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Latitudinal variations in the abundance, biomass, taxonomic composition and estimated production of epipelagic mesozooplankton along the 155°E longitude in the western North Pacific during spring

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A B S T R A C T

A total of 100 mesozooplankton samples collected with NORPAC nets from a 0 to 150-m depth at latitudinal stations (35–44°N) along 155°E each May from 2002 through 2011 were analyzed. The mesozooplankton abundance at each station varied from 39 to 1106 ind. m^{-3}. The mesozooplankton biomass was consistently higher (80–100 mg DM m^{-3}) in the transition domain (40–42°N) than the biomass in the other domains. An empirical metabolic rate-based carbon budget model indicated that production of mesozooplankton suspension feeders was highest (120–175 mg C m^{-2} d^{-1}) in the transition domain. A comparison between the production of the mesozooplankton suspension feeders and the food requirement of mesozooplankton carnivores indicated that the latter was well fulfilled by the former in the subarctic and transition domains. However, the food requirement of the mesozooplankton carnivores was near equal to or exceeded the production of mesozooplankton suspension feeders in the subtropical domain. As an annual event, the feeding migration of epipelagic fish to the transition and subarctic domains in summer may be interpreted by their utilization of the excess secondary production (production of mesozooplankton suspension feeders).

1. Introduction

The western North Pacific is known to be one of the largest nursery, feeding and growth grounds of pelagic fishes (i.e., Japanese sardine [*Sardinops melanostictus*], Pacific saury [*Cololabis saira*] and Pacific chub mackerel [*Scomber japonicus*]) (Odate, 1994; Kurita et al., 2004). Epipelagic mesozooplankton are an important food source for pelagic fishes (Taka et al., 1982; Sugisaki and Kurita, 2004). Because of their importance, various studies have been conducted concerning the mesozooplankton communities in this region. Within these particular communities, three topics have been extensively studied in detail: (1) the life cycles of the large boreal Copepoda (*Neocalanus* spp. and *Eucalanus bungii*) in the Oyashio region (Kobari and Ikeda, 1999, 2001a,b; Shoden et al., 2005), (2) the long-term changes in the zooplankton community in relation with climate change (Tadokoro et al., 2005; Chiba et al., 2006, 2008, 2009) and (3) the whole plankton community, from the surface down to greater depths (Yamaguchi et al., 2002a,b, 2004, 2005). However, despite their importance, the north/south differences in the epipelagic zooplankton community and their production have been little studied (cf. Ikeda and Motoda, 1978). Furthermore, the lack of information on zooplankton production in this region may prevent a better understanding of the marine ecosystem structure and availability of prey for pelagic fishes.

In the present study, based on 100 mesozooplankton samples collected with NORPAC nets from 0 to 150 m depth at latitudinal stations (35–44°N) along 155°E from May 2002 to May 2011, we evaluated the latitudinal changes in epipelagic mesozooplankton abundance, biomass, taxonomic composition, estimated production and food requirement. The energetic ratio between the production of suspension feeders and the food requirement of carnivores is an index of the amount of surplus food for pelagic fishes (Taniguchi, 1973). The latitudinal changes in these parameters were also analyzed and discussed from the viewpoint of mesozooplankton food resources for pelagic fishes.

2. Materials and methods

2.1. Field sampling

Zooplankton samples were collected by the vertical tow of a NORPAC net (mesh size of 335 μm, mouth diameter of 45 cm, Motoda, 1957) from 150 m to the sea surface each May from 2002 to 2011. There were 7–13 stations every 45 nautical miles

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between 35°N and 44°N along 155°E in each year, and there was a total of 100 stations (Table 1, Fig. 1). Sampling was conducted during day and night. Sampling was conducted during day (48%) and night (52%). There were no significant differences in the total zooplankton wet mass between day and night ($p = 0.25$, *U*-test). The NORPAC nets were equipped with a flow meter (Rigosha Co. Ltd.) in the net mouth to register the volume of water filtered. The filtration efficiency of the net was in the range of 84–100% (mean = 93%). The samples were preserved in 5% borax-buffered formalin seawater on board. Temperature and salinity data were obtained at each station using a CTD system (Sea-Bird SBE-911 Plus).

Table 1
Zooplankton sampling along 155°E in the western North Pacific during May of 2002–2011.

