2001a). Body sizes of the other two dominant *Neocalanus* spp.: *N. cristatus* and *N. plumchrus*, are also larger in the west and the north, and a low temperature is considered as a factor resulting in large-sized individuals (Tsuda *et al*., 2001a; Kobari *et al*., 2003a).

Thus, east–west differences in the mesozooplankton community of the subarctic Pacific have recently been clarified. However, compared with the extensive data available in the literature on oceanographic environmental variables and the phytoplankton community, data on the zooplankton community are still limited, partly because of methodological problems. In order to make quantitative comparisons for higher trophic levels, sampling methods (mesh size of net, sampling depth, time and season) need to be standardized (Tseitlin *et al*., 1997). In previous studies, large differences in sampling methods between east and west have prevented simple comparisons. Since mesozooplankton contribute more than half of the biomass of pelagic biota in the subarctic Pacific (Ikeda *et al*., 2008), east–west comparisons of the mesozooplankton abundance, biomass and community structure are of major importance. To make such comparisons possible, sets of zooplankton samples collected in almost the same seasons by identical sampling methods are essential for analysis.

In this study, to clarify east–west differences in the mesozooplankton community in the subarctic Pacific, transects along the 165°E line from 41°30′N to 49°30′N and 165°W line between 39°N and 53°30′N were surveyed using the same sampling gear (Twin NORPAC net) and the same sampling methods (0–150 m depth vertical tow) during the summers (June–August) of four consecutive years (2003–2006). Based on these samples, this study aims to clarify east–west differences in abundance, stage composition and body sizes of large calanoid copepods *N. cristatus*, *N. flemingeri*, *N. plumchrus*, *E. bungii* and *Metridia pacifica* which are abundant in the zooplankton biomass of the subarctic Pacific, and the primary factors leading to these differences are discussed.

METHOD

Field study

Oceanographic observations and plankton sampling were conducted along the 165°E and 165°W lines on board the T/S *Oshoro-Maru* of the Faculty of Fisheries, Hokkaido University in the summers of 2003–2006 (Fig. 1a). The number of sampling stations and sampling period along each transect varied among years. Along the 165°E line, samples were collected at 4–10 stations from 41°30′N through 49°30′N from 6 June to 8 July. Along the 165°W line, samples were collected at 5–16 stations from 39°00′N through 53°30′N from 30 June to 2 August (Fig. 1b). Zooplankton samples were collected by vertical hauls from 150 m to the surface using 45 cm net ring diameter, 335 and 100 μm mesh size Twin NORPAC net (Motoda, 1957), equipped with flowmeters (Rigosha Co., Ltd.). The net towing speed was 1 m s^{-1}. During each sampling, the wire angle was measured using a protractor, and the wire length was extended so the net reached 150 m. The samples were immediately preserved in 5% formaldehyde–seawater buffered with sodium tetraborate. The volume of water filtered was calculated from the flowmeter reading.

At each sampling station, vertical profiles of temperature and salinity from the surface to 800 m were monitored with a CTD (Sea-Bird Electronics, Inc., CTD-SBE 9plus) or XCTD (Tsurumi Seiki Co., Ltd.). The temperature and salinity data have been published elsewhere (Hokkaido University, 2004, 2005, 2006, 2007). At each station, 1 L surface water was collected with a bucket for Chl *a* measurement, and 1 L water samples from 10 discrete layers between the surface and 150 m (5, 10, 20, 30, 40, 50, 60, 75, 100, 150 m) were collected with Niskin bottles on the CTD frame. Each water sample was filtered onto a Whatman GF/F filter using a vacuum pressure differential of <100 mmHg. GF/F filter samples were immersed in *N*,*N*-dimethylformamide overnight in the dark for extraction of pigments. The fluorescence was measured with a Turner Designs fluorometer (Model 10-AU), and Chl *a* was calculated.

Sample analysis

In the onshore laboratory, each 335 μm mesh zooplankton sample was divided into two subsamples by using Motoda plankton splitter (Motoda, 1959). A subsample was filtered onto a 100 μm mesh using an aspirator, and the zooplankton wet mass was measured by an electronic balance with a precision of 0.01 g. Each 100 μm sample was well mixed, and then a 1/10 subsample was taken using a large bore pipette. This subsample was observed under a dissecting microscope, and large calanoid copepods, small calanoid copepods, cyclopoid copepods, poecilostomatoid copepods, harpacticoid copepods, copepod nauplii, amphipods,

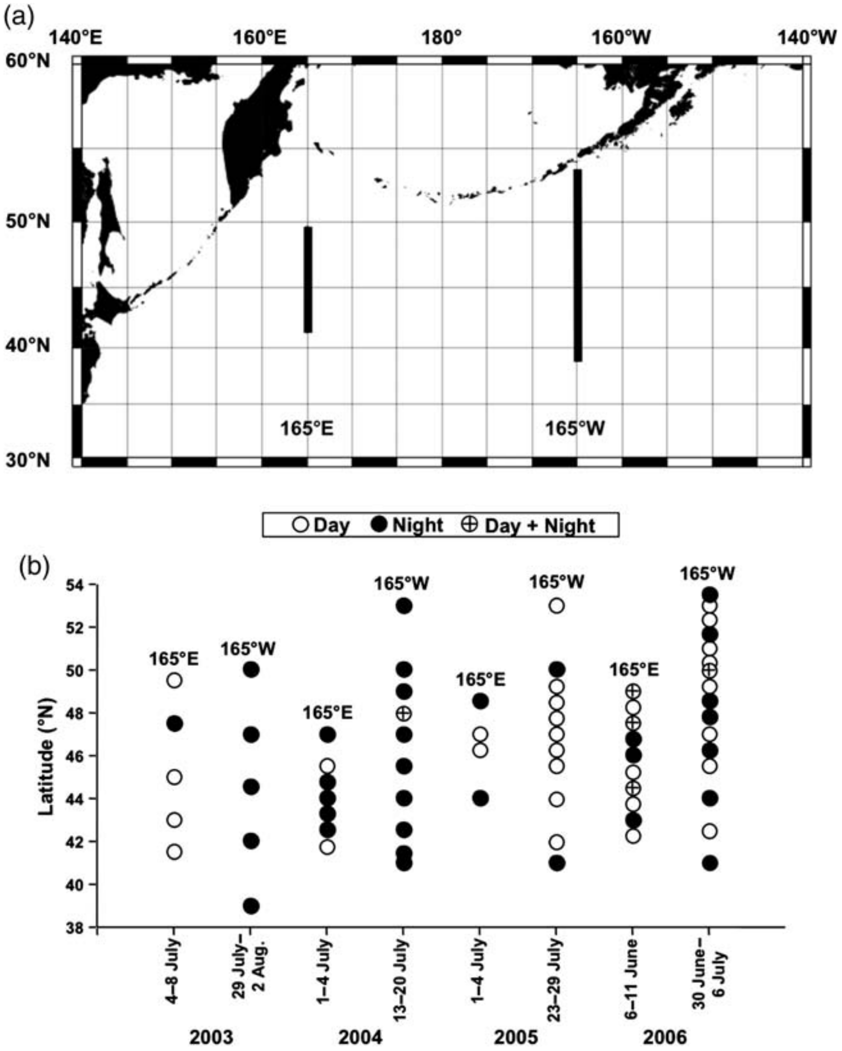

Fig. 1. (**a**) Sampling transects along 165°E and 165°W lines in the subarctic Pacific, and (**b**) sampling time (day, night and both day and night) along 165°E and 165°W lines during the summers of 2003–2006.

appendicularians, chaetognaths, doliolids, euphausiids, hydrozoans, molluscans, ostracods, polychaetes and salps were sorted and counted.

