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Vertical Distribution, Community Structure, and Active Carbon Flux of Two Macrozooplankton Taxa : Amphipods and Euphausiids in the Summer of the Western North Pacific

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Abstract

This study conducted diel vertical migration and active migration flux estimation of macrozooplanktonic amphipods and euphausiids at 0-250 m water column of the three stations in the western North Pacific during summer. For amphipods, 25 species belonging to 17 genera were identified. Their standing stock was 60-574 ind. m^{-2} during the daytime and 35-5,228 ind. m^{-2} at night-time. For euphausiids, 19 species belonging to 7 genera were identified. The standing stock of euphausiids was 80-382 ind. m^{-2} and 286-2,156 ind. m^{-2} during the day and at night, respectively. Feeding impacts during the night were estimated to be 0.19-11.76 mg C m^{-2} day^{-1} (amphipods) and 5.12-16.42 mg C m^{-2} day^{-1} (euphausiids). Respiration during the daytime accounted for 0.08-6.38 mg C m^{-2} day^{-1} (amphipods) and 2.33-7.70 mg C m^{-2} day^{-1} (euphausiids). The feeding impact and respiratory flux by active migration of macrozooplankton taxa were estimated as 8.34-28.18 mg C m^{-2} day^{-1} and 3.15-14.08 mg C m^{-2} day^{-1}, respectively. These values corresponded to 3.7-12.4% of primary production (feeding impact) and 2.4-10.7% of sinking passive flux from the euphotic zone (respiratory flux). Thus, this study emphasizes the importance of active flux by macrozooplankton for vertical material flux in the western North Pacific.

Key words : Active carbon flux, Biological pump, *Phronima* spp., *Themisto pacifica*, *Primno abyssalis*, *Vibilia gibbosa*, *Euphausia* spp., *Nematoscelis* spp., *Thysanoessa* spp., *Stylocheiron* spp.

Introduction

Vertical material flux in the ocean occurs mainly through biological activity and is called a "biological pump". The main driving source of a biological pump is the passive sinking flux mediated by gravity ; that is, CO_2 dissolved in seawater is converted to a particulate organic material by the photosynthesis of phytoplankton, which sinks from the ocean surface and settles in the deep layer (Longhurst, 1991). As a component of the biological pump, the biological activity of zooplankton is also important. Zooplankton feed near the surface layer of the ocean and enhance vertical material transport by egesting fast-sinking faecal pellets (Ducklow et al., 2001). The diel vertical migration (DVM) of zooplankton is also considered to play an important role in the biological pump. Diel migrant zooplankton feed near the surface layer at night and descend to the deep layer during the day ; then their metabolic respiration at the deep layer accelerates vertical material flux (Longhurst et al., 1990). Vertical material transport due to the DVM of zooplankton is called active flux, which contradicts passive flux by gravity. Active flux is an important process in the quantitative evaluation of a biological pump, and its quantitative measurement is being conducted at various locations (Steinberg et al., 2000 ; Al-Mutairi and Landry, 2001).

Macrozooplanktonic amphipods and euphausiids are known to be important prey of pelagic fishes (Yamamura et al., 2002 ; Brodeur et al., 2007 ; Uchikawa et al., 2008), squids (Watanabe et al., 2004), seabirds (Ogi, 1980 ; Ogi et al., 1980 ; Springer et al., 1996, 1999), and baleen whale (Murase et al., 2007 ; Konishi et al., 2009). On the other hand, they feed on microplankton (euphausiids) and mesozooplankton (amphipods) (Nakagawa et al., 2001 ; Dalpadado et al., 2008 ; Noyon et al., 2009). Thus, macrozooplankton

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plays a role in the transfer of lower trophic production to higher trophic organisms in the marine ecosystem. Macrozooplankton is known to perform large DVMs (Thurston, 1976a, 1976b ; Mauchline, 1980). The active flux by the DVM of macrozooplankton is estimated to reach 71% of gravity passive flux (Steinberg et al., 2000). These facts suggest that macrozooplankton have an important role in pelagic food web and material flux in marine ecosystems.

The western North Pacific Ocean is characterized by large-scale phytoplankton blooms occurring in spring, and it is known to be an area with actively driving biological pumps due to its high nutrient supply and high new primary production (Longhurst, 1998). Despite their importance, the estimation of active flux by zooplankton DVM in this region is scarce (Takahashi et al., 2009). For macrozooplanktonic taxa, the estimation of active flux is only limited in the subtropical area (Al-Mutairi and Landry, 2001 ; Hidaka et al., 2001).

In this study, day-night MOCNESS samplings were conducted at three stations in the western North Pacific Ocean during summer, and DVM of macrozooplanktonic amphipods and euphausiids were observed. For the dominant species, the body size and weight (wet, dry and ash-free) were measured, then the weight-body size equations were calculated. Based on the body size measurement and application equations, the biomass was also estimated. The metabolism (respiration carbon) was estimated by applying an empirical model varied by taxon (Ikeda, 2014). Assuming the assimilation efficiency and gross growth efficiency, the feeding impact at the near-surface layer during the night and the respiration at the deep layer during the daytime were assessed. Thus, the estimated active flux by the macrozooplankton DVM was compared with primary production in the same area, and the role of macrozooplankton in the vertical material flux was evaluated.

Material and methods

Field sampling

Samplings were conducted on R/V *Shunyo-Maru* (National Research Institute of Far Seas Fisheries, Japan Fisheries Research and Education Agency). Day and night sampling with oblique tow of MOCNESS (1 m^2 opening, 0.33 mm mesh equipped, Wiebe et al., 1985) were conducted from eight depths (0-20, 20-40, 40-60, 60-80, 80-100, 100-150, 150-200 and 200-250 m) at three stations (39°N [St. 39N], 41°N [St. 41N] and 44°N [St. 44N]) along the 158°E line in the western North Pacific during 16-25 June 2003 (Fig. 1). After collection, samples were immediately fixed with 10% borax-buffered formalin. For each station, the temperature and salinity were measured by CTD (Seabird Electronics).

