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An east-west comparison of the zooplankton community in the subarctic Pacific during summers of 2003-2006.

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Abstract

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* while the eastern region by high temperature and low chlorophyll-*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 0.335 and 0.100 mm mesh size Twin NORPAC net during the summers of 2003-2006. East-west differences in the zooplankton community were characterized as: 1) greater total zooplankton abundance in the west-and 2) larger body size of calanoid copepods within 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.

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 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 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 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 (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 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 the east (Shiomoto and Asami, 1999). Greater

primary productivity in the west leads to the POC flux being higher in the west than the east (Kawakami et al., 2010). Recent multi-sensor satellite data (Goes et al., 2004) also revealed higher Chl-*a* and primary production in the west than the east.

HNLC in the subarctic Pacific is attributed to the low iron concentration (Martin and Fitzwater, 1988). Iron is an important biochemical 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 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 fauna 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 understood. Species with identical life spans in the east and the west (*Neocalanus cristatus*: Kobari and Ikeda, 1999, *N. 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 (*N. 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). *N. 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 low temperature is considered as a factor of large-sized individuals (Tsuda et al., 2001a; Kobari et al., 2003a).

Thus, east-west differences in the mesozooplankton community of 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 is still limited, partly because of methodological problems. In order to make quantitative comparisons for higher trophic levels than zooplankton, 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 set 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 *M. pacifica* which are abundant in the zooplankton biomass (wet mass) 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 Faculty of Fisheries, Hokkaido University during the North Pacific cruises 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 June 6 to July 8. Along 165°W line, samples were collected at 5-16 stations from 39°00′N through 53°30′N from June 30 to August 2 (Fig. 1b). Zooplankton samples were collected by vertical hauls from 150 m to the surface using 45 cm net ring diameter, 0.33 and 0.10 mm 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 CTD (Sea-Bird Electronics, Inc., CTD-SBE9plus) or XCTD (Tsurumi Seiki Co., Ltd.). The temperature and salinity data have been published elsewhere (Hokkaido University, 2004, 2005, 2006, 2007). At each station, 1L surface water was collected with a bucket for chlorophyll-*a* (Chl-*a*) measurement, and 1L water samples from 10 discrete layers between the surface and 150 m (5, 10, 20, 30, 40, 50, 60, 75, 125, 150 m) were collected with Niskin bottles equipped to the CTD frame. Each water sample was filtered onto a Whatman GF/F filter using a vacuum pressure differential of less than 100 mm Hg. Filtered GF/F filter was immersed in N,N-Dimethylformamide (DMF) overnight in the dark for extraction of pigments. The fluorescence was measured by a Turner Designs fluorometer (Model 10-AU), and Chl-*a* was calculated.

Sample analysis

In the onshore laboratory, each 0.335 mm mesh zooplankton sample was divided into two subsamples by using Motoda plankton splitter (Motoda, 1959). A subsample was filtered onto a 0.10 mm mesh using an aspirator, and the zooplankton wet mass was measured by an electronic balance with a precision of 0.01 g. Each 0.100 mm mesh zooplankton sample was well mixed, and then 1/10 subsample was taken using a large bore pipet. This 1/10 subsample was observed under a dissecting microscope, and large calanoid copepods, small calanoid copepods, cyclopoid copepods, poecilostomatoid copepods, harpacticoid copepods, copepod nauplii, hydrozoans, amphipods, appendicularians, chaetognaths, doliolids, euphausiids, molluscans, ostracods, polychaetes and salps were sorted and counted.

In this study, the following five species were treated as large calanoid copepods: *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 have little day-night change in depth distribution (Kobari and Ikeda, 1999; 2001a, b; 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 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 (Fig. 2). 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, Fig. 2). 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,

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

where *MS* is mean copepodid stage; *i* is copepodid stage; N_i is 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 0.10 mm precision.

The wet masses of large calanoid copepods were calculated, and the compositions in the zooplankton biomass were computed. The wet masses of large calanoid copepods were calculated by multiplying the abundance of each copepodid stage by 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 test (PLSD).

Results

Hydrography

The subarctic front (boundary of subarctic current system [SA] and transition domain [TR]), where 4°C isothermal line 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 (Fig. 3). 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. 4). 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 (Figs. 3, 4).

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 (Fig. 3). Chl-*a* in other stations in the western subarctic Pacific was low, < 1 mg m^{-3} (Fig. 3). 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. 4). 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. 4).

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 in 42°N in 2003 (Fig. 5a). 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 0-150 m were compared between the east and the west, showed Chl-*a* was higher in the west (Fig. 5b). 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 total zooplankton community ranged 2,047-5,044 ind. m^{-3} in the western and 193-5,067 ind. m^{-3} in the eastern subarctic Pacific (Fig. 6). 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 total zooplankton community ranged 45-1,357 mg m^{-3} in the western and 16-2,600 mg m^{-3} in the eastern subarctic Pacific (Fig. 7). In 2003-2005, large calanoid copepods *N. cristatus* and *N. plumchrus* were abundant in the east and the west, and in 2004-2005. 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. 6), the wet mass did not show significant difference (Fig. 7).

Copepod population structure

N. cristatus abundance and mean copepodid stage did not show a significant east-west difference (Fig. 8). 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 low. The mean stage was earlier than in the northern TR, and C3 dominated in the eastern subarctic Pacific of 2004 and 2006.

N. 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 (Fig. 9). In 2006, the mean copepodid stage also showed a significant east-west difference. Thus, early copepodid stages (C1-C3) were abundant in the west while only C5 occurred in the east. In 2003-2005, only a few *N. flemingeri* C5 were observed during the sampling periods.

N. 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 (Fig. 10, $p < 0.05$). 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 stage (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 (Fig. 10).

E. bungii abundance showed a significant east-west difference in the TR of 2004, and 2-9 times greater abundance observed in the western than in the eastern subarctic Pacific (Fig. 11, $p < 0.05$). In the SA of 2005, both the abundance and mean copepodid stage showed a significant east-west difference, and had 5-6 times greater abundance of early copepodid stages in the east than 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.

M. pacifica abundance and mean copepodid stage did not show east-west differences in every sampling year and domain (Fig. 12). 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 (prosome length)

PL of 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. *N. 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. flemigeri* 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 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). *E. 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 ($p < 0.05$). *M. 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.

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 large calanoid copepods *N. cristatus* and *M. pacifica* did not vary between in 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 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 grazing food chain is driven, 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. 5b). Throughout the stations, the zooplankton community was dominated by small-sized cyclopoid copepods and calanoid nauplii (Fig. 6). 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 (Fig. 7).

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. *N. flemingeri* has a life span of one year in the east (Miller and Clemons, 1988) while some individuals have a life span of two years in the west (Tsuda et al., 1999) and C4 and C6F overwinter as diapause stage (Miller and Terazaki, 1989; Tsuda et al., 1999). *N. 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. 5a) prevents 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 bloom, 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 (Fig. 9).

N. 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). *N. plumchrus* abundance was greater in the east than in the west in 2006 (Fig. 10). 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. 5a). Since few *N. plumchrus* occurred in the west of 2006, and the east-west difference (greater in east) was observed only for this year.

E. bungii abundance was greater in the west in 2004 but was greater in the east in 2005 (Table I). This species, similar to *N. flemingeri*, differs in life spans between eastern and western subarctic Pacific. In the west, most individuals live for one year while some live for two years (Tsuda et al., 2004; Shoden et al., 2005). In the east, most individuals live for two 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. *E. 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. 5b) 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 prosome length (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). The hydrozoan *A. digitale* had two cohorts with different body sizes, and both cohorts were larger in the west than in the east.

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 prosome length (mm), *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. 13). 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. *N. 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). *M. 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. 13). *N. flemingeri* has different generation lengths in the eastern and western subarctic Pacific, and some individuals in the west live for two years (Tsuda et al., 1999; Kobari and Ikeda, 2001b). The PL of *N. flemingeri* with multiple-year life span may be 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. *E. bungii* C4-C6 PL and local temperature also did not have any relationship (Fig. 13). 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 had 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. 14). However, their coefficient of determination (r^2) was relatively lower than the relationships with temperature (Figs. 13, 14). 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. *N. flemigeri* has variable generation lengths in the eastern and western subarctic Pacific. In the west, some individuals live for two years (Tsuda et al., 1999; Kobari and Ikeda, 2001b), therefore; phytoplankton density during sampling year may not have direct impact on the PL. *N. plumchrus* is known to be herbivorous as 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 prosome length. *M. pacifica* is small in size and has a short generation length of less than one 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 three characteristics: 1) greater zooplankton abundance in the west, and 2) larger PL of calanoid copepods within same copepodid stage in the west. Differences in zooplankton abundance 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 are needed to be evaluated from a perspective of the influence on higher trophic levels and 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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417 **References**

418 Anma, G., Masuda, K., Kobayashi, G. *et al.* (1990) Oceanographic structures and changes around the
419 transition domain along 180° longitude, during June 1979-1988. *Bull. Fac. Fish. Hokkaido*
420 *Univ.*, **41**, 73-88.

421 Aramaki, T., Watanabe, S., Kuji, T. *et al.* (2001) The Okhotsk-Pacific seawater exchange in the
422 viewpoint of vertical profiles of radiocarbon around the Bussol' Strait. *Geophys. Res. Lett.*, **28**,
423 3971-3974.

424 Banse, K. and English, D. C. (1999) Comparing phytoplankton seasonality in the eastern and western
425 subarctic Pacific and the western Bering Sea. *Prog. Oceanogr.*, **43**, 235-288.

426 Batchelder, H. P. (1985) Seasonal abundance, vertical distribution, and life history of *Metridia pacifica*
427 (Copepoda: Calanoida) in the oceanic subarctic Pacific. *Deep-Sea Res.*, **32**, 949-964.

428 Batten, S. D., Welch, D. W. and Jonas, T. (2003) Latitudinal differences in the duration of development
429 of *Neocalanus plumchrus* copepodites. *Fish. Oceanogr.*, **12**, 201-208.

430 Batten, S. D., Hyrenbach, K. D., Sydeman, W. J. *et al.* (2006) Characterising meso-marine ecosystems
431 of the North Pacific. *Deep-Sea Res. II*, **53**, 270-290.