In this study, the following five species of large calanoid copepods were considered: *N. cristatus*, *N. flemingeri*, *N. plumchrus*, *E. bungii* and *M. pacifica*. These species are known to constitute ca. 70% of the total mesozooplankton biomass in the subarctic Pacific (Ikeda *et al.*, 2008). For these large copepods, *Neocalanus* spp. were counted according to copepodid stage 1–6 (C1–C6). In addition to these copepodid stages, distinction of females and males was made for *E. bungii* and *M. pacifica* C4–C6. Nauplii of *E. bungii* which are morphologically different from the other species (Johnson, 1937) were also counted.

Large calanoid copepods *N. cristatus*, *N. flemingeri*, *N. plumchrus* and *E. bungii* usually show little day–night change in depth distribution (Kobari and Ikeda, 1999, 2001a, 2001b; Shoden *et al.*, 2005). However, *M. pacifica* is known to perform diel vertical migration in summer (Hattori, 1989; Yamaguchi *et al.*, 2004; Padmavati *et al.*, 2004; Takahashi *et al.*, 2009). In this study, zooplankton samples were collected during both day and night (Fig. 1b). To allow quantitative comparisons among stations of *M. pacifica* abundance, it is necessary to standardize to either the day or the night value. In each domain along each transect, differences in day and night abundances of every copepodid stage of *M. pacifica* were tested with *U* test (see online supplementary data Fig. S1). As a result, only *M. pacifca* C6F showed a significantly greater abundance at night in each domain ($P < 0.05$). In each domain, day:night ratio in abundance was calculated (0.003–0.076, see online supplementary data Fig. S1). Using these factors, the nighttime values of *M. pacifica* C6F were converted to daytime values.

Mean copepodid stages were calculated from copepodid stage abundances using the equation below:

$$\mathrm{MS} = \frac{\sum_{i=1}^{6} i \times N_i}{\sum_{i=1}^{6} N_i},$$

where MS is the mean copepodid stage, i the copepodid stage and N_i the abundance (ind. m^{-3}) in each copepodid stage (cf. Marin, 1987). In the calculation of the mean copepodid stage, *E. bungii* nauplii were not taken into account.

Regarding large calanoid copepod diapause stages (stage C5 of the three *Neocalanus* spp., C4F/M, C5F/M and C6F of *E. bungii* and C6F of *M. pacifica*), prosome length (PL) was measured. If at least 30 individuals were found in a sample, 30 individuals were randomly selected. If less than 30 individuals were found in a sample, then all the individuals were used. PL was measured under a dissecting microscope using an eyepiece micrometer with a 10 μm precision.

The wet masses of large calanoid copepods were calculated, and their contributions to the total zooplankton biomass were also computed. The wet masses of large calanoid copepods were calculated by multiplying the abundance of each copepodid stage by the wet mass of each stage (for *E. bungii*, *M. pacifica* and the three *Neocalanus* spp. referring to Shoden, unpublished data, Padmavati, unpublished data and Kobari *et al.*, 2003b, respectively).

Statistical analysis

The east–west differences in zooplankton abundance and wet mass, and large calanoid copepods were tested by U test. The regional differences in PL of large calanoid copepods at each station were analyzed by one-way ANOVA and an ex post facto test by Fisher's protected least significant difference (PLSD) test.

RESULTS

Hydrography

The subarctic front [boundary of subarctic current system (SA) and transition domain (TR)], where the 4°C isothermal is located vertically below 100 m (Favorite *et al.*, 1976; Anma *et al.*, 1990), was found near 45°30′N in 2003, 45°N in 2004, 44°30′N in 2005 and 45°N in 2006 along the 165°E line (see online supplementary data Fig. S2). Along the 165°W line, the subarctic front was observed near 49°N in 2003, 47°30′N in 2004 and 2005 and 48°N in 2006 (Fig. 2). The subarctic front in the east was located more northward than in the west, and the transition domain spread further north. Salinity did not show a clear latitudinal change as seen in temperature. While the surface layer in high latitudes was low in salinity, 33.5 PSU isohaline line was observed in depth of 100–200 m in both the eastern and western subarctic Pacific (see online supplementary data Fig. S2 and Fig. 2).

Chl *a* was relatively high (2 mg m^{-3}) above 50 m in 2003, in the south of 44°N in 2004 and in the north of 48°N in 2005 in the western subarctic Pacific (see online supplementary data Fig. S2). Chl *a* at the other stations in the western subarctic Pacific was low, <1 mg m^{-3} (see online supplementary data Fig. S2). In the eastern subarctic Pacific, high Chl *a* (2 mg m^{-3}) was only observed in 25–50 m near 47°N in 2003 (Fig. 2). During the other sampling periods, Chl *a* in the eastern subarctic Pacific was low (0.50–0.75 mg m^{-3}) above 25–50 m and <0.25 mg m^{-3} below 100 m (Fig. 2).

Integrated mean temperature from the surface to 150 m was higher in the eastern subarctic Pacific than in the western subarctic Pacific in every sampling year and domain, except for 42°N in 2003 (Fig. 3a). The east–west differences in the temperature were 2.4–3.4°C in the TR of 2005, 1.7–3.1°C in the SA of 2005, 1.5–2.0°C in the SA and 2.0–5.7°C in the TR of 2006. Overall, the temperature in the east was significantly higher than in the west (U test, $P < 0.05$). Chl *a* standing stocks integrated from 0 to 150 m were compared between east and west, showing that Chl *a* was higher in the west (Fig. 3b). The east–west differences in Chl *a* were 3–34 mg m^{-2} in the SA of 2005, 11–17 mg m^{-2} in the TR and 15–24 mg m^{-2} in the SA of 2006. Overall, the Chl *a* in the west was significantly higher than in the east (U test, $P < 0.05$).

Zooplankton abundance and biomass

Abundance of the total zooplankton community ranged from 2047 to 5044 ind. m^{-3} in the western and 193 to 5067 ind. m^{-3} in the eastern subarctic Pacific (Fig. 4). In every year and domain, cyclopoid copepods and copepod nauplii were abundant. In 2006, poecilostomatoid copepods were also abundant in the west. Zooplankton abundances in the TR of 2003, 2004 and 2006 were significantly different between east and west (U test, $P < 0.05$), and the abundances in the west were 2.7–3.9, 2.5–12.5 and 1.8–2.1 times greater than in the east, respectively.