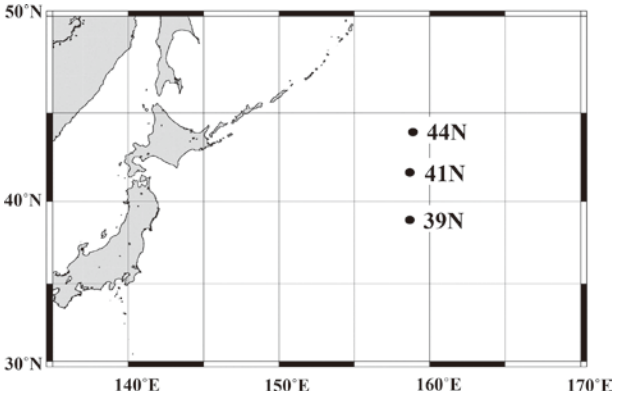

Fig. 1. Location of the sampling stations (39°N, 41°N and 44°N) along 158°E in the western North Pacific.

Quantification and body size measurement

Based on the sub-samples (1/1 to 1/420, which varied with the number of samples), amphipods and euphausiids were sorted, and the species were identified and counted. For amphipods, the body lengths (BL : mm) of six dominant genera (*Cyphocaris*, *Eupronoe*, *Phronima*, *Primno*, *Themisto* and *Vibilia*) were measured as the maximal distance between the tip of head to the distal end of the uropod (or telson for *Cyphocaris* spp.) of the straightened body. For euphausiids, the body lengths (BL : mm) of five dominant genera (*Euphausia*, *Nematoscelis*, *Stylocheiron*, *Tessarabrachion* and *Thysanoessa*) were measured from the posterior margin of the eye notch to the terminal end of the sixth abdominal segment. All measurements were made to the nearest 0.1 mm under a dissecting microscope with an eyepiece micrometre or with a slide gauge.

Weight measurement

For dominant species, namely, 7 species belonging to 6 genera in amphipods (*Cyphocaris challengeri*, *Eupronoe minuta*, *Phronima atlantica*, *Phronima sedentaria*, *Primno abyssalis*, *Themisto pacifica*, *Vibilia gibbosa*) and 5 species of 5 genera in euphausiids (*Euphausia pacifica*, *Nematoscelis difficilis*, *Stylocheiron longicorne*, *Tessarabrachion oculatum*, *Thysanoessa inspinata*), a batch of specimens was prepared with sufficient BL intervals, and wet weight (WW), dry weight (DW) and ash-free dry weight (AFDW) were determined. WW was determined for batches of pooled specimens after rinsing the animals briefly in distilled water, blotting them on a filter paper, and then placing them into a pre-weighed combusted aluminium pan. The specimens were then dried in a drying oven at 60°C for 5 h to obtain the DW. To obtain the AFDW, the ash content was determined by weighing the specimens before and after combustion at 480°C for 5 h. A microbalance (Mettler Toledo, MT5) was used to weigh to a precision of 1 µg. For each species, regressions between weights (Y : WW, DW, AFDW, mg) and

BL (X : mm) were expressed with :

$$Y = aX^b \tag{1}$$

where a and b are fitted constants. Each of the regressions is presented as either Appendix 1 (amphipods) or Appendix 2 (euphausiids).

Abundance and biomass

Based on the counted number (n) of each species in the subsamples with split rate (s) and filtering volume (F, m^3) of the sample, the abundance at each sampling layer (N, ind. m^{-3}) was calculated as follows :

$$N = \frac{n}{s \times F} \tag{2}$$

By multiplying the depth of each sampling layer (20 or 50 m), the abundance in density (N, ind. m^{-3}) was converted to the standing stock (ind. m^{-2}). Using BL data and DW–BL relationships (Appendix 1 and 2), the individual DWs (mg DW ind.$^{-1}$) were calculated, then the individual DW was multiplied with the density or standing stock, and the biomass (mg DW m^{-3} or mg DW m^{-2}) were calculated.

Active flux estimation

To evaluate the active flux by DVM of amphipods and euphausiids, feeding at the epipelagic zone (≤250 m) during the night and respiration at the deep-sea (>250 m) during the daytime were estimated. First, the time durations at day and night depths were calculated. At each sampling station, the sunrise was from 4 : 42 to 4 : 59, and the sunset was from 19 : 53 to 20 : 13 ; therefore, the daytime and night-time were calculated as 15 hours and 9 hours, respectively. Next, the time required for the zooplankton DVM was determined by the swimming speed and the DVM distance, and the residence time of the zooplankton in each layer was determined by subtracting it from the above day and night time. In this study, the daytime distribution depth was assumed to be 400 m, which corresponded with the reported daytime distribution depths for each taxon (Yamada and Ikeda, 2000 ; Yamada et al., 2002, 2004 ; Taki, 2008). The distribution layer at night was determined by the distribution centre ($D_{50\%}$, Pennak, 1943), which varied by species. Thus, the DVM distance (m) was calculated as : daytime distribution depth (400 m) – $D_{50\%}$. For the swimming speed, we applied eight times BL per second, which was reported for euphausiids (Kils, 1979). Since we could not find comparable information on amphipods, their swimming speed was calculated by the same criteria of euphausiids (eight times of BL per second). This swimming speed of amphipods corresponded well with the reported swimming speed (0.172 m s^{-1}) of *Phronima* spp. (Davenport, 1994), which was abundant in this region.

The individual respiration rates of amphipods and euphausiids were calculated by the following equations (Ikeda, 2014) :

$$\ln R = 18.775 + 0.766 \times \ln BM - 5.256 \times 1000/Temp - 0.113 \times \ln Depth + 0.416 \text{ (amphipods)} \tag{3}$$

$$\ln R = 18.775 + 0.766 \times \ln BM - 5.256 \times 1000/Temp - 0.113 \times \ln Depth + 0.697 \text{ (euphausiids)} \tag{4}$$

where ln R is the logarithm (base e) of the respiration rate (µl O$_2$ ind.$^{-1}$ h^{-1}), ln BM is the logarithm of the individual dry weight (mg DW ind.$^{-1}$), $Temp$ is the habitat temperature (K), and ln $Depth$ is the logarithm of the habitat depth (m).

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

$$F_{night} = R \times \frac{12}{22.4} \times 0.97 \times \frac{1}{0.4} \times \frac{1}{1000} \times h_{night} \tag{5}$$

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), 1/0.4 is the F/R, 10^{-3} is a unit conversion from µg to mg, and h_{night} is the residence time at 0–200 m during the night (h [9 hours – time required for DVM]). By multiplying the individual feeding rate (F_{night}) by the night-time standing stock (N_{night}, ind. m^{-2}), the daily feeding rate of the water column (mg C m^{-2} d^{-1}) was calculated.

