HOKKAIDO UNIVERSITY

Title	Abundance and biomass of mesozooplankton along north-south transects (165° E and 165° W) in summer in the North Pacific: an analysis with an optical plankton counter
Author(s)	Matsuno, Kohei; Yamaguchi, Atsushi
Citation	Plankton and Benthos Research, 5(4), 123-130 https://doi.org/10.3800/pbr.5.123
Issue Date	2010-11
Doc URL	https://hdl.handle.net/2115/52333
Rights	© 2010 Plankton Society of Japan
Type	journal article
File Information	2-Matsuno and Yamaguchi 2010.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

Plankton Benthos Res 5(4): 123–130, 2010

Plankton & Benthos Research
© The Plankton Society of Japan

Abundance and biomass of mesozooplankton along north-south transects (165°E and 165°W) in summer in the North Pacific: an analysis with an optical plankton counter

KOHEI MATSUNO* & ATSUSHI YAMAGUCHI

Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido University, 3–1–1 Minatomachi, Hakodate, Hokkaido 041–8611, Japan

Received 13 November 2009; Accepted 2 July 2010

Abstract: Zooplankton abundance and biomass along 165°E and 165°W in the North Pacific were estimated using an optical plankton counter on preserved samples collected with a plankton net of 335 μm mesh-size from 0.150 m at 89 stations from the subarctic to subtropical regions during the summers of 2003–2006; the stations were grouped into subarctic (SA), transitional (TR) and subtropical (ST) regions for latitudinal comparisons. The two-way ANOVA and a post hoc test showed that total abundance and biomass were significantly larger in SA and smaller in ST stations, respectively, than in the other regions, but were not significantly different between 165°E and 165°W. Total ranges of abundance and biomass were: 34×10^3–65×10^3 indiv. m^{-2} and 2.9–7.9 g dry mass m^{-2}, respectively. The variation in abundance was mainly governed by the variation of 0.34–1.00 mm equivalent spherical diameter (ESD) size class zooplankton, but total biomass variations were due mainly to the 2.00–3.00 mm ESD size class, which corresponds to the calanoid copepod *Neocalanus* spp. copepodid stage 5 (C5) that had a greater abundance in SA and TR than in ST. Despite possibly higher abundances of *Neocalanus* C5 in TR than in SA, abundance and biomass of the 2.00–3.00 mm ESD size class were not significantly different between the two regions. Size reduction of individuals due to higher temperatures in TR than in SA may be a possible explanation.

Key words: abundance, biomass, optical plankton counter, size, zooplankton

Introduction

In the last decade, east-west differences in the plankton community have been reported for the subarctic Pacific. For example, rates of primary production and phytoplankton concentration are reported to be higher for the western, than the eastern region (Shiomoto & Asami 1999, Shiomoto & Hashimoto 2000). These east-west differences in the phytoplankton community and production are considered to be caused by the differences in the iron concentration (higher in the west, Harrison et al. 1999, Suzuki et al. 2002). This east-west difference in the phytoplankton community may also reflect differences in the grazing pressure of the zooplankton community (Mackas & Tsuda 1999, Takahashi et al. 2008). Energy transfer efficiency between trophic levels is reported to be higher in the western region (Taniguchi 1999), the life cycles of the dominant copepod taxa are known to vary between east-west (Kobari & Ikeda 2001, Tsuda et al. 2004, Shoden et al. 2005), and the body size of copepods also varies (Tsuda et al. 2001, Kobari et al. 2003b). In these studies the regional variations in copepod ecology are attributed to regional variations in temperature and magnitude of the spring phytoplankton bloom (cf. Tsuda et al. 2004).

Regional differences in the plankton community structure have also been reported between the north and south of the North Pacific. For example, the phytoplankton concentration and biomass are higher in the subarctic than in the transition or subtropical regions (Odate T 1994) and the north-south differences in zooplankton biomass are attributable to faunal differences (Odate K 1994). The zooplankton biomass of the subarctic and transition regions is dominated by the large copepod *Neocalanus* spp., and their abundance is highest in the transitional region (Nagasawa et al. 2001, Kobari et al. 2003a). The developmental rate of copepods is

* Corresponding author: Kohei Matsuno; E-mail, k.matsuno@fish.hokudai.ac.jp 6

also reported to be faster in the south, which may be caused by the higher temperature there than in the northern regions (Batten et al. 2003).

The reported east-west and north-south differences in mesozooplankton communities (Mackas & Tsuda 1999, Batten et al. 2003) suggest that there are also regional differences in abundance and biomass of total zooplankton between these regions. However information especially on regional variations in abundance and biomass according to zooplankton size have not been evaluated in detail, because quantitative comparison of previous studies between east and west regions is difficult due to differences in sampling methodologies such as mesh size of plankton nets used, sampling depth and season.

In the present study, we analyzed samples collected with the same sampling methodologies in the same season, and made east-west and north-south comparisons of abundance and biomass of mesozooplankton among regions of the North Pacific Ocean during the summers of 2003 to 2006. We did the analysis with an optical plankton counter (OPC) on net-collected samples to estimate zooplankton abundance and biomass. Regional differences (north vs south or east vs west) of abundance and biomass were tested with two-way ANOVA, and are discussed.