Wet masses of the total zooplankton community ranged from 45 to 1357 mg m^{-3} in the western and 16

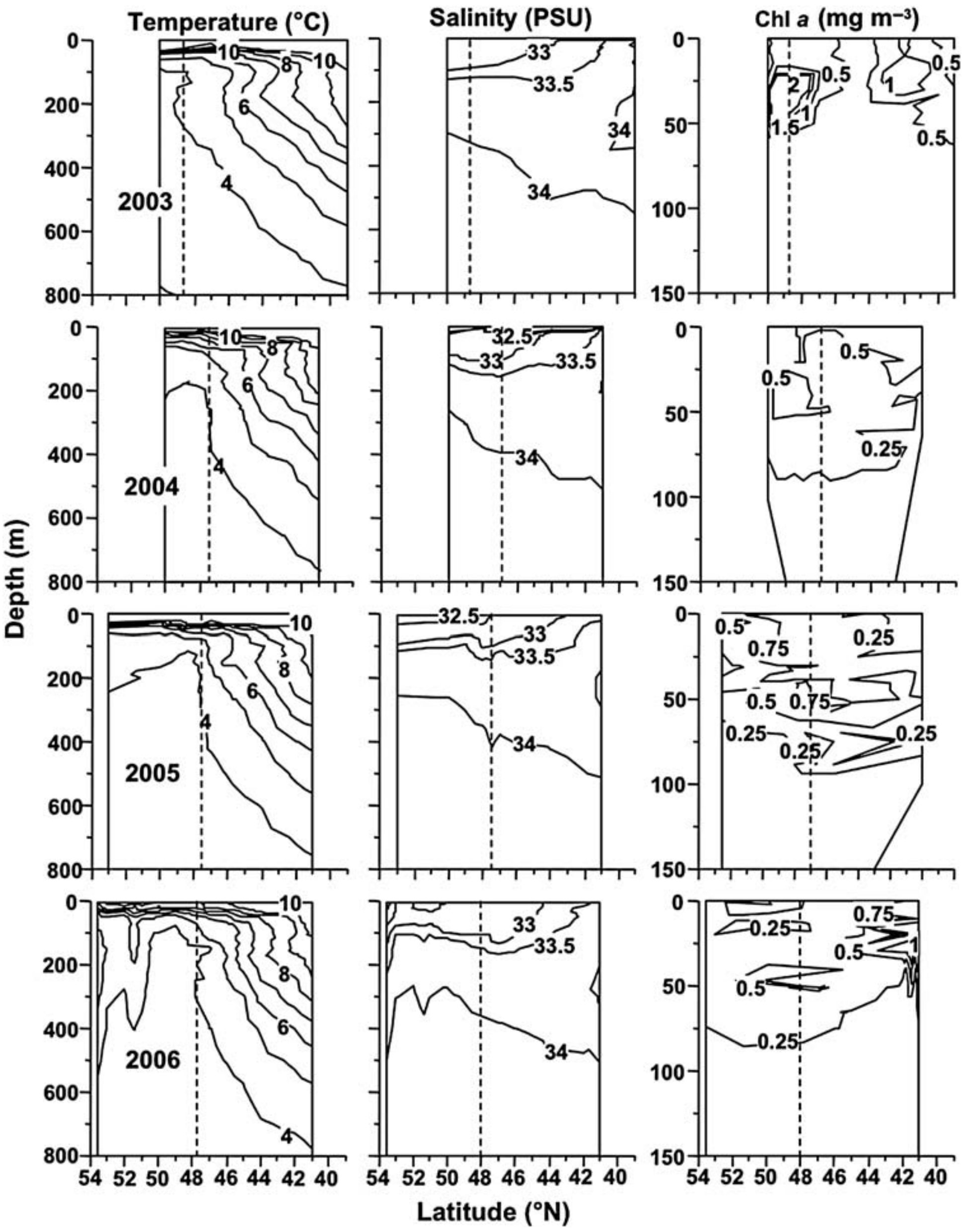

Fig. 2. Vertical profiles of temperature, salinity and chlorophyll *a* along 165°W in the eastern subarctic Pacific during the summers of 2003–2006. Note that the depth scale differs for Chl *a*. Vertical dashed lines indicate approximate position of the subarctic front identified from the 4°C isothermal lines.

to 2600 mg m^{-3} in the eastern subarctic Pacific (see online supplementary data Fig. S3). In 2003–2005, large calanoid copepods *N. cristatus* and *N. plumchrus* were abundant in the east and the west. In 2006, in addition to the above two *Neocalanus* spp., *N. flemingeri* was also abundant. While significant east–west difference was seen in the abundance (Fig. 4), the wet mass did not show a significant difference (see online supplementary data Fig. S3).

Copepod population structure

Neocalanus cristatus abundance and mean copepodid stage did not show a significant east–west difference (Fig. 5). Their copepodid stage structure varied between SA and TR. In the SA, early copepodid stages (C1–C3) were abundant, and the mean stage was low (2–3). In the TR, late copepodid stages, especially C5, dominated and the mean stage was high (4–5). In the southern TR, abundance of *N. cristatus* was extremely

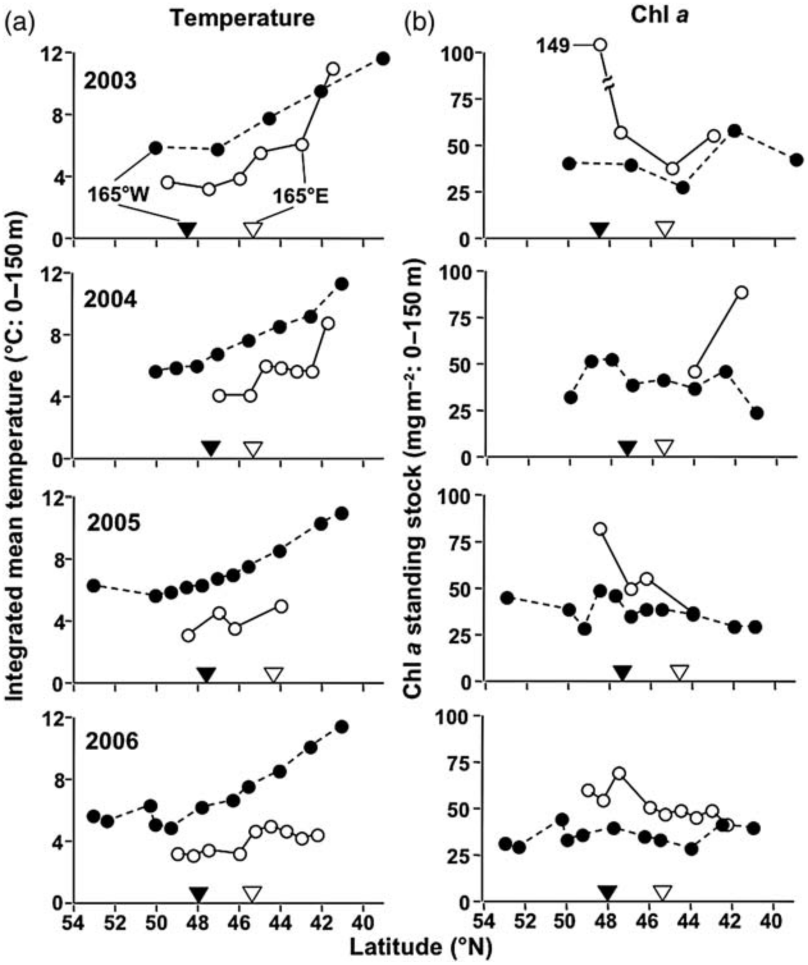

Fig. 3. (a) Integrated mean temperature and (b) Chl *a* standing stock over the 150 m water column in the western (165°E, open circle) and eastern (165°W, solid circle) subarctic Pacific during the summers of 2003–2006. Triangles (165°E, open symbol; 165°W, solid symbol) indicate the approximate positions of the subarctic front (cf. online supplementary data Fig. S2 and Fig. 2).

low. The mean stage was earlier than in the northern TR, and C3 dominated in the eastern subarctic Pacific of 2004 and 2006.