The respiration rate during daytime (R_{day} : mg C ind.$^{-1}$ d^{-1}) was calculated by using the following equation :

$$R_{day} = R \times \frac{12}{22.4} \times 0.97 \times \frac{1}{1000} \times h_{day} \tag{6}$$

where h_{day} is the residence time at the deep-layer during the daytime (h [15 hours – time required for DVM]). Multiplying the individual respiration rate (R_{day}) by the standing stock, which performs DVM (N_{night}–N_{Day}, ind. m^{-2}), and the daily respiratory flux (mg C m^{-2} d^{-1}) was calculated.

Results

Hydrography

The water temperature between 0–500 m of each station was 5.3–16.7°C for 39N, 4.3–10.4°C for 41N and 4.0–10.5°C for 44N, and thermocline development was observed at approximately 30 m of 41N (Fig. 2a). The salinity at sea surface ranged between 33.3 and 34.4, and increased with increasing depth at 41N and 44N, and decreased with increasing depth at 39N (Fig. 2b). Throughout the station, the salinity settled approximately 34.0 at 500 m depths. A T-S diagram showed that the water mass at 39N was a subtropical domain, while those at 41N and 44N were transitional domains (Anma et al., 1990) (Fig. 2c).

Amphipods

The standing stock of amphipods in the 0–250 m water col-

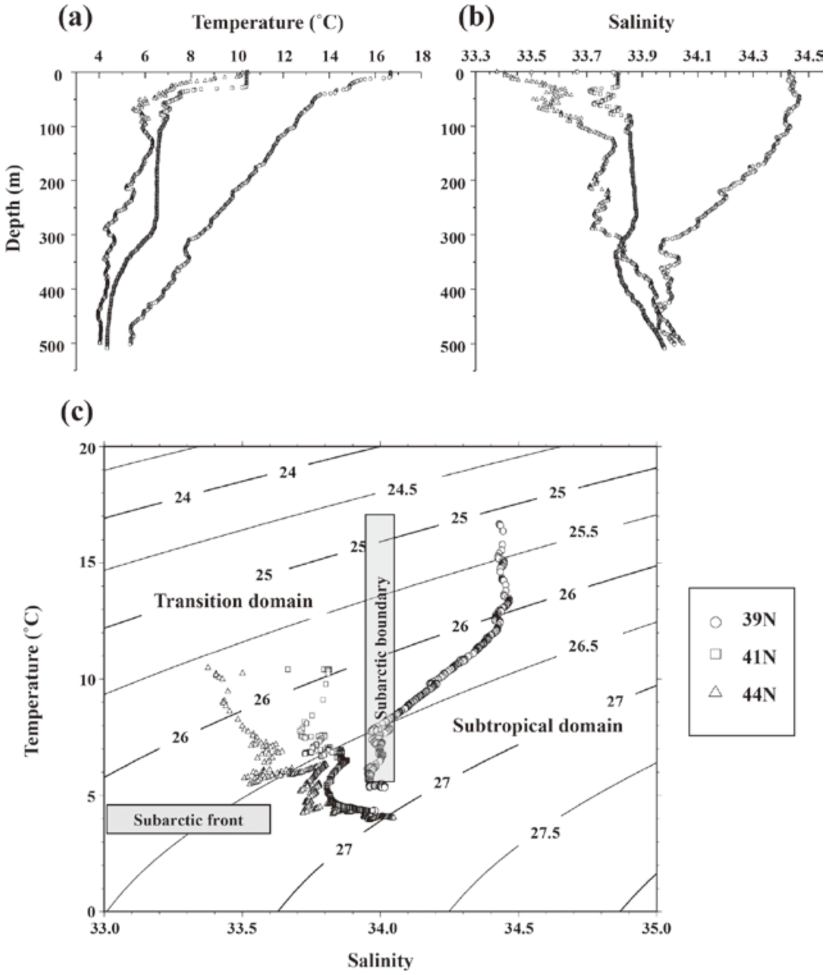

Fig. 2. Vertical profiles of temperature (a) and salinity (b) and T-S diagram (c) at each station in the western North Pacific during 16–25 June 2003. Numbers in the panel (c) indicate water densities (sigma-T). Boundaries of water masses (Anma et al., 1990) are shown in the panel (c).

umn ranged between 60 ind. m^{-2} (39N) and 574 ind. m^{-2} (44N) for daytime, and 35 ind. m^{-2} (39N) and 5,228 ind. m^{-2} (41N) for night-time (Table 1). Throughout the stations, 25 species belonging to 17 genera of amphipods occurred. The number of species was high (21 species) at the southern station (39N) and decreased with the higher latitude station (11 species at 44N) (Table 1). At 39N, *Phronima* spp. was abundant and followed *T. pacifica*. The number of species was high at night-time. At 41N and 44N, *T. pacifica* was the predominant species, both day and night, and *C. challengeri* and *V. gibbosa* showed high abundance, especially at night. Vertical distribution of the biomass of six dominant amphipod species (*C. challengeri, E. minuta, Phronima* spp.*, P. abyssalis, T. pacifica* and *V. gibbosa*) and their species compositions are shown in Fig. 3. Biomass through the 0–250 m water column ranged between 26 mg DW m^{-2} (39N) and 110 mg DW m^{-2} (44N) at daytime, and 18 mg DW m^{-2} (39N) and 1,178 mg DW m^{-2} (41N).

At 39N, the amphipod biomass was high at 80–200 m depths, during both the day and night (Fig. 3a). *Phronima* spp. dominated 47–100% of the amphipod biomass during the daytime, and their concentration was high, especially below 85 m. *V. gibbosa* occurred at the deepest depth during the daytime and constituted 48–76% of the biomass at 0–60 m during the night. *E. minuta* occurred only at 39N and constituted 5–26% of the biomass at 0–80 m during the daytime and 7–23% at 20–100 m during the night, thus showing no DVM.

At 41N, the highest biomass (0.74–0.91 mg DW m^{-3}) was seen at 20–60 m during the daytime, and a prominent increase (21.39 mg DM m^{-3}) was seen at 150–200 m at night (Fig. 3b). During daytime, *T. pacifica* predominated at 20–100 m, and *Phronima* spp. and *P. abyssalis* dominated below 100 m. At night, *V. gibbosa* dominated at 0–100 m and constituted 47% of the high-biomass in the 150–200 m layer. As day-night differences, the species concentrations of *C. challengeri* and *V. gibbosa* in the biomass increased at night throughout the layers.

