

Different vertical distribution of zooplankton community between North Pacific Subtropical Gyre and Western Pacific Warm Pool: its implication to carbon flux

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Abstract

The mesozooplankton in both epipelagic and mesopelagic zones is essentially important for the study of ecosystem and biological carbon pump. Previous studies showed that the diel vertical migration (DVM) pattern of mesozooplankton varied among ecosystems. However, that pattern was largely unknown in the Western Pacific Warm Pool (WPWP). The vertical distribution, DVM and community structure of mesozooplankton from the surface to 1 000 m were compared at Stas JL7K (WPWP) and MA (North Pacific Subtropical Gyre, NPSG). Two sites showed similarly low biomass in both epipelagic and mesopelagic zones, which were in accordance with oligotrophic conditions of these two ecosystems. Stronger DVM (night/day ratio) was found at JL7K (1.31) than that at MA (1.09) on surface 0–100 m, and an obvious night increase of mesopelagic biomass was observed at JL7K, which was probably due to migrators from bathypelagic zone. Active carbon flux by DVM of zooplankton was estimated to be 0.23 mmol/(m²·d) at JL7K and 0.16 mmol/(m²·d) at MA. The community structure analysis showed that calanoid copepods, cnidarians and appendicularians were the main contributors to DVM of mesozooplankton at both sites. We also compared the present result with previous studies of the two ecosystems, and suggested that the DVM of mesozooplankton was more homogeneous within the WPWP and more variable within the NPSG, though both ecosystems showed typically extremely oligotrophic conditions. The different diel vertical migration strength of mesozooplankton between NPSG and WPWP implied different efficiency of carbon pump in these two ecosystems.

Key words: mesopelagic zone, diel vertical migration, biological pump, vertical distribution, active carbon flux

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1 Introduction

The pelagic ecosystem is important in regulating the air-sea exchange flux, as well as the transfer of organic carbon into the deep sea. Within this ecosystem, mesozooplankton play a key role in influencing the fate of primary production and linking that with higher trophic levels (such as macrozooplankton and micronekton). Recent studies focused on their roles in the biological pump and ocean carbon cycle, such as fecal pellet production, ontogenetic or diel vertical migration, feeding on sinking particles or “marine snow”, sinking of carcasses and respiration in deep waters (e.g., Ohtsuka et al., 1996; Kobari et al., 2008, 2016; Takahashi et al., 2009; Lebrato et al., 2013; Cavan et al., 2017). Although zooplankton community shows significant diversity in taxonomy, life history, size spectrum and trophic ecology, their roles are always simplified in many biogeochemical models (Steinberg and Landry, 2017). Especially, mesozooplankton has

been considered to be important in determining the sinking efficiency of particulate organic carbon by grazing or crushing, and supplying extra energy to the mesopelagic zone by diel vertical migration (DVM) (Steinberg et al., 2008b; Cavan et al., 2017). However, the knowledge of their abundance, biomass, community structure and trophic ecology in mesopelagic zone is limited, compared with those in epipelagic zone (Yamaguchi et al., 2002; Steinberg et al., 2008a).

The information on vertical distribution of abundance, biomass and community structure of zooplankton in mesopelagic zone is fundamentally important for the study of biological carbon pump, especially in the open sea. First, some detritus feeders were observed to ingest sinking particles. For example, *Oncaea* spp. ingested appendicularian houses and possibly affected the POC flux (Ohtsuka et al., 1996; Nishibe et al., 2015). Similarly, Svensen and Nejstgaard (2003) also observed that cyc-

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lopoids ingested copepod fecal pellets in field experiment. Second, several salps were confirmed to filter small-size particles (2.5 μm in diameter) with high efficiency (Kremer and Madin, 1992), while copepods and other mesozooplankton could only feed larger particles (5–12 μm in diameter) effectively (Nival and Nival, 1976). Therefore, different community structure inferred differences in energy transfer efficiency in pelagic ecosystem, especially in oligotrophic subtropical gyre, in which the picophytoplankton contributed most of total primary production (Liu et al., 1997). Third, carnivores in mesopelagic zone would repack their prey into fast-sinking fecal pellets, and thus influenced the POC flux (Wilson et al., 2008). The mesopelagic carnivore layer was found to be distinct in the subarctic North Pacific Ocean (Steinberg et al., 2008a). Fourth, some taxa with significant ontogenetic or diel vertical migration could cause remarkably active carbon flux in mesopelagic zone (Kobari et al., 2008; Takahashi et al., 2009; Jónasdóttir et al., 2015). Finally, sinking of gelatinous zooplankton biomass was considered as an important component of biological pump, while sinking rates of different taxa were varied (Lebrato et al., 2013).

The North Pacific Subtropical Gyre (NPSG) is the largest contiguous biome on the earth (Karl, 1999). The surface water of NPSG is a typical oligotrophic zone, characterized by low nutrient concentration and low standing stocks of phytoplankton (Suzuki et al., 1997; Zhang et al., 2012). The Western Pacific Warm Pool (WPWP), located at the western part of Equatorial Pacific, is also an oligotrophic zone. However, the difference is that the warm pool is also characterized by low salinity, low nitrate concentration, high surface temperature and deep thermocline (Hénin et al., 1998; Le Borgne et al., 2002). Recent studies showed that a large number of overlapping species between the mesozooplankton communities in NPSG and WPWP, regardless of in epipelagic zone or in mesopelagic zone (Yamaguchi et al., 2015; Sun and Wang, 2017). This suggested a potentially close relationship between these two pelagic ecosystems.

Although growing evidence confirmed the significant role of WPWP and western NPSG in global marine carbon cycle (Kawahata et al., 2000), the studies about mesopelagic mesozooplankton abundance, biomass and community structure in western NPSG were quite limited compared with those in eastern Equatorial Pacific or eastern NPSG (e.g., Roman et al., 1995; Steinberg et al., 2008a). Vertical distribution of “metazooplankton” (>90 μm) biomass, sketchy community structure (copepods, chaetognaths and cnidarians) and chemical composition of biomass were studied (Yamaguchi et al., 2004, 2005). Recently, the vertical distribution of calanoid copepods community structure was also re-

ported (Yamaguchi et al., 2015). At the subtropical time-series Sta. S1, the mesozooplankton biomass and community structure were studied (Kobari et al., 2013; Kitamura et al., 2016). Recently, the abundance and size spectra of zooplankton down to 3 000 m along the Pacific western boundary currents was reported (Dai et al., 2017). Among all these results, the diel vertical migration of mesopelagic mesozooplankton was only studied in detail at subtropical Sta. S1, and a detail comparison of mesopelagic mesozooplankton communities in the western NPSG and WPWP was still lacking. This limited further study of biological pump and biogeochemistry in the western subtropical and tropical Pacific.

In this study, the mesozooplankton communities (0–1 000 m) between the western NPSG and WPWP were compared. Zooplankton samples were collected during the day and night at two sites in the western NPSG and one site in the northern WPWP. The vertical changes of community structure and diel vertical migration pattern were studied, and their potential significance to biological pump was also discussed.

2 Materials and methods

2.1 Sampling sites

The investigation was conducted in the western North Pacific Ocean, including two sites at southwestern NPSG (Sta. MA, around 15°N, 155°E; Sta. MP-NA, around 19°N, 161°E) and one site at northern WPWP was Sta. JL7K (around 11°N, 142°E) (Fig. 1 and Table 1).

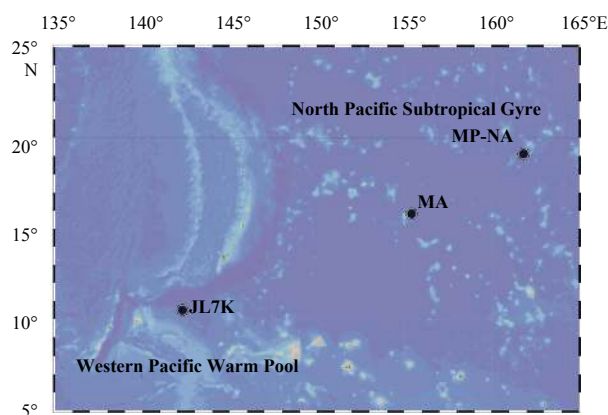


Fig. 1. Map of sampling stations. JL7K, MA and MP-NA were three sampling sites in the present investigation.

