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Vertical distribution, standing stocks, and taxonomic accounts of the entire plankton community, and the estimation of vertical material flux via faecal pellets in the southern Okhotsk Sea

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ABSTRACT

The faecal pellets egested by zooplankton are essential as they influence the vertical material flux in oceans. As mesozooplankton are dominant within the plankton community in the southern Okhotsk Sea during early summer, the vertical material flux via mesozooplankton is expected to be substantial. However, quantitative information on their faecal pellets is currently lacking. In this study, we evaluated the taxonomic accounts of the entire plankton community, including microplankton, mesozooplankton, and macrozooplankton, in the 0–1000 m water column. The ingestion and egestion rates of the zooplankton were also estimated. We used a fine-mesh (63 μm) plankton net along with an imaging technique (with ZooScan) to quantify the amount of *in-situ* faecal pellets. Furthermore, on-board experiments were conducted to estimate the faecal pellet egestion by the dominant zooplankton species. Cosmopolitan diatom species were found to dominate the microplankton biomass, whereas the large-sized calanoid copepod *Metridia okhotensis*, which performs nocturnal ascent diel vertical migration, dominated the mesozooplankton biomass. Two euphausiid species with different body sizes, namely the small-sized *Thysanoessa inermis* and the large-sized *Euphausia pacifica,* were found to be dominant among the macrozooplankton. The highest density and mass of faecal pellets (1888 pellets m^{-3}, 2.96 mg C m^{-3}) was observed in the 0–100 m layer during the daytime. Throughout the layer, the volumes of the faecal pellets peaked at 0.010–0.015 mm^3, which corresponded with the size of the pellets egested by *M. okhotensis* in the on-board laboratory experiments. The large-sized faecal pellets (>0.2 mm^3), which were inferred to be egested by euphausiids, were only observed during the night-time. Based on the on-board experiments, the faecal pellets egested by all the meso- and macrozooplankton species contained phytoplankton cells that possessed a fluorescent ability. Furthermore, cyanobacteria were the most common taxa (26–65% in number) observed in the faecal pellets. Coprophagy (feeding on faecal pellets) was observed for the calanoid copepod *Gaetanus variabilis*, which was collected from depths of 500–1000 m. The estimated daily ingestion rates of meso- and macrozooplankton corresponded with 21% of the standing stock of microplankton. In contrast, their daily egestion rates accounted for 40–112% of the *in-situ* faecal pellet masses. Faecal pellet collection by the gentle vertical towing of a fine-mesh plankton net and quantification through imaging analysis can provide new insights for the evaluation of the number and mass of faecal pellets in the field. The findings of the present study suggest that these techniques have the potential to successfully quantify faecal pellets in the water column.

Abbreviations: DST, Drifting sediment trap; VMPS, Vertical Multiple Plankton Sampler; MOHT, Matsuda-Oozeki-Hu Trawl; TL, Total length; DVM, Diel vertical migration.

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1. Introduction

The vertical material transport in oceans theoretically occurs via two routes: fluxes due to physical mixing, and fluxes mediated by biological activities, the latter of which is also known as the "biological pump" (Longhurst and Harrison, 1989). The biological pump has been reported to be the most important driving force behind vertical material flux in oceans (Ducklow et al., 2001). It can be further divided into active and passive transport (Steinberg et al., 2008; Kobari et al., 2016). The main mechanisms for active transport include respiration, egestion, and mortality of zooplankton at different depths owing to their vertical migration (Ducklow et al., 2001; Takahashi et al., 2009). Passive transport, which is the larger type of flux, includes the sinking of faecal pellets that are egested by zooplankton rather than the direct sinking of phytoplankton (Wilson et al., 2008; Turner, 2015). This is partly due to their size differences—faecal pellets are much larger than phytoplankton cells.