Neocalanus flemingeri abundance showed significant east–west differences in both SA and TR of 2006 (*U* test, $P < 0.05$), and those in the western subarctic Pacific were 2.6–12.2 and 1.8–4.6 times greater than in the eastern subarctic Pacific, respectively (see online supplementary data Fig. S4). In 2006, the mean copepodid stage also showed a significant east–west difference. Thus, early copepodid stages (C1–C3) were abundant in the west, whereas only C5 occurred in the east. In 2003–2005, only a few *N. flemingeri* C5 were observed during the sampling periods.

Neocalanus plumchrus abundance showed a significant east–west difference in the SA of 2006, and 12–25 times greater abundance was observed in the eastern than in the western subarctic Pacific (see online supplementary data Fig. S5, $P < 0.05$). The subarctic front also divided their copepodid stage structure into two patterns. In the SA, the mean copepodid stage was low (2–3), and early copepodid stages (C1–C3) were abundant, while in the TR, the mean copepodid stage was high (3–5), and late copepodid stages (C5) were abundant. Similar to *N. cristatus*, few *N. plumchrus* were observed in the southern TR and early copepodid stages dominated. Nevertheless in 2006, in the west, the abundance of *N. plumchrus* in SA was lower than TR and dominated by early copepodid stages (see online supplementary data Fig. S5).

Eucalanus bungii abundance showed a significant east–west difference in the TR of 2004, and two to nine times greater abundance observed in the western than in the eastern subarctic Pacific (Fig. 6, $P < 0.05$). In the SA of 2005, both the abundance and mean copepodid stage showed a significant east–west difference and had five to six times greater abundance of early copepodid

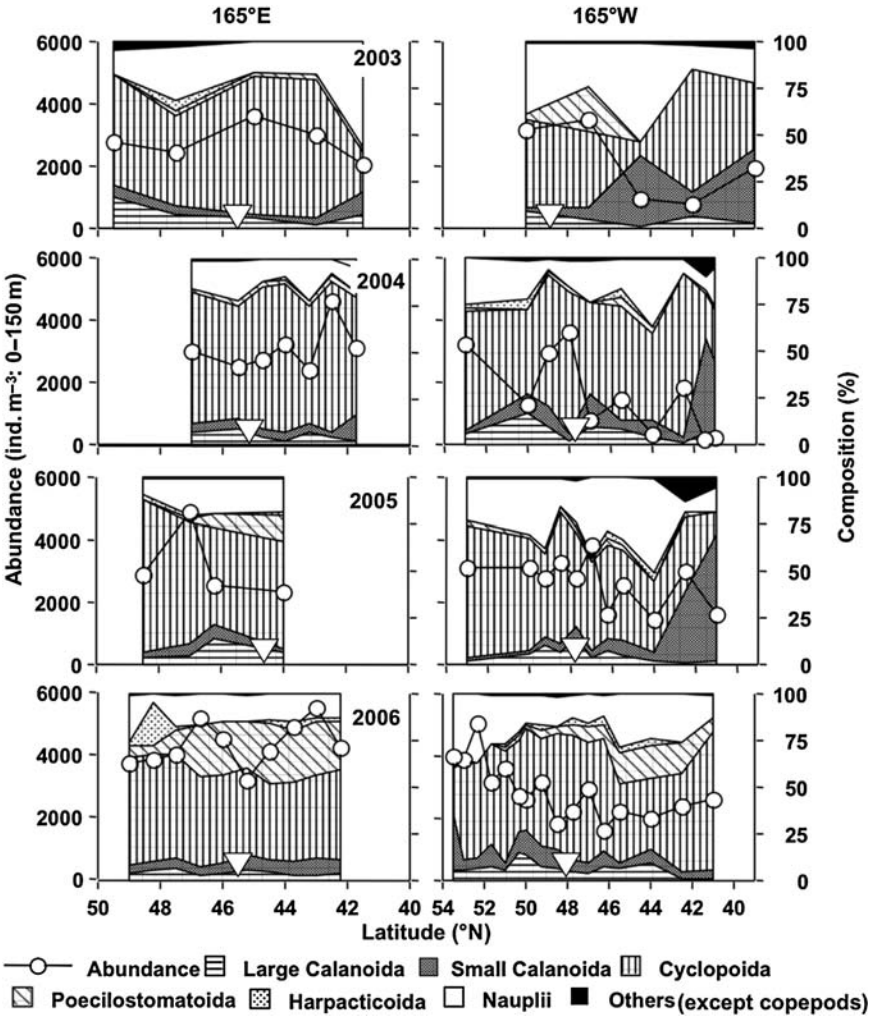

Fig. 4. Abundance of total zooplankton and taxonomic composition (orders of copepods and others) in the western (165°E, left) and the eastern (165°W, right) subarctic Pacific during the summers of 2003–2006. Triangles indicate the approximate positions of the subarctic front (cf. online supplementary data Fig. S2 and Fig. 2).

stages in the east than in the west ($P < 0.05$). The copepodid stage structure of *E. bungii* was dominated by C3 in the SA, while dominated by late copepodid stages (C4 and C5) in the TR, as was seen in the east of 2005 and in both the east and west of 2006.

Metridia pacifica abundance and mean copepodid stage did not show east–west differences in every sampling year and domain (see online supplementary data Fig. S6). In most years and transects, north–south differences in copepodid stage were not clear. For *M. pacifica*, early copepodid stages (C1–C3) always dominated, and the mean copepodid stage was low, around 2.

Copepod body size (PL)

PL of the large calanoid copepods *N. cristatus*, *N. flemingeri* and *N. plumchrus* C5, *E. bungii* C4F/M, C5/M, C6F and *M. pacifica* C6F showed significant regional differences which were consistent among stations in every sampling year. *Neocalanus cristatus* PL was larger in the western (6.38–6.93 mm) than in the eastern subarctic Pacific (5.70–6.78 mm) within the same latitudes in the TR of 2004, in the SA of 2005, in both SA and TR of 2006 (Table I, one-way ANOVA, Fisher's PLSD, $P < 0.01$). Within the same longitudes, *N. cristatus* C5 showed a consistent geographical trend that was larger in the north than the south. PL of *N. flemingeri* C5 was larger in the west (2.96–3.72 mm) than in the east (2.83–3.03 mm) in both the SA and the TR in 2006 ($P < 0.05$). However, there was no east–west difference for *N. flemingeri* C5 in 2003–2005. Similar to *N. cristatus* C5 PL, *N. plumchrus* C5 PL was larger in the west (3.64–3.93 mm) than in the east (3.37–3.83 mm), and significant east–west differences in *N. plumchrus* PL were observed for the TR in 2003, both SA and