432 Corkett, C. J. and McLaren, I. A. (1978) The biology of *Pseudocalanus*. *Adv. Mar. Biol.*, **15**, 1-231.

433 Duce, R. A. and Tindale, N. W. (1991) Atmospheric transport of iron and its deposition in the ocean.
434 *Limnol. Oceanogr.*, **36**, 1715-1726.

435 Favorite, F., Dodimead, A. J. and Nasu, K. (1976) Oceanography of the subarctic Pacific region, 1960-
436 71. *Bull. Int. North Pac. Fish. Comm.*, **33**, 1-187.

437 Frost, B. W. and Kishi, M. J. (1999) Ecosystem dynamics in the eastern and western gyres of the
438 Subarctic Pacific - a review of lower trophic level modeling. *Prog. Oceanogr.*, **43**, 317-333.

439 Goes, J. I., Sasaoka, K., Gomes, H. R. *et al.* (2004) A comparison of the seasonality and interannual
440 variability of phytoplankton biomass and production in the western and eastern gyres of the
441 subarctic Pacific using multi-sensor satellite data. *J. Oceanogr.*, **60**, 75-91.

442 Harrison, P. J., Boyd, P. W., Varela, D. E. *et al.* (1999) Comparison of factors controlling
443 phytoplankton productivity in the NE and NW subarctic Pacific gyres. *Prog. Oceanogr.*, **43**,
444 205-234.

445 Harrison, P. J., Whitney, F. A., Tsuda, A. *et al.* (2004) Nutrient and plankton dynamics in the NE and
446 NW gyres of the subarctic Pacific Ocean. *J. Oceanogr.*, **60**, 93-117.

447 Hashimoto, S. and Shiomoto, A. (2000) High-west and low-east in April and no trend in August in
448 chlorophyll *a* concentration and standing stock in the subarctic Pacific in 1999. *Bull. Jap. Soc.*
449 *Fish. Oceanogr.*, **64**, 161-172.
450 Hattori, H. (1989) Bimodal vertical distribution and diel migration of the copepods *Metridia pacifica*,
451 *M. okhotensis* and *Pleuromamma scutullata* in the western North Pacific Ocean. *Mar. Biol.*,
452 **103**, 39-50.
453 Hokkaido University. (2004) *Data Record of Oceanographic Observation and Exploratory Fishing No.*
454 *47*. Saitoh, S.-I. (ed.), Faculty of Fisheries, Hokkaido University, Hakodate, 282 pp.
455 Hokkaido University. (2005) *Data Record of Oceanographic Observation and Exploratory Fishing No.*
456 *48*. Saitoh, S.-I. (ed.), Faculty of Fisheries, Hokkaido University, Hakodate, 303 pp.
457 Hokkaido University. (2006) *Data Record of Oceanographic Observation and Exploratory Fishing No.*
458 *49*. Saitoh, S.-I. (ed.), Faculty of Fisheries, Hokkaido University, Hakodate, 255 pp.
459 Hokkaido University. (2007) *Data Record of Oceanographic Observation and Exploratory Fishing No.*
460 *50*. Saitoh, S.-I. (ed.), Faculty of Fisheries, Hokkaido University, Hakodate, 285 pp.
461 Ikeda, T., Shiga, N. and Yamaguchi, A. (2008) Structure, biomass distribution and trophodynamics of
462 pelagic ecosystem in the Oyashio region, western subarctic Pacific. *J. Oceanogr.*, **64**, 339-354.
463 Johnson, M. W. (1937) The developmental stages of the copepod *Eucalanus elongatus* Dana var.
464 *bungii* Giesbrecht. *Trans. Am. Microsc. Soc.*, **56**, 79-98.
465 Kawakami, H., Honda, M. C., Matsumoto, K. *et al.* (2010) East-west distribution of POC fluxes
466 estimated from ^{234}Th in the northern North Pacific in autumn. *J. Oceanogr.*, **66**, 71-83.
467 Kitayama, S., Kuma, K., Manabe, E. *et al.* (2009) Controls on iron distributions in the deep water
468 column of the North Pacific Ocean: iron (III) hydroxide solubility and marine humic-type
469 dissolved organic matter. *J. Geophys. Res.*, **114**, C08019, doi: 10.1029/2008JC004754.
470 Kobari, T. and Ikeda, T. (1999) Vertical distribution, population structure and life cycle of *Neocalanus*
471 *cristatus* (Crustacea: Copepoda) in the Oyashio region, with notes on its regional variations.
472 *Mar. Biol.*, **134**, 683-696.
473 Kobari, T. and Ikeda, T. (2000). Life cycle of *Neocalanus* species in the Oyashio region. *Bull.*
474 *Plankton Soc. Jpn.*, **47**, 129-135.
475 Kobari, T. and Ikeda, T. (2001a) Ontogenetic vertical migration and life cycle of *Neocalanus*
476 *plumchrus* (Crustacea: Copepoda) in the Oyashio region, with notes on regional variations in
477 body sizes. *J. Plankton Res.*, **23**, 287-302.

478 Kobari, T. and Ikeda, T. (2001b). Life cycle of *Neocalanus flemingeri* (Crustacea: Copepoda) in the
479 Oyashio region, western subarctic Pacific, with notes on its regional variations. *Mar. Ecol.*
480 *Prog. Ser.*, **209**, 243-255.
481 Kobari, T., Tadokoro, K., Shiomoto, A. *et al.* (2003a) Geographical variations in prosome length and
482 body weight of *Neocalanus* copepods in the North Pacific. *J. Oceanogr.*, **59**, 3-10.
483 Kobari, T, Shinada, A. and Tsuda, A. (2003b). Functional roles of interzonal migrating
484 mesozooplankton in the western subarctic Pacific. *Prog. Oceanogr.*, **57**, 279-298.
485 Kobari, T., Tadokoro, K., Sugisaki, H. *et al.* (2007) Response of *Eucalanus bungii* to oceanographic
486 conditions in the western subarctic Pacific: retrospective analysis of the Odate Collections.
487 *Deep-Sea Res. II*, **54**, 2748-2759.
488 Longhurst, A. R. (2007) *Ecological Geography of the Sea*. 2nd edn. Academic Press, Oxford, 527 pp.
489 Mackas , D. L. and Tsuda, A. (1999) Mesozooplankton in the eastern and western subarctic Pacific:
490 community structure, seasonal life histories, and interannual variability. *Prog. Oceanogr.*, **43**,
491 335-363.
492 Marin, V. (1987) The oceanographic structure of the eastern Scotia Sea-IV. Distribution of copepod
493 species in relation to hydrography in 1981. *Deep-Sea Res. I*, **34**, 105-121.
494 Martin, J. H. and Fitzwater, S. E. (1988) Iron deficiency limits phytoplankton growth in the north-east
495 Pacific subarctic. *Nature*, **331**, 341-343.
496 McLaren, I. A., Corkett, C. J. and Zillioux, E. J. (1969) Temperature adaptations of copepod eggs from
497 the arctic to the tropics. *Biol. Bull.*, **137**, 486-493.
498 Miller, C. B., Frost, B. W., Batchelder, H. P. *et al.* (1984). Life histories of large, grazing copepods in
499 a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in
500 the Northeast Pacific. *Prog. Oceanogr.*, **13**, 201-243.
501 Miller, C. B. and Clemons, M. J. (1988). Revised life history analysis for large grazing copepods in
502 the subarctic Pacific Ocean. *Prog. Oceanogr.*, **20**, 293-313.
503 Miller, C. B. and Terazaki, M. (1989). The life histories of *Neocalanus flemingeri* and *Neocalanus*
504 *plumchrus* in the Sea of Japan. *Bull. Plankton Soc. Jpn*, **36**, 27-41.
505 Miller, C. B., Frost, B. W., Wheeler, P. A. *et al.* (1991) Ecological dynamics in the subarctic Pacific, a
506 possibly iron-limited ecosystem. *Limnol. Oceanogr.*, **36**, 1600-1615.
507 Motoda, S. (1957) North Pacific standard plankton net. *Inf. Bull. Planktol. Jpn.*, **4**, 13-15.
508 Motoda, S. (1959) Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.*, **7**, 73-94.

509 Nishikawa, J., Nishida, S., Moku, M. et al. (2001) Biomass, abundance, and vertical distribution of
510 micronekton and large gelatinous zooplankton in the subarctic Pacific and the Bering Sea
511 during the summer of 1997. J. Oceanogr., 57, 361-375.
512 Nishioka, J., Ono, T., Saito, H. *et al.* (2007) Iron supply to the western subarctic Pacific: importance of
513 iron export from the Sea of Okhotsk. *J. Geophys. Res.*, **112**, C10012,
514 doi:10.1029/2006JC004055.
515 Padmavati, G. and Ikeda, T. (2002) Development of *Metridia pacifica* (Crustacea: Copepoda) reared at
516 different temperatures in the laboratory. *Plankton Biol. Eco.*, **49**, 93-96.
517 Padmavati G., Ikeda, T. and Yamaguchi, A. (2004) Life cycle, population structure and vertical
518 distribution of *Metridia* spp. (Copepoda: Calanoida) in the Oyashio region (NW Pacific Ocean).
519 *Mar. Ecol. Prog. Ser.*, **270**, 181-198.
520 Pearcy, W. G., Fisher, J. P., Anma, G. *et al.* (1996) Species associations of epipelagic nekton of the
521 North Pacific Ocean, 1978-1993. *Fish. Oceanogr.*, **5**, 1-20.
522 Raven, J. A., Evans, M. C. W. and Korb, R. E. (1999) The role of trace metals in photosynthetic
523 electron transport in O_2-evolving organisms. *Photosyn. Res.*, **60**, 111-150.
524 Shinada, A., Ikeda, T., Ban, S. *et al.* (2001) Seasonal dynamics of plankton food chain in the Oyashio
525 region, western subarctic Pacific. *J. Plankton Res.*, **23**, 1237-1248.
526 Shiomoto, A. and Asami, H. (1999) High-west and low-east distribution patterns of chlorophyll *a*,
527 primary productivity and diatoms in the subarctic North Pacific surface waters, midwinter 1996.
528 *J. Oceanogr.*, **55**, 493-503.
529 Shiomoto, A. and Hashimoto, S. (2000) Comparison of east and west chlorophyll *a* standing stock and
530 oceanic habitat along the Transition Domain of the North Pacific. *J. Plankton Res.*, **22**, 1-14.
531 Shoden, S., Ikeda, T. and Yamaguchi, A. (2005) Vertical distribution, population structure and life
532 cycle of *Eucalanus bungii* (Copepoda: Calanoida) in the Oyashio region, with notes on its
533 regional variations. *Mar. Biol.*, **146**, 497-511.
534 Suzuki, K., Liu, H. and Saino, T. *et al.* (2002) East-west gradients in the photosynthetic potential of
535 phytoplankton and iron concentration in the subarctic Pacific Ocean during early summer.
536 *Limnol. Oceanogr.*, **47**, 1581-1594.
537 Tadokoro, K. (2000) Geographical variation of Chl-*a* seasonality in the subarctic North Pacific Ocean.
538 *Bull. Plankton Soc. Jpn.*, **47**, 111-115.