Drifting sediment traps (DSTs) are commonly used in the field for the quantitative collection of faecal pellets (Trull et al., 2008; Wilson et al., 2008; Laurenceau-Cornec et al., 2015). A DST is shaped as a cylinder with a small diameter; therefore, only a small number of faecal pellets are collected in DSTs, and long-drifting mooring (two to three days) is required. This can mask the differences in the faecal pellet abundance between day and night in the field (Emerson and Roff, 1987). As most zooplankton have a diel feeding pattern (Mauchline, 1998), it is expected that diel changes may influence the number of faecal pellets in the field. However, due to the methodological limitations (i.e. mooring for several days) of DSTs, field information on the diel changes in faecal pellet abundance and on the passive flux of materials by faecal pellets is currently lacking.

The faecal pellet volume has a positive relationship with zooplankton body size, which can be expressed using log-to-log equations (Uye and Kaname, 1994; Turner, 2002, 2015). Similarly, the sinking rates of faecal pellets can be expressed using log-to-log equations that consider faecal pellet volume (Komar et al., 1981; Turner, 2002, 2015). The sinking rates of faecal pellets are related to differences in the pellet constituents and density, and they may vary among species (Fowler and Small, 1972; Fender et al., 2019). Furthermore, coprophagy and coprorhexy by other zooplankton are also important factors that affect the sinking rate (Noji et al., 1991; Suzuki et al., 2003; Iversen and Poulsen, 2007). In addition, the faecal pellets that sink from the overlying water layers are also considered to be an important food source for the zooplankton living in the food-limited deep sea (Harding, 1974; Yamaguchi et al., 2007; Abe et al., 2012). To evaluate the nutritional importance and sinking rates of faecal pellets, it is essential to obtain information on their constituents. For example, observations using epifluorescence microscopes have revealed that the digestive tracts of deep-sea zooplankton in the subarctic and subtropical North Pacific contain a high density of pico-sized cells such as cyanobacteria (Wilson and Steinberg, 2010). Although information on the contents of zooplankton faecal pellets is important for understanding the vertical material flux in oceans, little information is currently available.

To quantitatively evaluate passive material flux via the zooplankton community, it is necessary to obtain estimates of the ingestion and egestion rates of faecal pellets, both of which are commonly expressed in units of mg C m^{-2} day^{-1}. These rates are widely calculated according to a physiological method that utilises empirical equations to estimate growth or respiration rates by applying independent variables (body weight and temperature) and combining them under assumed assimilation and net growth efficiencies (Steinberg et al., 2008; Kobari et al., 2016). The respiration rate, which is estimated from body weight, water temperature, and habitat depth, has been reported for zooplankton worldwide (13 taxa including copepods) using empirical equations (Ikeda, 2014). In the western subarctic Pacific, several studies on zooplankton ingestion and egestion estimation have conducted sensitivity tests by manipulating the assimilation and net growth efficiencies (Wilson et al., 2008; Takahashi et al., 2009). However, few attempts have been made to estimate zooplankton ingestion and egestion by applying habitat depth through new physiological methods (Ikeda, 2014).

Several projects focused on biological pump estimation, such as the VERTIGO, A-line, and K2S1, have been undertaken in the western subarctic Pacific (Wilson et al., 2008; Takahashi et al., 2009; Kobari et al., 2016). In contrast, few such attempts have been made in the Okhotsk Sea, which is a marginal sea adjacent to the western subarctic Pacific. The Okhotsk Sea is located at the southern end of the seasonally ice-covered ocean in the Northern Hemisphere, and it is reported to have high biological productivity (Pinchuk and Paul, 2000). Since the depth of the southern Okhotsk Sea is $>$ 3000 m, the function of the biological pump is expected to be large. However, information on the biological pump in this sea is lacking. Taxonomic accounts of the microplankton (Shimizu, 2009; Kasai et al., 2010; Shiomoto, 2011) and meso- and macrozooplankton (Gorbatenko et al., 2014; Yamaguchi, 2015; Arima et al., 2016; Mizukami et al., 2019) are available for this region. However, such taxonomical studies have focused on targeted taxa, and no study has been conducted to obtain a taxonomic account of the whole plankton community (e.g. microplankton, mesozooplankton, and macrozooplankton) on one occasion.