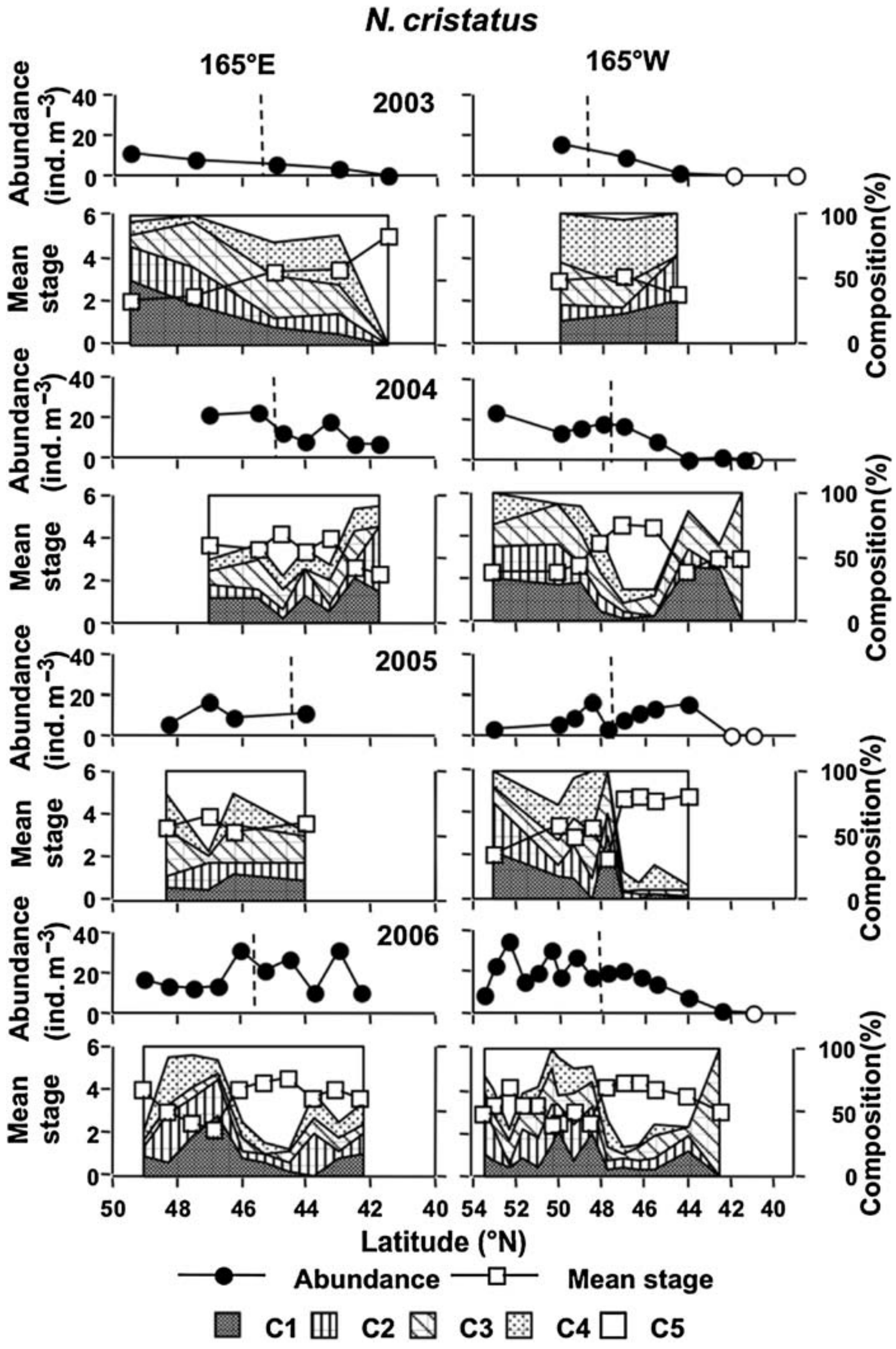

Fig. 5. Abundance, composition of each copepodid stage (C1–C5) and mean stage of *N. cristatus* in the western (165°E, left) and eastern (165°W, right) subarctic Pacific during the summers of 2003–2006. Vertical dashed lines indicate the approximate positions of the subarctic front (cf. online supplementary data Fig. S2 and Fig. 2). Open symbols in abundance indicate no occurrence.

TR in 2004, TR in 2006 ($P < 0.05$). Within the same longitudes, *N. plumchrus* C5 showed a clear geographical pattern being larger in the north than in the south (Table I). *Eucalanus bungii* C4F, C4M, C5F, C5M and C6F did not show clear geographical trends (Table I). A significant difference in PL of *E. bungii* larger in the west was only observed for C6F in SA of 2006 ($P < 0.05$). *Metridia pacifica* C6F PL showed a similar geographical variation as *N. cristatus* and *N. plumchrus* (Table I). In both SA and TR of 2005 and 2006, *M. pacifica* C6F was larger in the west (2.08–2.16 mm) than in the east (1.74–2.14 mm) ($P <$ 0.05) and was larger in the north than in the south.