539 Takahashi, K., Kuwata, A., Sugisaki, H. *et al.* (2009) Downward carbon transport by diel vertical
540 migration of the copepods *Metridia pacifica* and *Metridia okhotensis* in the Oyashio region of
541 the western subarctic Pacific Ocean. *Deep-Sea Res. I*, **56**, 1777-1791.
542 Takata, H., Kuma, K., Saitoh, Y. *et al.* (2006) Comparing the vertical distribution of iron in the eastern
543 and western North Pacific Ocean. *Geophys. Res. Lett.*, **33**, L02613, doi:
544 10.1029/2005GL024538.
545 Tseitlin, V. B., Rudyakov, Y. A. and Kitain, V. Y. (1997) Zooplankton biomass distribution in the
546 surface layer of the Pacific Ocean. *Russ. Acad. Sci. Oceanol.*, **37**, 75-82.
547 Tsuda, A., Saito, H. and Kasai, H. (1999) Life histories of *Neocalanus flemingeri* and *Neocalanus*
548 *plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. *Mar. Biol.*, **135**, 533-544.
549 Tsuda, A., Saito, H. and Kasai, H. (2001a) Geographical variation of body size of *Neocalanus cristatus*,
550 *N. plumchrus* and *N. flemingeri* in the subarctic Pacific and its marginal seas: implications for
551 the origin of large form of *N. flemingeri* in the Oyashio area. *J. Oceanogr.*, **57**, 341-352.
552 Tsuda, A., Saito, H. and Kasai, H. (2001b) Life history strategies of subarctic copepods *Neocalanus*
553 *flemingeri* and *N. plumchrus*, especially concerning lipid accumulation patterns. *Plankton Biol.*
554 *Ecol.*, **48**, 52-58.
555 Tsuda, A., Saito, H. and Kasai, H. (2004) Life histories of *Eucalanus bungii* and *Neocalanus cristatus*
556 (Copepoda: Calanoida) in the western subarctic Pacific Ocean. *Fish. Oceanogr.*, **13**, 10-20.
557 Vinogradov, M. E. (1970) *Vertical Distribution of the Oceanic Zooplankton.* Israel Program for
558 Scientific Translations, Jerusalem, 339 pp.
559 Whitney, F. A., Wong, C. S. and Boyd, P. W. (1999) Interannual variability in nitrate supply to surface
560 waters of the North-east Pacific Ocean. *Mar. Ecol. Prog. Ser.*, **170**, 15-23.
561 Yamaguchi, A., Ikeda, T., Watanabe, Y., et al. (2004) Vertical distribution patterns of pelagic copepods
562 as view from the predation pressure hypothesis. *Zool. Stud.*, **43**, 475-485.

Table and Figure legends

Table I. Range and median of prosome length (mm, mean ± sd.) of *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus* C5, *Eucalanus bungii* C4F- C6F and *Metridia pacifica* C6F along 165°E and 165°W lines in the North Pacific during the summers of 2003-2006. 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. Trend, years and domains with significant east-west differences are shown. SA: Subarctic current system, TR: Transition domain.

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

Fig. 2. *Metridia pacifica* abundance (mean ± 1 sd) of each copepodid stage during day and night in the subarctic current system (SA) and transitional domain (TR) along 165°E and 165°W lines. Significant differences are marked with asterisks (*U*-test; $p < 0.05$), and their day:night ratios are also shown.

Fig. 3. Vertical profiles of temperature, salinity and chlorophyll-*a* along 165°E line in the western 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.

Fig. 4. Same as Fig. 3, but for 165°W in the eastern subarctic Pacific.

Fig. 5. Integrated mean temperature (a) and chlorophyll-*a* standing stock (b) 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 approximate positions of the subarctic front (cf. Figs. 3, 4).

Fig. 6. 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 approximate positions of the subarctic front (cf. Figs. 3, 4).

592 Fig. 7. Zooplankton wet mass and the composition of large copepods and hydrozoan *Aglantha digitale*
593 in the western (165°E, left) and eastern (165°W, right) subarctic Pacific during the summers of
594 2003-2006. Triangles indicate approximate positions of the subarctic front (cf. Figs. 3, 4).
595 Fig. 8. Abundance, composition of each copepodid stage (C1-C5) and mean stage of *Neocalanus*
596 *cristatus* in the western (165°E, left) and eastern (165°W, right) subarctic Pacific during the
597 summers of 2003-2006. Vertical dashed lines indicate approximate positions of the subarctic
598 front (cf. Figs. 3, 4). Open symbols in abundance indicate no occurrence.
599 Fig. 9. Same as Fig. 8, but for *Neocalanus flemingeri.*
600 Fig. 10. Same as Fig. 8, but for *Neocalanus plumchrus.*
601 Fig. 11. Same as Fig. 8, but for *Eucalanus bungii*.
602 Fig. 12. Same as Fig. 8, but for *Metridia pacifica*.
603 Fig. 13. Relationship between prosome length (mean ± 1 sd) of *Neocalanus cristatus*, *N. flemingeri*
604 and *N. plumchrus* C5, *Eucalanus bungii* C4F-C6F and *Metridia pacifica* C6F and integrated
605 mean temperature in each sampling station along 165°E (open circles) and 165°W (solid
606 circles) lines in the North Pacific during the summers of 2003-2006. Analyses of regressions
607 (Bêlehrádek equations) are shown for significant species/stages.
608 Fig. 14. Relationship between prosome length (mean ± 1 sd) of *Neocalanus cristatus*, *N. flemingeri*
609 and *N. plumchrus* C5, *Eucalanus bungii* C4F-C6F and *Metridia pacifica* C6F and chlorophyll-*a*
610 standing stock in each sampling station along 165°E (open circles) and 165°W (solid circles)
611 lines in the North Pacific during the summers of 2003-2006. Analyses of linear regressions are
612 shown for significant species/stages.

Table I (Saito *et al.*)

Speices	Stag	West (165°E) Range	West (165°E) Median	Trend	East (165°W) Range	East (165°W) Median	Year (Domain)
Neocalanus 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, 2006 (TR)
Eucalanus 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
Metridia pacifica	C6F	2.08-2.16	2.11	>	1.74-2.14	2.04	2005, 2006 (SA, TR)

Table II (Saito *et al.*)

Parameters	West (165°E) Range	West (165°E) Median	Trend	East (165°W) Range	East (165°W) 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)
Chlorophyll-*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})	2,047-	3,217	>	193-2,928	2,592	2003 (TR), 2004 (TR), 2006 (TR)
Wet mass (mg m^{-3})	45-1,357	459	≠	16-2,600	405	NS
Copepod abundance (ind. m^{-3})						
Neocalanus 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)
Eucalanus 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)
Metridia pacifica	19.8-232.7	63.6	≠	2.3-277.6	65.9	NS

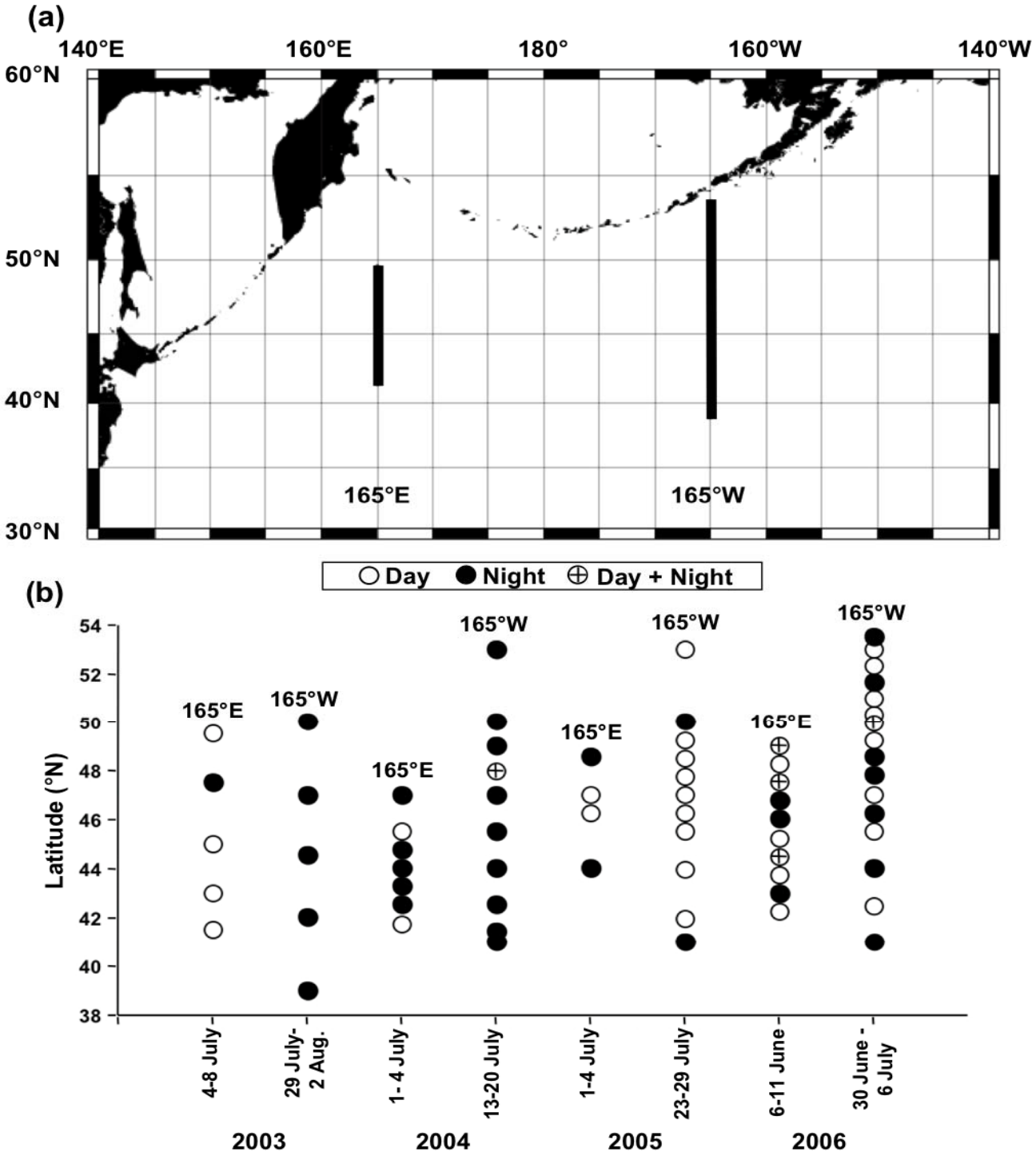


Fig. 1 (Saito *et al.*)