Year	Period	Latitude (*N*)	Number of station
2002	22–27 May	35°00′–44°00′	13
2003	14–18 May	38°00′–44°00′	8
2004	11–16 May	36°30′–44°00′	12
2005	13–20 May	35°45′–44°00′	12
2006	12–17 May	38°00′–44°00′	9
2007	11–16 May	38°00′–44°00′	9
2008	10–17 May	38°45′–44°00′	8
2009	11–16 May	34°15′–44°00′	11
2010	12–17 May	36°30′–44°00′	11
2011	15–20 May	38°00′–44°00′	7

2.2. Abundance and biomass

After each cruise, the various types of zooplankton in the samples were sorted into following taxa: small Copepoda (<5 mm total length), large Copepoda (⩾5 mm total length), Amphipoda, Euphausiacea, Mysidacea, Cnidaria, Appendicularia, Salpida, Doliolida, Chaetognatha and others. The sorted samples were filtered onto a 100-μm mesh under low vacuum, and the wet mass (WM) was measured using an electronic microbalance with precision of 0.01 g. The water content of each taxon was assumed to be 80% for Copepoda, Amphipoda, Euphausiacea and Mysidacea; 90% for Chaetognatha; 96% for Cnidaria, Appendicularia, Salpida and Doliolida; and 80% for the others (Postel et al., 2000). The WM data were converted to dry mass (DM) units using these constants.

2.3. Production and food requirements

The zooplankton production (*G*) and food requirements (*I*) were estimated from the empirical respiration rate and the carbon budget model (cf. Ikeda and Motoda, 1978). The respiration rate was calculated using the following equation:

$$\ln R = -0.2512 + 0.7886 \ln B + 0.0490T \qquad (1)$$

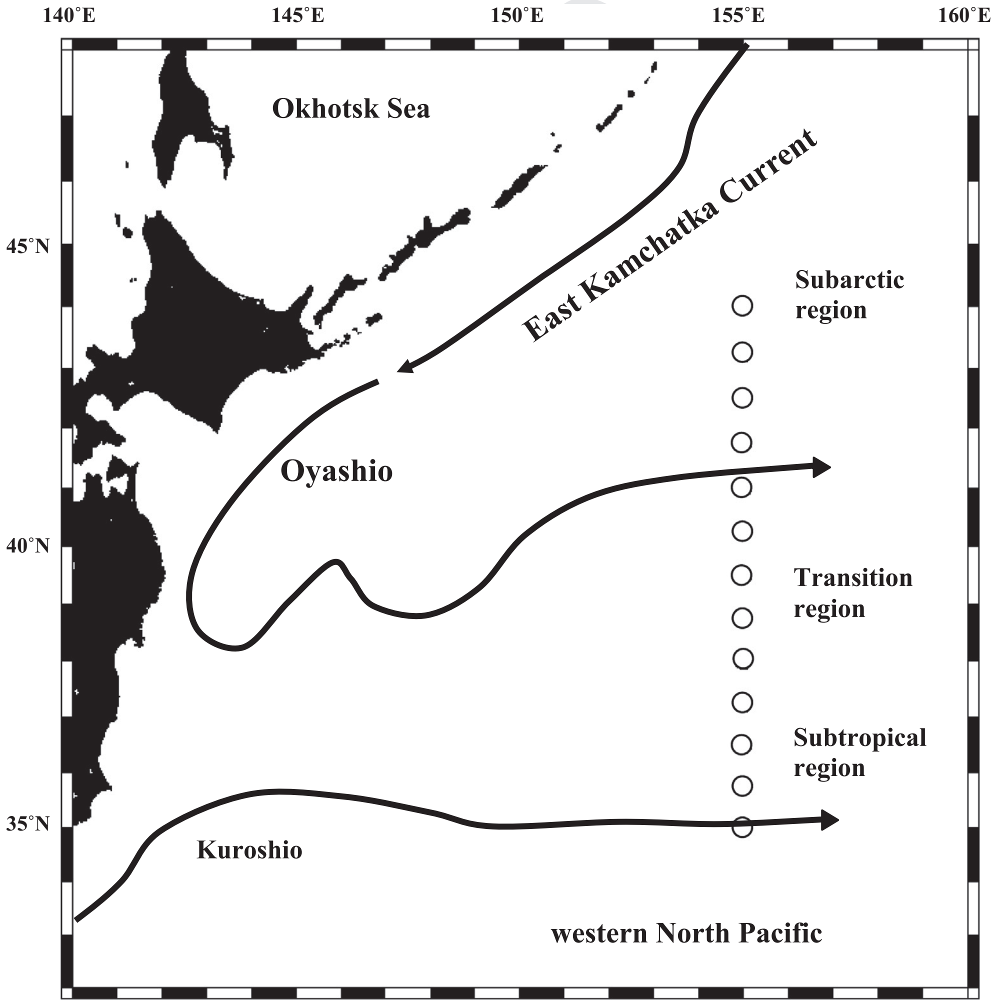

Fig. 1. Location of the sampling stations (35–44°N) along 155°E in the western North Pacific each May from 2002 to 2011. The approximate mean position of the current system and the regions are also shown.