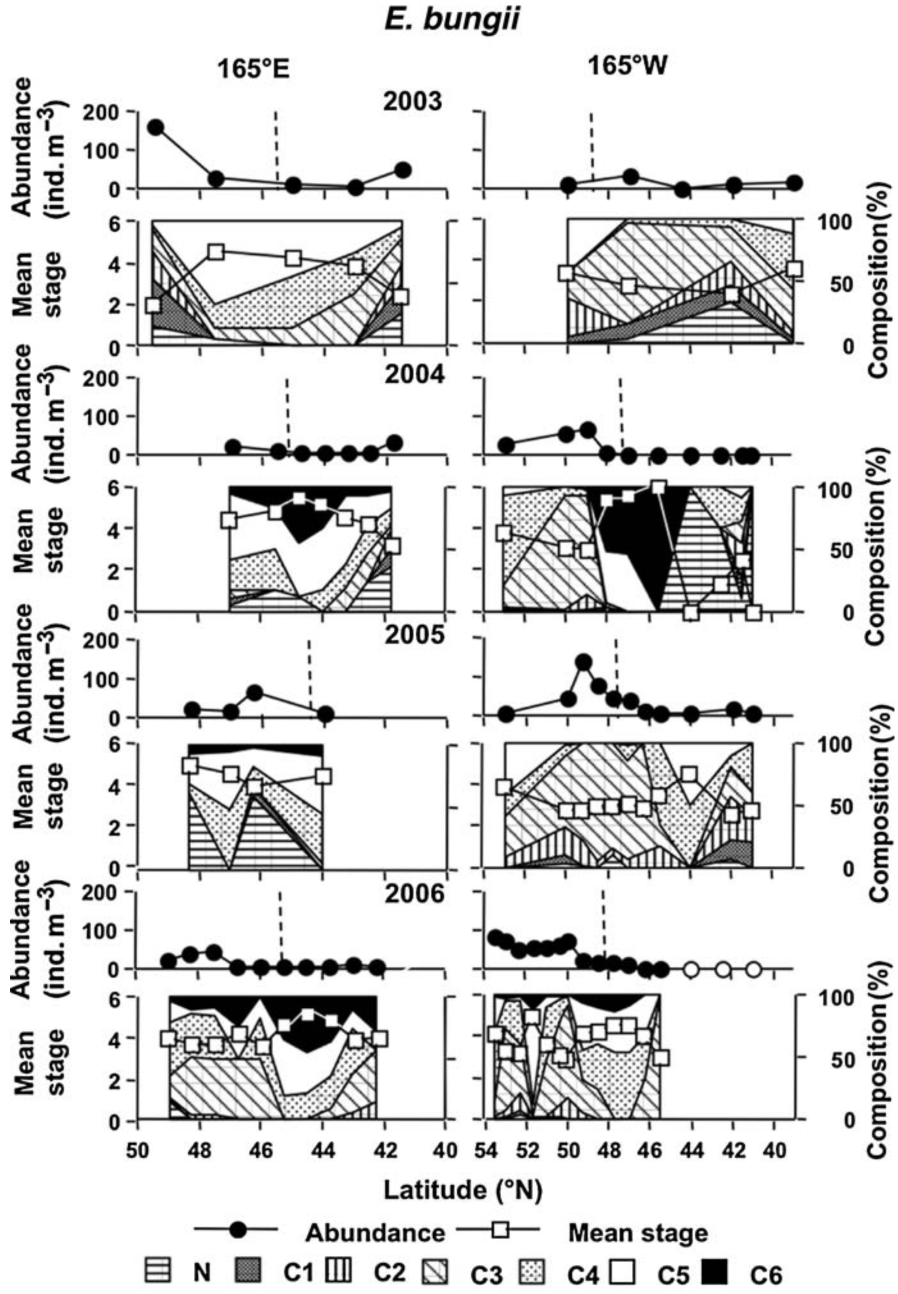

Fig. 6. Same as Fig. 5, but for *E. bungii*.

DISCUSSION

East–west differences in zooplankton abundance and biomass

Table II summarizes the east–west differences in oceanographic environments and zooplankton abundance and biomass in the North Pacific during the summers of 2003–2006. Temperature was higher in the eastern than in the western subarctic Pacific but Chl *a* was higher in the west than in the east (Table II). Zooplankton abundance was greater in the west than in the east in most of the years though the wet mass did not show any east–west difference. Abundance of the large calanoid copepods *N. cristatus* and *M. pacifica* did not vary between the east and the west. Abundance of *N. flemingeri* was greater in the west than in the east in both SA and TR of 2006 while abundance of *N. plumchrus* was greater in the east than in the west in the SA

Table I: Range and median of PL (mm) of N. cristatus, N. flemingeri, N. plumchrus C5, E. bungii C4F–C6F and M. pacifica C6F along 165°E and 165°W lines in the North Pacific during the summers of 2003–2006

		West (165°E)			East (165°W)		
Speices	Stage	Range	Median	Trend	Range	Median	Year (domain)
N. cristatus	C5	6.38–6.93	6.68	>	5.70–6.78	6.21	2004 (TR), 2005 (SA), 2006 (SA, TR)
N. flemingeri	C5	2.96–3.72	3.64	>	2.83–3.03	3.14	2006 (SA, TR)
N. plumchrus	C5	3.64–3.93	3.81	>	3.37–3.83	3.53	2003 (TR), 2004 (SA, TR), 2006 (TR)
E. bungii	C6F	5.97–6.41	6.27	>	5.70–6.11	5.95	2006 (SA)
	C5F	4.21–4.69	4.63	≒	4.28–5.17	4.50	NS
	C5M	3.89–4.71	4.54	≒	4.00–4.80	4.39	NS
	C4F	3.10–3.69	3.51	≒	3.22–3.73	3.42	NS
	C4M	3.03–3.77	3.48	≒	3.26–3.67	3.41	NS
M. pacifica	C6F	2.08–2.16	2.11	>	1.74–2.14	2.04	2005, 2006 (SA, TR)

Trend, years and domains with significant east–west differences are shown. SA, subarctic current system; TR, transition domain.

Table II: Summary of the east–west comparisons of hydrography, zooplankton abundance and biomass in the North Pacific during the summers of 2003–2006

	West (165°E)			East (165°W)		
Parameters	Range	Median	Trend	Range	Median	Year (domain)
Hydrography						
Temperature (°C)	3.1–8.8	4.9	<	4.8–11.4	6.6	2004 (TR), 2005 (SA), 2006 (SA, TR)
Chl *a* (mg m^{-2})	41.8–82.4	59.7	>	28.1–48.7	38.2	2005 (SA), 2006 (SA, TR)
Zooplankton						
Abundance (ind. m^{-3})	2047–5504	3217	>	193–2928	2592	2003 (TR), 2004 (TR), 2006 (TR)
Wet mass (mg m^{-3})	45–1357	459	≒	16–2600	405	NS
Copepod abundance (ind. m^{-3})						
N. cristatus	0.4–31.4	12.2	≒	0–35.0	13.8	NS
N. flemingeri	18.6–59.2	38.5	>	0–18.1	7.2	2006 (SA, TR)
N. plumchrus	0–84.3	2.4	<	0–118.1	15.9	2006 (SA)
E. bungii	1.9–29.9	2.8	>	0.3–1.4	0.5	2004 (TR)
	13.1–66.0	21.6	<	5.6–135.7	44.6	2005 (SA)
M. pacifica	19.8–232.7	63.6	≒	2.3–277.6	65.9	NS

Trend, years and domains with significant east–west differences are shown. SA, subarctic current system; TR, transition domain.

of 2006. Abundance of *E. bungii* was greater in the west than in the east in the TR in 2004 but was greater in the east than in the west in the SA of 2005.

The east–west difference in total zooplankton abundance may be caused by the east–west difference in primary production. In the west, the iron concentration is higher than in the east (Suzuki *et al.*, 2002; Takata *et al.*, 2006; Kitayama *et al.*, 2009), and phytoplankton blooms of large-sized species are observed in spring (Tadokoro, 2000); therefore, the food chain is driven by grazing, especially in spring (Shinada *et al.*, 2001). In the east, because of iron limitation, small-sized phytoplankton blooms are observed from the late summer through autumn (Banse and English, 1999; Tadokoro, 2000). Shiomoto and Asami (1999) reported that the amount of primary production was greater in the west than in the east. Primary productivity is also higher in the west (Kawakami *et al.*, 2010). In the present study, Chl *a* was also higher in the west than in the east (Fig. 3b). Throughout the stations, the zooplankton community was dominated by small-sized cyclopoid copepods and calanoid nauplii (Fig. 4). Since their body sizes are small, they are considered to be able to quickly respond to changes in the amount of local primary production. Their greater abundance in the west than the east may therefore be a reflection of the higher Chl *a* stock and greater primary production in the west.

Zooplankton biomass did not show east–west differences (Table II), partly suggesting that the cyclopoid copepods and copepod nauplii are small in size and have little impact on the zooplankton biomass. Actually, large calanoid copepods (Mackas and Tsuda, 1999) and gelatinous zooplankton (Nishikawa *et al.*, 2001) are known to contribute mostly to the total zooplankton biomass, consistent with the present study (see online supplementary data Fig. S3).