At 44N, the highest biomass was seen at 100–150 m, during both the day and night (1.26 mg DW m^{-3} at daytime and

Table 1. List of amphipod species and their abundance (ind. m^{-2}) at 0–250 m water column of three stations along 158°E in the western North Pacific during 16–25 June 2003.

Species	39N		41N		44N	
	Day	Night	Day	Night	Day	Night
Cranocephalus scleroticus		0.08				
Cyphocaris challengeri		0.69	0.11	98.44	28.01	
Eupronoe minuta	4.53	3.31				
Hyperioides longipes		0.07				
Hyperia medusarum				0.72		
Hyperoche medusarum				0.18		
Mimonectes loveni		0.08				
Oxycephalus clausi		0.07				
Paraphronima crassipes		0.07		2.79		0.37
Paraphronima gracilis	0.34	0.28		2.79	0.26	0.94
Phronima atlantica	8.11	5.45	1.26	23.29	1.42	2.36
Phronima colletti		0.26				0.50
Phronima sedentaria	6.79	6.54	1.40	4.39	1.62	3.05
Phronima spp.	31.97	7.80				
Phronima stebbingi	0.62					
Phrosina semilunata	0.11	0.23				
Platyscelus serratulus		0.12				
Primno abyssalis	2.27	0.35	6.70	13.81	1.67	1.22
Scina crassicornis				2.79		
Streetsia steenstrupi	0.34	0.21				
Themisto pacifica	4.70	6.31	194.58	4,738.60	568.93	315.85
Vibilia australis		0.08				
Vibilia caeca				5.57	0.08	0.18
Vibilia gibbosa		2.29	0.42	323.83	0.48	95.02
Vibilia pyripes		0.85				0.57
Vibilia viatrix				11.42		
Total amphipods	59.8	35.1	204.5	5,228.6	574.47	448.1

2.97 mg DW m^{-3} at night, Fig. 3c). During the daytime, *T. pacifica* predominated the amphipod biomass (constituting 95–100% of the biomass), especially at 0–200 m depths. At night, the concentration of *T. pacifica* decreased ; on the other hand, the concentrations of *C. challengeri* and *V. gibbosa* increased. Within the biomass, *V. gibbosa* dominated at 20–150 m depths and constituted 67–89% of the amphipod biomass at night. Thus, while the amphipod biomass peak was seen same depths of 100–150 m during both the day and night, the biomass composition varied greatly ; *T. pacifica* dominated during the daytime, while *V. gibbosa* dominated at night.

Euphausiids

The standing stock of euphausiids in the 0–250 m water column ranged from 80 ind. m^{-2} (41N) to 382 ind. m^{-2} (44N) during the daytime and from 286 ind. m^{-2} (39N) to 2,156 ind. m^{-2} (41N) at night (Table 2). Throughout the region, 19 species belonging 7 genera euphausiid species occurred. The number of euphausiid species was the highest at the subtropical station (39N). At that station, the number of species increased at night. At 39N, *Euphausia* spp., especially *E. pacifica,* was the most numerous species. At 41N and 44N, the most abundant species was *Thysanoessa* spp., and *E. pacifica* increased in abundance at night. The vertical distribution of the biomasses of five dominant euphausiid species (*Euphausia* spp., *Nematoscelis* spp., *Stylocheiron* spp., *Thysanoessa* spp. and *Tessarabrachion oculatum*) and their species concentrations are shown in Fig. 4. At the subtropical station, a prominent day–night contrast (extremely high concentrations at night) was observed in the case of the euphausiid biomass in the 0–250 m water column.

At 39N, the euphausiid biomass was high (2.51 mg DW m^{-3}) at 100–150 m depth during the daytime, was concentrated at ≤100 m and was especially high (8.6–10.9 mg DW m^{-3}) at 0–40 m at night (Fig. 4a). These high densities were mainly composed of *E. pacifica,* which accounted for 81–100% of the euphausiid biomass at 100–200 m during the

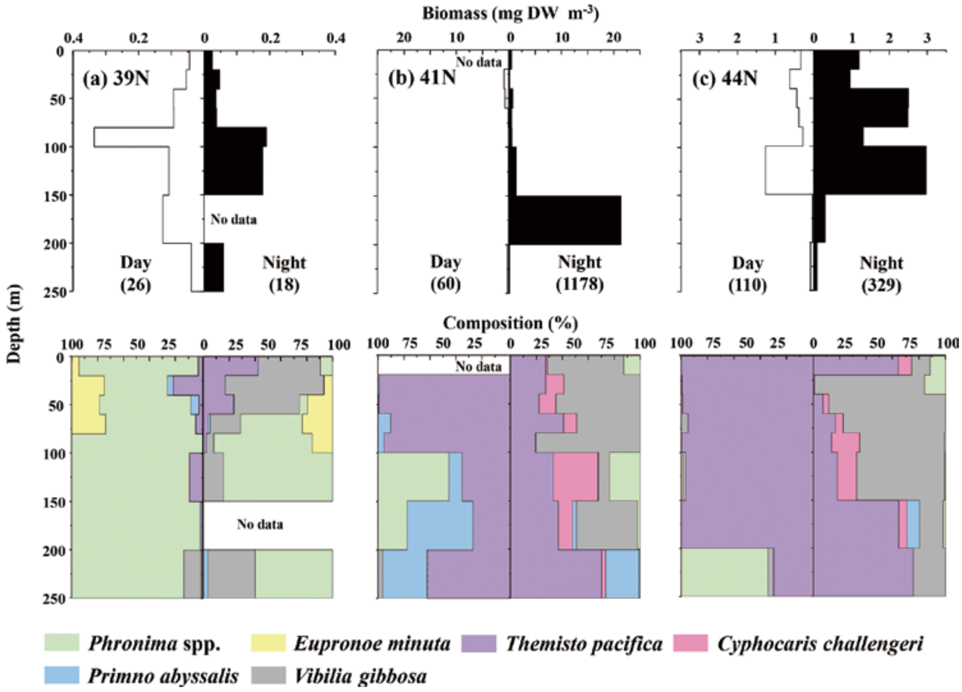

Fig. 3. Vertical distribution in the biomass (upper panels) and species composition (lower panels) of dominant amphipods in terms of biomass at 39°N (a), 41°N (b), 44°N (c) along 158°E in the western North Pacific during 16–25 June 2003. The integrated mean biomass (0–250 m, mg DM m^{-2}) is shown in the parentheses in the upper panels.