Table 1. Summary of sampling information

Area	Station	North latitude	East longitude	Sampling date	Day/Night
WPWP	JL7K-01	10.500 8°	142.299 9°	2012-06-16	day
	JL7K-02	11.157 2°	142.273 6°	2012-06-18	night
	JL7K-03	11.759 0°	142.329 1°	2012-06-20	night
	JL7K-04	11.296 6°	142.317 2°	2012-06-23	day
NPSG	MA-01	15.815 0°	155.413 6°	2012-07-21	day
	MA-02	15.893 4°	155.553 6°	2012-07-21	day
	MA-03	15.918 4°	155.610 8°	2012-07-22	day
	MA-04	15.627 4°	154.915 8°	2012-07-14	night
	MA-06	15.579 2°	154.711 6°	2012-07-16	night
	MA-07	15.208 9°	154.376 7°	2012-07-19	day
	MA-08	16.066 7°	154.902 9°	2012-07-24	night
	MP-NA-01	19.681 0°	161.733 9°	2012-07-27	night
MP-NA-04	19.121 6°	161.827 9°	2012-08-01	day	

2.2 Sample collection

Physical, chemical and biological investigations were conducted by the R/V *Haiyang 6* around the above two areas during June and July 2012, as a part of DY27 Cruiser (COMRA). Four, seven and two sampling tows were deployed at JL7K, MA and MP-NA, respectively (Table 1). Mesozooplankton were collected using a five-net multiple plankton sampler, MultiNet (Hydro-Bios Co. Ltd.), which had a 0.25 m² mouth opening area and a mesh size of 200 μm. At each station, the following depth intervals were sampled on the upcast: 0–50 m, 50–100 m, 100–200 m, 200–500 m, and 500–1 000 m. The towing speed when sampling was about 0.6 m/s and the filtered water volume of each sample was estimated by a flow meter located at the mouth of MultiNet. The collected samples were preserved immediately in 5% (v/v) buffered formalin-seawater solution. Temperature and salinity were recorded using a CTD system (SBE 911 plus, Seabird Co. Ltd.) to depth of 1 000 m and averaged into 1 m vertical intervals. Seawater used for the analysis of chlorophyll *a* concentration was collected from 2, 10, 30, 50, 75, 100, 125, 150, 175 and 200 m depths. At MA and MP-NA, the chlorophyll *a* concentration of 30 m layer was not measured. These samples were filtered through Whatman GF/F filter (nominal pore size, 0.7 μm). Chlorophyll *a* on each filter was measured using a Trilogy Laboratory Fluorometer (Model 7200, Turner Designs Co. Ltd.) after overnight extraction with 90% aqueous acetone at –20°C in the dark (Parsons et al., 1984).

2.3 Zooplankton abundance, biomass and diversity

Large gelatinous zooplankton (such as *Pyrosoma* sp.), macrozooplankton (body length > 20 mm, except Chaetognaths) and small nekton were removed before analysis and measurement. Subsamples of mesozooplankton were obtained using a Folsom Plankton splitter. A half of each sample was filtered using a mesh (mesh size of 200 μm) and redundant water was removed using absorbent papers. These samples were dried under 60°C for 24 h. The dry weight was measured using an electronic microbalance (MS105DU, METTLER-TOLEDO Co. Ltd.) with precision of 0.1 mg. In laboratory, 1% to 50% of the total mesozooplankton samples were identified to species or genus level when possible and counted using a stereomicroscope (M205c, Leica Co. Ltd.). All the specimens from large-size taxonomic groups, such as euphausiids, were identified and counted. The biomass and abundance of mesozooplankton were expressed as mg/m³ (dry biomass) and ind./m³, respectively. Due to the limitation of relatively small net mouth area in the present work, the sampling effectiveness for some active swimming taxa with strong escape ability (so-called “net avoidance”), such as euphausiids and amphipods, would be underestimated in the present sampling (Sameoto et al., 2000), though they were identified and counted. Besides, a part of euphausiids specimens were damaged by the net, thus were only counted but not identified to species or genus level. Therefore, the community structure data of above two taxa were not discussed. For MP-NA, only two net tows (day and night) were finished completely. Therefore, only the biomass and abundance data of MP-NA was showed, and community structure data and diel vertical migration was not analyzed and discussed.

Because some other studies only showed the carbon content biomass of zooplankton, we used the average ratio of carbon content (36%) for mesozooplankton in NPSG (calculated from Table 2 in Landry et al. (2001)) to standardize the carbon content data from literatures to dry weight biomass data.

2.4 Active carbon flux by DVM

We chose 100 m as the threshold depth for day- and night-

Table 2. Mean dry weight biomass (SD) during day and night, and the diel vertical migration indices of mesozooplankton at each depth layer at Stas JL7K, MA and MP-NA

Sites and depths/m	Mean dry weight biomass (SD)/mg·m ⁻³		N:D ratio
	Day	Night	
JL7K			
0–50	3.28 (0.95)	4.89 (0.33)	1.49
50–100	2.80 (0.39)	3.04 (0.50)	1.08
100–200	2.93 (0.37)	1.93 (0.90)	0.66
200–500	0.65 (0.22)	0.71 (0.12)	1.09
500–1 000	0.31 (0.01)	0.48 (0.05)	1.54
(0–100)	3.04 (0.67)	3.97 (0.08)	1.31
(0–200)	2.98 (0.52)	2.95 (0.41)	0.99
(200–1 000)	0.44 (0.09)	0.56 (0.08)	1.29
MA			
0–50	2.94 (1.44)	4.76 (2.16)	1.62
50–100	3.95 (1.03)	2.76 (1.79)	0.70
100–200	2.51 (0.62)	1.78 (0.39)	0.71
200–500	1.19 (0.09)	0.54 (0.32)	0.45
500–1 000	0.53 (0.06)	0.43 (0.10)	0.81
(0–100)	3.45 (1.14)	3.76 (1.82)	1.09
(0–200)	2.98 (0.61)	2.77 (0.94)	0.93
(200–1 000)	0.78 (0.03)	0.47 (0.15)	0.60
MP-NA			
0–50	2.53	3.47	1.38
50–100	1.50	2.21	1.47
100–200	2.21	1.00	0.45
200–500	0.88	0.65	0.74
500–1 000	0.70	0.32	0.46

Note: (0–100), (0–200) and (200–1 000) indicated the integrated biomass at the depths of 0–100 m, 0–200 m and 200–1 000 m, respectively.

time biomass of migrators, based on the vertical community structure profiles. To estimate the contribution of mesozooplankton DVM to the vertical carbon flux (also named as “active carbon flux”), we followed below procedure (Dam et al., 1995; Al-Mutairi and Landry, 2001).

First, oxygen consumption rate of mesozooplankton were estimated following the empirical relationships of Ikeda (1985).

$$\ln RO = -0.2512 + 0.7886 \ln DW + 0.049T,$$

where *RO* is the oxygen consumption rate (μL/(ind·h)), *DW* is the dry mass (mg) and *T* is the mean environmental temperature (°C). We assumed that the daytime depth range of migrating mesozooplankton was 150–300 m in oligotrophic subtropical oceans (Ohman and Romagnan, 2016).

Second, the oxygen consumption rate was converted to respiratory carbon rate (*RC*, μmol/(ind·h)) as

$$RC = RO \times RQ / 22.4,$$

where *RQ* (respiratory quotient) is the molar ratio of carbon produced to oxygen utilized, and 22.4 is the molar volume. In the present study, *RQ* of 0.97 was assumed (Isla et al., 2015; Kobari et al., 2016).

Third, the downward flux of carbon respired by migrators below 100 m was estimated by applying the below equation:

$$F = B \times RC \times t,$$

where *F* is the respired carbon flux of zooplankton at the depth of 100 m (μmol/(m²·d)); *B* is the biomass of diel-migrating mesozooplankton biomass at the surface 100 m (*DW*, mg/m²), calculated as the difference between day and night samples; and *t* is

the average number of daytime hours (12.5 h and 13 h in JL7K and MA, respectively).

Fourth, the downward active flux of dissolved organic carbon (DOC) by migrant zooplankton ($\mu\text{mol}/(\text{ind.}\cdot\text{h})$) was calculated as 31% of downward active flux of respired carbon (dissolved inorganic carbon, DIC) (Steinberg et al., 2000). The active carbon flux of migrant mesozooplankton was the sum of DOC and DIC.