In the present study, we conducted a species-level taxonomic survey of the entire plankton community, including microplankton, mesozooplankton, and macrozooplankton, for a 0–1000 m water column in the southern Okhotsk Sea during early summer. Vertical stratified samples for meszooplankton were collected during the daytime and night-time. To quantitatively estimate the ingestion and egestion of meso- and macrozooplankton, we used physiological methods that utilised respiration rates. *In-situ* faecal pellets were collected by the gentle towing of a fine-mesh-equipped vertical stratification net (63 μm) with a large filtration volume (19–108 m^3). Next, faecal pellets were identified and their size and volume were measured using imaging analysis (ZooScan). In addition, on-board experiments on the egestion of the meso- and macrozooplankton were conducted by rearing live specimens, and the collected faecal pellets were examined for their ingredient contents. There were two main aims of this study: (i) to explore a new approach for estimating the standing stocks of faecal pellets, and (ii) to characterise the impacts of predominant metazoans on the biogeochemical cycles of the Okhotsk Sea.

2. Material and methods

2.1. Field sampling

Field observations were made at two stations: St. D2 (44°16′ N, 145°34′ E; water depth: 2264 m) and St. E1 (44°12′ N, 145°27′ E; water depth: 1859 m) (Fig. 1) in the southern Okhotsk Sea on 29 and 30 June 2019. To sample the microplankton, 1-L water samples were collected at St. D2 using a bucket from the sea surface and a conductivity-temperature-depth profiler with rosette multi-bottle samplers (CTD-RMS) from the maximum fluorescence layer (at a depth of 10 m). The samples were preserved by adding glutaraldehyde at 1% in final concentration, and they were stored under dark and cold conditions until further analysis. Additionally, 250-mL water samples were collected, filtered through a GF/F grade glass microfibre filter, and extracted in N, N-dimethylformamide. Then, chlorophyll *a* (Chl. *a*) was measured with a fluorometer (10-AU; Turner Designs, San Jose, CA, USA). Mesozooplankton samples were collected by vertical stratified sampling from three layers (0–100, 100–500, and 500–1000 m) using a vertical multiple plankton sampler (VMPS; Tsurumi Seiki Co. Ltd., Kanagawa, Japan) (Terazaki and Tomatsu, 1997) with a mouth-opening of 0.25 m^2. The VMPS was equipped with 63-μm mesh and non-filtered cod ends at night (St. D2) and during the day (St. E1). The filtered volumes were measured using a flowmeter for each sample, and the values ranged between 19.3 and 108.2 m^3 (Table 1). After recovering the VMPS, each

zooplankton sample was immediately split in half using a Motoda splitter (Motoda, 1959). Then, one aliquot containing live zooplankton individuals was used for the on-board rearing of zooplankton for faecal pellet egestion experiments. The remaining samples were preserved by adding 5% (v/v) borax-buffered formalin immediately after splitting.

In the on-board rearing for the faecal pellet egestion experiments, four copepod species (*Metridia okhotensis* C6F, *Neocalanus cristatus* C5, *Neocalanus plumchrus* C5, *Gaetanus variabilis* C5M, C6F) and one euphausiid species (*Thysanoessa inermis*), which were dominant in the collected samples, were sorted into 50 mL bottles that were then filled with chilled filtered seawater and equipped with a 300-μm mesh on the bottom to prevent coprophagy or coprorhexy. The specimens were reared for one day under dark conditions in an incubator set at 3 °C. The egested faecal pellets were preserved by adding glutaraldehyde at 1% in the final concentration and stored under cool and dark conditions until further analysis.