Table 2. List of euphausiid species and their abundance (ind. m^{-2}) at 0–250 m water column of three stations along 158˚E in the western North Pacific during 16–25 June 2003.

Species	39N		41N		44N	
	Day	Night	Day	Night	Day	Night
Euphausia brevis	0.26					
Euphausia diomedeae	0.87	0.28				
Euphausia hemigibba	0.81	0.16				
Euphausia mutica	0.78	1.29				
Euphausia pacifica	68.18	166.09	2.62	203.77	5.58	41.39
Euphausia pseudogibba	2.08	22.80				
Euphausia recurva	4.43	6.32				
Euphausia similis	1.17	9.19				
Euphausia spp.	97.80	16.14	0.42	45.25		5.07
Nematobrachion flexipes	1.05	1.83				
Nematoscelis difficilis	0.13	11.81				
Nematoscelis spp.	0.59	1.92				
Stylocheiron abbreviatum						0.12
Stylocheiron carinatum				0.19	0.11	
Stylocheiron elongatum		0.07				
Stylocheiron longicorne	5.28	9.74		0.23	0.36	0.19
Stylocheiron maximum						0.13
Stylocheiron spp.	4.17	1.85	2.17	3.18	7.15	3.17
Tessarabrachion oculatum	4.59	3.58	4.16	12.22	4.08	7.60
Thysanoessa inspinata	0.90	0.87	1.97	16.49	23.52	23.60
Thysanoessa longipes					1.14	0.10
Thysanoessa spp.	3.54	13.85	12.49	1,705.57	192.76	611.12
Thysanopoda aequalis		0.16				
Unidentified euphausiids	135.68	18.05	56.01	169.11	147.06	128.50
Total euphausiids	332.3	286.0	79.8	2,156.0	381.8	821.0

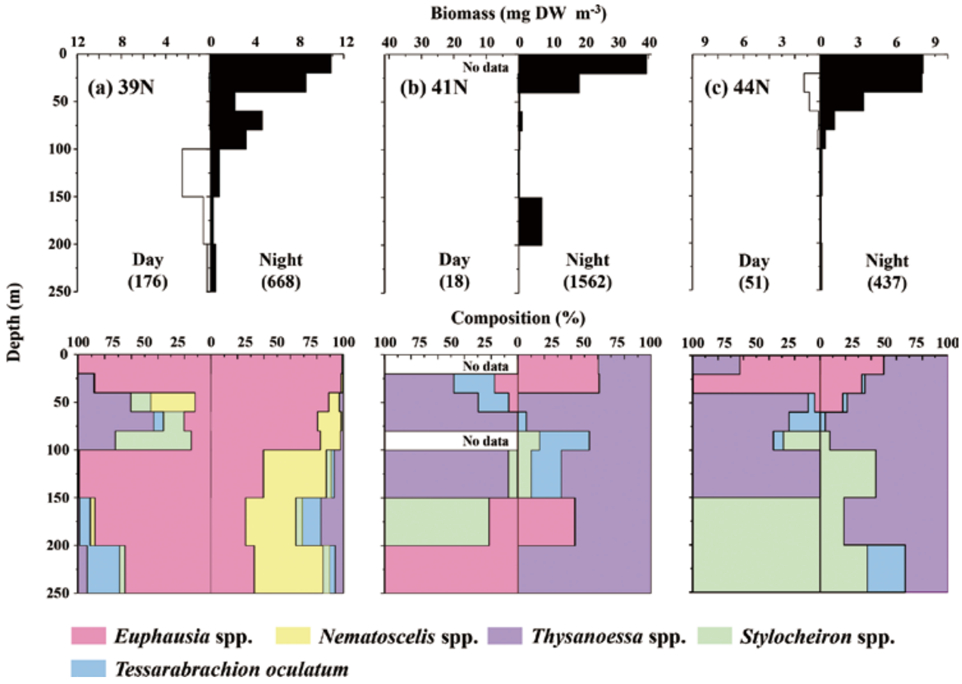

Fig. 4. Vertical distribution in biomass (upper panels) and species composition (lower panels) of dominant euphausiids in terms of biomass at 39°N (a), 41°N (b), 44°N (c) along 158°E in the western North Pacific during 16–25 June 2003. The integrated mean biomass (0–250 m, mg DM m^{-2}) are shown in the parentheses in the upper panels.

daytime and at 0–100 m during the night-time. Within the dominant species, *Nematoscelis* spp. occurred only at 39N. *Nematoscelis* spp., constituted 33% of the euphausiid biomass at 40–60 m during the daytime, formed a substantial concentration at 40–250 m and constituted 52% of the biomass at 200–250 m at night.

At 41N, the euphausiid biomass was low (0.005–0.24 mg DW m^{-3}) during the daytime, while having a high density (maximum reached 39.43 mg DW m^{-3} at 0–25 m) for 0–100 m depths at night (Fig. 4b). During the daytime, *Thysanoessa* spp. dominated at 20–150 m, *Stylocheiron* spp. dominated at 150–200 m, and *Euphausia* spp. predominated at 200–250 m. At night-time, *Thysanoessa* spp. showed a high concentration (39–100% of the biomass) throughout the layer, and it should be noted that *Euphausia* spp. dominated (40–60%) at 0–40 m and 150–200 m depths, where the euphausiid biomasses were high.

At 44N, the euphausiid biomass ranged from 0.003–1.28 mg DW m^{-3} during the daytime and from 0.06–8.05 mg DW m^{-3} at night (Fig. 4c). In the daytime, the euphausiid biomass was high at 20–60 m depths. At night, the euphausiid biomass increased for the whole layers and was concentrated at 0–60 m. For the biomass composition, *Thysanoessa* spp. dominated at 40–150 m of daytime and at all layers at night. *Euphausia* spp. occurred only at 0–60 m depths during both day and night and constituted 4–99% and 18–50% of the euphausiid biomass during day and night, respectively. *Stylocheiron* spp. occurred below 80 m and constituted 28–100% of the biomass at 80–100 m and 150–200 m during the daytime and 8–44% of the biomass below 80 m during the night-time.