3 Results

3.1 Physical oceanography and chlorophyll *a* concentration

At JL7K, the mixed layer depth was 75 m, and the surface temperature was above 29.5°C. Below the mixed layer, the water temperature decreased very slowly to approximately 115 m, then followed by a rapid drop to 350 m, and finally entered a stage of slow decrease below 350 m. The surface salinity was lower, ranged from 34.3 to 34.6 between 0 to 100 m. The salinity increased to 35.3 at the depth of 172 m, and decreased to 34.3 rapidly at around 300 m. Then, the salinity remained relatively constant (around 34.5). For the chlorophyll *a*, the surface concentration was extremely low (around 0.03 $\mu\text{g}/\text{L}$), and the maximum value was 0.18 $\mu\text{g}/\text{L}$ at the depth of 125 m. The vertically integrated chlorophyll *a* in the epipelagic layer was 0.08 $\mu\text{g}/\text{L}$ (15.20 mg/m^2) (Fig. 2).

At MA, the mixed layer depth was 46 m, and the surface temperature was above 29.1°C. Below the mixed layer, the water temperature decreased rapidly to around 500 m, and then decreased quite slowly below this zone. The surface salinity was around 35.0, which was significantly higher than that at JL7K. The salinity decreased below 170 m, with the minimum value occurred at the depth of 500 m. The salinity of midwater was lower than that at JL7K. For chlorophyll *a*, the surface concentration was also extremely low (0.04–0.05 $\mu\text{g}/\text{L}$), and the maximum value was 0.20 $\mu\text{g}/\text{L}$ at the depth of 125 m. The vertically integrated chlorophyll *a* in the epipelagic layer was 0.08 $\mu\text{g}/\text{L}$ (16.90 mg/m^2) (Fig. 2). At MP-NA, the water temperature profile was similar with that at MA, but a lower water temperature was found at the depth of 50–250 m. The salinity profile was also similar with that at MA, but with a slightly higher surface salinity (around 35.2). For the chlorophyll *a* concentration profile, a shallower maximum value was observed at the depth of 100 m. The vertically integrated

chlorophyll *a* in the epipelagic layer was also extremely low, approximate 0.08 $\mu\text{g}/\text{L}$ (16.93 mg/m^2) (Fig. 2).

3.2 Biomass and abundance

Vertical profiles of dry weight biomass at JL7K, MA and MP-NA were showed in Fig. 3 and Table 2, which illustrated some vertical differences among sites. First, both JL7K and MA exhibit surface (0–50 m) peaks in biomass at night (4.89 mg/m^3 for JL7K and 4.76 mg/m^3 for MA), while there was a significant subsurface peak (50–100 m) in biomass for MA in the day. Second, the integrated mesozooplankton biomass of epipelagic zone (0–200 m) were very close between two sites (2.77–2.98 mg/m^3 at MA and 2.95–2.98 mg/m^3 at JL7K). Third, for mesopelagic layers, the biomass at JL7K (0.71 mg/m^3 for 200–500 m and 0.48 mg/m^3 for 500–1 000 m) was higher than those at MA (0.54 mg/m^3 for 200–500 m and 0.43 mg/m^3 for 500–1 000 m) at night; while an opposite trend occurred during the day (JL7K: 0.65 mg/m^3 for 200–500 m and 0.31 mg/m^3 for 500–1 000 m; MA: 1.19 mg/m^3 for 200–500 m and 0.53 mg/m^3 for 500–1 000 m). Besides, the biomass at MP-NA were lower than those at MA at most layers; a similar vertical distribution was also observed, but a deeper subsurface peak (100–200 m) in biomass was found in the day at MP-NA.

The DVM of mesozooplankton was obvious at all sites, though there were also differences (Fig. 3 and Table 2). At JL7K, the biomass of surface 0–50 m and mesopelagic 500–1 000 m at night was 49% and 54% higher than those during the day, while the biomass of 100–200 m layer at night was obviously lower than that during the day (only 66%). At MA, the biomass of surface 0–50 m at night was 62% higher than those during the day, with a corresponding decrease in below layers. The vertical trend of biomass at Sta. MP-NA was basically similar with that at MA, but with a higher night/day ratio of 50–100 m layer. The integrated biomass at the surface 0–100 m and the whole epipelagic zone (0–200 m) between JL7K and MA were also compared. A stronger DVM (night/day ratio) of 0–100 m was found at JL7K (1.31) than that at MA (1.09), while the strength of DVM at the depths of 0–200 m was not pronounced or very weak at both sites (JL7K: 0.99; MA: 0.93).

Different from the vertical distribution of mesozooplankton biomass, the vertical profiles of abundance were fundamentally

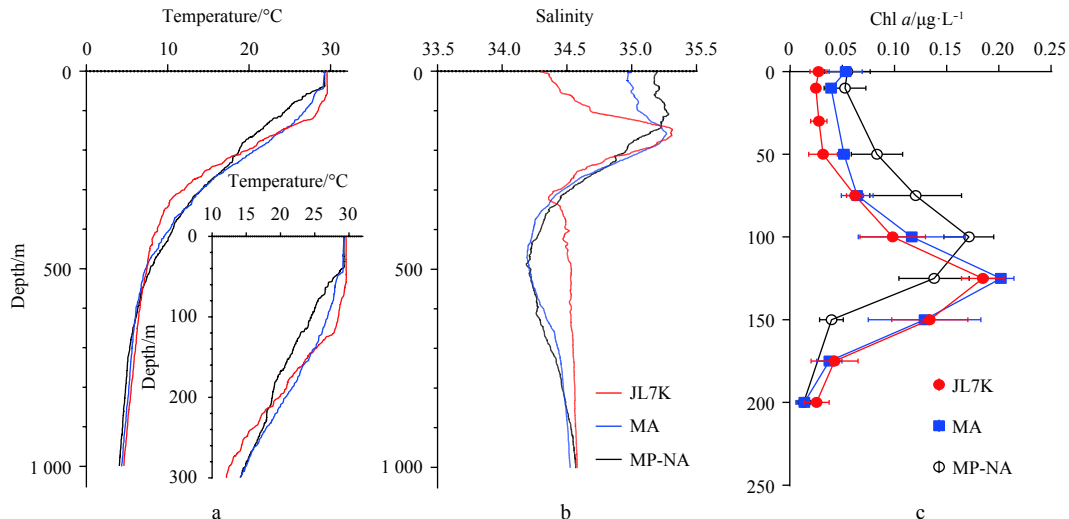


Fig. 2. Vertical profiles of temperature, salinity and chlorophyll *a* concentration of Stas JL7K, MA and MP-NA.

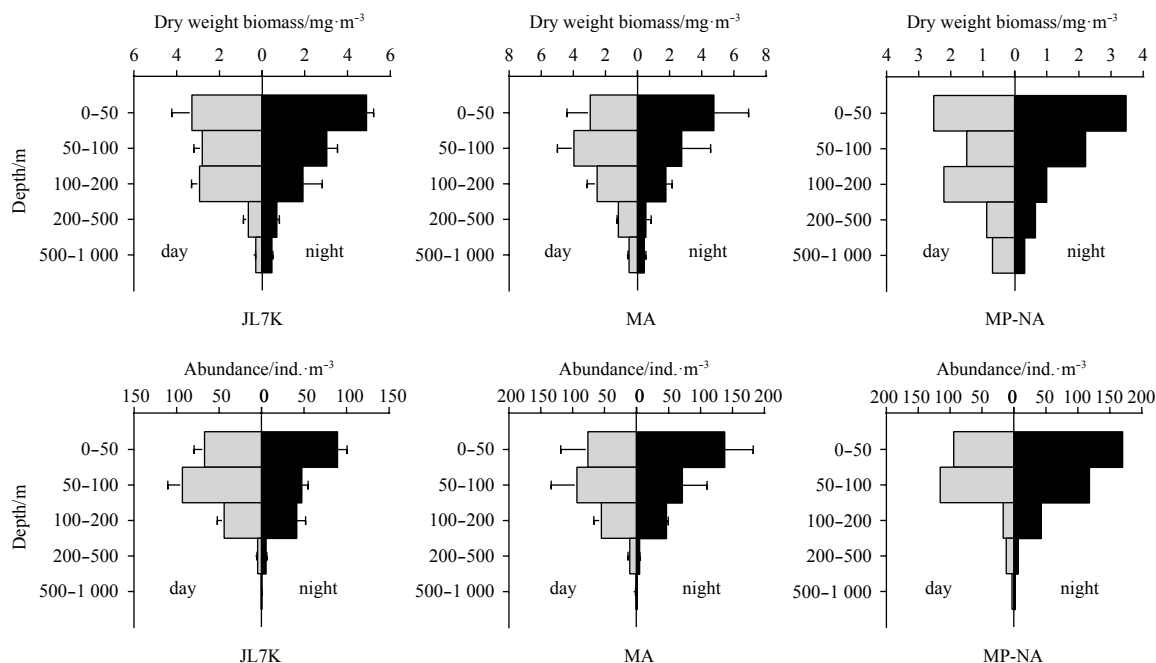


Fig. 3. Vertical distribution of dry weight biomass and abundance of Stas JL7K, MA and MP-NA, during the day and at night.

similar at JL7K, MA and MP-NA (Fig. 3). At night, an obviously surface peak and a decrease trend in below layers were found at all sites. The abundance of JL7K, which ranged from 0.4 ind./m³ (500–1 000 m) to 90.4 ind./m³ (0–50 m), was lower than those at MA, which ranged from 0.4 ind./m³ (500–1 000 m) to 138.1 ind./m³ (0–50 m). During the day, a pronounced subsurface peak (50–100 m) and a similar decrease trend in below layers were detected at all sites. The abundance at JL7K, which ranged from 0.3 ind./m³ (500–1 000 m) to 93.0 ind./m³ (50–100 m), was lower than those at MA, which ranged from 0.6 ind./m³ (500–1 000 m) to 93.1 ind./m³ (0–50 m). The DVM of mesozooplankton abundance was also obvious at the depths of 0–100 m, but weak DVM of abundance was observed from deeper waters.