Abundance of large calanoid copepods showed occasional east–west differences for a particular species and year (Table II). In 2006, *N. flemingeri* abundance was greater in the west, while *N. plumchrus* abundance was greater in the east. This may be attributed to the east–west differences in their phenology. *Neocalanus flemingeri* has a life span of 1 year in the east (Miller and Clemons, 1988) while some individuals have a life span of 2 years in the west (Tsuda *et al*., 1999) and C4 and C6F overwinter as diapause stages (Miller and Terazaki, 1989; Tsuda *et al*., 1999). *Neocalanus flemingeri* begins to store lipid from early copepod stages (Tsuda *et al*., 2001b) and grows more slowly than *N. plumchrus* (Tsuda *et al*., 1999; Kobari and Ikeda, 2001b). In addition to these factors, low temperature in the west (Fig. 3a) prevents the growth of *N. flemingeri* to the late copepodid stage for one year, instead it diapauses at C4 (Miller and Terazaki, 1989; Kobari and Ikeda, 2001b). In 2006, zooplankton sampling was conducted one month earlier than in the other years (Fig. 1b), and *N. flemingeri*, which occurs near to the surface in early phytoplankton blooms, increased their abundance in the surface. In 2006, the individuals in the west overwintering as C4 and those which recruited in the sampling year simultaneously appeared, accordingly the abundance in the west tended to be greater than in the other years (see online supplementary data Fig. S4).

Neocalanus plumchrus, similar in body size to *N. flemingeri*, appears in the surface layer three months later than *N. flemingeri* in the western subarctic Pacific (Miller and Clemons, 1988; Tsuda *et al*., 1999; Kobari and Ikeda, 2000, 2001a). *Neocalanus plumchrus* abundance was greater in the east than in the west in 2006 (see online supplementary data Fig. S5). The earlier sampling period in 2006 (Fig. 1b) may have led to the higher abundance of *N. flemingeri* but lower abundance of *N. plumchrus*. This influence is considered to be greater in the west, where temperature was low (Fig. 3a). Since few *N. plumchrus* occurred in the west of 2006, and the east–west difference (greater in the east) was observed only for this year.

Eucalanus bungii abundance was greater in the west in 2004 but was greater in the east in 2005 (Table II). This species, similar to *N. flemingeri*, differs in life spans between the eastern and western subarctic Pacific. In the west, most individuals live for 1 year while some live for 2 years (Tsuda *et al*., 2004; Shoden *et al*., 2005). In the east, most individuals live for 2 years, and some live for 3 years (Miller *et al*., 1984). Since the longevity is longer in the east, it may lead to greater abundance in the east. *Eucalanus bungii* reproduces in the surface layer (Shoden *et al*., 2005), and the magnitude of reproduction has been shown to be largely influenced by the local phytoplankton concentration (Kobari *et al*., 2007). The high Chl *a* in the west (Fig. 3b) might relate to the high abundance of *E. bungii* in the west. The higher abundances observed for *E. bungii* in both east and west in different years may be caused by these ambivalent factors that made abundance high in both the east and west.

East–west differences in zooplankton body size

Comparing PL of large calanoid copepods between the eastern and the western subarctic Pacific, *Neocalanus* spp. and *M. pacifica* were larger in the west than in the east in several sampling years and domains (Table I).

As the factors limiting the PL of large calanoid copepods, local temperature and Chl *a* are considered. Temperature and body size of aquatic invertebrates, including copepods, are known to have an inverse relationship (cf. Corkett and McLaren, 1978). For calanoid copepods, their relationships can be shown using the Bêlehrádek equation, $PL = a\,(T - \alpha)^b$, where PL is in millimeter, T is temperature (°C), a, α and b are parameters (Corkett and McLaren, 1978). For many copepods, b is known to be -2.05 (McLaren *et al*., 1969). The relationship between integrated mean temperature from 150 m to the surface and the average PL of large calanoid copepods were analyzed, and *N. cristatus* C5, *N. plumchrus* C5, *E. bungii* C5F/M and C6F and *M. pacifica* C6F showed significant inverse relationships with the temperature, expressed with Bêlehrádek equation (Fig. 7). Previously, inverse relationships between temperature and PL of *N. cristatus* and *N. plumchrus* C5 (Tsuda *et al*., 2001a; Kobari *et al*., 2003a) and *M. pacifica* C6F (Padmavati and Ikeda, 2002) have been reported. *Neocalanus cristatus* and *N. plumchrus* have almost identical life histories in the east and west: one generation per year (Kobari and Ikeda, 1999, 2001a). Therefore, local temperature in a sampling year is considered to have a direct impact on individual body size (Kobari *et al*., 2003a). *Metridia pacifica* has an east–west difference in generation length. The species has two generations per year in the west (Padmavati *et al*., 2004) but three generations per year in the east (Batchelder, 1985). Since *M. pacifica* can grow in a short time in the surface during summer (Padmavati *et al*., 2004), similar to *N. cristatus* and *N. plumchrus*, the PL of *M. pacifica* C6F is considered to be influenced by the temperature during sampling years.

In contrast, *N. flemingeri* C5 and *E. bungii* C4–C6 PL did not have significant relationships with the local temperature (Fig. 7). *Neocalanus flemingeri* has different generation lengths in the eastern and western subarctic Pacific, and some individuals in the west live for 2 years (Tsuda *et al*., 1999; Kobari and Ikeda, 2001b). The PL of *N. flemingeri* with multiple-year life span may be

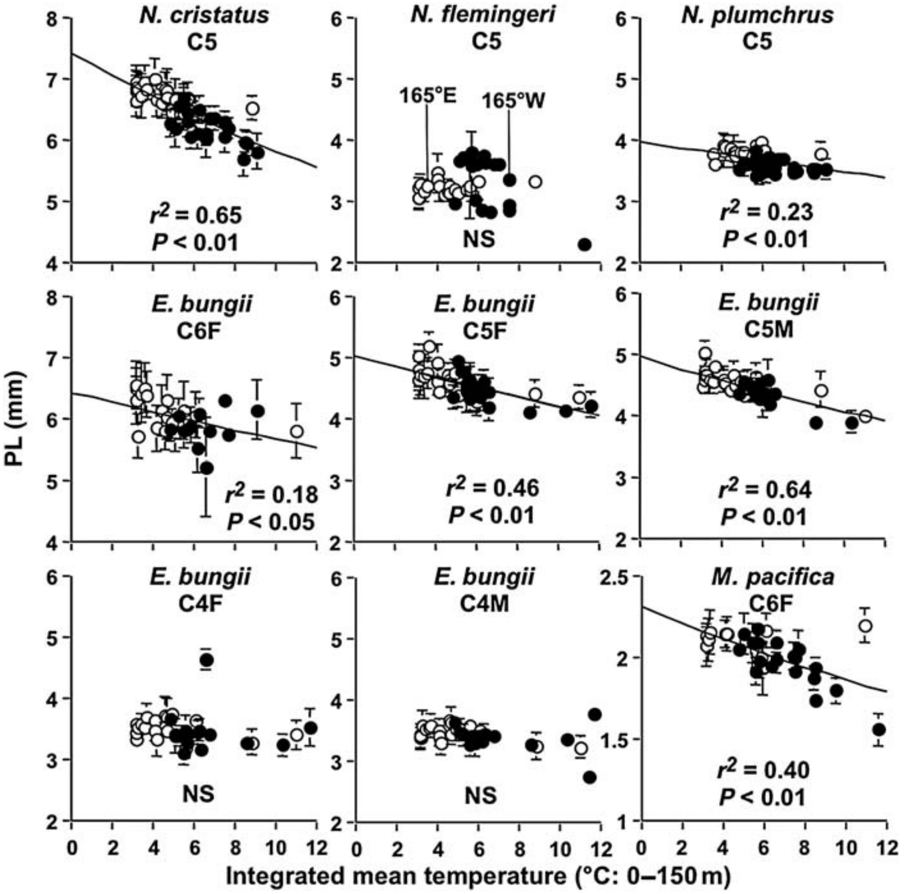

Fig. 7. Relationship between PL (mean ± 1 sd) of *N. cristatus*, *N. flemingeri* and *N. plumchrus* C5, *E. bungii* C4F–C6F and *M. pacifica* C6F and integrated mean temperature in each sampling station along 165°E (open circles) and 165°W (solid circles) lines in the North Pacific during the summers of 2003–2006. Analyses of regressions (Bêlehrádek equations) are shown for significant species/stages.