Materials and Methods

Sampling of zooplankton

Zooplankton samplings were conducted at 4–10 stations (36°00′N–49°30′N) along the 165°E line and at 11–20 stations (22°00′N–53°30′N) along 165°W in the North Pacific during the cruises of the T/S *Oshoro-Maru* in the summers of 2003–2006 (total: 96 samples at 89 stations, Fig. 1). Zooplankters were collected by vertical hauls of a NORPAC net (mouth diameter 45 cm, mesh size 0.335 mm, Motoda 1957) from the upper 150 m during day and/or night. The volume of water filtered through the net was estimated using a flow-meter (Rigosha Co. Ltd.) mounted in the net mouth. Volume of water filtered ranged between 15.6 and 47.7 m^3 (mean±sd: 25.0±4.6 m^3). Zooplankton samples were immediately fixed with 5% buffered formalin. At each station, profiles of water temperature and salinity were obtained with a Sea-Bird SBE 911 Plus CTD system.

OPC analysis

After the cruise, formalin-preserved zooplankton samples were processed with an Optical Plankton Counter (OPC, Model OPC-1L: Focal Technologies Corp.). The OPC can measure the number of particles with 4096 size categories between 0.250–20 mm with a precision of 0.001–0.021 mm. The OPC measurements were made with 1/2–1/8 sub-samples. For avoiding phytoplankton and detritus detection, the measurements were done at a flow rate and particle density of about 10 L min^{-1} and <10 counts $sec.^{-1}$, respectively, using the procedure of Mullin et al. (2000) and Yokoi et al. (2008).

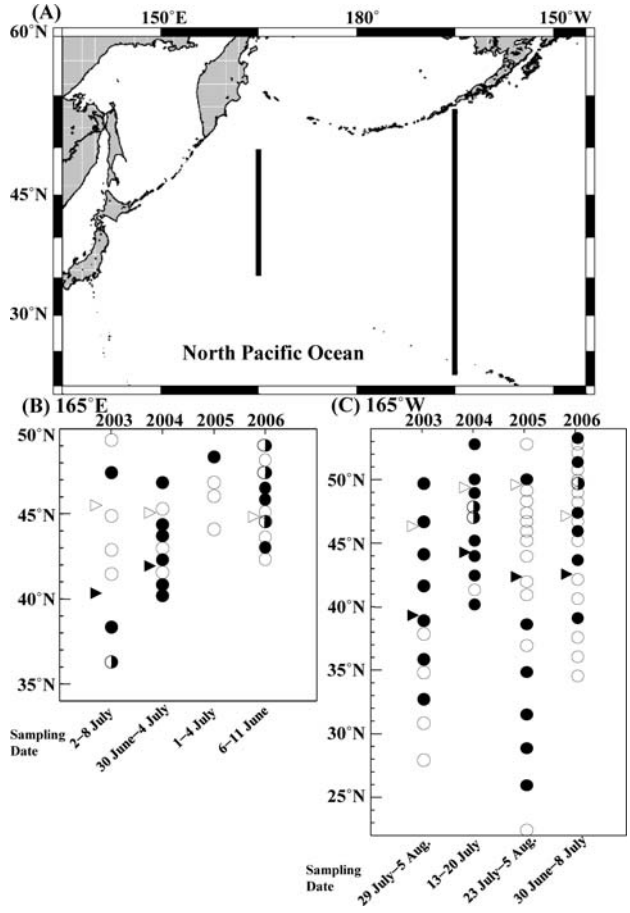


Fig. 1. Location of sampling transects along 165°E and 165°W in the North Pacific (A). Sampling stations along 165°E (B) and 165°W (C) during 2003–2006. Open, solid and half-solid symbols denote stations where day, night and both day and night samplings were conducted, respectively. Open and solid triangles indicate approximate positions of the subarctic front and subarctic boundary, respectively.

Abundance

Abundance per square meter (N, indiv. m^{-2}) for each of the 4096 equivalent spherical diameter (ESD) size categories was calculated from the following equation:

$$N = \frac{n \times 150}{s \times F}$$

where n is the number of particles (=zooplankton indiv.), s is the split factor of each sample, F is the filtered volume of the net (m^3) and 150 is the length of the vertical net tow (m). Because the regional differences in abundance were greater than the day-night differences (see Results below and Fig. 4), we made no conversion according to day-night regime. For the stations where both day and night samplings were conducted (Fig. 1), we used the mean values for the day-night data.