3.3 Community structure

3.3.1 Copepods

Copepods were the most abundant mesozooplankton taxa at all sites. At night, it constituted 82.0%–87.3% and 73.2%–78.3% of the total mesozooplankton abundance in the epipelagic zone (0–200 m) and mesopelagic zone (200–1 000 m) respectively at JL7K, and 70.8%–81.4% and 74.2%–82.8% at MA. During the day, it constituted 75.4%–87.0% and 80.1%–88.7% of the total mesozooplankton abundance in the epipelagic zone (0–200 m) and mesopelagic zone (200–1 000 m) respectively at JL7K, and 80.2%–83.4% and 74.3%–82.2% at MA (Fig. 4). The average proportion of copepods to the total abundance was higher at JL7K (night: 83.3%±5.5%; day: 80.9%±5.4%) than that of MA (night: 76.4%±5.4%; day: 80.7%±3.8%) (all samples integrated).

Calanoid copepods were the most abundant taxa of copepods at both sites (Fig. 5). At night, it constituted 50.3%–63.9% and 69.9%–83.0% of the total abundance of copepods in the epipelagic zone (0–200 m) and mesopelagic zone (200–1 000 m) respectively at JL7K, and 53.5%–56.2% and 57.8%–66.8% at MA. During the day, it constituted 38.3%–51.8% and 33.8%–91.7% of the total abundance of copepods in the epipelagic zone (0–200 m) and mesopelagic zone (200–1 000 m) respectively at JL7K, and

35.0%–43.3% and 44.0%–66.6% at MA. Several small species, including *Clausocalanus* spp. and *Paracalanus* spp., were the dominant groups at both sites. Besides, calanoids included several subordinate dominant and middle-sized taxa with obvious DVM behavior, such as *Pleuromamma* spp., *Lucicutia* spp. and *Euchaeta* spp. Therefore, the DVM of calanoids was obvious at both sites in the present study (Fig. 6). A similar vertical distribution between JL7K and MA was found: the peak value occurred in the surface layer (0–50 m) at night and in the subsurface layer (50–100 m) during the day, at both sites. The N:D ratios at the depths of 0–50 m and 0–100 m were 1.7 and 1.0 respectively at JL7K, and 2.1 and 1.3 at MA. The N:D ratios at the upper mesopelagic zone (200–500 m) were 2.3 at JL7K and 0.6 at MA (Table 3). Some bathypelagic species (including copepods and euphausiids) migrating up into the mesopelagic zone were also observed at JL7K (Table 4), which caused an obviously night increase (N:D ratio=1.54) of biomass in the layer of 500–1 000 m.

Poecilostomatoid copepods were the second abundant taxa of copepods at both sites (Fig. 5). They also exhibited similar vertical distribution between JL7K and MA: the peak value both occurred in the surface layer (0–50 m) and the abundance decreased rapidly with depth during both day and night (Fig. 6). Poecilostomatoid copepods were mostly from the genus *Corycaeus*, *Farranula* and *Oncaea* at both sites. The N:D ratios at the depths of 0–50 m and 0–100 m were 1.1 and 0.9 respectively at both sites, which indicated a weak DVM for Poecilostomatoid copepods at both sites (Table 3).

Cyclopoid copepods were the third abundant taxa of copepods, which were almost from the genus *Oithona* at both sites (Fig. 5). During the day, a similar vertical distribution was observed at both sites: an obvious subsurface peak (50–100 m) was found. However, the vertical profiles of Cyclopoid abundance at night were different: the depth of maximum abundance at MA (100–200 m) was deeper than that at JL7K (50–100 m) (Fig. 6). The N:D ratios at the depths of 0–50 m and 0–100 m were 0.9 and 0.6 respectively at JL7K, and 1.0 and 0.6 at MA. This indicated no DVM for Cyclopoid copepods at both sites (Table 3).

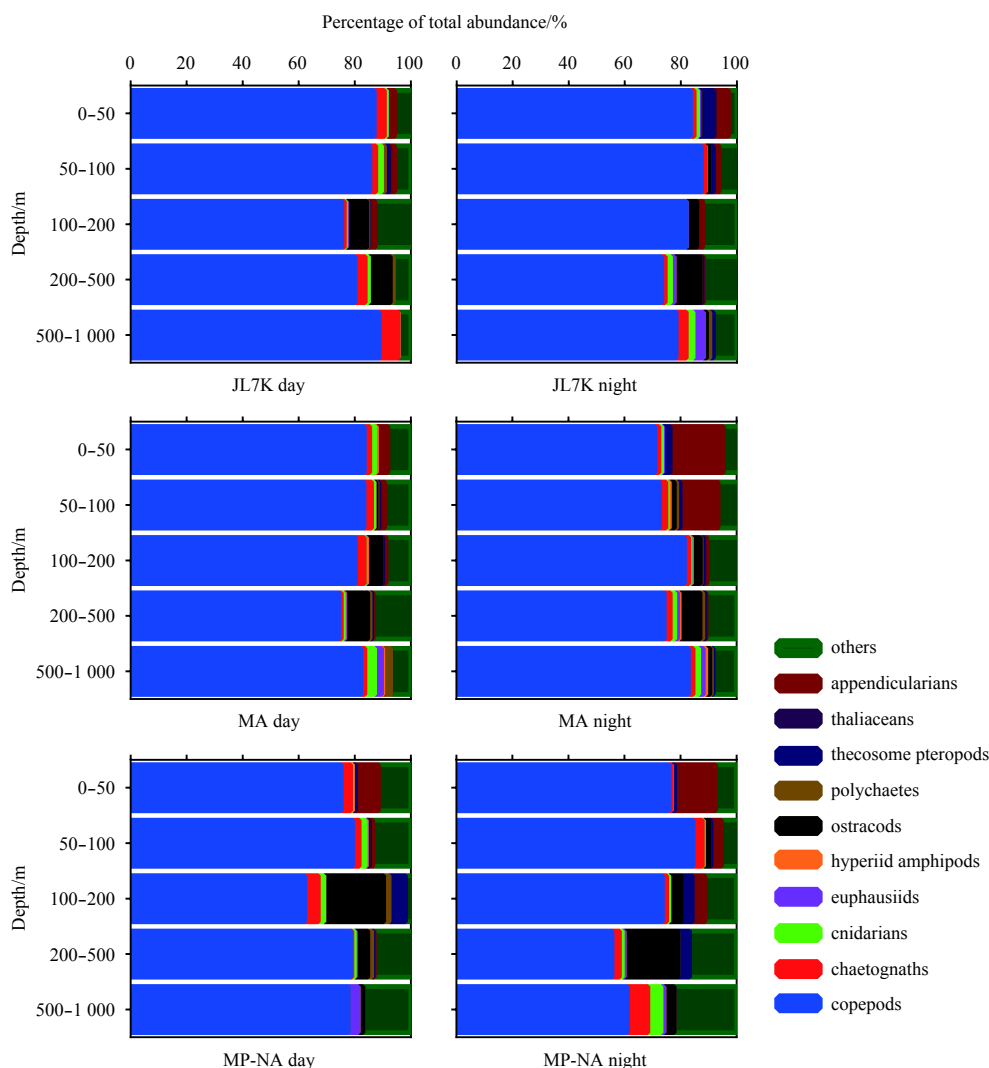


Fig. 4. Percentage of total abundance at Stas JL7K, MA and MP-NA, during the day and at night. “Others” mainly include planktonic larvae, fish eggs, small ichthyoplankton, and *Lucifer* spp.