Active flux

For active flux, the feeding impact near the surface layer during night and respiration at the deep-layer during daytime were computed (Table 3). The feeding impact of amphipods was 0.19–11.76 mg C m^{-2} day^{-1}, and that of euphausiids was 5.12–16.42 mg C m^{-2} day^{-1}. The respiration rate of amphipods was 0.08–6.38 mg C m^{-2} day^{-1}, and that of euphausiids was 2.33–7.70 mg C m^{-2} day^{-1}. For both the feeding impact and the respiration rate, values at 41N were the largest, which was due to the largest biomass at that station being observed for both amphipods and euphausiids (1,178 or 1,562 mg DW m^{-2}). Common for the whole station, the ingestion and respiration rates of euphausiids were greater than those of amphipods. For the total of active flux by macrozooplankton, the ingestion rate was 8.34–28.18 mg C m^{-2} day^{-1} and the respiration rate was 3.15–14.08 mg C m^{-2} day^{-1}.

Discussion

Amphipods

The abundance of amphipods was high at high latitude and decreased with low latitude (Table 1). Within the dominant species, *T. pacifica* is known to be a boreal subarctic species (Nagata, 1997) that inhabits a wide geographical range including the Bering Sea, Okhotsk Sea and northern North Pacific (Bowman, 1960 ; Nagata, 1997). The abundance of

Table 3. Biomass at night and active carbon transport by diel vertical migration of amphipods and euphausiids ; nighttime ingestion and daytime respiration were calculated.

Taxon/station	Biomass at night (mg DW m^{-2})	Ingestion (mg C m^{-2} day^{-1})	Respiratory flux (mg C m^{-2} day^{-1})
Amphipods			
39N	18	0.19	0.08
41N	1,178	11.76	6.38
44N	329	3.34	1.68
Euphausiids			
39N	668	8.14	3.07
41N	1,562	16.42	7.70
44N	437	5.12	2.33
Total			
39N	686	8.34	3.15
41N	2,740	28.18	14.08
44N	766	8.46	4.00

T. pacifica was low at the low latitude station (39N) and was high at 41N and 44N, with *T. pacifica* being the dominant species at those stations. These facts suggest that latitudinal changes in the abundance may have primarily govern the latitudinal distribution of *T. pacifica*. Common for *T. pacifica*, *C. challengeri* and *V. gibbosa*, their abundances showed clear increases at night (Table 1). These three species are known to perform DVM, which is characterized by nocturnal ascent (Thurston, 1976a, 1976b ; Yamada, 2002). Thus, the drastic increase in abundance of these species may be interpreted as the result of their nocturnal ascent DVM. For the biomass of amphipods, their night-time peak was seen for 75-150 m, which is comparable to that of surface swarming euphausiids (Figs. 3 and 4). Next, we discuss the six dominant species in the amphipod biomass.

C. challengeri were extremely few in number in the daytime, while occurring throughout the 0-250 m layer of 41N and 44N at night (Fig. 3b, c). *C. challengeri* is known to distribute throughout the oceans worldwide (Hughes and Lowry, 2015). In low latitude areas, their vertical distribution is reported to become deep (Thurston, 1976a). The thermal and saline range of the *C. challengeri* distribution is reported to be <10°C and <34.5, respectively. In the Oyashio region, *C. challengeri* distributes at 200-400 m depth during daytime, then migrates upward and distributes approximately 0-150 m at night (Yamada, 2002). This day-night distribution of *C. challengeri* corresponds well with those at 41N and 44N for this study (Fig. 3b, c). Since the temperature of 0-250 m depths at 39N was 9.4-16.7°C (Fig. 2a), to avoid the high thermal condition, the abundance of *C. challengeri* was extremely low at that station.

E. minuta is classified as a warm-water species in the western North Pacific (Nagata, 1997). *E. minuta* occurred only at the southern 39N (Fig. 3a). *E. minuta* distributed in the upper 100 m depths both day and night, which corresponded with the previously reported vertical distribution of this species (Cornet and Gili, 1993).

For *P. abyssalis*, the presence of DVM is reported (Yamada, 2002). In this study, *P. abyssalis* occurred for daytime at 39N and 41N, and no evidence was detected for the DVM. Since the abundance of *P. abyssalis* peaks at approximately 400 m depths both day and night (Yamada, 2002), the shallower sampling depths of this study (0-250 m) made it impossible to collect their main population or to detect their DVM.

T. pacifica is an epipelagic amphipod, and their distribution in the western subarctic Pacific was concentrated at shallower depths than 200 m in the daytime and shallower than 50 m at night (Yamada, 2002). At 39N of this study, the biomass of *T. pacifica* shifted to <100 m depths at night (Fig. 3a), which corresponded with this DVM pattern. At 41N and 44N, *T. pacifica* composed the main species of the amphipod biomass <100 m depths during daytime, while their composition decreased at night (Fig. 3b, c), which may be partly due to the body size of *T. pacifica* being smaller than that of the other species ; thus, because of the dominance of the large body size of other species, the contribution of *T. pacifica* in the amphipod biomass decreased at night.

Phronima spp. (*P. atlantica* and *P. sedentaria*) is reported to distribute at 0-1,000 m depths in the Canary Islands, and *P. atlantica* has abundance peaks <200 m and 600-1,000 m, while *P. sedentaria* concentrates at <400 m, and both species perform small DVM (Thurston, 1976b). In this study, *Phronima* spp. had a high composition in the amphipod biomass, especially for the high biomass layer at 39N (Fig. 3a), and the vertical distribution and DVM of amphipods at that station may be governed by *Phronima* spp. *Phronima* spp. is known to feed on small salps and enter barrels, which is the remains of gelatinous zooplankton living inside of barrels (Harbison et al., 1977). Since the distributions of *Phronima* spp. and gelatinous zooplankton, which is a source of the barrel, are well corresponded (Gasca and Haddock, 2004), the distribution of *Phronima* spp. May be governed and determined by the distribution of gelatinous zooplankton.