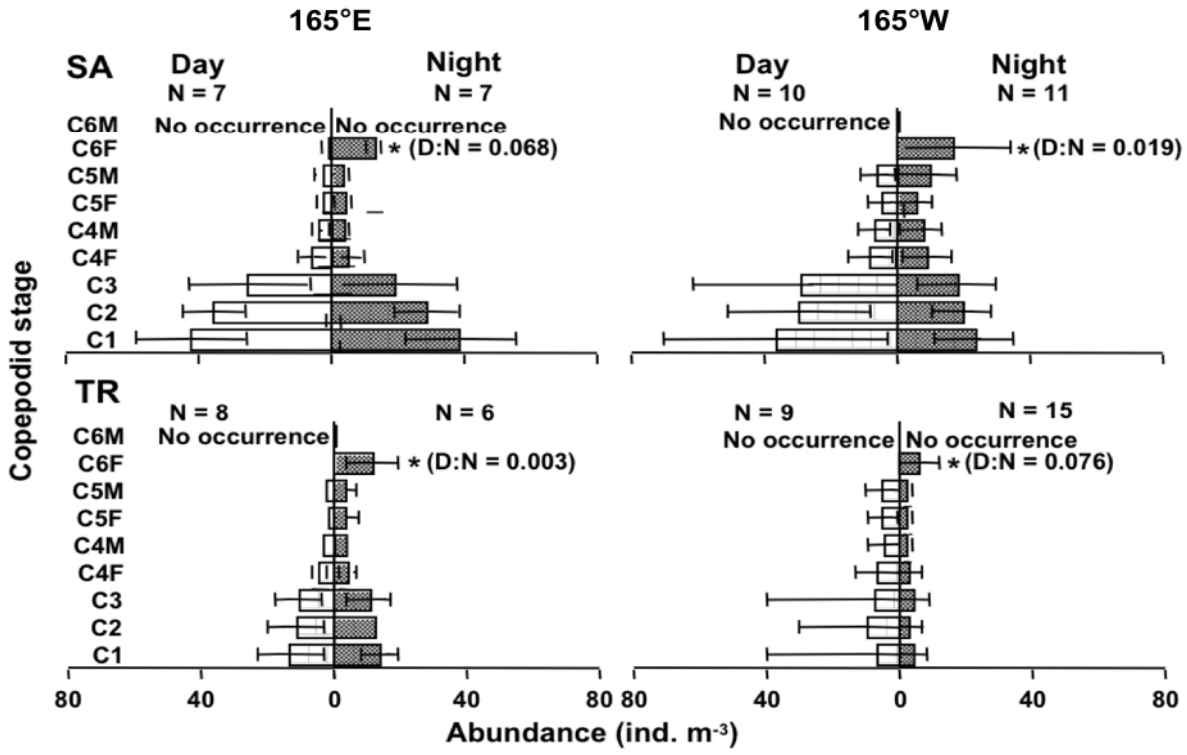


Fig. 2 (Saito *et al.*)

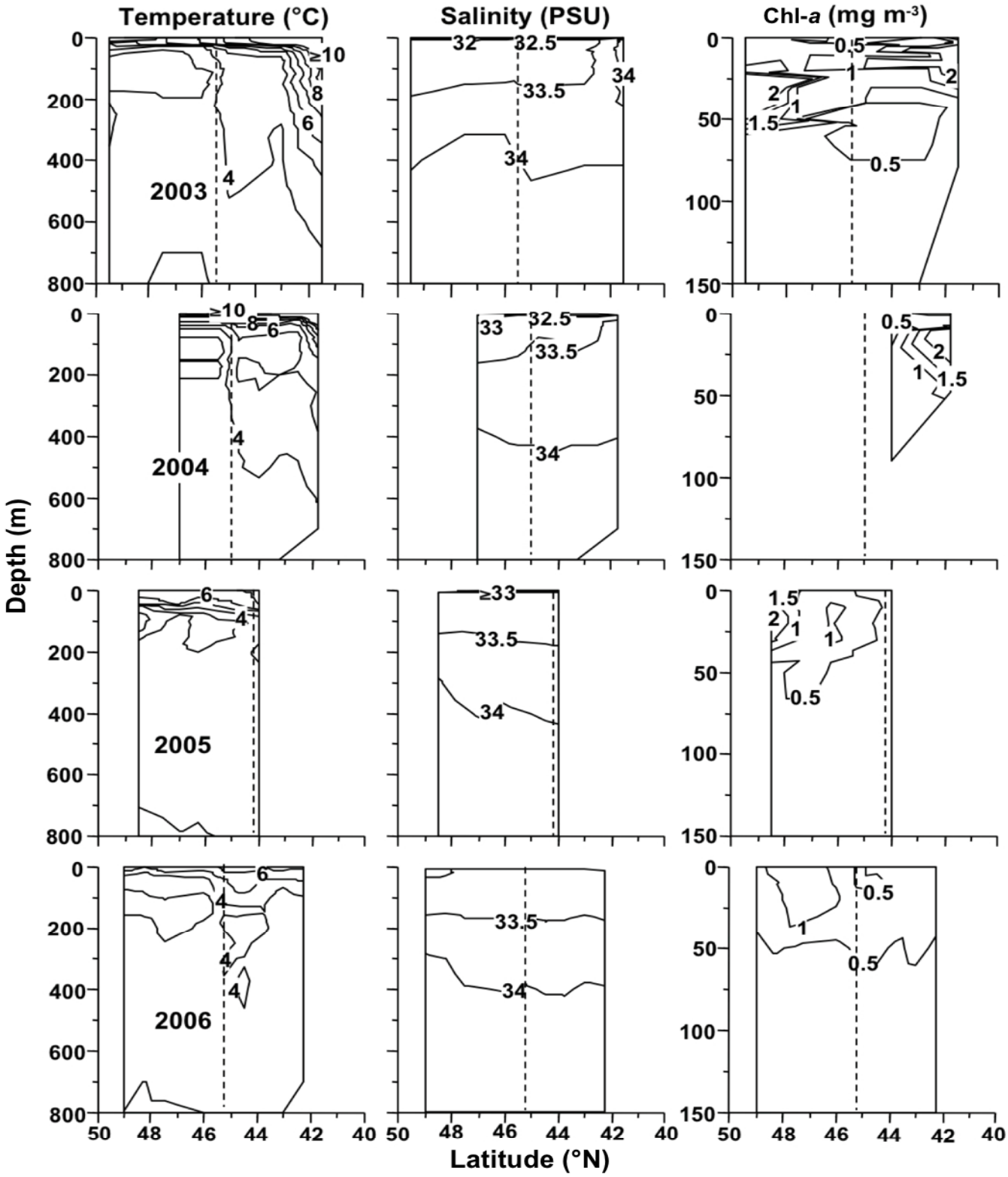


Fig. 3 (Saito *et al*.)