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where R is the oxygen consumption rate (μl O_2 ind.$^{-1}$ h^{-1}), B is the biomass (mg DM ind.$^{-1}$) and T is temperature (°C) ($r^2 = 0.94$, Ikeda, 1985), where T is the integrated mean temperature of the net towed depth (0–150 m).

Assuming the assimilation efficiency ($[G + R]/I$) and the gross growth efficiency (G/I) to be 70% and 30%, respectively (Ikeda and Motoda, 1978), growth (=production) in mg C ind.$^{-1}$ d^{-1} was calculated using the following equation:

$$G = R \times \frac{12}{22.4} \times 0.97 \times \frac{0.3}{0.4} \times 10^{-3} \times 24 \qquad (2)$$

where 12/22.4 is the weight of carbon (12 g) in 1 mol (22.4 L) carbon dioxide, 0.97 is the respiratory quotient (CO_2/O_2, Gnaiger, 1983), 0.3/0.4 is the G/R, 10^{-3} is a unit conversion from μg to mg, and 24 is the time unit conversion from hourly to daily (×24). The food requirement was computed with the following equation:

$$I = R \times \frac{12}{22.4} \times 0.97 \times \frac{1}{0.4} \times 10^{-3} \times 24 \qquad (3)$$

This equation was used to obtain the individual growth and food requirement (mg C ind.$^{-1}$ d^{-1}) with abundance data (ind. m^{-2}); we estimated the zooplankton production and food requirement (mg C m^{-2} d^{-1}). For the feeding modes, we separated zooplankton taxa into two primary categories: suspension feeders and carnivores. For the suspension feeders, we included Copepoda, Euphausiacea, Appendicularia, Salpida and Doliolida. For the carnivores, we included Amphipoda, Mysidacea, Cnidaria and Chaetognatha. Note that there are exceptions for several taxa (carnivorous copepods *Paraeuchaeta, Heterorhabdus* and carnivorous euphausiids *Stylocheiron*); however, because the contribution of such exceptions was minor, we applied the above primary feeding categories in this study. Using these feeding categories, we compared the production of suspension feeders and the food requirement of carnivores because it is an index of the surplus food for pelagic fish resources (Taniguchi, 1973; Ikeda and Motoda, 1978).

Because the sampling stations were fixed and visited annually during this study (Fig. 1), the 10-year mean of each parameter (temperature, salinity, abundance and biomass) was calculated for each station. Then, the anomaly from the 10-year mean was calculated for each station. In the following, the results on mesozooplankton (abundance, biomass and production/food requirement) are presented, as in the 10-year mean values. For details of the raw data at each station/year, see Electronic supplements 1–3.

3. Results

3.1. Hydrography

The hydrography along the 155°E line was characterized by high temperature and high salinity at low latitudes, and both decreased as the latitude increased (Fig. 2). The magnitudes of the anomalies at each latitude were ±3.5 °C for temperature and ±0.4 PSU for salinity. Temperature and salinity anomalies were positively correlated ($r^2 = 0.82$, $p < 0.0001$, Fig. 2). This correlation between the temperature and salinity anomalies indicates that the variability was caused by north–south shifts of subarctic and subtropical water masses and the variable position of the fronts in each year.

3.2. Abundance

The zooplankton abundance ranged between 38.6–1106 ind. m^{-3} (Fig. 3). Small Copepoda were numerous at most of the stations, while the other taxa were abundant only in several regions/years. The anomalies from the mean abundance at each station varied between −300 and 800 ind. m^{-3} and had no correlation with the anomalies of temperature or salinity mentioned previously ($p = 0.31$–0.57). The 10-year means at each latitude indicated that the zooplankton abundance was lowest at low latitudes and was higher at approximately 38–44°N. The zooplankton taxonomic composition, based on 10-year mean abundance, exhibited a predominance (>80%) of small Copepoda especially north from 41°N (Fig. 3). Cnidaria represented a greater portion of the taxonomic composition (ca. 10–15%) at 37–40°N, and Doliolida represented a similar fraction (ca. 10–15%) at 36°30′–39°30′N.