Macrozooplankton samples were collected by horizontal towing at a ship speed of 2–3 knots. Midwater trawling was conducted using the Matsuda-Oozeki-Hu trawl (MOHT) with a mouth area of 5 m^2 (Oozeki et al., 2004) at depths of 53–69 m (monitored using acoustics) at St. D2 during the night (Table 1). The MOHT was equipped with 1.4 mm mesh and a flowmeter. The collected samples were immediately preserved on board by adding 10% (v/v) borax-buffered formalin. Additionally, the water temperature, salinity, and fluorescence were measured at both stations at depths between 0 and 1000 m using a CTD profiler (SBE–911 Plus, Sea-Bird Electronics, Bellevue, WA, USA) and a fluorometer (Seapoint Chlorophyll Fluorometer, Seapoint Sensors, Exeter, NH, USA). Based on the Chl. *a* measurement data obtained throughout the cruise, we obtained the conversion factor between Chl. *a* and fluorescence ($r^2 = 0.96$, $p < 0.0001$, $n = 84$) and expressed Chl. *a* in mg m^{-3} in 1-m intervals.

2.2. Microscopic observations

In the land laboratory, the 1-L water samples were allowed to sit undisturbed on a stone table for more than one day to allow the microprotist cells to settle at the bottoms of the bottles. Then, the samples were concentrated to 20 mL using a siphon over 48 h under cool dark conditions. Subsamples (0.1–0.5 mL) were mounted on a glass slide and examined with an inverted microscope under 200–400 × magnification. Microplankton (diatoms, dinoflagellates, and ciliates [Oligotrichia and Tintinnida]) were identified to the species level and counted. For each taxon, the lengths along the major and minor axes were measured with 0.01 μm precision using Nikon NIS Elements, and the cell volumes were calculated using geometric models that varied for different genera (Sun and Liu, 2003). Then, the volume data were converted to carbon units (mg C m^{-3}) using volume-carbon conversion factors, which varied depending on the taxa (Strathmann, 1967; Menden-Deuer and Lessard, 2000).

For mesozooplankton samples, 1/4–1/136 (examined fraction/whole sample in volume) subsamples (varied with the sample amount), which were created using a wide-bore pipette, were examined under a stereomicroscope. The number of specimens were counted, and the species and the developmental stages were identified for calanoid copepods, which were the dominant taxa in the collected samples. The total length (TL) of the adults of each copepod species was previously reported by Brodskii (1967). To obtain the TL values for the juvenile stages, we used the moult increment data at each stage by Mauchline (1998) to compute the developmental stage factors. The values of each stage were calculated by multiplying the adult TL with the following factors: 0.318 (copepodite stage 1: C1), 0.411 (C2), 0.513 (C3), 0.648 (C4), and 0.813 (C5). For cyclopoid, poecilostomatoid, and harpacticoid copepods, species identification was not conducted, and the TL values were measured using an eyepiece micrometre with a precision of 0.01