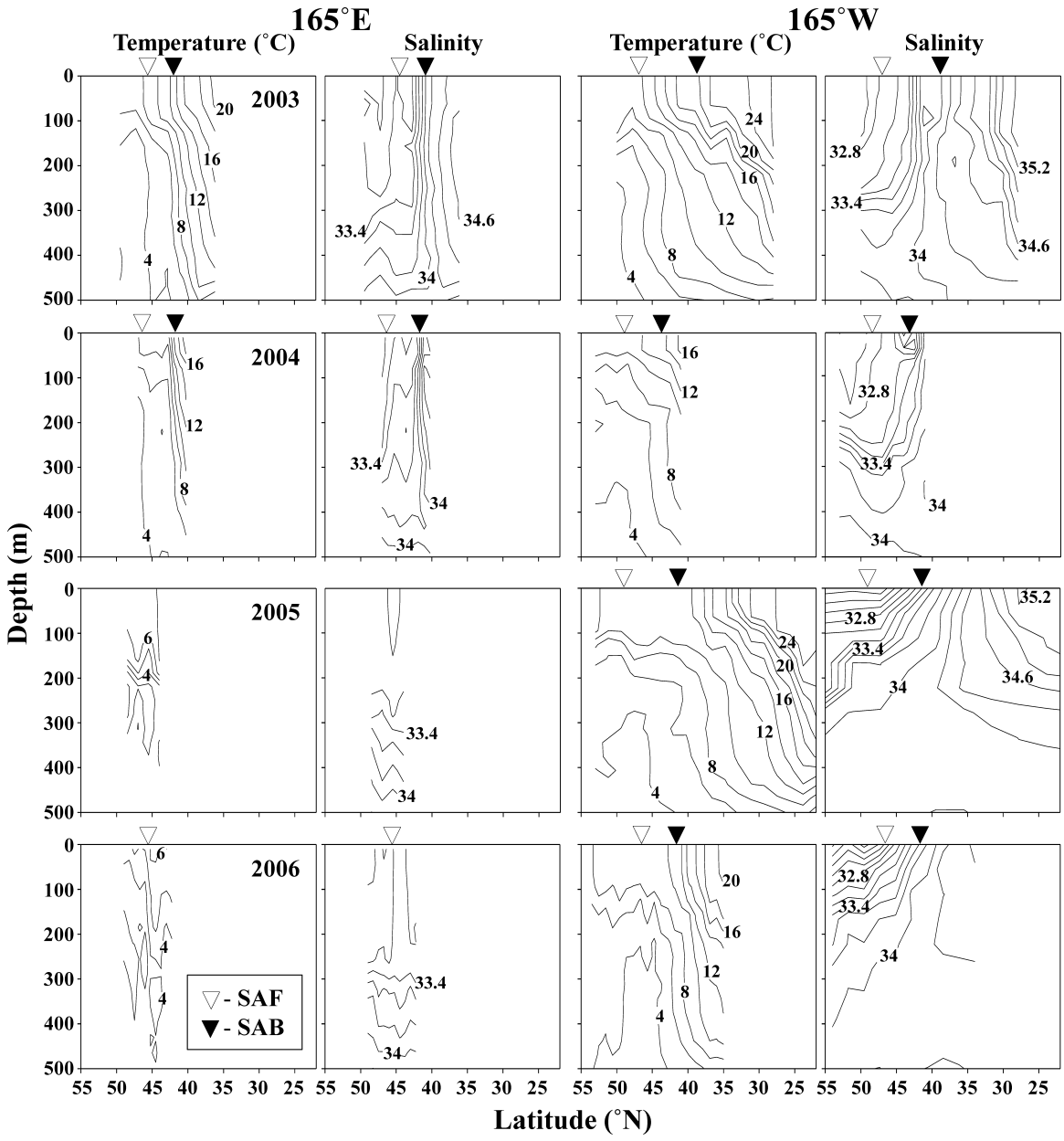


Fig. 2. Vertical profiles of temperature and salinity along 165°E and 165°W in the North Pacific during summers of 2003–2006. Approximate positions of the subarctic front (SAF) and subarctic boundary (SAB) are shown with open and solid triangles, respectively.

Biomass

Wet mass (WM) of the zooplankton community in the 4096 size categories was calculated from ESD data by assuming the relative density of zooplankton to be equal to seawater (=1 mg mm^{-3}). WM was converted to dry mass (DM) assuming that the water content of zooplankton was 90% (DM=0.1×WM), which is the mean water content of zooplankton from subarctic to subtropical areas in the North Pacific Ocean above 1,000 m (Yamaguchi et al. 2005, Matsuno et al. 2009). For calibration of OPC derived biomass, direct WM measurements were made on all samples with a precision of 10 mg.

Statistical analysis

To make regional comparisons of abundance and biomass data, we further binned the data from the 4096 size categories obtained with the OPC into five size classes (0.34–1.00, 1.00–2.00, 2.00–3.00, 3.00–4.00 and 4.00–5.00 mm ESD) and the total. For each size class, we used a two-way ANOVA to test for regional differences in the estimated variables. We used the definitions of Favorite et al. (1976) for the subarctic front (SAF; 4°C isotherm from 100

m to 500 m depth) and the subarctic boundary (SAB; 34 PSU isohaline in the upper 150 m depth) to define the three regions. Thus the subarctic region (SA) was north of the SAF, the transitional region (TR) was between the SAF and the SAB and the subtropical region (ST) was south of the SAB. In the present study, we treated six regions as independent variables of two-way ANOVA, e.g. east-west (165°E and 165°W) and north-south (SA, TR and ST). If the ANOVA indicated there were significant differences between regions, then a post hoc test by Fisher's Protected Least Significant Difference test (PLSD) was carried out.