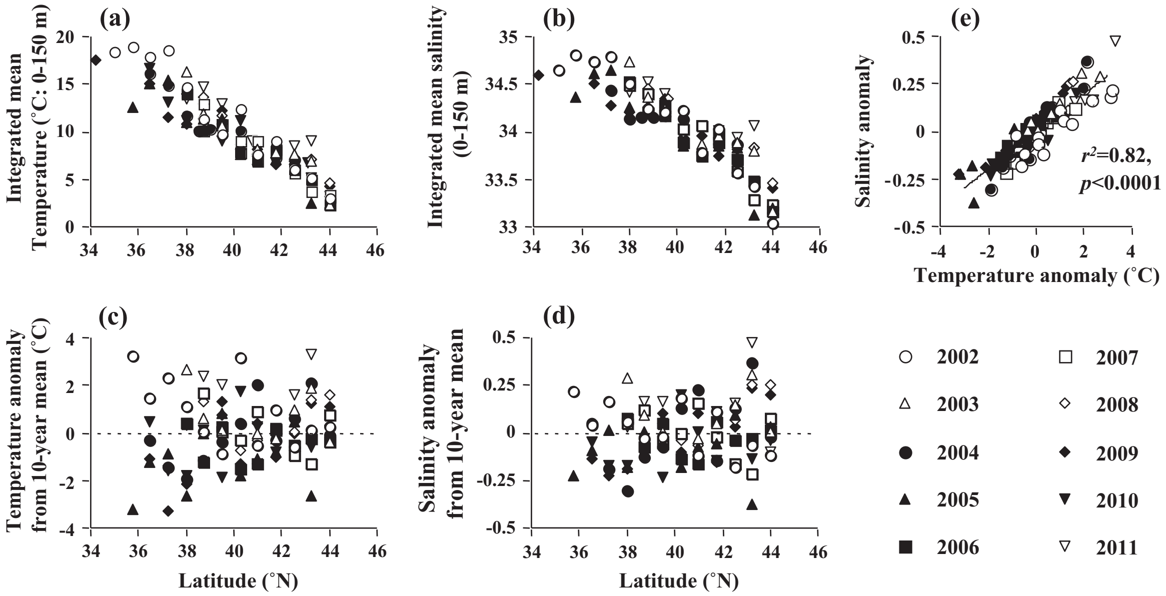

Fig. 2. Latitudinal changes in the integrated mean temperature (a) and mean salinity (b) at 0–150 m depths along 155°E in the western North Pacific each May from 2002 to 2011. Anomalies from the 10-year mean were also calculated for temperature (c) and salinity (d). The relationship between the salinity anomaly and the temperature anomaly (e).

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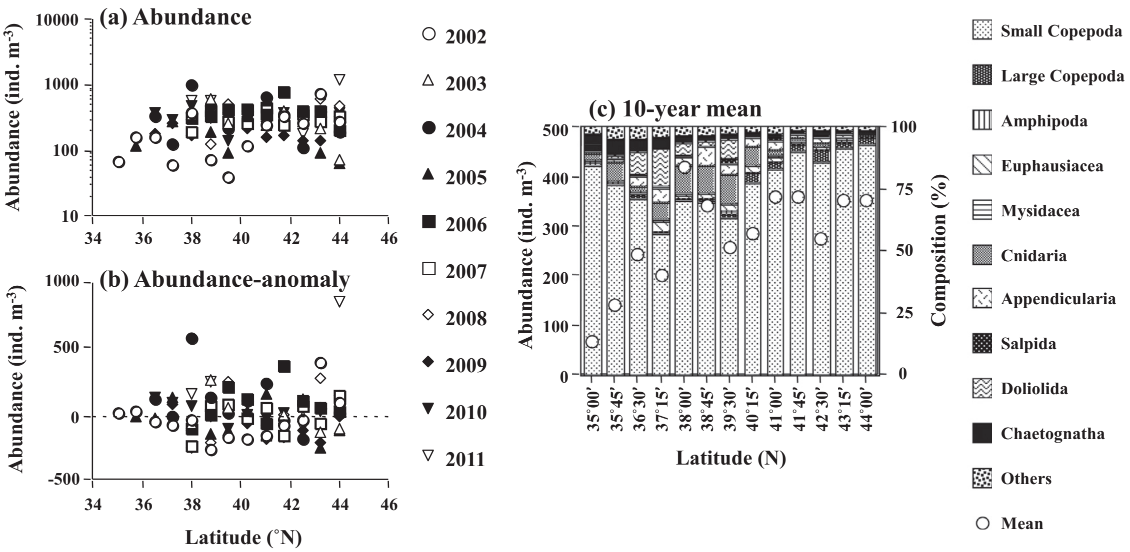