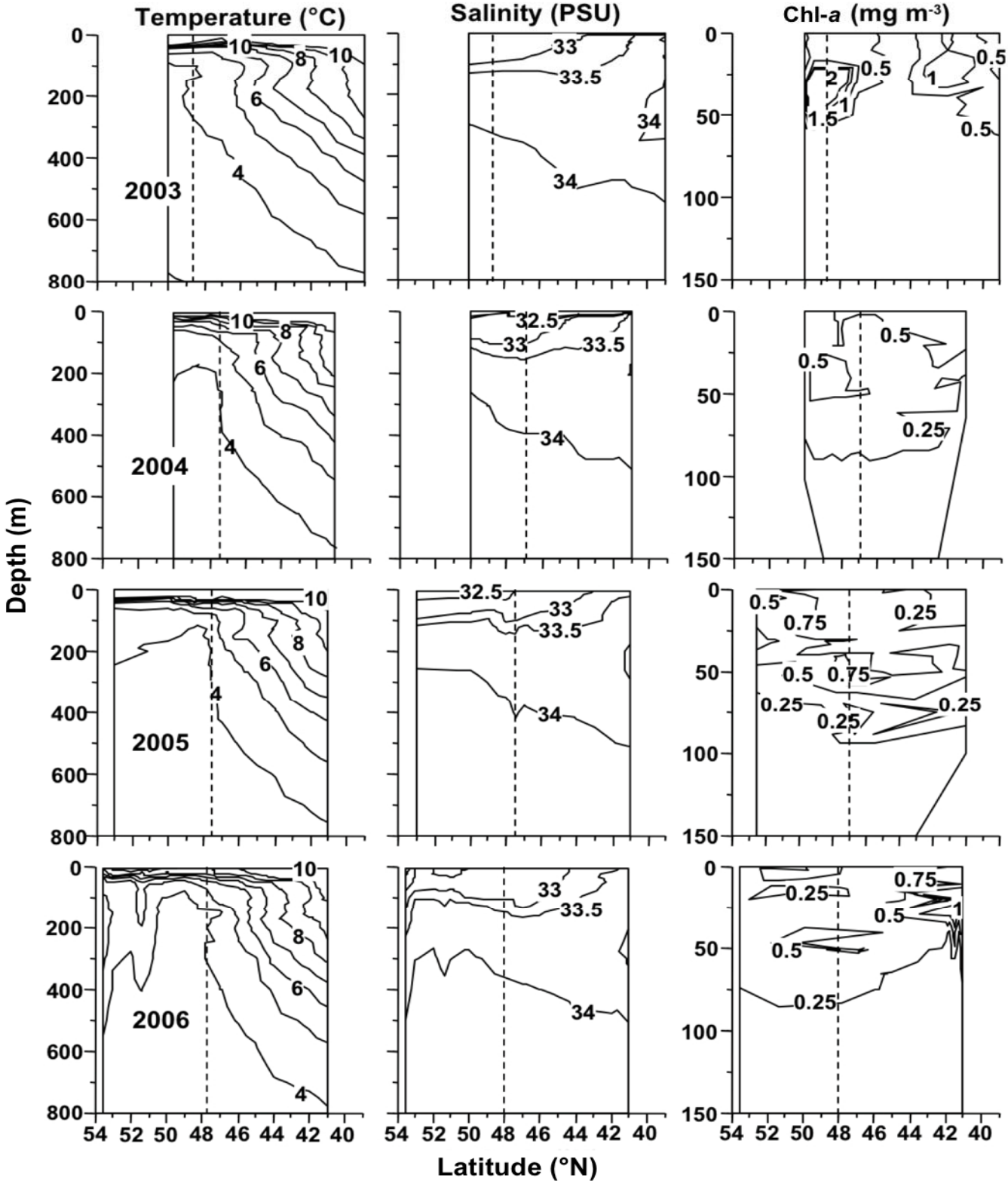


Fig. 4 (Saito *et al.*)

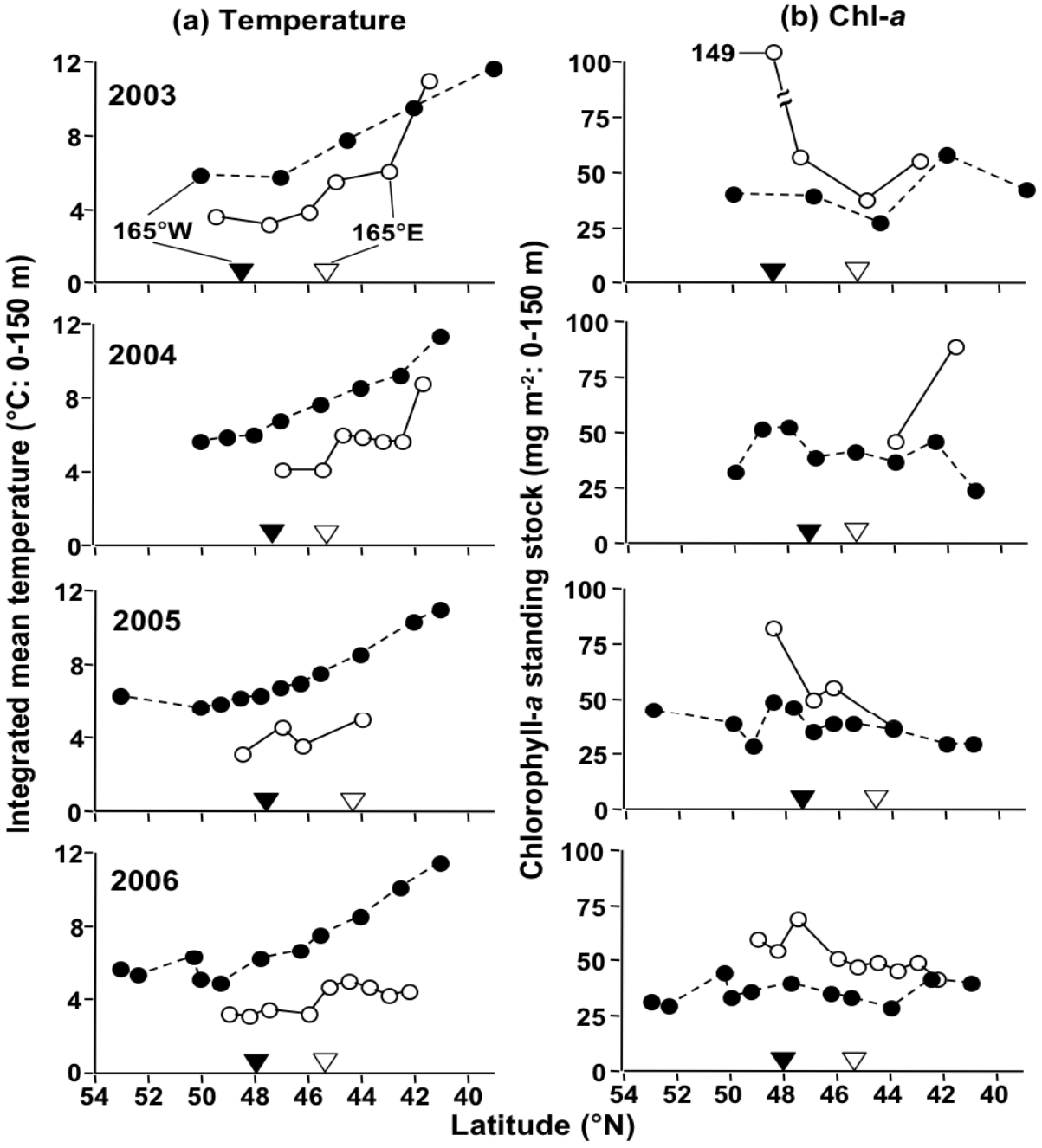


Fig. 5 (Saito *et al.*)

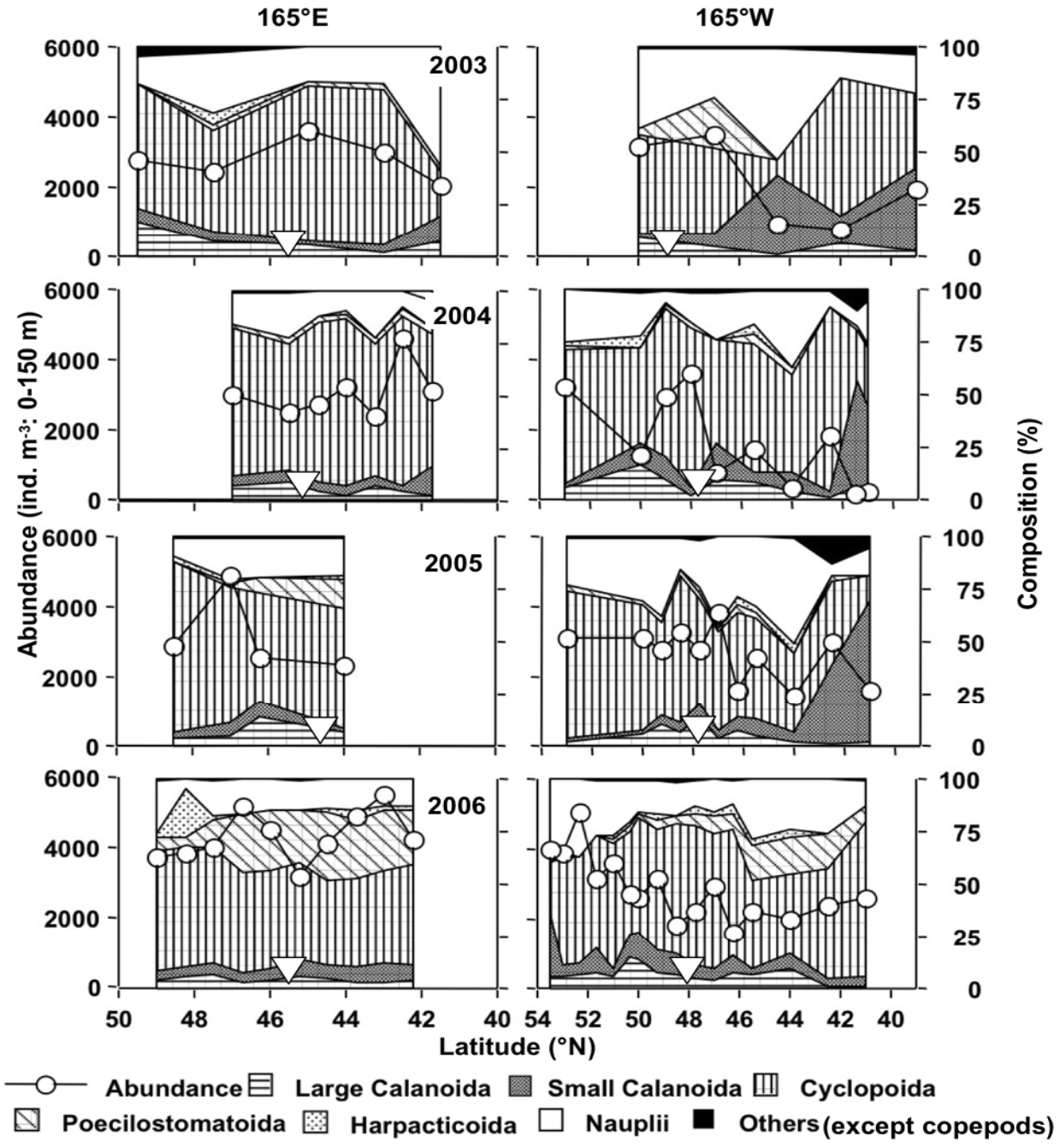


Fig. 6 (Saito *et al.*)