Results

Hydrography

The temperature in the upper 150 m varied greatly with latitude (1.6–19.6°C on 165°E, and 3.3–27.0°C on 165°W) (Fig. 2). The position of the SAF, which is the northern boundary of the TR, was stable around 45°N on the 165°E line in 2003, 2004 and 2006, whereas on the 165°W line it was located further north and varied between years (47–49°N). In 2005 on 165°E, the SAF was not observed. The position of the SAB, which is at the southern end of TR, was 40–42°N on 165°E in 2003 and 2004, but varied from 39–44°N on 165°W between years. In 2005 and 2006 on 165°E, the SAB was not observed. Thus the hydrographic variation was greater for the 165°W line.

Zooplankton abundance and biomass

The result of the comparison between direct measured wet-mass and estimated OPC derived wet-mass is shown in Fig. 3. A highly significant correlation ($r^2=0.79$, $p<0.0001$) was observed between these variables (Fig. 3). The slope of the regression line was 1.16, indicating that the OPC data overestimated by 16% on average compared to directly measured mass.

Because interannual variations of the mean zooplankton abundance and biomass were not significant on any of the transect lines (Kruskal Wallis test, $p=0.07$–0.64), the following analysis for regional and day-night differences was made on the four years' data combined in order to increase the data size for a statistical comparison. Variations in mean day and night abundances of each ESD size in each region are shown in Fig. 4. Day-night differences in total zooplankton abundance were not detected in any of the regions (U-test, $p=0.50$–0.99). Interestingly, most of the N:D ratios were lower than 1 in the SA and ST. For the TR, high N:D ratios were observed commonly on 165°E and 165°W transects, while the ESD sizes with high N : D ratios differed between the transects; high ratios were observed in large zooplankton on the 165°E transect but in small zooplankton on the 165°W transect. Because these high N : D ratios indicate that zooplankton undergo diel vertical migration, the difference in high N : D ratios depending on size between the transects may indicate the zooplankton were of different species and/or that they were copepodid stages.

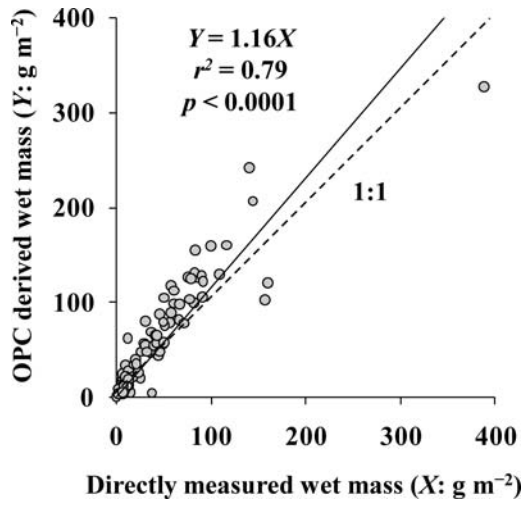


Fig. 3. Relationship between OPC derived (Y) and directly measured (X) wet mass. Solid and dashed lines indicate the regression line and position of 1 : 1, respectively.

Zooplankton abundances generally decreased with the ESD size. In the TR on both transects, however, distinct inflections in the decreasing curves were observed around 3.00 mm ESD (Fig. 4). A similar but smaller scale inflection around 3.00 mm ESD was seen in the SA, while it was not observed in the ST. Such a size spectrum pattern was common both at day and night within each region, indicating that the difference in the pattern was more remarkable between the regions than between day and night.

Figures 5 and 6 show size and latitudinal distribution of zooplankton abundance and biomass in the upper 150 m along 165°E and 165°W, respectively. The abundance was the highest in the smallest size class (0.34–1.00 mm ESD) in all regions and years. In contrast, the maximum biomasses were attributed to the middle to large size classes (2.00–5.00 mm ESD) in most of the cases. Thus, size distribution of abundance and biomass was very different.

Total abundance and biomass of zooplankton showed a statistically significant north-south difference (two-way ANOVA, $p<0.05$, Table 1), while east-west differences in each latitudinal region and size class were not significant ($p=0.15$–0.96). Total abundance ranged from 34×10^3 to 65×10^3 indiv. m^{-2}, and was significantly higher in the SA than in the TR and ST (Table 1). The smallest size class comprised the major portion (62–84%) of total abundance, and its latitudinal differences represented 62–183% of the differences in total abundance. Abundances of the 2.00–3.00 and 4.00–5.00 size classes were significantly lower in the ST than the other regions.