Fig. 3. Annual changes in zooplankton abundance along 155°E in the western North Pacific each May from 2002 to 2011 (a), anomaly from the 10-year mean (b) and the 10-year mean abundance and taxonomic composition (c).

3.3. Biomass

The zooplankton biomass ranged between 10.4–256 mg DM m^{-3} (Fig. 4). The 10-year mean indicated that zooplankton biomass was the lowest at low latitudes, peaked (95 mg DM m^{-3}) at approximately 41°N, and then remained high for higher latitudes. The 10-year mean zooplankton taxonomic composition in biomass indicated that small Copepoda represented the largest (30–55%) percentage of the composition, followed by large Copepoda (ca. 20%) north of 40°N (Fig. 4). South of 40°N, Chaetognatha represented ca. 20% of the total zooplankton biomass. Anomalies from the 10-year mean zooplankton biomass ranged from −70 to 160 mg DM m^{-3} and were marked by an outbreak of Salpida (mainly the aggregate form [blastozooids] of *Salpa fusiformis*) at 39°30′N in 2003 (Fig. 4).

3.4. Production and food requirement

The production (=growth) of suspension feeders (G_{SF}) and the food requirement (=ingestion) of carnivores (I_C) ranged between 26–250 mg C m^{-2} d^{-1} and 10–249 mg C m^{-2} d^{-1}, respectively (Fig. 5). Their ratio (G_{SF}/I_C) was the index of surplus food for pelagic fishes (cf. Taniguchi, 1973) and ranged from 0.2 to 10. The ratio from the 10-year mean exhibited a clear latitudinal pattern, i.e., the ratio was nearly 1 (G_{SF} was well balanced with I_C; little surplus food would be available for migratory pelagic fishes) south of 40°N, but was high (2.2–4.4) north of 40°N (G_{SF} was higher than the I_C; surplus food would be available for migratory pelagic fishes) (Fig. 5). This latitudinal change (south of 40°N vs. north of 40°N) in the ratio was highly significant ($p < 0.0001$, *U*-test).

4. Discussion

4.1. Abundance

Although our sampling, which occurred in May each year, provides us with a consistent dataset, note that these data represent just one snapshot of the seasonal cycle. Zooplankton are highly

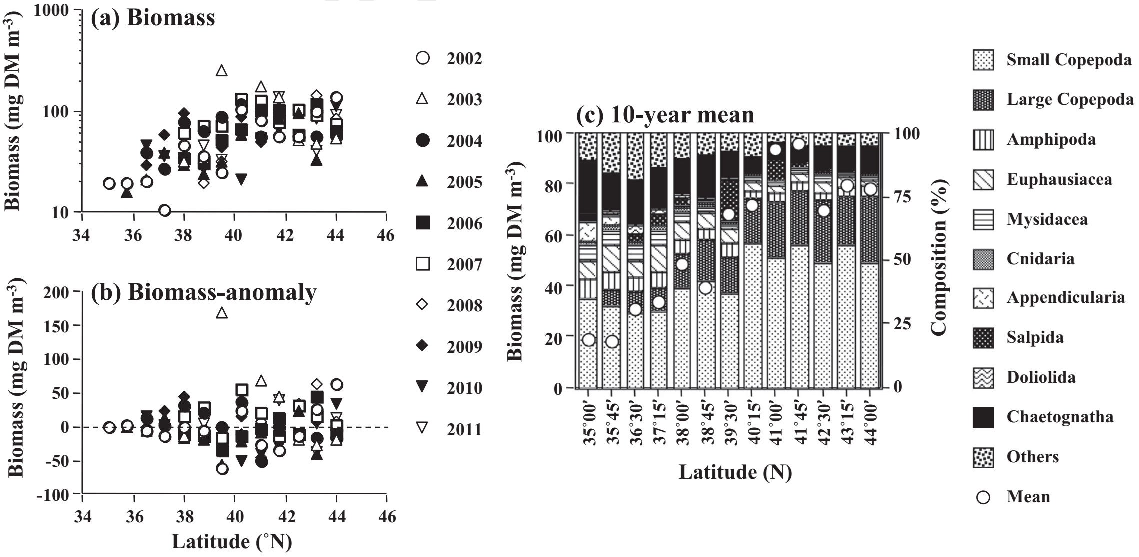

Fig. 4. Annual changes in zooplankton biomass along 155°E in the western North Pacific each May from 2002 to 2011 (a), anomaly from the 10-year mean (b) and the 10-year mean abundance and taxonomic composition (c).