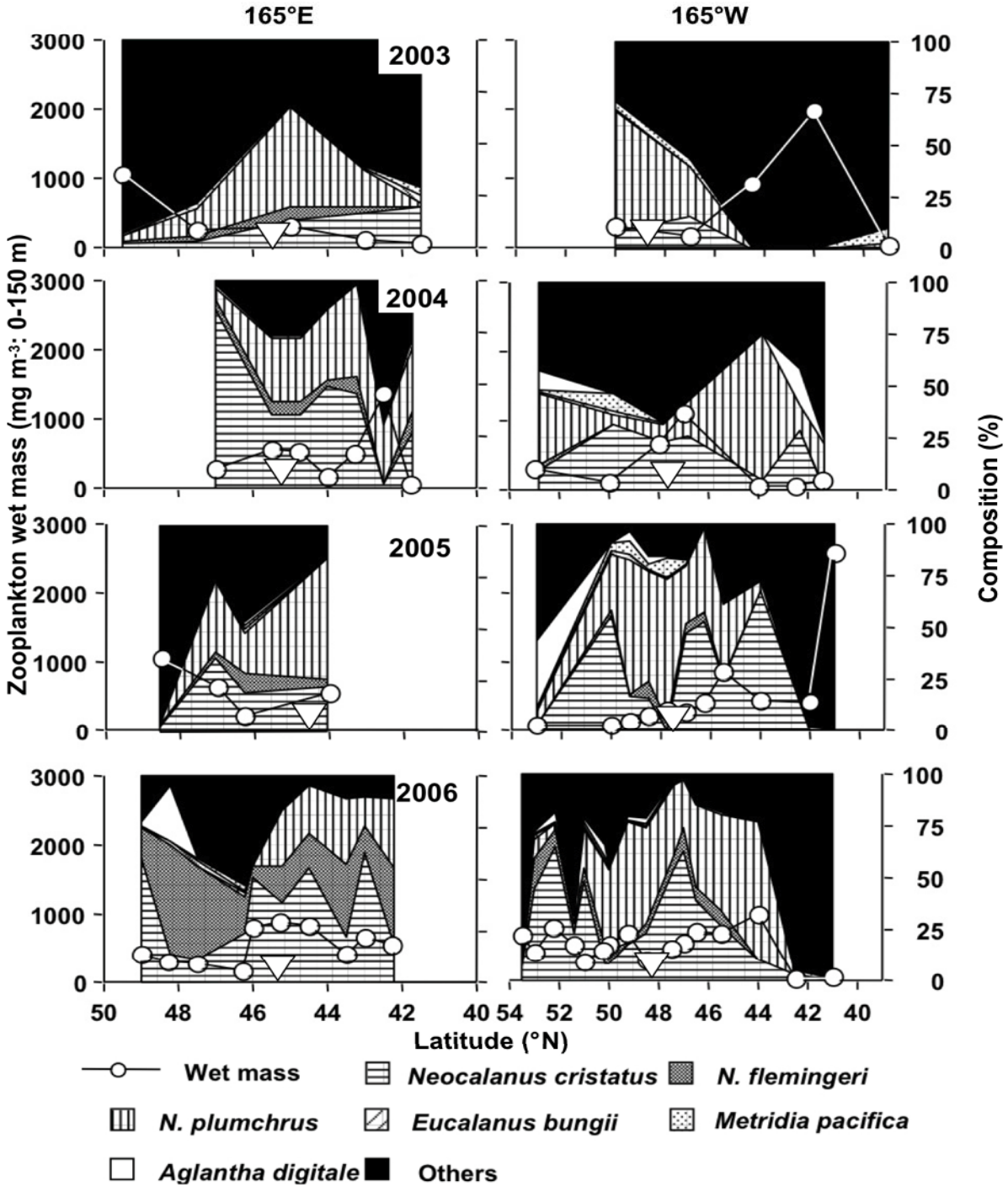


Fig. 7 (Saito *et al.*)

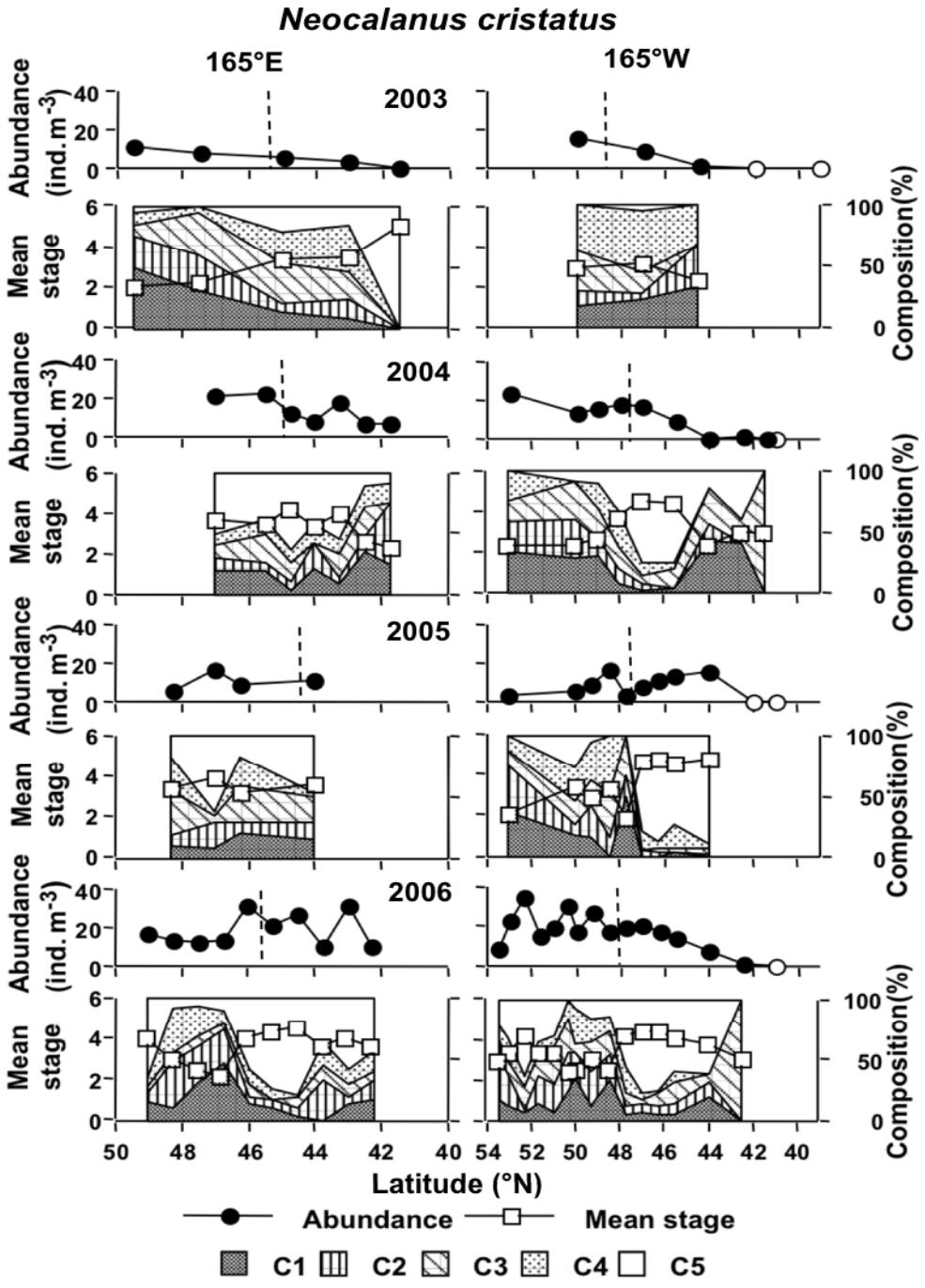


Fig. 8 (Saito *et al.*)

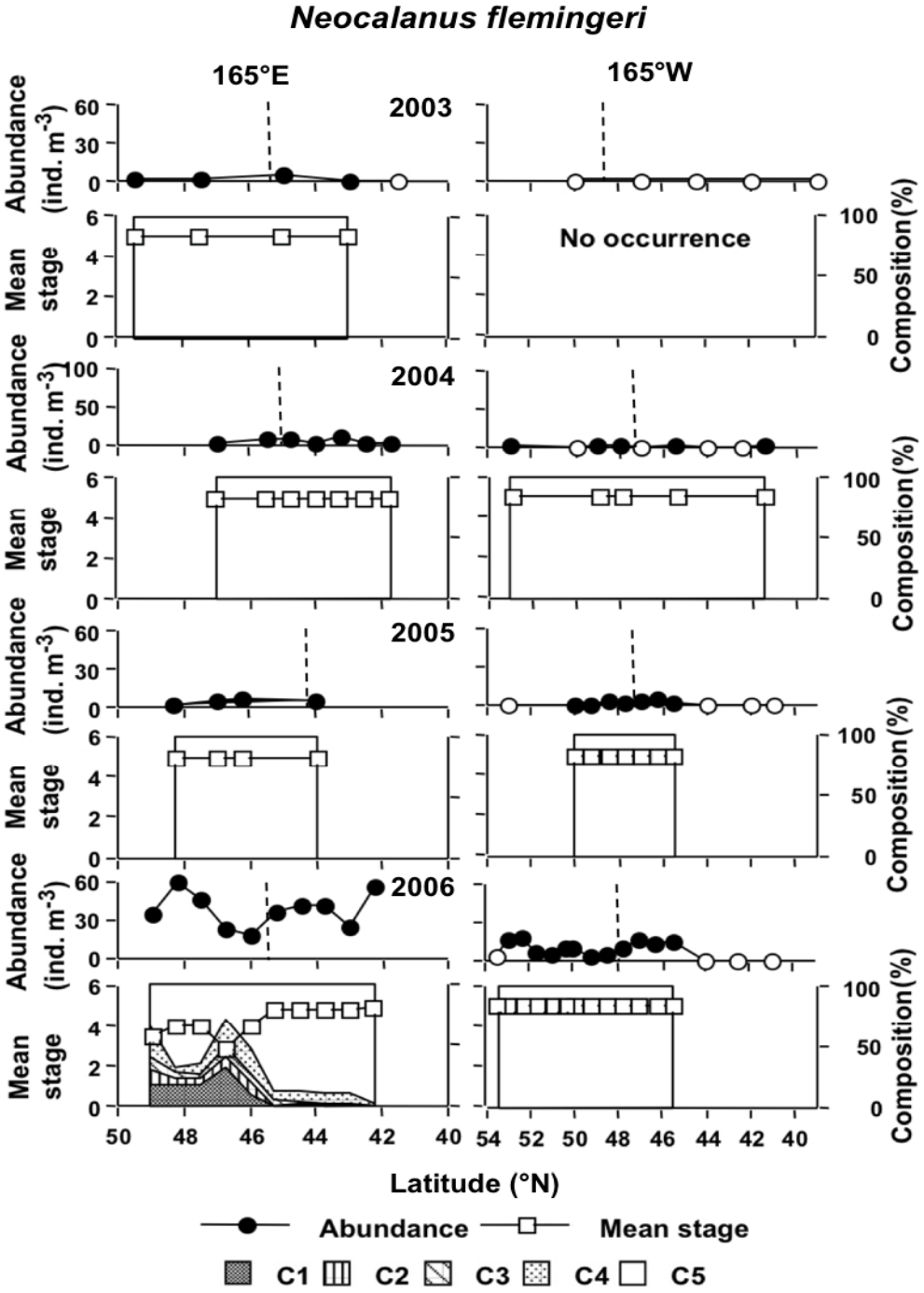


Fig. 9 (Saito *et al.*)