Total biomass ranged from 2.9 to 7.9 g DM m^{-2}, and was significantly lower in the ST than in the SA and TR. The 2.00–3.00 mm size class had the largest biomass in the SA and TR, comprising the major portion (28–48%) of the

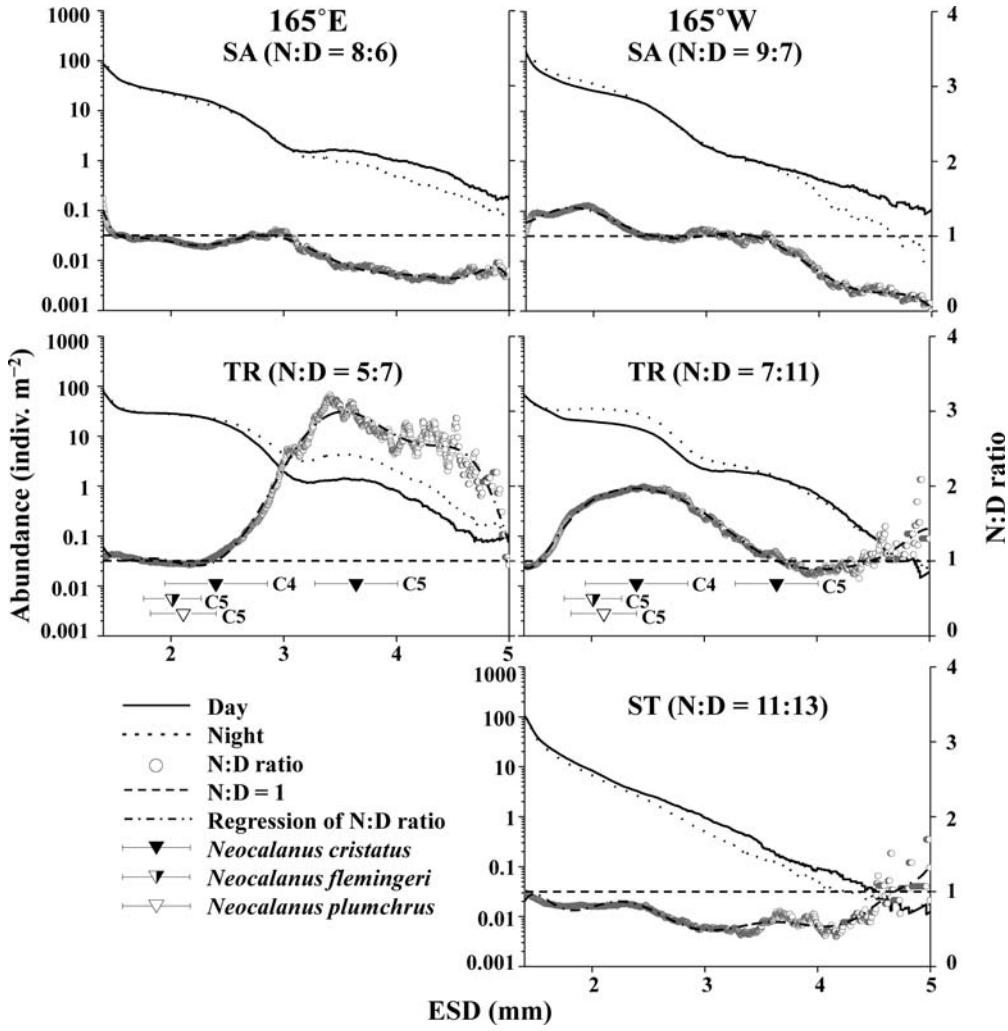


Fig. 4. Mean day and night abundance along with ESD size range in the 165°E (left) and 165°W (right) lines of North Pacific during summers of 2003–2006. N : D ratios are also shown. Horizontal dashed lines indicate positions of N : D = 1. SA: Subarctic, TR: Transition and ST: Subtropical regions. Numbers of samples in day and night are shown in the (N : D), 12 samples were omitted from the calculation where gelatinous zooplankton were abundant. Mean (symbols) and sd (bars) of ESD of late copepodid stages of *Neocalanus* spp. (Ohgi & Yamaguchi, unpubl) are superimposed in the middle panels (TR). C4 and C5 indicate copepodid stage 4 and 5, respectively.

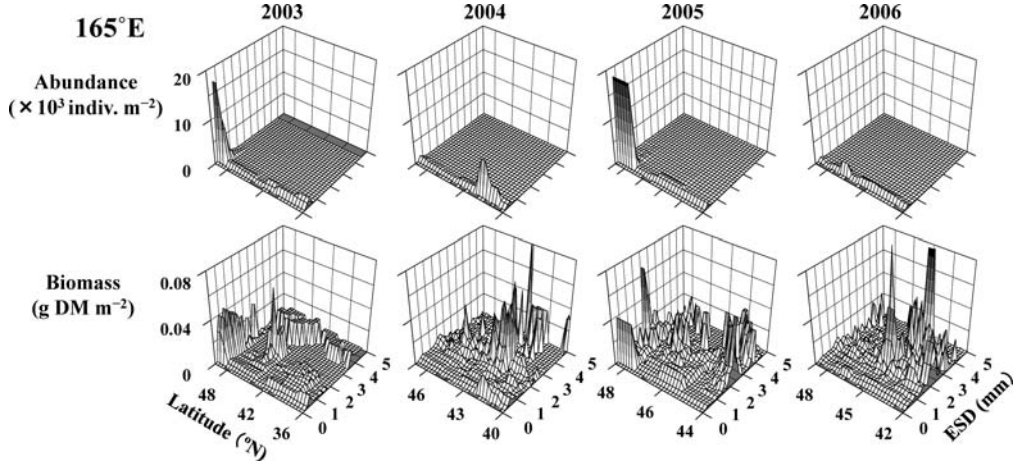


Fig. 5. Latitudinal changes in abundance and biomass with each size class along 165°E in the western North Pacific during summers of 2003–2006.