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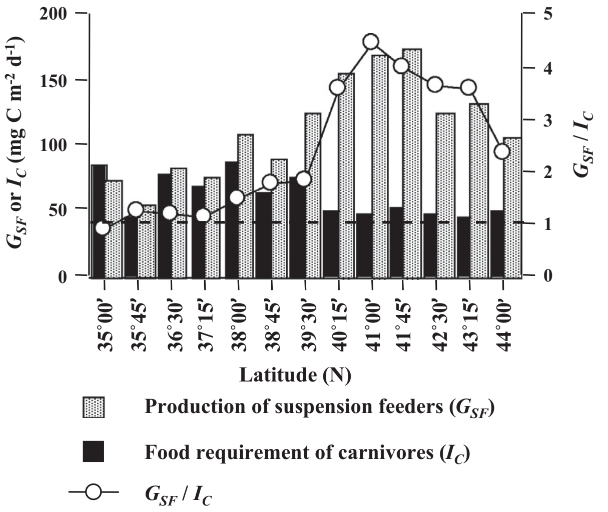

Fig. 5. Latitudinal changes in the production (=growth) of suspension feeders (G_{SF}), the food requirement (=ingestion) of carnivores (I_C) and their ratio (G_{SF}/I_C) along 155°E in the western North Pacific each May from 2002 to 2011. Horizontal dashed line indicates position of 1 ($G_{SF} = I_C$). All of the values are 10-year mean.

variable with season, particularly in the more northerly regions. Depending on the interannual variability in climate, May of one year may resemble April or June of another year. Thus, we may be sampling the zooplankton community at slightly different parts of their seasonal evolution in different years. Mackas et al. (1998, 2007), for example, found a 6-week difference among years in the seasonal timing of the large *Neocalanus* copepods at Station P in the eastern North Pacific. Similar variability of the developmental timing of large *Neocalanus* copepods was also reported in the western North Pacific (Chiba et al., 2004; Tadokoro et al., 2005). When considering our sampling in May, this type of potential timing variability should be considered. However, our sampling periods concentrated within a 3-week (Table 1) and close correlation between temperature and salinity during sampling period (Fig. 2e) suggests that the north–south changes in water masses are more important factors to control zooplankton community in this region. Since the common north–south patterns were recognized for all of the year (see electronic supplement 1–3), we considered that the effect of yearly changes in phenology was smaller than the north–south pattern during the study period, and treated whole zooplankton data to create 10-year means for evaluation general north–south trend along 155°E (Figs. 3 and 4).

Other north/south transects in the North Pacific indicated that zooplankton abundance is lower at low latitudes and is higher at high latitudes (Yokoi et al., 2008; Matsuno and Yamaguchi, 2010; Saito et al., 2011; Fukuda et al., 2012). Where the zooplankton abundance is the lowest, the number of species and species diversity are reported to be higher in the subtropical and tropical oceans for various zooplankton taxa, i.e., Copepoda (Heinrich, 1969), Euphausiacea, Pteropoda and Chaetognatha (Fager and McGowan, 1963).

The increase in species diversity at lower latitude could be explained by evolution of these taxa. According to Briggs (1974), there are three explanations for the high species diversity at low latitudes: (1) competition theory, (2) theory of climatic stability and (3) availability of comparatively large geographic areas. These three theories may not have only one cause, but the combination of the theories may affect the zooplankton evolutionary processes. Because the climatic and oceanographic condition of tropical and subtropical oceans is stable for long periods, the natural selection of species may have the tendency to increase inter-species competition for food. Under such conditions, each species may adapt to a smaller niche, which would then induce an increase in the species number and diversity.

In the arctic and subarctic regions, there are greater seasonal changes in the climate and physical oceanography, and zooplankton have to adapt to the high variability in the environmental conditions. Under such conditions, natural selection of species may function to increase zooplankton egg production (reproductive success). This selection is considered to be a possible cause of the high mesozooplankton abundance in the subarctic region of this study. From these viewpoints, species differentiation, diversity and marine ecosystem structure are established for the tropical and subtropical regions.