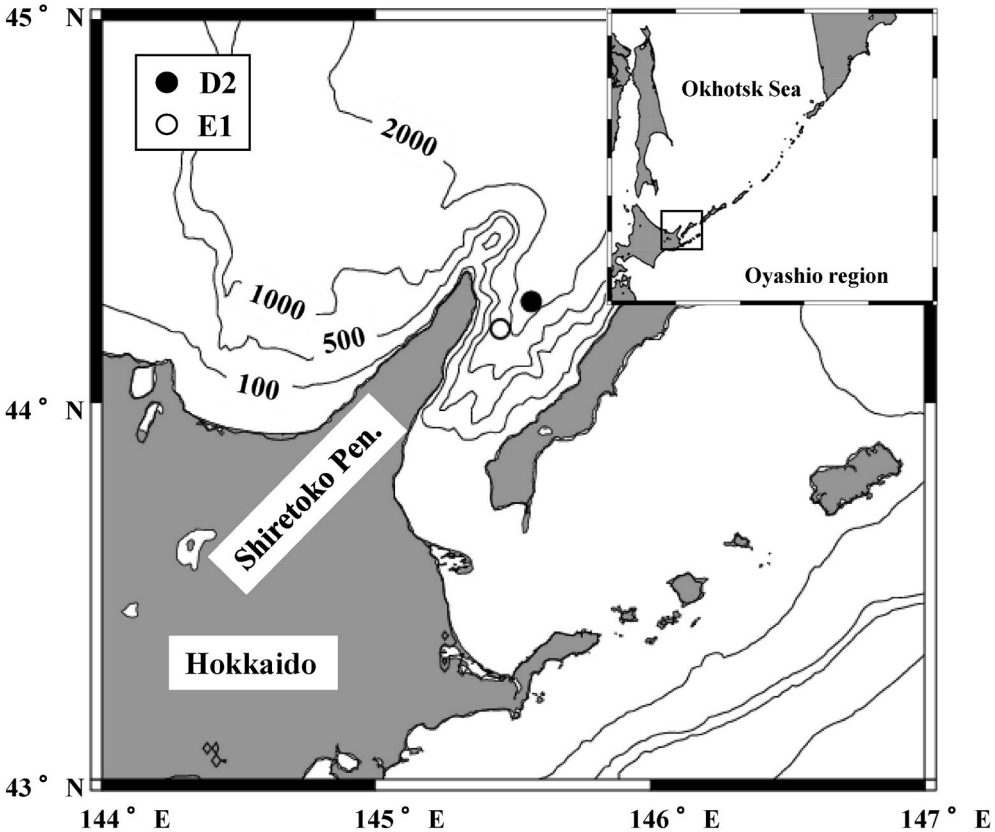

Fig. 1. Location of the sampling stations (St. D2 and E1) in the southern Okhotsk Sea during 29–30 June 2019. Depth contours are superimposed. For details of the sampling items at each station, see Table 1.

mm for 30 individuals. The TL data were converted to the carbon unit (mg C ind.$^{-1}$) by applying the carbon-TL regressions for calanoid, cyclopoid, and poecilostomatoid copepods that were previously reported by Nakamura et al. (2017), and that for harpacticoid copepods as reported by Uye et al. (2002). The carbon biomass (mg C m^{-3}) was quantified by multiplying the carbon mass of an individual with the abundance of each species/stage.

The macrozooplankton samples were divided into 1/32 (examined fraction/whole sample in volume) subsamples using a Motoda splitter, and the euphausiid species, the dominant taxa in the collected samples, were identified and counted under a stereomicroscope. The TL of all euphausiid individuals was measured under a stereomicroscope using a scale with a precision of 0.5 mm. The TL data for the euphausiids were converted to carbon units (mg C ind.$^{-1}$) by applying the carbon-TL relationship reported by Ross (1982). The data were then expressed as carbon biomass (mg C m^{-3}), which allowed the data to be comparable to that of the other taxa.

In the land laboratory, faecal pellets egested by the zooplankton during the on-board rearing experiments were examined under an inverted fluorescence microscope. The constituents of the faecal pellets were identified to the lowest taxonomic levels whenever possible. The counting procedure used was that of Wilson and Steinberg (2010). Cells containing red fluorescence (chlorophyll) and yellow fluorescence (phycoerythrin and phycocyanin of the cyanobacteria) were identified and counted. For flagellates and dinoflagellates, cells with red autofluorescence were treated as autotrophs and green cells were treated as heterotrophs. The hard parts of the cells were used to identify them as diatoms or dinoflagellates, and tintinnid loricae were also identified and quantified. The long and short axes of the faecal pellets were measured with a precision of 1 μm, and then the faecal pellet volume (mm^3) was calculated using the volumetric formula for ellipsoids. The cell number contained in each faecal pellet was expressed as the number of cells per unit volume of the faecal pellet (cells mm^{-3}). The faecal pellet sedimentation rate (*SR*; m day^{-1}) was also estimated from the volume of the faecal pellet (*V*; mm^3) using the formula given by Small et al. (1979):