Few *V. gibbosa* occurred at each station during the daytime, while being observed for whole layers throughout the station at night (Fig. 3). Throughout the station, *V. gibbosa* had a high composition at <50 m depths and was the dominant species at biomass peak depths of 41N and 44N (Fig. 3b, c). There is little information available on the DVM of *Vibilia* spp. In the Canary Islands, vertical distribution of *Vibilia* spp. extends down to 600 m and reaches 800 m, and the DVM is reported for *V. armata*, which is the dominant species there (Thurston, 1976b). These facts suggest that *V. gibbosa* in the western North Pacific may be distributed below 250 m during the daytime, perform DVM and occur at <250 m depths in this study (Fig. 3). *V. gibbosa* is also reported to distribute in the body of salps, and they feed on particle matter, which is collected by salps (Madin and Harbison, 1977). These facts suggest that the distribution of *V. gibbosa* may be related with gelatinous zooplankton, especially salps,, while ecological information on *V. gibbosa* is rare in the western North Pacific, considering their high composition ; thus, more study is required in the future.

Euphausiids

For euphausiids, 19 species belonging to 7 genera were identified in this study (Table 2). Since euphausiids in this study contain many unidentified specimens (Table 2), there are some possibilities that the species list of this study may increase. The abundance of euphausiids increased at night, especially at 41N and 44N (Table 2). The night-time euphausiid abundance was dominated by *Thysanoessa* spp., followed by *Euphausia* spp., especially *E. pacifica*. At all stations, these two genera (*Thysanoessa* spp. and *Euphausia* spp.) dominated in abundance (Table 2). These facts indicate that the euphausiid abundance in this region is shaped mainly by these two genera. For the euphausiid biomass, few peaks were detected during the daytime, while forming clear peaks at 0–40 m depths (Fig. 4). These facts suggest that a clear DVM was the case for three stations in this study. Next, we discuss the DVM of the biomass-dominated 5 genera species.

Euphausia spp. is reported to have a clear DVM in various locations (Mauchline, 1980 ; Taki, 2008). During the night, *Euphausia* spp. distributes at the surface and feeds on phytoplankton, microzooplankton and detritus (Mauchline, 1980). The night-time distribution depth of *Euphausia* spp. is known to vary with the amount of primary production (Hirota, 1987). Dominance of *Euphausia* spp. at the shallowest depths (0–20 m) at night throughout the station corresponds to these findings (Fig. 4). Throughout the station, vertical changes in the euphausiid biomass were well synchronized with the dominance of *Euphausia* spp. These facts suggest that the euphausiid biomass in this region is mainly governed by *Euphausia* spp.

Nematoscelis spp. is reported to be distributed mainly in the subtropical region, while the distribution depths varied by species and with the performance of DVM (Mauchline, 1980 ; Sawamoto, 1997). Also found in this study was that *Nematoscelis* spp. occurred only at the subtropical station (39N) (Fig. 4a). Vertical distribution of *N. difficilis*, which is the abundant species in this study, is reported to be 50–400 m, both day and night (Sawamoto, 1997). At 39N, the night-time increase of *Nematoscelis* spp. in composition with the euphausiid biomass may reflect upward migration from below 250 m at night.

Stylocheiron spp. is distributed below 50 m depths and occurred deeper than the other genera (Fig. 4). Within *Stylocheiron* spp., *S. longicorne* was the most abundant species (Table 2). *S. longicorne* is known to have no DVM and is characterized by mesopelagic carnivores (Mauchline, 1980), while feeding on faecal pellets (Nemoto, 1967 ; Hirota and Nemoto, 1989). Because of these feeding modes (feed on faecal pellets and zooplankton), the vertical distribution depths of *Stylocheiron* spp. may be deeper than that of the other euphausiid species.

T. oculatum showed deeper distribution depths at night than during the daytime (reverse DVM) for all stations (Fig. 4). These reverse DVM patterns of *T. oculatum* have been reported by Mauchline (1980). Since the main distribution depth of *T. oculatum* is reported to be a much deeper layer (below 200 m depth during the daytime and below 400 m depth at night) (Mauchline, 1980 ; Sawamoto, 1997), the sampling design of this study (0–250 m depths) may have failed to accurately detect the distribution depths of this species.

Thysanoessa spp. composed a small percentage of the euphausiid biomass at 39N, while having high percentages at 41N and 44N. For high biomass layers at 41N and 44N, the composition of *Thysanoessa* spp. in the euphausiid biomass was followed by *Euphausia* spp. For *Thysanoessa* spp., species identification was difficult for most of the specimens because of the incomplete species identification of body parts. Since both the abundance and biomass of *Thysanoessa* spp. increased clearly at night (Table 2, Fig. 4), DVM characterized by nocturnal ascent from below 250 m depth may the case for this genus.

Active flux

The estimated macrozooplankton ingestion at night and respiration during the daytime were the highest at 41N, which may have been caused by the highest biomass occurring at that station (Table 3). For the second largest biomass station (44N), the daytime respiration was higher than that in 39N, while night-time ingestion was similar for that in 39N (Table 3), which may be due to differences in the temperature between the two stations (Fig. 2).

As information on primary production in this region, the value at St. KNOT (44°N, 155°E) during June–August : 227 mg C m^{-2} day^{-1} has been reported (Imai et al., 2002). Estimated ingestion by macrozooplankton in this study (8.3–28.2 mg C m^{-2} day^{-1}, Table 3) corresponded with 3.7–12.4% of primary production. If we assume the f-ratio to be 0.58 (cf. Fujii et al., 2007), passive POC flux from the euphotic layer is estimated to be 132 mg C m^{-2} day^{-1}. Estimated respiration by macrozooplankton in this study (3.2–14.1 mg C m^{-2} day^{-1}, Table 3) accounted for 2.4–10.7% of passive POC flux.

Active carbon flux by respiration of zooplankton DVM is estimated to be 1.5–20 mg C m^{-2} day^{-1} for oceans worldwide (Table 4). An estimation by this study contains only four

Table 4. Comparison of active carbon flux (respiratory only, not included egestion or motality at depth) by diel migrant zooplankton. All migratory flux are means and are compared with mean sedimentary passive C flux at each region. Numbers in parentheses are values of amphipods and euphausiids, respectively.