Harpacticoid copepods and Mormonilloid copepods constituted an extremely small part of total abundance of copepods in epipelagic zone, and their contribution increased in mesopelagic zone at both sites (Fig. 5). Harpacticoid copepods and Mormonilloid copepods constituted 0%–1.6% and 0.2%–9.7% of total abundance of copepods in epipelagic zone at JL7K and MA respectively.

3.3.2 Chaetognaths

Chaetognath was one of the dominant carnivorous groups (Fig. 4). The vertical profiles of chaetognaths were obviously different between two sites. At night, a surface peak (0–50 m) was found at both sites. However, a subsurface peak (50–100 m) occurred at MA during the day, in contrast with a surface peak (0–50 m) at JL7K (Fig. 7). The DVM for chaetognaths was not obvious at JL7K (N:D=0.9), and weak at MA (N:D=1.3) in the surface (Table 3).

3.3.3 Cnidarians

At both sites, the cnidarians mainly consisted of siphonophores, but the vertical distribution was different: the peak abundance occurred at surface both during the day and at night

at MA, while the diel vertical migration was evident in epipelagic zone at JL7K (N:D=2.3 at 0–50 m) (Fig. 7 and Table 3).

3.3.4 Ostracods

After copepods, ostracods were the second most abundant group (Fig. 4), which constituted 2.1% and 1.9% of total mesozooplankton abundance at JL7K and MA, respectively. Their contributions to the total community peaked at the depths of 200–500 m, in which they constituted 8.6% and 7.1% of total mesozooplankton abundance at JL7K and MA, respectively. The DVM of this group was evident, especially at surface (0–100 m) at both sites (Fig. 7 and Table 3).

3.3.5 Appendicularians

Appendicularians were an important group in epipelagic zone at both sites, which constituted 2.7% and 5.3% of total mesozooplankton abundance at JL7K and MA, respectively (Fig. 4). The N:D ratios at the depths of 0–50 m and 0–100 m were 2.3 and 1.4 respectively at JL7K, and 8.7 and 7.4 at MA (Table 3). This indicated a much greater strength of DVM for appendicularians at MA in epipelagic zone.

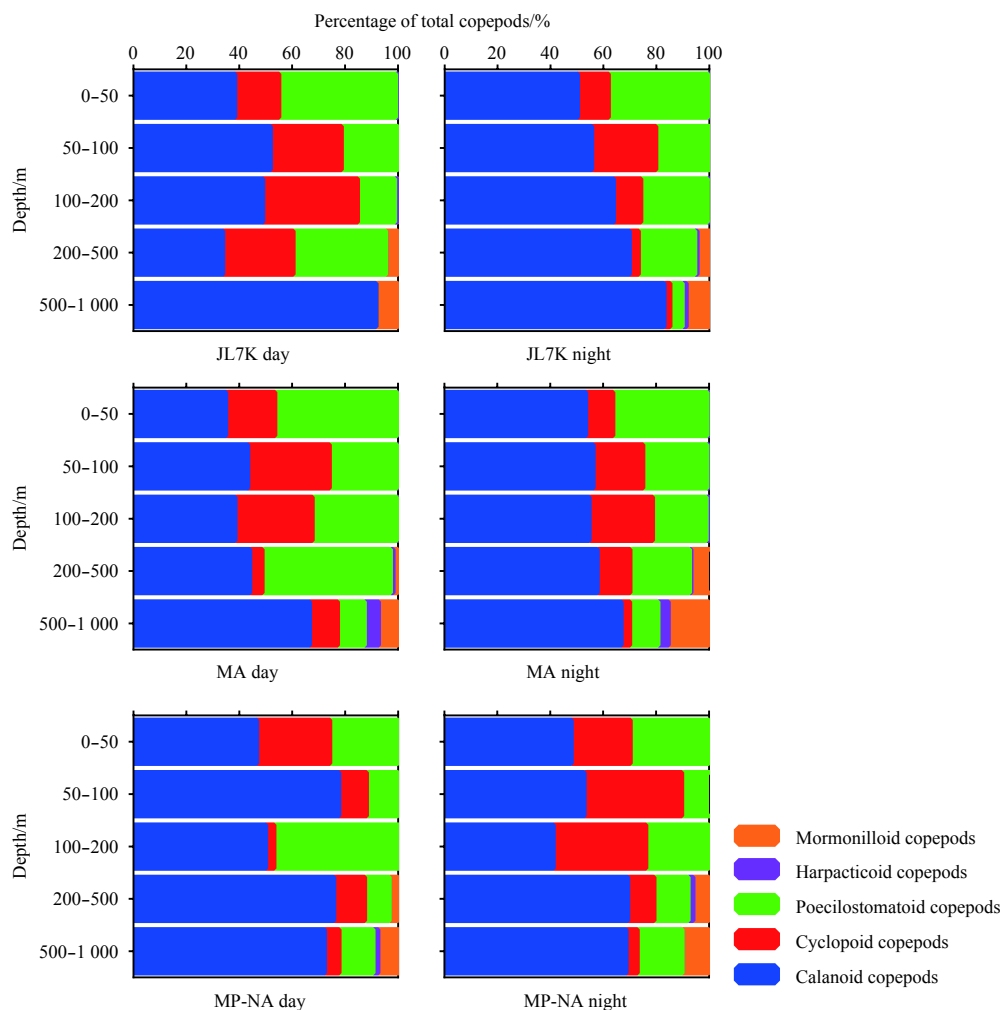


Fig. 5. Percentage of copepod abundance at Stas JL7K, MA and MP-NA, during the day and at night.

3.4 Active carbon flux

The total active carbon flux (DOC+DIC) by migrating mesozooplankton was higher in JL7K than that of MA, which was (0.23 ± 0.14) mmol/(m²·d) and (0.16 ± 0.41) mmol/(m²·d), respectively (Table 5).

4 Discussion

4.1 Comparison of mesozooplankton communities at JL7K and MA

In this study, an obvious difference in physical oceanographic characteristics between the two sites was found. A deeper mixed layer, higher temperature and lower salinity in epipelagic zone generally occurred at JL7K than that of MA. These physical oceanographic characteristics well reflected the differences between the NPSG and WPWP in summer (Cravatte et al., 2009). The vertical distribution of chlorophyll *a*, which showed a deep-water maximum layer (100–125 m) and low concentration in both sites, was also consistent with general characteristics of NPSG and WPWP from previous results (Ishizaka et al., 1994; Blanchot et al., 2001). Therefore, that similar phytoplankton standing stock reasonably resulted in similar dry weight biomass of mesozooplankton in epipelagic zone at both sites. In mesopelagic zone, the biomass of MA was slightly higher than that of JL7K in the day, while an opposite trend was found at night. Overall, the biomass in 0–1 000 m layers was low, which was con-

sistent with other results from oligotrophic Pacific (Steinberg et al., 2008a; Kitamura et al., 2016).

The diel vertical migration of mesozooplankton was always significant in tropical and subtropical oceans (Hays, 2003; Ohman and Romagnan, 2016). Our study also confirmed that pattern: the N:D ratios of biomass in 0–100 m layer were 1.31 and 1.09 at JL7K and MA, respectively, which indicated an evident DVM in epipelagic zone. Nonetheless, there was a less consistent pattern of vertical migration between two sites. The N:D ratio was 1.62 in the layer of 0–50 m and less than 1.0 in deeper layers at MA, while at JL7K, it exceeded 1.0 in most layers, except in the layer of 100–200 m. The increase of biomass in mesopelagic zone at night was probably due to the ascending migration of copepods and euphausiids (including *Euchirella* spp., *Haloetilus longicirrus*, *Lucicutia longiserrata*, *Pleuromamma xiphias*, *Xanthocalanus pulcher* and *Thysanopoda pectinate*) from bathypelagic zone at JL7K (Table 4). The N:D ratio of these species exceeded two times in the layer of 500–1 000 m at this site. At MA, these species showed different DVM pattern, which the N:D ratio in the layer of 500–1 000 m was significantly lower than that of JL7K. The temperature profile of this depth layer was extremely similar between two sites, and the relatively tiny salinity difference of this depth layer was also unlikely to cause this obvious difference in community structure. For the mesopelagic zooplankton, their food mostly consisted of sinking particulate organic matter and