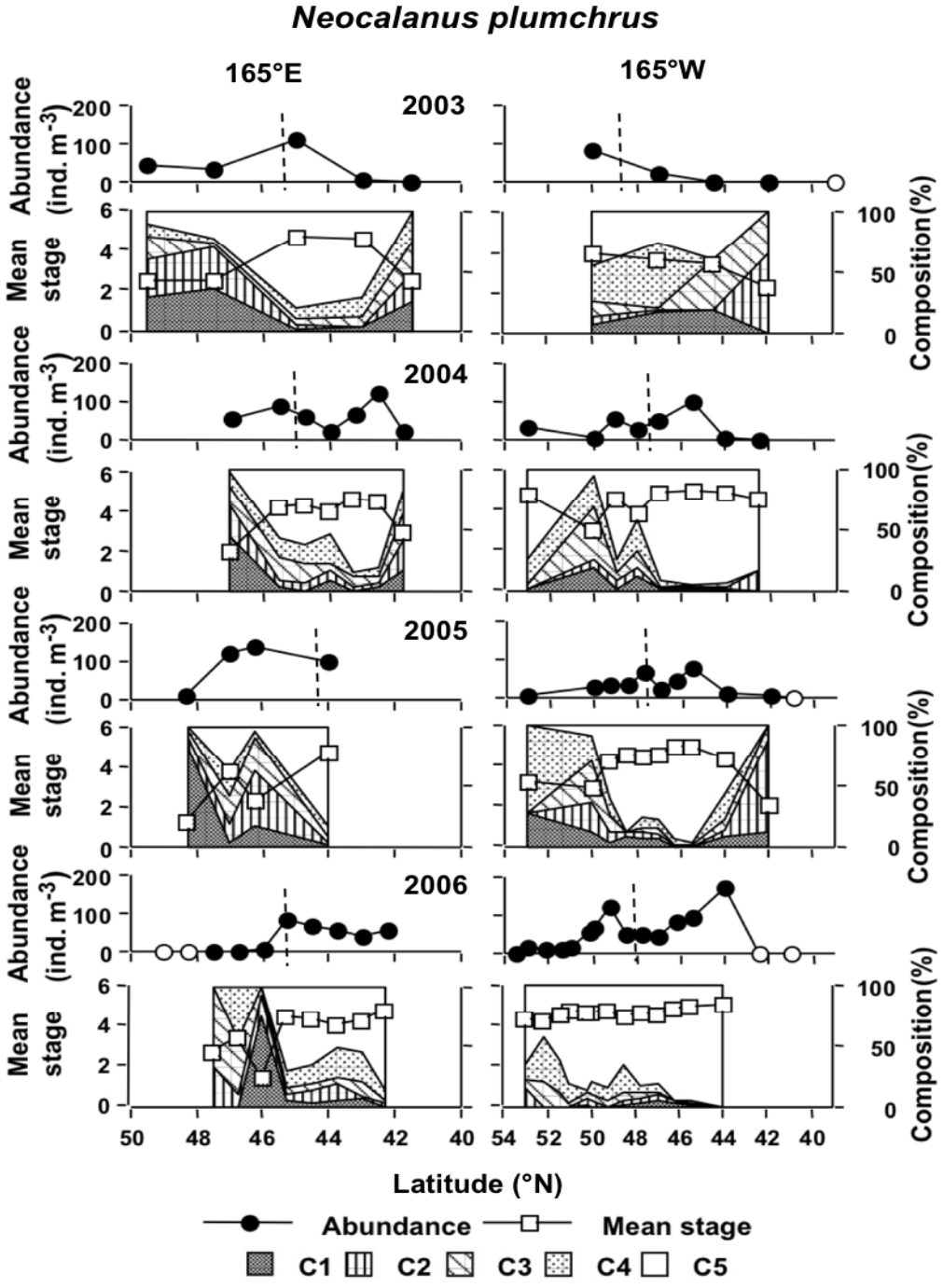


Fig. 10 (Saito *et al.*)

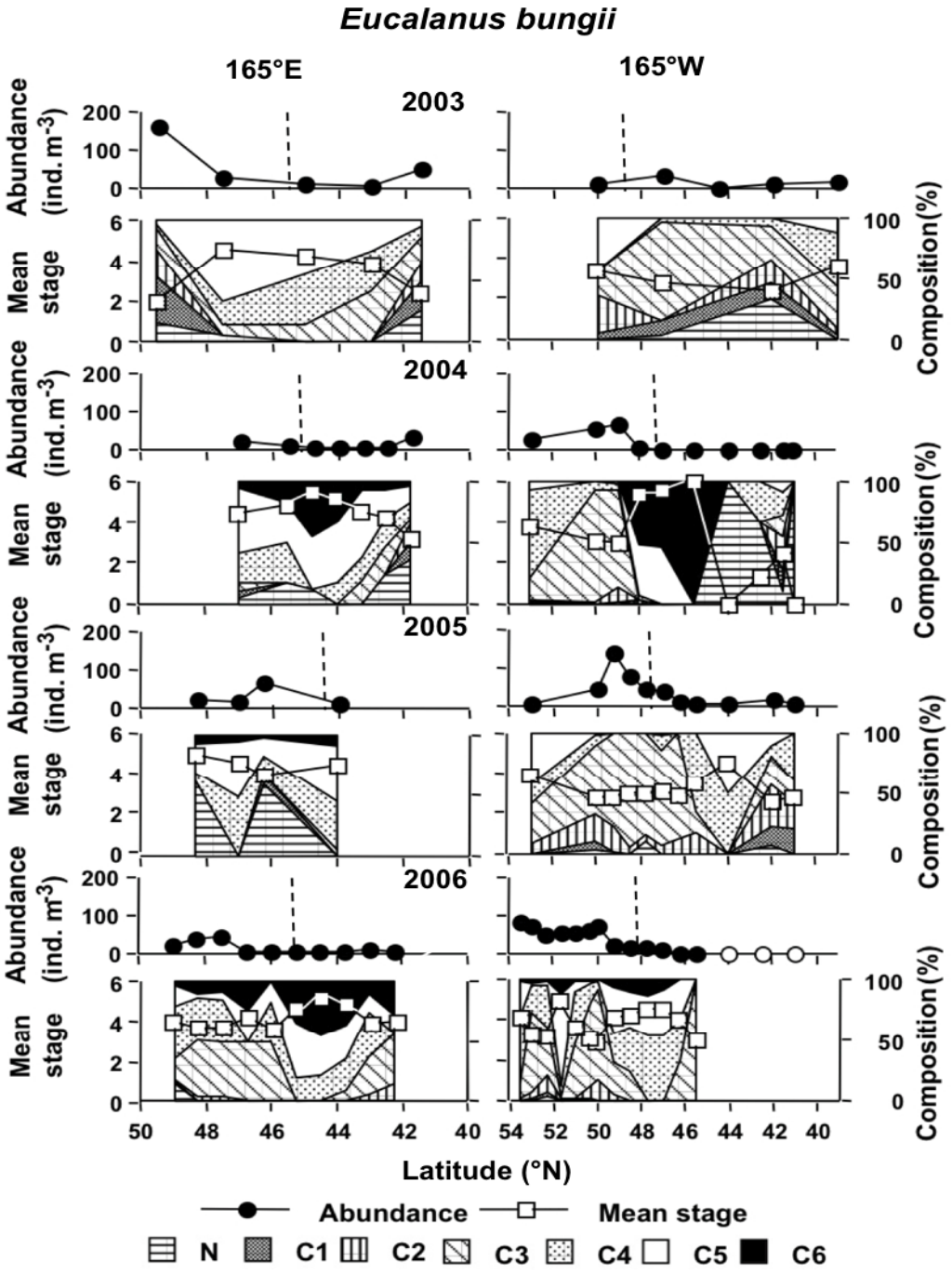


Fig. 11 (Saito *et al.*)