Location	Migrant Biomass		Migratory flux (mg C m^{-2} day^{-1})	Compared with POC flux		Source
	(mg C m^{-2})	Component		%	Depth (m)	
Atlantic Ocean						
BATS	191	Mesozooplankton	15	34	150	Dam et al. (1995)
BATS	49	Mesozooplankton	1.5	6	150	Steinberg et al. (2000)
Pacific Ocean						
Eastarn Equator	96	Mesozooplankton	4.2	18	150	Zhang and Dam (1997)
Eastarn Equator	155	Mesozooplankton	7.3	25	150	Zhang and Dam (1997)
ALOHA	126	Meso- and macrozooplankton	3	18	150	Steinberg et al. (2008)
K2	1,280	Meso- and macrozooplankton	20	72	150	Steinberg et al. (2008)
K2	116	*Metridia pacifica*	3.0	10	150	Kobari et al. (2008)
39N	274*	Amphipods+euphausiids	3.2 (0.1+3.1)	2	–	This study
41N	1,096*	Amphipods+euphausiids	14.1 (6.4+7.7)	11	–	This study
44N	306*	Amphipods+euphausiids	4.0 (1.7+2.3)	3	–	This study

*Calculated from Table 3, assuming C=0.4×DM (Peters and Downing, 1984).

amphipods and euphausiids, whose respiration flux (3.2–14.1 mg C m^{-2} day^{-1}) is at the range of the reported value. The respiration flux at 41N is very close to the value on zooplankton community at St. K2 (47°N, 161°E) in the western subarctic Pacific (Steinberg et al., 2008). As characteristics of the present estimation, active carbon flux was small relative to the biomass. For instance, the active carbon flux in the central equatorial Pacific (Zhang and Dam, 1997) is same value at 44N in this study (4.0 mg C m^{-2} day^{-1}, Table 3). However, the zooplankton biomass was 96 mg C m^{-2} in the equatorial Pacific (Zhang and Dam, 1997), while it was 306 mg C m^{-2} at 44N (Table 4). These discrepancies may be due to differences in the mass-specific respiration, which is primarily governed by habitat temperature (cf. Ikeda, 1985). For a calculation of the habitat temperature in the equatorial Pacific, Zhang and Dam (1997) used 13°C, while it was 4.5°C at 44N (Fig. 2). Thus, the mass-specific metabolism is high in the warm low latitude region, and the contribution of zooplankton respiration flux may be high in these regions.

There are several shortcomings in the present estimation of active carbon flux. First, we assumed the vertical migration distance to be : 400 m – $D_{50\%}$. However, the magnitude of DVM is known to vary by species, body size and developmental stages (Thurston, 1976b ; Mauchline, 1980 ; Yamada, 2002). To make a more accurate estimation, the vertical migration distance, which varied by body size, and information on the swimming velocity would be required. Second, active carbon flux in this study only included respiration of zooplankton, and fluxes due to predation, mortality and excretion were not considered. Among other types of flux, active flux via dissolved organic carbon (DOC) was reported to be important. According to Steinberg et al. (2000), active flux via DOC accounts for 31% of respiration flux. Zhang and Dam (1997) also noted that mortality flux may account for one-third of the zooplankton DVM flux. Considering this information and since the present estimate is only based on respiration flux, this estimate might be an underestimation because it lacks consideration for the DOC and mortality flux, but it may difficult to estimate those factors using the data set of this study.

With these shortcomings considered, the respiration flux in this study is estimated to account 2.4–10.7% of the passive sinking flux in this region. Based on the calculation of this study, the importance of active carbon flux of macrozooplankton is evident. The biomass of Macrozooplankton, such as amphipods and euphausiids, is difficult to estimate accurately by ordinary zooplankton sampling. To collect macrozooplankton quantitatively, largemouth sampling gear, such as MOCNESS, may be required. Because of the large-body size, macrozooplankton perform large DVM and may have an important role in the vertical material flux of oceans.

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Appendix 1. Relationships between body mass (Y: wet mass [WM], dry mass [DM] and ash-free dry mass [AFDM], all in mg) and body length (X, mm) of dominant amphipods in the western North Pacific Ocean. Note that the all regressions are highly significant ($p < 0.01$).

Species	Body mass unit	n	$Y= aX^b$		r^2
			a	b	
Cyphocaris challengeri	WM	18	0.00969	3.12	0.97
	DM	18	0.00082	3.30	0.97
	AFDM	18	0.00078	3.26	0.97
Eupronoe minuta	WM	11	0.04583	2.67	0.99
	DM	11	0.00628	2.58	0.99
	AFDM	11	0.00538	2.56	0.99
Phronima atlantica	WM	21	0.02986	2.47	0.92
	DM	21	0.00467	2.06	0.91
	AFDM	21	0.00506	1.84	0.91
Phronima sedentaria	WM	15	0.01029	3.05	0.99
	DM	15	0.00083	2.98	0.99
	AFDM	15	0.00069	2.91	0.98
Primno abyssalis	WM	19	0.02598	2.84	0.99
	DM	19	0.00372	2.93	0.96
	AFDM	19	0.00258	3.03	0.97
Themisto pacifica	WM	19	0.02398	2.98	0.99
	DM	19	0.00440	2.82	0.99
	AFDM	19	0.00376	2.65	0.99
Vibilia gibbosa	WM	19	0.03805	2.72	0.88
	DM	19	0.00039	3.90	0.95
	AFDM	19	0.00019	4.06	0.93

Appendix 2. Relationships between body mass (Y: wet mass [WM], dry mass [DM] and ash-free dry mass [AFDM], all in mg) and body length [X, mm] of dominant euphausiids in the western North Pacific Ocean. Note that the all regressions are highly significant ($p<0.01$).

Species	Body mass unit	n	$Y=aX^b$		r^2
			a	b	
Euphausia pacifica	WM	21	0.00420	3.23	0.99
	DM	21	0.00056	3.27	0.99
	AFDM	21	0.00055	3.22	0.99
Nematoscelis difficilis	WM	21	0.01454	2.77	0.99
	DM	21	0.00160	2.89	0.98
	AFDM	21	0.00144	2.87	0.97
Stylocheiron longicorne	WM	21	0.01211	2.82	0.97
	DM	21	0.00187	2.79	0.97
	AFDM	21	0.00177	2.73	0.97
Tessarabrachion oculatum	WM	20	0.00422	3.25	0.99
	DM	20	0.00080	3.17	0.99
	AFDM	20	0.00098	2.96	0.99
Thysanoessa inspinata	WM	21	0.01048	2.93	0.98
	DM	21	0.00194	2.86	0.97
	AFDM	21	0.00208	2.74	0.97