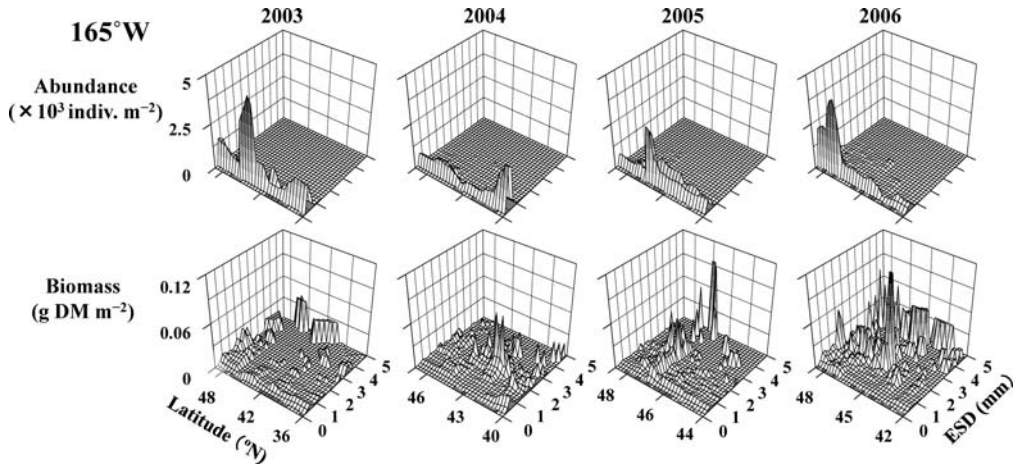


Fig. 6. Latitudinal changes in abundance and biomass with each size class along 165°W in the eastern North Pacific during summers of 2003–2006.

Table 1. North-south differences in abundance and biomass of zooplankton in the North Pacific during summers of 2003–2006. Since the east-west differences were not evident, data of both 165°E and 165°W are combined in this calculation and statistical analysis. "Differences" is the results of two-way ANOVA and between region differences were tested by post-hoc test of Fisher's PLSD. The letters assigned to each region label indicate the significant of difference; the region labels having different letters are significantly different from each other. Values are mean±sd. Numbers in parentheses indicate the number of stations included in each region. *: $p<0.05$, **: $p<0.01$. NS: not significant. SA: Subarctic, TR: Transitional and ST: Subtropical region.

Zooplankton	Region			Differences	Fisher's PLSD		
Size class	SA (30)	TR (28)	ST (31)				
Abundance ($\times 10^3$ indiv. m^{-2})							
Total	64.64±66.79	33.95±18.37	41.74±32.27	*	SA (a)	TR (b)	ST (b)
0.34–1.00 mm	49.42±61.15	20.90±15.84	35.13±24.93	*	SA (a)	TR (b)	ST (ab)
1.00–2.00 mm	10.51±7.03	6.35±3.46	5.09±6.34	**	SA (a)	TR (b)	ST (b)
2.00–3.00 mm	3.96±3.36	5.63±4.68	1.09±2.17	**	SA (a)	TR (a)	ST (b)
3.00–4.00 mm	0.60±0.64	0.92±1.00	0.40±1.63	NS			
4.00–5.00 mm	0.16±0.22	0.14±0.21	0.03±0.11	*	SA (a)	TR (a)	ST (b)
Biomass (g DM m^{-2})							
Total	6.95±4.15	7.85±5.46	2.86±6.14	**	SA (a)	TR (a)	ST (b)
0.34–1.00 mm	0.46±0.52	0.23±0.19	0.34±0.27	*	SA (a)	TR (b)	ST (ab)
1.00–2.00 mm	1.83±1.29	1.24±0.79	0.75±0.98	**	SA (a)	TR (b)	ST (b)
2.00–3.00 mm	2.65±2.27	3.78±3.06	0.80±1.70	**	SA (a)	TR (a)	ST (b)
3.00–4.00 mm	1.31±1.47	2.04±2.30	0.83±3.43	NS			
4.00–5.00 mm	0.70±0.93	0.56±0.86	0.14±0.42	*	SA (a)	TR (a)	ST (b)

mean total biomass, and its latitudinal pattern was the same as that of the total biomass, representing 45–126% of the differences in the mean total biomass. The 3.00–4.00 mm ESD had the second largest biomass in the TR, and the biomass of the 2.00–3.00 plus 4.00–5.00 size classes comprised 74% of the mean total biomass.

Discussion

In the subarctic Pacific, east-west differences have been reported for the oceanic environment: low temperature in the west (Favorite et al. 1976), phytoplankton and primary productivity: high in the west (Shiomoto & Asami 1999, Shiomoto & Hashimoto 2000), zooplankton life cycles: different periods necessary to complete their life cycles (Kobari & Ikeda 2001, Tsuda et al. 2004, Shoden et al. 2005) and zooplankton body size: larger in the west (Tsuda et al. 2001, Kobari et al. 2003b). Regardless of these east-west differences, east-west differences were not detected for total zooplankton abundance and biomass in this study. It should be noted that the study period varied slightly between 165°E and 165°W (ca. two weeks earlier in 165°E, cf. Fig.