4.2. Biomass

Based on the 17,242 zooplankton samples collected from the Tohoku Sea Area (33–46°N latitude, Japan coastline-160°E longitude) during 1951–1990, Odate (1994) reported that the zooplankton biomass peaked in May throughout the regions (subarctic, transition and subtropical regions). Within the three regions, seasonal variability in zooplankton biomass was the greatest for the subarctic region, moderate for the transition region and lowest for the subtropical region (Odate, 1994). Greater seasonality in the subarctic region is mainly caused by the boreal large Copepoda (e.g., *Neocalanus* spp. and *E. bungii*), which is only found in the subarctic and transition regions (Odate, 1994). These large Copepoda grow near the surface layer during spring and then descend to the meso- and bathypelagic layers to undergo diapause from summer to winter (Kobari and Ikeda, 1999, 2001a,b; Shoden et al., 2005). Because all of the samples of this study were collected in May, the zooplankton biomass in this study might indicate the maximum biomass in this region.

The outbreak of Salpida at 40°N in 2003 was a remarkable feature of the zooplankton biomass in that year. The transition region including 40°N generally has dominance of Doliolida and Cnidaria (Fig. 3). These taxa are described as “gelatinous zooplankton” (cf. Postel et al., 2000). The atmospheric and physical oceanographic characteristics of the transition region are unstable where storms, streams, streamers and fronts are frequently changing the spatial/vertical distribution of water masses (Anma et al., 1990; Roden, 1991). These characteristics in the transition region may affect the abundance of the various gelatinous zooplankton taxa that occur there.

Previous laboratory experiments have shown that Salpida are filter feeders that are capable of ingesting particles larger than 3–4 μm (Harbison and McAlister, 1979; Caron et al., 1989; Kremer and Madin, 1992). Because Salpida has a large body size, it can collect various wide-sized particles of food. These feeding characteristics of Salpida may provide a unique niche for this taxon in oligotrophic oceanic environments. Salp blooms have been observed at various locations such as upwelling regions or fronts (Deibel, 1985; Paffenhöfer et al., 1987) and in a warm core ring (Tsuda and Nemoto, 1992). Because their distribution may be governed by the meso-scale (ca. 50–60 km) oceanographic conditions (Haury et al., 1978), the Salpida spatial distribution may also be affected by these oceanographic conditions (cf. Berner, 1967).

4.3. Production/food requirement

In this study, we estimated the production and food requirements from an empirical metabolism equation, with temperature and body mass as independent variables ($r^2 = 0.939$, Ikeda, 1985). The estimation assumed values for assimilation and gross growth efficiencies (Ikeda and Motoda, 1978). As an alternative, several equations to directly estimate the growth rate from the temperature, body mass or chlorophyll *a* are reported (Hirst and Lampitt,

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1998; Hirst and Bunker, 2003), however, the coefficients of determination of these equations are extremely low ($r^2 = 0.435$ or 0.289) and limited for use only with Copepoda. Because our data included 12 taxa, application of other equations may be difficult (note that all taxa in this study are included for the metabolism equation in Ikeda, 1985).

To test the estimation accuracy, we also calculated the production of Copepoda by using other equations (Hirst and Lampitt, 1998; Hirst and Bunker, 2003). These calculations resulted in similar production values (the values from these equations were at factors of 0.431–1.382 of the values of this study [grand mean was 0.901]). While our samples were collected using a net tow from 0 to 150 m, mesozooplankton may not be expected to be distributed evenly through the 0–150 m water column. Thus, the problem with the choice of applying temperature in the equation is inevitable for these calculations (all the equations require temperature data). To overcome these problems, in the future, these types of calculation should be performed based on the abundance/biomass data with fine depth scale (1 m interval), which is available from *in-situ* vehicles, such as the Video Plankton Recorder (VPR) (Gallager et al., 1996).

Comparison of the suspension feeder production and the carnivorous food requirement revealed that south of 40°N, there remained little surplus food for migratory pelagic fishes, while there was a significant surplus of food for the migratory pelagic fishes available north of 40°N (Fig. 5). The dominance of the boreal large-sized Copepoda in the subarctic and transition region has been reported for various studies based on north/south transects in the North Pacific (Kobari et al., 2003; Yokoi et al., 2008; Matsuno and Yamaguchi, 2010; Saito et al., 2011; Fukuda et al., 2012). In contrast to the north, the high proportion of Chaetognatha in the zooplankton biomass south of 40°N (Fig. 4) may induce low surplus production of suspension feeders. The high composition of the carnivorous zooplankton compared with the total zooplankton biomass in the tropical and subtropical regions has been reported for several oceans, including the North Pacific (Taniguchi, 1973) and the Indian Ocean (Timonin, 1971).