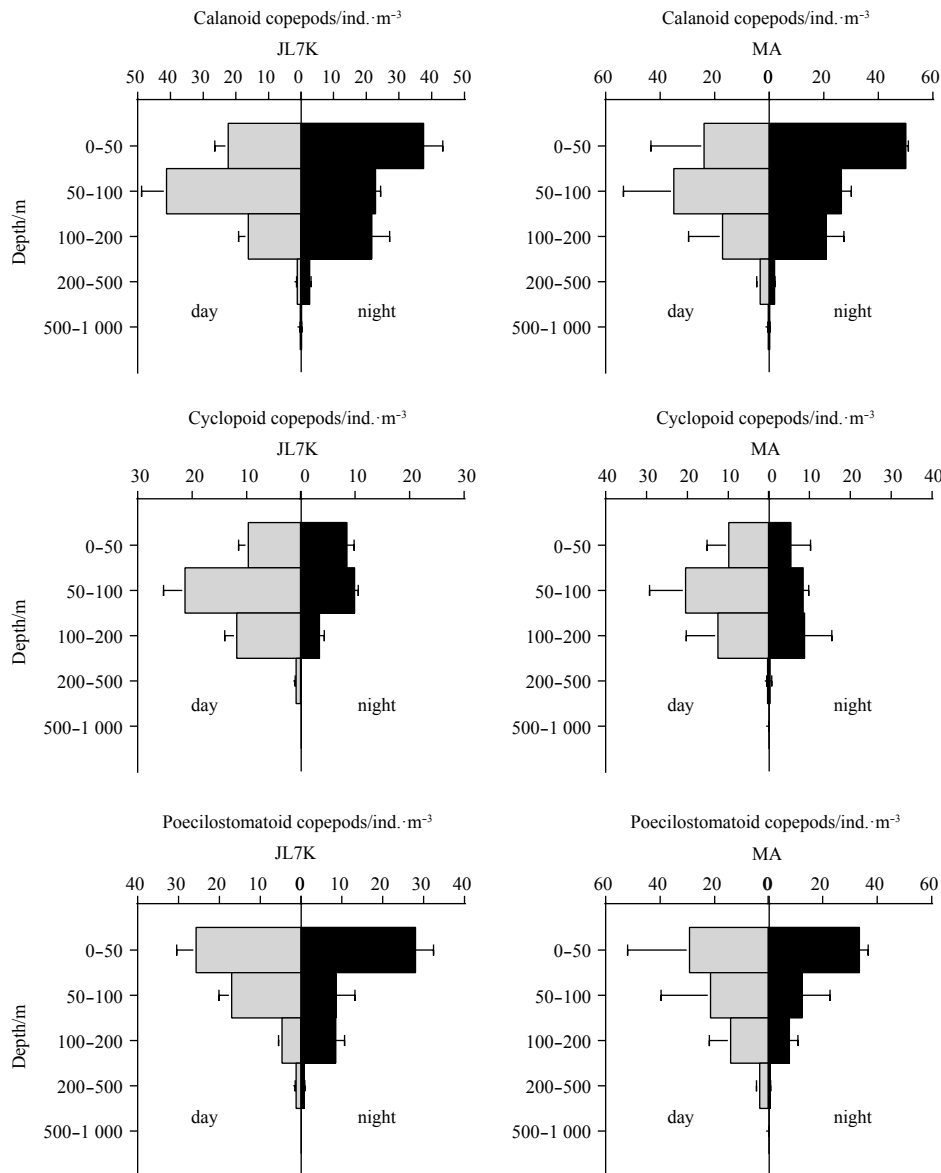


Fig. 6. Vertical distribution of Calanoid copepods, Cyclopoid copepods and Poecilostomatoid copepods.

DVM of zooplankton from epipelagic zone (Steinberg et al., 2008b; Koppelman et al., 2009; Ariza et al., 2015; Hannides et al., 2015). The export of POM from epipelagic zone to deep sea and its efficiency were different between NPSG and WPWP (Schlitzer, 2000). It may be a possible explanation for this difference in community structure of mesopelagic zone.

The vertical distribution and DVM strength (indicated by N:D ratio) of zooplankton were obviously various among taxa and between two sites. Most of calanoids were herbivorous or filter feeders. Therefore a subsurface biomass peak in the day and a surface biomass peak at night well met the “hunger-satiation” hypothesis (Pearre, 2003), and the DVM strength of this taxa was usually remarkable (Andersen et al., 2001). By contrast, cyclopoids and poecilostomatoids, which were generally regarded as suspension-feeders, usually ingested various slowing-moving particles, such as faecal pellets of other zooplankton (González and Smetacek, 1994) or discarded appendicularian houses (Nishibe et al., 2015). Therefore, none- or weak DVM was obvious for these groups (Table 3). Similar patterns were also widely

observed in other sea areas (Yamaguchi et al., 2002; Steinberg et al., 2008a). Recently, Ohman and Romagnan (2016) found that there was a significant relationship between body size, transparency of sea water and strength of DVM in copepods in the upper ocean of 0–450 m. In their study, intermediate-sized species showed stronger DVM, while smallest or largest copepods showed weaker DVM. In our study, the small-sized copepods (<1 mm) mainly consisted of *Clausocalanus* spp., *Oithona* spp., *Corycaeus* spp. and *Oncaea* spp., which were observed to be weak or non-migrators at both sites. This result also confirmed Ohman and Romagnan’s hypothesis.

Both vertical peaks of two main carnivorous taxa, chaetognaths and cnidarians, occurred in the epipelagic zone. This homogeneous distribution of carnivores directly followed the vertical distribution of their preys (such as copepods and various planktonic larvae). It should be noted that an obvious DVM for cnidarians was found at JL7K (Fig. 7 and Table 3). The cnidarians mainly consisted of Siphonophore at both sites. As carnivorous zooplankton, they located their prey by tactile stimuli. Therefore,

Table 3. Diel vertical migration indices (N:D ratio of abundance) of main mesozooplankton taxa at each depths at Stas JL7K and MA

Taxa	Sites	N:D ratio				
		0–50	(0–100)	(0–200)	200–500	500–1 000
Calanoid copepods	JL7K	1.7	1.0	1.1	2.3	1.1
	MA	2.1	1.3	1.3	0.6	0.8
Cyclopoid calanoids	JL7K	0.9	0.6	0.5	0.1	–
	MA	1.0	0.6	0.6	1.2	0.2
Poecilostomatoid calanoids	JL7K	1.1	0.9	1.0	0.7	–
	MA	1.1	0.9	0.8	0.2	0.7
Chaetognaths	JL7K	0.9	0.8	0.9	0.8	1.4
	MA	1.3	1.0	0.7	0.5	1.0
Cnidarians	JL7K	2.3	0.6	0.8	2.0	–
	MA	1.2	1.0	1.0	0.5	0.1
Ostracods	JL7K	–	–	0.6	1.5	–
	MA	4.0	2.1	0.7	0.3	2.2
Appendicularians	JL7K	2.3	1.4	1.3	–	–
	MA	8.7	7.4	6.5	0.2	–

Note: – indicates that the given taxon did not occur at a certain layer during the day or at night.

Table 4. The abundance (ind./100 m³) of several main ascending migration species in the layer of 500–1 000 m at two sites, during the day and at night

Species	Abundance/ind.·(100 m ³) ⁻¹			
	JL7K		MA	
	Night	Day	Night	Day
Copepods				
<i>Euchirella</i> spp.	2.4	0	1.5	1.0
<i>Haloptilus longicirrus</i>	2.4	0	1.2	1.6
<i>Lucicutia longiserrata</i>	2.4	0.6	1.5	2.9
<i>Pleuromamma xiphius</i>	5.4	0.6	2.7	6.0
<i>Xanthocalanus pulcher</i>	1.2	0	0.6	0
Euphausiids				
<i>Thysanopoda pectinate</i>	1.2	0	0.6	0.5

light was unlikely to be a necessary condition for their predation (Hays, 2003). Similar vertical migration of Siphonophore was also found in another study (Silguero and Robison, 2000). However, the exact mechanism was still unknown.

Ostracods were always observed as strong diel vertical migrators in the open sea (Kaeriyama and Ikeda, 2002; Steinberg et al., 2008a) and considered as omnivorous animals, which consumed marine snow and phytoplankton (Lampitt et al., 1993; Angel, 1999). Besides, they were also opportunistic feeders, which would ingest almost any encountered large pieces (Vannier et al., 1998). The vertical distribution of ostracods indicated complex trophic condition in the present study: the peak of abundance occurred in the layer of 100–200 m both during the day and at night, and an obvious diel vertical migration was also found at the surface 0–100 m. The stable bulk biomass in the layer of 100–200 m possibly attributed to the marine snow feeders or opportunistic feeders, while the biomass with significant DVM might be caused by herbivores. The sharp decline of biomass in the layer of 500–1 000 m reflected the significant food limitation in lower mesopelagic zone.