influenced by temperature prior to the sampling year. Thus, the PL of *N. flemingeri* may have little relationship with the temperature in the sampling years. *Eucalanus bungii* C4–C6 PL and local temperature also did not have any relationship (Fig. 7). Similar to *N. flemigeri*, the generation length of *E. bungii* is known to be multiple years. The generation length of *E. bungii* is 1–2 years in the west (Tsuda *et al.*, 2004; Shoden *et al.*, 2005) but 2–3 years in the east (Miller *et al.*, 1984). The PL of *E. bungii* C4–C6 showed no relationship with the local temperature (Table I). It may be partly because of the temperature prior to the sampling year affected the PL; therefore, the local temperature in a given year may have little effect on their PL.

The PL of *N. cristatus* C5, *E. bungii* C5F/M and C6F had positive relationships with Chl *a* standing stock from 150 m to the surface (Fig. 8). However, their coefficient of determination (r^2) was relatively lower than the relationships with temperature (Figs 7 and 8). The number of species/copepodid stage with a significant relationship with Chl *a* was fewer than with temperature. In a previous study, the PL of *N. cristatus* C5, a herbivorous copepod, was influenced by the local phytoplankton concentration (Kobari *et al.*, 2003a), and such a result agrees with this study. *Neocalanus flemigeri* has variable generation lengths in the eastern and western subarctic Pacific. In the west, some individuals live for 2 years (Tsuda *et al.*, 1999; Kobari and Ikeda, 2001b); therefore, phytoplankton density during sampling year may not have direct impact on the PL. *Neocalanus plumchrus* is known to be herbivorous as are the other *Neocalanus* spp. According to Tsuda *et al.* (2001b), however, *N. plumchrus* also grazes on ciliates and small crustaceans. Thus, only Chl *a* during sampling year may not explain the variability in their PL (Kobari *et al.*, 2003a). The PL of *E. bungii* C4F/M and Chl *a* had no relationship since the different generation lengths between east and west (Tsuda *et al.*, 2004; Shoden *et al.*, 2005) result in the Chl *a* during the sampling years did not directly impact on their PL.

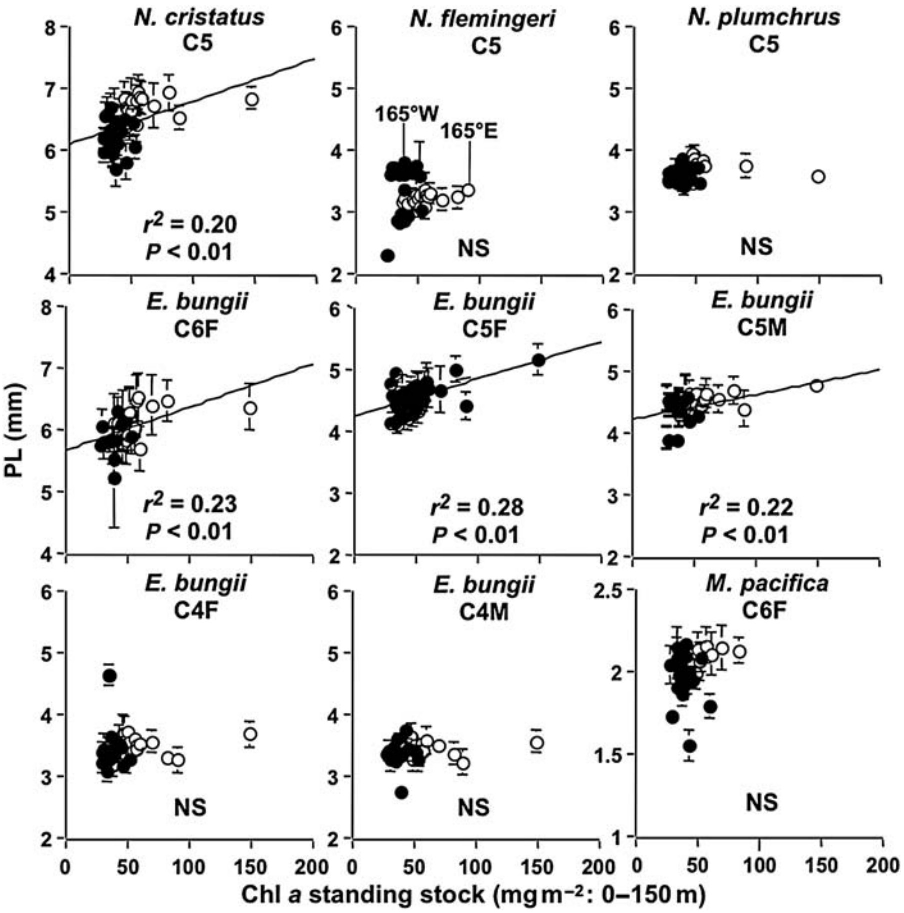

Fig. 8. Relationship between PL (mean ± 1 sd) of *N. cristatus*, *N. flemingeri* and *N. plumchrus* C5, *E. bungii* C4F–C6F and *M. pacifica* C6F and Chl *a* standing stock in each sampling station along 165°E (open circles) and 165°W (solid circles) lines in the North Pacific during the summers of 2003–2006. Analyses of linear regressions are shown for significant species/stages.

Metridia pacifica is small in size and has a short generation length of less than 1 year (Padmavati *et al*., 2004). Since they reproduce in the surface layer, it is more efficient that their C6F use acquired energy for reproduction than their growth. Thus, the PL of *M. pacifica* C6F may not have a clear relationship with Chl *a*.

CONCLUSION

In this study, in addition to previously reported east–west differences in oceanographic environments and the phytoplankton community, the east–west differences in the zooplankton community were analyzed. The east–west differences in zooplankton community were mainly characterized by the following two characteristics: (i) greater zooplankton abundance in the west and (ii) larger PL of calanoid copepods within same copepodid stage in the west. Differences in zooplankton abundances may be attributed to the east–west differences in the magnitude of primary production and the size of primary producers. Large body sizes of calanoid copepods in the west were primarily attributed to low temperature. Thus, the east–west differences in oceanographic environments, and phytoplankton community influence zooplankton abundance and body size. In the future, east–west differences in the zooplankton community should be evaluated from a perspective of the influence on higher trophic levels and the vertical carbon cycle for a more complete understanding of the ecosystem. Further studies are also needed on the east–west differences in the zooplankton community structure below 150 m as well as that in other seasons.

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