1), this may have had some effect on east-west differences, however, it is difficult to fully assess these effects.

According to Saito (2010), zooplankton abundance based on samples collected with a net with smaller mesh (0.10 mm) carried out simultaneously with the present study was higher on the 165°E line than on 165°E by a factor of 1.8 to 12.5, mainly due to the dominance of nauplii and cyclopoid copepods. In contrast to his study, the present study using 0.335-mm mesh net indicated that zooplankton abundances were not significantly different between 165°E and 165°W. The difference between the two studies are undoubtedly due to the difference in the net used, and indicates that the longitudinal pattern in zooplankton abundance in the North Pacific was different between smaller and larger zooplankton.

The zooplankton communities in both the SA and TR were characterized by the dominance of large, cold-water copepods (e.g. *Neocalanus* spp.), whereas the community of the ST was characterized by a completely warm-water fauna comprised of much smaller taxa (Odate K 1994). These north-south differences in zooplankton fauna are considered as the cause of the regional differences in size spectra; the inflection point around 3.00 mm ESD was observed in the SA and TR, while no such inflections occurred in the ST. This inflection point in the SA and TR probably resulted from a paucity of copepods in that size class. The ESD of *Neocalanus flemingeri* Miller, *Neocalanus plumchrus* (Marukawa) copepodid stage 5 (C5) and *Neocalanus cristatus* (Krøyer) C4 was 2.0–2.4 mm and that of *N. cristatus* C5 was 3.6 mm (Fig. 4). The inflection around 3.00 mm ESD is just between the discrete size ranges of large and small *Neocalanus* spp. Absence of a corresponding inflection point in the ST is possibly explained by the absence of *Neocalanus* spp.

It is interesting that the total abundance of zooplankton was significantly lower in the TR and ST than in the SA whereas the total biomass was significantly higher in the SA and TR than in the ST. The high total biomass in the TR in contrast to the low total abundances is considered to be due to high abundances of *Neocalanus* spp., because the mean biomass of the 2.00–4.00 mm ESD, which corresponds to C4 and C5 of *Neocalanus* spp., comprised 74% of the total biomass and exhibited the same north-south pattern as the total biomass. Indeed, *Neocalanus* spp. dominated most of the samples in the TR (checked by eye during OPC analysis).

In regard to the north-south differences of *Neocalanus* spp., it may be important to consider their temperature-dependent growth rate. Batten et al. (2003) showed that in waters from Alaska to California the peak biomass of *N. plumchrus* C5 occurred five weeks earlier in California than in Alaska, and suggested that higher temperature in California by about 4°C than in Alaska results in a reduced development duration to reach C5 and consequently in their earlier occurrence. In the present study, the integrated mean temperature of the upper water column (0–150 m) was <4°C in the SA, while it was 6–12°C in the TR. According to the study using a 0.10-mm mesh plankton net made simultaneously with the present study (Saito R. pers comm), C5 of *N. cristatus* and *N. plumchrus* were more abundant in the TR than in the SA. Regardless of the difference in temperature and abundance of *Neocalanus* spp. C5, both the abundance and biomass in the present study were not significantly different between the SA and TR. One reason for this discrepancy may be explained by a negative correlation between body size of copepods and habitat temperature (cf. Corkett & McLaren 1978). Kobari et al. (2003a) investigated the body size (prosome length) of *Neocalanus* spp. C5 between 51°N to 37°N along 180° longitude, and revealed that mean prosome lengths of *Neocalanus* spp. C5 stages decreased with lower latitude, ranging between 6.1 and 7.2 mm for *N. cristatus*, 3.5–3.9 mm for *N. plumchrus* and 2.9–3.4 mm for *N. flemingeri* (Kobari et al. 2003a, read from Fig. 7). The ratio of biomass:abundance of the 2.00–4.00 mm ESD, which corresponds to *Neocalanus* spp. C5, was almost the same between the SA and TR (0.87 in SA and 0.89 in TR calculated from Table 1), indicating that the mean individual size was not different between the SA and TR. Smaller size of *Neocalanus* spp. C5 in the TR than in SA may have offset the expected increase in their biomass from their abundance.

The present study revealed that the TR was characterized by low abundances and high biomass of zooplankton. A similar situation has also been reported for early summer along 155°E in the western North Pacific Ocean (Yokoi et al. 2008). Because this situation in the TR has been observed on both sides of the North Pacific Ocean, it can be considered as a general pattern of the TR over the central North Pacific Ocean.

Acknowledgements

We thank Dr. Jeffery M. Napp (NOAA) for kindly reviewing an earlier version of this paper. We thank the captain, officers and crews of the T/S *Oshoro-Maru* for their help in zooplankton sampling. This study was supported by a Grant-in-Aid for Young Scientists (B) 21780173 by the Japan Society for the Promotion of Science.

References

Batten SD, Welch DW, Jonas T (2003) Latitudinal difference in the duration of development of *Neocalanus plumchrus* copepodites. Fish Oceanogr 12: 201–208.

Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. Adv Mar Biol 15: 1–231.