Appendicularians were considered to be able to exploit picophytoplankton effectively (Nakamura et al., 1997), and transferred energy to copepods and higher trophic levels through direct predation of their eggs and juveniles by Calanoid copepods

(López-Urrutia et al., 2004) or indirect ingestion of their discarded houses and fecal pellet by Poecilostomatoid copepods (Gorsky et al., 1999; Nishibe et al., 2015). Therefore, they were important secondary producers with high energy transfer efficiency between small primary producers and higher consumers, especially in oligotrophic conditions (Nakamura et al., 1997; Sato et al., 2008). In both sites, strong DVM of appendicularians was observed (Table 3). In the field, it was suggested that appendicularian population dynamics would be distinctly controlled by calanoid copepods (Sommer et al., 2003). This pronounced DVM might reflect a balance between predation risk and herbivorous efficiency, though no evidence supported visual or light dependence in the predation relationship between copepods and appendicularians. In addition, the abundance during the day was seriously higher than that of night at MA (N:D ratio=6.5). It was unlikely that such high N:D ratio was simply due to diel vertical migration of appendicularians. Two possible reasons were suggested here. Firstly, due to their high filter efficiency for picophytoplankton and short generation time (Uye and Ichino, 1995; Nakamura et al., 1997), they would show a quick response to appropriate microhabitat and generate a higher population density in short time. Secondly, it might be caused by the patchiness of plankton community, which would be discussed below.

The comparison between JL7K and NPSG was listed in Table 6.

4.2 Comparison of mesozooplankton community at JL7K and MA with other results from the tropical and subtropical Pacific

In the tropical and subtropical Pacific, many studies demonstrated the vertical distribution of zooplankton (Yamaguchi et al., 2005, 2015; Hwang et al., 2007; Dai et al., 2017); however, detail results about DVM of zooplankton down to mesopelagic zone were still relatively limited. In epipelagic zone, Landry et al. (2001) reported that the 0–150 m integrated dry biomass was 3.24 mg/m³ during the day and 5.55 mg/m³ at night in the eastern subtropical Pacific (Sta. ALOHA), which was similar with the result of Steinberg et al. (2008a) (3.38 mg/m³ during the day and 5.43 mg/m³ at night, respectively). In the western subtropical Pacific (Sta. S1), Kitamura et al. (2016) reported that the 0–200 m integrated dry biomass was 1.25 mg/m³ during the day and 3.47 mg/m³ at night, which was lower than those in eastern Pacific. In our research, the 0–200 m integrated biomass was 2.98 mg/m³ during the day and 2.77 mg/m³ at night, which was consistent with the above results. Those results reflected a uniform and extremely low primary productivity level in the whole NPSG (Antoine et al., 1996; Karl, 1999), while the biomass seemed to be even lower in the western NPSG than those in the eastern NPSG. In mesopelagic zone, 150–1 000 m integrated dry biomass was 0.64 mg/m³ during the day and 0.53 mg/m³ at night in the eastern subtropical Pacific (Sta. ALOHA). While in the western subtropical Pacific (Sta. S1), the 200–1 000 m integrated dry biomass was observed to be higher (1.28 mg/m³ during the day and 0.87 mg/m³ at night, respectively). We found that the 200–1 000 m integrated dry biomass at Sta. MA was 0.78 mg/m³ during the day and 0.47 mg/m³ at night. Two characteristics in mesopelagic zone were discussed here. On the one hand, the N:D ratio was lower in western NPSG than that in eastern NPSG (western: 0.60 at Sta. MA and 0.68 at Sta. S1; eastern: 0.83 in Sta. ALOHA). Based on empirical data from other research (Steinberg et al., 2000; Isla et al., 2015), it might imply a higher proportion of active carbon flux to deep sea by mesozooplankton in the western NPSG than that in eastern NPSG, though more detail results were still required. On the other hand, mesopelagic biomass was lower at Sta. MA than at Sta. S1, while much comparable with those in the

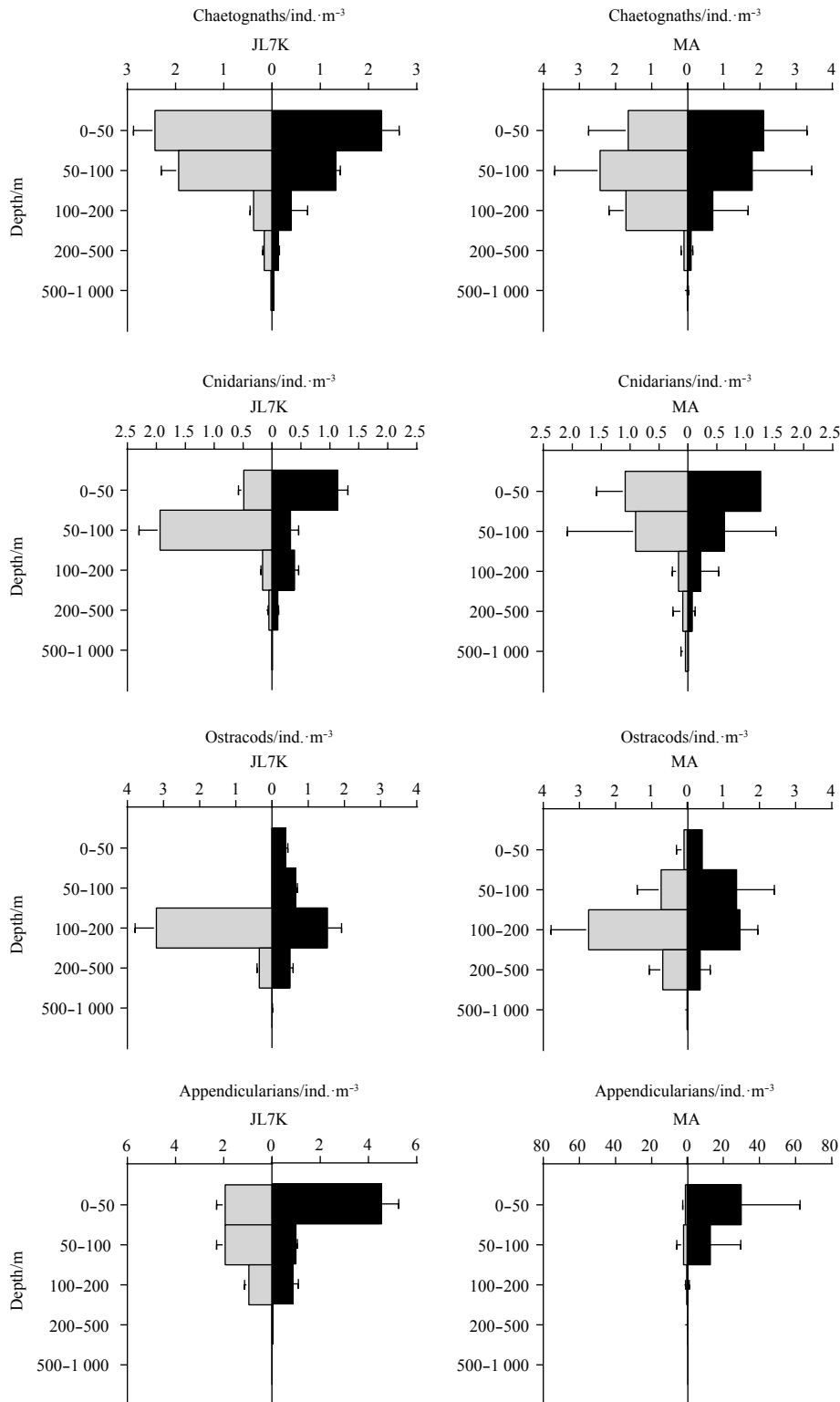


Fig. 7. Vertical distribution of chaetognaths, cnidarians, ostracods and appendicularians.

eastern Pacific.

In the WPWP, few studies demonstrated the vertical distribution and diel vertical migration down to mesopelagic zone. [Le Borgne and Rodier \(1997\)](#) studied the DVM of mesozooplankton down to 500 m at 165°–167°E at equator. The Sta. PROPPAC 1 in their study was in well accordance with general characters of warm pool (named as “typical tropical structure” in their paper).