Reduced seasonality in the zooplankton community at low latitudes (Odate, 1994) may provide a stable food web structure within the mesozooplankton community. In a stable marine ecosystem, the proportion of carnivores is expected to be balanced and maximized (Vinogradov, 1970). This seasonal stability in the zooplankton community could be a possible cause of the dominance of carnivorous Chaetognatha at low latitude regions (Timonin, 1971; Taniguchi, 1973). Regarding the seasonality in the high latitude region, the biomass of boreal large Copepoda has a large peak in May and exhibits a sudden decrease with their descent into a deep layer during summer (Odate, 1994; Kobari and Ikeda, 1999, 2001a,b; Shoden et al., 2005). Because of this large seasonality in zooplankton biomass, most of the production of large Copepoda would not be consumed by carnivorous zooplankton and thus remains as surplus food for pelagic fishes. This seasonal change may explain why the amount of the surplus food for pelagic fishes is greater north of 40°N in May (Fig. 5).

Most of the important pelagic fishes in this region (Japanese sardine, Pacific saury and Pacific chub mackerel) reproduce in the subtropical region and then migrate northward, which is termed "feeding migration" (Fukushima, 1979; Kurita et al., 2004). While a slight preference of feeding habits is present between species, that is, Japanese sardine prefer diatoms and small Copepoda (Yoshida, 1987), Pacific saury prefer large Copepoda, and Pacific chub mackerel prefer large mesozooplankton (Iizuka, 1987), boreal large Copepoda (*Neocalanus* spp. and *E. bungii*) in the subarctic region are known to be a sufficient food for all of these migratory pelagic fishes (Taka et al., 1982; Odate, 1994; Sugisaki and Kurita, 2004). From the bioenergetics estimation of migratory pelagic fishes, Odate (1994) noted that the annual mean consumption of zooplankton by Pacific saury was 1.55×10^6 tons during 1979–1985, and Tadokoro et al. (2005) noted that Japanese sardine consumed 32–138% of daily *Neocalanus* production during summer of 1984. Recently, advances in modeling (NEMURO and NEMURO.FISH) enabled the development of the bioenergetics models of Japanese sardine (Okunishi et al., 2009) and of Pacific saury (Ito et al., 2004, 2007; Mukaia et al., 2007) in this region. The large surplus production of suspension feeders north of 40°N strongly supports the sufficient food condition for pelagic fishes at high latitude regions in the western North Pacific. The above modeling studies well corresponded with the findings of this study. To evaluate detailed biological phenology, further studies on the variability of timing of copepod diapauses and the timing of predatory fish arrival are needed in this region.

5. Conclusion

The latitudinal characteristics of epipelagic mesozooplankton abundance, biomass, taxonomic composition and estimated production were evaluated in the western North Pacific each May from 2002 to 2011. Zooplankton abundance was lowest in the south and increased northward. Small-sized Copepoda (<5 mm total length) was the most abundant taxon (>80%) of the taxonomic composition. Zooplankton biomass was also lower in the south, peaked at approximately 41°N, and remained high further north. For zooplankton biomass, small Copepoda was also dominant, but to a lesser extent (30–55%), followed by the large Copepoda in the subarctic region and the Chaetognatha in the subtropical region. The highest biomass of gelatinous zooplankton (Salpida, Doliolida and Cnidaria) was observed in the transition region. The latitudinal differences in the second abundant taxa induced latitudinal differences in the marine ecosystem structure. Thus, in the subtropical region, abundant carnivores (Chaetognatha) may consume most of the production of suspension feeders, and the food requirement of carnivores was well balanced with the production of suspension feeders. These data suggest that there was less surplus food for pelagic fishes in the subtropical region. However, in the subarctic region, the dominance of large Copepoda (*Neocalanus* spp. and *E. bungii*) provided a higher amount of suspension feeder production than the food requirement of carnivores. As an annual event, the feeding migration of epipelagic fish to the transitional and subarctic domains in summer may be interpreted as a utilization of the excess production of mesozooplankton suspension feeders.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2015.04.011.

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