Favorite F, Dodimead AJ, Nasu K (1976) Oceanography of the subarctic Pacific region 1960–1971. Bull Int North Pac Fish Comm 33: 1–187.

Harrison PJ, Boyd PW, Varela DE, Takeda S, Shiomoto A, Odate T (1999) Comparison of factors controlling phytoplankton productivity in the NE and NW subarctic Pacific gyres. Prog

Oceanogr 43: 205–234.

Kobari T, Ikeda T (2001) Life cycle of *Neocalanus flemingeri* (Crustacea: Copepoda) in the Oyashio region, western subarctic Pacific, with notes on its regional variations. Mar Ecol Prog Ser 209: 243–255.

Kobari T, Ikeda T, Kanno Y, Shiga N, Takagi S, Azumaya T (2003a) Interannual variations in abundance and body size in *Neocalanus* copepods in the central North Pacific. J Plankton Res 25: 483–494.

Kobari T, Tadokoro K, Shiomoto A, Hashimoto S (2003b) Geographical variations in prosome length and body weight of *Neocalanus* copepods in the North Pacific. J Oceanogr 59: 3–10.

Mackas DL, Tsuda A (1999) Mesozooplankton in the eastern and western subarctic Pacific: Community structure, seasonal life histories, and interannual variability. Prog Oceanogr 43: 335–363.

Matsuno K, Kim HS, Yamaguchi A (2009) Causes of under- or overestimation of zooplankton biomass using Optical Plankton Counter (OPC): effect of size and taxa. Plankton Benthos Res 4: 154–159.

Motoda S (1957) North Pacific standard net. Inform Bull Planktol Japan 4: 13–15. (in Japanese with English abstract)

Mullin MM, Goetze E, Beaulieu SE, Lasker JM (2000) Comparisons within and between years resulting in contrasting recruitment of Pacific hake (*Merluccius productus*) in the California Current System. Can J Fish Aquat Sci 57: 1434–1447.

Nagasawa K, Ohtsuka S, Saeki S, Ohtani S, Zhu GH, Shiomoto A (2001) Abundance and *in-situ* feeding habits of *Neocalanus cristatus* (Copepoda: Calanoida) in the Central and Western North Pacific Ocean in summer and winter. Bull Natl Res Inst Far Seas Fish 38: 37–52.

Odate K (1994) Zooplankton biomass and its long-term variation in the western North Pacific Ocean, Tohoku Sea Area, Japan. Bull Tohoku Natl Fish Res Inst 56: 115–173. (in Japanese with English abstract)

Odate T (1994) Plankton abundance and size structure in the northern North Pacific Ocean in early summer. Fish Oceanogr 3: 267–278.

Saito R (2010) East-west comparison of zooplankton community in the subarctic Pacific during summers of 2003–2006. Master's thesis of Graduate School of Fisheries Sciences, Hokkaido University.

Shiomoto A, Asami H (1999) High-west and low-east distribution patterns of chlorophyll *a*, primary productivity and diatoms in the subarctic North Pacific surface waters, midwinter 1996. J Oceanogr 55: 493–503.

Shiomoto A, Hashimoto S (2000) Comparison of east and west chlorophyll *a* standing stock and oceanic habitat along the Transition Domain of the North Pacific. J Plankton Res 22: 1–14.

Shoden S, Ikeda T, Yamaguchi A (2005) Vertical distribution, population structure and life cycle of *Eucalanus bungii* (Copepoda: Calanoida) in the Oyashio region, with notes on its regional variations. Mar Biol 146: 497–511.

Suzuki K, Liu H, Saino T, Obata H, Takano M, Okamura K, Sohrin Y, Fujishima Y, (2002) East-west gradients in the photosynthetic potential of phytoplankton and iron concentration in the subarctic Pacific Ocean during early summer. Limnol Oceanogr 47: 1581–1594.

Takahashi K, Kuwata A, Saito H, Ide K (2008) Grazing impact of the copepod community in the Oyashio region of the western subarctic Pacific Ocean. Prog Oceanogr 78: 222–240.

Taniguchi A (1999) Differences in the structure of the lower trophic levels of pelagic ecosystems in the eastern and western subarctic Pacific. Prog Oceanogr 43: 289–315.

Tsuda A, Saito H, Kasai H (2001) Geographical variation of body size of *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri* in the subarctic Pacific and its marginal seas: Implications for the origin of large form of *N. flemingeri* in the Oyashio area. J Oceanogr 57: 341–352.

Tsuda A, Saito H, Kasai H (2004) Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Copepoda: Calanoida) in the western subarctic Pacific Ocean. Fish Oceanogr 13: 10–20.

Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Maeda M, Ishizaka J, Ikeda T, Takahashi MM (2005) Biomass and chemical composition of net-plankton down to greater depths (0–5800 m) in the western North Pacific Ocean. Deep-Sea Res I 52: 341–353.

Yokoi Y, Yamaguchi A, Ikeda T (2008) Regional and inter-annual change in the abundance, biomass and community structure of mesozooplankton in the western North Pacific in early summer; as analyzed with an optical plankton counter. Bull Plankton Soc Japan 55: 9–24. (in Japanese with English abstract)