They found that the DVM strength (N:D ratio) was 1.49 at the surface layer (0–100 m), while it decreased to 0.99 in the whole epipelagic zone (0–200 m). Our investigation at Sta. JL7K also showed a similar DVM pattern (N:D ratio: 1.31 in 0–100 m, 0.99 in 0–200 m) in epipelagic zone. Besides, in the study of zooplankton biovolume down to 3 000 m in the western boundary currents of the western tropical North Pacific, [Dai et al. \(2017\)](#)

Table 5. Active flux of dissolved carbon (mmol/(m²·d)) (mean±SD) caused by DVM of mesozooplankton

	DIC	DIC+DOC
JL7K (WPWP)	0.17±0.11	0.23±0.14
MA (NPSG)	0.12±0.32	0.16±0.41

Note: DIC indicates the downward respired carbon flux of zooplankton at the depth of 100 m; and DOC the downward active flux of excretion (dissolved organic carbon) of migrating mesozooplankton, which was calculated as 31% of downward active flux of DIC (Steinberg et al., 2000).

Table 6. A comparison between JL7K and NPSG

	JL7K (WP)	MA (NPSG)
Environment	surface temperature	higher
	mixed layer depth	deeper
	surface salinity	lower
	integrated Chl <i>a</i> of 0–200 m	similar
Biomass	integrated biomass of 0–200 m	similar
	integrated biomass of 200–500 m	lower
	integrated biomass of 500–1 000 m	higher
DVM	DVM strength of 0–100 m	higher
	DVM strength of 0–200 m	similar
	active flux of dissolved carbon	higher

demonstrated that the peak value of biovolume occurred at the surface even during the day, which suggested that a weak DVM also occurred at 130°E of tropical Pacific. In mesopelagic zone, the N:D ratio of 0–500 m integrated biomass was 1.23 (calculated from Table 2 in Le Borgne and Rodier (1997)) in Sta. PROPPAC 1,

Table 7. The effects of mouth area and mesh size of plankton net on the strength of diel vertical migration at two ecological provinces

Ecological province	Mouth area of plankton net/m ²	Mesh size of plankton net/μm	Layers/m	Strength of DVM (N:D ratio)	Reference
WPWP	0.25	200	0–100	1.5	Le Borgne and Rodier (1997)
	0.25	200	0–100	1.3	the present study
	0.25	200	0–200	1.0	Le Borgne and Rodier (1997)
	0.25	200	0–200	1.0	the present study
NPSG	0.16	90	0–100	1.1	Yamaguchi et al. (2004)
	0.16	90	0–200	0.6	Yamaguchi et al. (2004)
	0.25	200	0–100	1.1	the present study
	0.25	200	0–200	0.9	the present study
	1.0	200	0–150	1.7	Landry et al. (2001)
	1.0	335	0–150	1.7	Steinberg et al. (2008a)
	1.5	330	0–200	2.8	Kitamura et al. (2016)

Note: WPWP represents Western Pacific Warm Pool, and NPSG North Pacific Subtropical Gyre.

Active transport of carbon by vertical migration was likely to be more important for the ecosystem of JL7K, not only due to a higher flux value but also because of the special vertical community structure of this site. In oligotrophic seasons, both the sinking carbon flux of POC and the loss of sinking POC are always low and are impossible to meet the metabolic demand of microorganisms and zooplankton (Steinberg et al., 2008b; Hanides et al., 2015), then the active carbon flux by DVM of mesozooplankton was a reasonable and substantial supply to mesopelagic zone. The significance of this active carbon flux by DVM is probably more prominent at JL7K than that of MA, because a significant night-increase (29%) of mesozooplankton biomass was found in mesopelagic zone (especially at the layer of 500–1 000 m) at JL7K (Table 2). Community structure analysis indicated some bathypelagic species (including copepods and euphausiids) were

which indicated that some taxa migrated up into the layer of 0–500 m at night. At JL7K, the N:D ratio of that layer was 1.01, which suggested fewer migrators up into this layer at night. But some bathypelagic species (including copepods and euphausiids) migrating up into the mesopelagic zone were also observed at JL7K (Table 4). This phenomenon was not well recorded in the WPWP before. Above data indicated a relatively stable DVM strength across the WPWP, in epipelagic zone. However, the dwelling depths of zooplankton migrated from bathypelagic zone at night might show spatial variations.

4.3 Active carbon flux by DVM of mesozooplankton

Generally, the migrant biomass of mesozooplankton and sinking carbon flux of POC is more pronounced under higher primary production and weaker in oligotrophic conditions, however, the contribution of active carbon flux by DVM to total downward carbon flux is not consistent with this pattern (Kobari et al., 2016). Our results showed that the active carbon flux caused by DVM of mesozooplankton should not be ignored in extreme oligotrophic areas, which was consistent with previous results (e.g., Steinberg et al., 2000; Al-Mutairi and Landry, 2001; Kobari et al., 2013, 2016). The active carbon fluxes of MA and JL7K in our study are well within the range of previous estimation for migrating mesozooplankton under oligotrophic conditions, which were from 0.1 to 1.1 mmol/(m²·d) (Table 7 in Isla et al. (2015)). Although the phytoplankton stocks and mesozooplankton biomass of upper ocean were almost under a same level, the active carbon fluxes were found to be different for both two sites. This difference was attributed to a greater biomass of migrating zooplankton at JL7K (Table 2).

the main contributors to that night-increase biomass (Table 4). These species might prey other mesozooplankton, ingest POC or filter microzooplankton in mesopelagic zone, but anyway, the majority of food for mesopelagic zooplankton was proved to be surface derived, by sinking POC or DVM of zooplankton (Hanides et al., 2013). Hence, the active transport of carbon by vertical migration from epipelagic zone to mesopelagic zone might largely support these migrating bathypelagic species at JL7K.

4.4 Limitations of the present study

Several potential factors, which might cause error in estimating biomass and community structure of deep sea zooplankton, had been discussed in previous study (Angel and Pugh, 2000). Those included fragile gelatinous organisms, net avoidance, vertical migration from deeper waters and high patchiness of zo-

oplankton. Those factors were discussed here. Firstly, gelatinous organisms usually occupied a significant proportion in the open sea; however, their contribution to dry biomass or carbon content was low (Moriarty et al., 2013; Lucas et al., 2014). Besides, appendicularians, one of the most fragile organisms, were well preserved in our samples. Therefore, possible underestimation of gelatinous organisms was impossible to influence the biomass estimation in the present study. Secondly, Hydro-Bios Multinet multiple net systems (0.25 m² mouth opening area and 200 μm mesh size) were used in our sampling. On the one hand, according to Sameoto et al. (2000), smaller mouth opening area tended to cause heavier net avoidance. We also compared some vertical sampling studies using multiple net systems with different mouth opening area in the WPWP and NPSG (Table 7). Le Borgne and Rodier (1997) used a same multiple net system with our study, and a similar DVM strength was estimated. When a plankton net with smaller mouth area was used, weaker DVM strength was found (Yamaguchi et al., 2004). While stronger DVM strength was found when larger mouth area plankton net was used (Landry et al., 2001; Steinberg et al., 2008a; Kitamura et al., 2016). Considering that larger-sized zooplankton always have stronger DVM ability (Steinberg et al., 2008a; Ariza et al., 2015) and escaping ability (Clutter and Anraku, 1968; Sameoto et al., 2000), above difference in estimation of DVM strength might be due to higher sampling efficiency of larger mouth area systems. On the other hand, when the mesh size of plankton net varied from 90 μm to 335 μm, no obvious mesh size effect was found (Table 7). Thirdly, we found some bathypelagic animals migrating up into mesopelagic zone at night at JL7K (Table 4), which caused an obvious night increase of mesopelagic integrated biomass (Table 2). While at MA, this phenomenon was not pronounced because of little day-night difference of 0–1 000 m integrated biomass. Lastly, patchiness of zooplankton, which may be caused by hydrodynamic or biological factors, is common in lakes and oceans (Folt and Burns, 1999). This factor is able to be a great source of error for estimation of biomass. In our study, extreme high N:D ratio of appendicularians was observed at MA (Fig. 7 and Table 3). This was possible due to patchiness of appendicularians. Besides, no other taxa were observed to show pronounced patchiness behavior.

5 Conclusions

We compared the 0–1 000 m mesozooplankton biomass and community structure at two sites in the NPSG (Sta. MA) and WPWP (Sta. JL7K). The two sites showed similarly low biomass in both epipelagic and mesopelagic zones, which was in accordance with oligotrophic conditions of these two ecosystems. However, the pattern of diel vertical migration was different between the two sites, especially in mesopelagic zone. Simultaneously, a higher active carbon flux by DVM of mesozooplankton was found at JL7L than that of MA. We also compared our results with previous studies in the WPWP and NPSG, and found that the DVM pattern of mesozooplankton was similar within the same ecosystem and varied between different ecosystems.

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