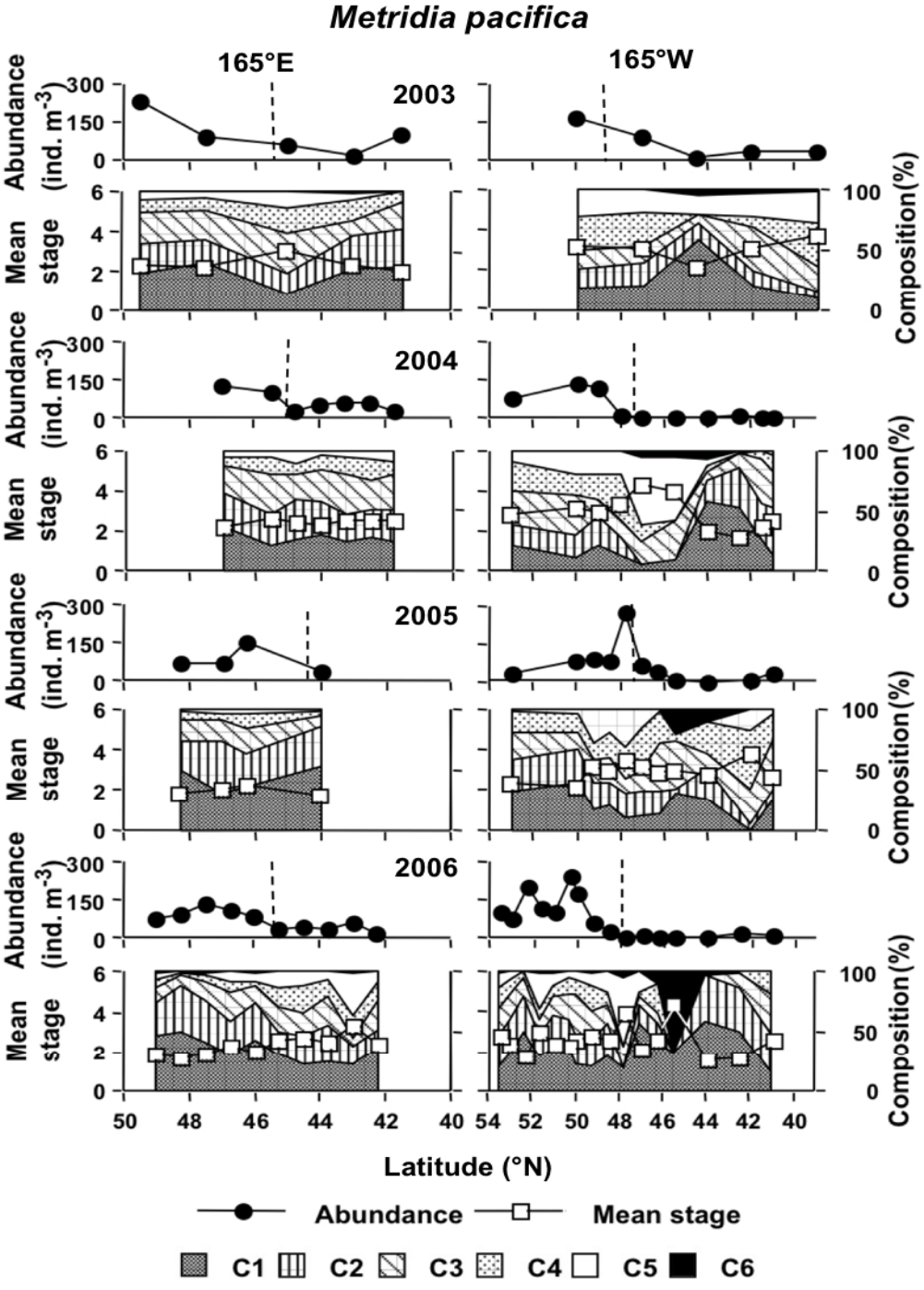


Fig. 12 (Saito *et al*.)

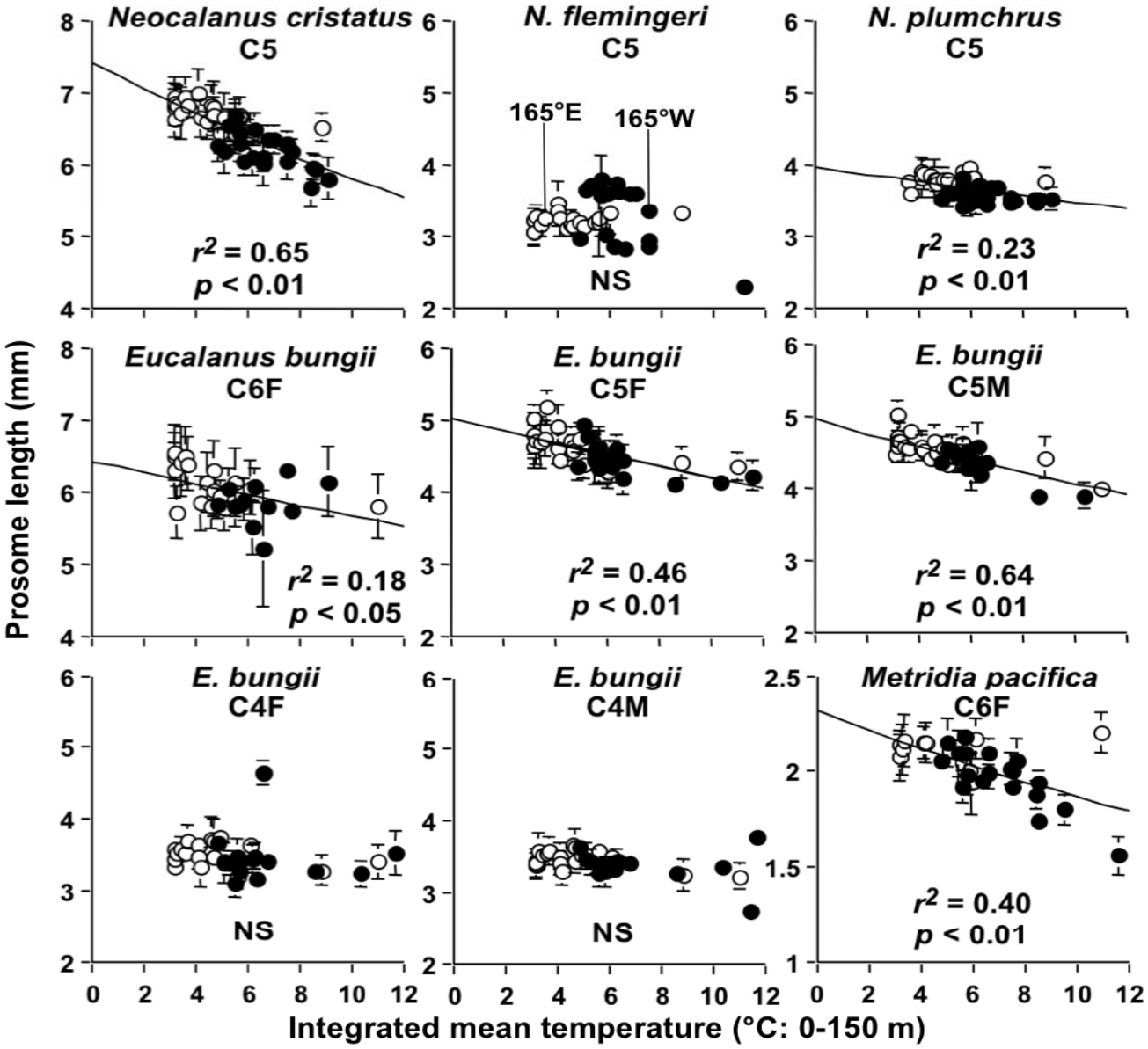


Fig. 13 (Saito *et al.*)

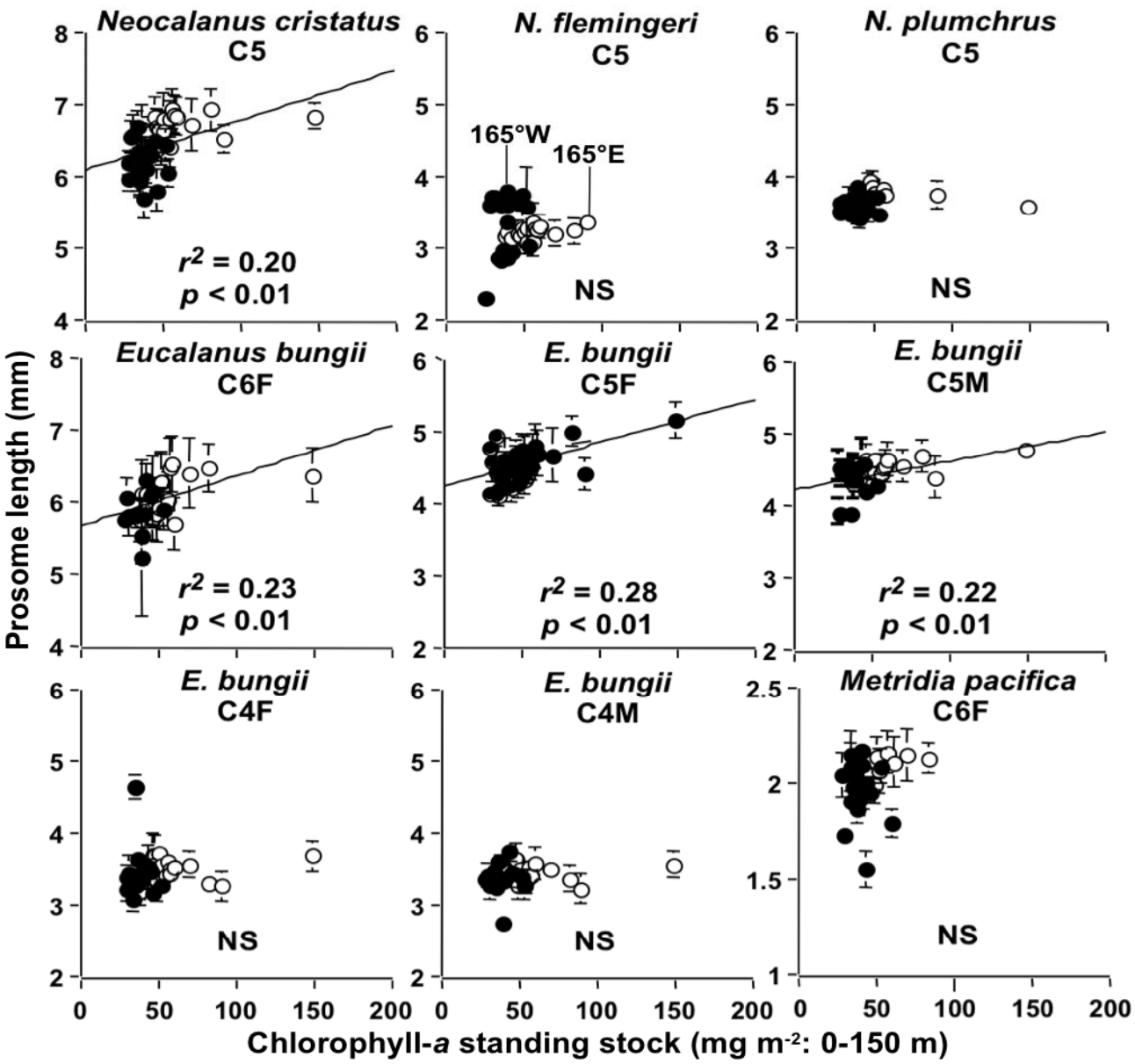


Fig. 14 (Saito *et al*.)