$$\log_{10} SR = 0.513 \log_{10} V - 1.214$$

2.3. In-situ quantification of faecal pellets (ZooScan measurements)

Multiple faecal pellets were observed in the mesozooplankton samples collected by VMPS (Fig. 2a). This may be attributed to the use of VMPS with a fine mesh size (63 μm) as well as gentle vertical towing of the non-filtered cod end. A wide-bore pipette was used to create 1/88–1/162 (examined fraction/whole sample in volume; varied according to the size of the samples) subsamples for the image scanning measurements. Images of the faecal pellet samples were scanned using ZooScan (ZooScan MIII, 127 Hydroptic Inc., France) to quantify the number and volume of the faecal pellets under *in-situ* conditions, according to the method reported by Gorsky et al. (2010). Before each measurement, background measurements were made using deionised water. The sample images were digitised at a 2400-dpi resolution (one pixel corresponded to 10.58 μm). All obtained images were then uploaded to the EcoTaxa website (http://ecotaxa.obs-vlfr.fr/prj/) and the faecal pellets were identified (Fig. 2b–e).

The faecal pellet sizes were measured using the major axis length (L_{major}: mm) and minor axis length (L_{minor}: mm). As most faecal pellets were elliptical, their volume (*V*: mm^3) was calculated using the following equation:

$$V = \frac{4}{3}\pi \times \left(\frac{L_{major}}{2}\right) \times \left(\frac{L_{minor}}{2}\right)^2$$

The carbon-to-volume conversion factor of faecal pellets (0.08 mg C mm^{-3}), which was reported by Wilson et al. (2008) for the western subarctic Pacific during summer, was used to calculate the faecal pellet carbon mass (mg C m^{-3}) at each sampling layer.

2.4. Ingestion and egestion rates

The ingestion and egestion rates of mesozooplankton (copepods) and macrozooplankton (euphausiids) were estimated using physiological methods (respiration rates) by applying three independent variables: water temperature, individual carbon mass, and habitat depths (Ikeda, 2014). Because the mass contributions for the other taxa were extremely low (<5%), we only focused on the fluxes of these two taxa in each plankton community. To estimate the ingestion and egestion rates, we used an assimilation efficiency (*AE*) and a net growth efficiency of 60% and 50%, respectively (Steinberg et al., 2008; Giering et al., 2014). Further, mean water temperature (*T*:°C) was calculated for a 1-m interval at each layer of VMPS and MOHT sampling.

The respiratory rates (*R*: μL O_2 ind.$^{-1}$ h^{-1}) of copepods and euphausiids were calculated using the following equations (Ikeda, 2014):

$$\ln R = 23.079 + 0.813 \times \ln\frac{CM}{1000} - 6.248 \times \frac{1000}{K} - 0.136 \times \ln D \text{ (copepods)}$$

$$\ln R = 23.079 + 0.813 \times \ln\frac{CM}{1000} - 6.248 \times \frac{1000}{K} - 0.136 \times \ln D + 0.600 \text{ (euphausiids)}$$

where *CM* is the carbon mass per individual (μg C ind.$^{-1}$), *K* is the absolute temperature (*K*: *T* + 273.15) at each layer, and *D* is the intermediate depth of the sampling layer (m).

Assuming a respiratory quotient of 0.97 (Gnaiger, 1983), the ingestion (*I*: mg C m^{-3} day^{-1}) and egestion (*E*: mg C m^{-3} day^{-1}) rates at night were calculated using the following equations:

$$I = \frac{R}{1000} \times 0.97 \times \frac{12}{22.4} \times \frac{1}{0.3} \times Abu \times 8.52$$

Table 1
Sampling data for each plankton sample collected in the southern Okhotsk Sea. Five types of data collections were made: microscopic quantification of microplankton (A) and calanoid copepods (B), faecal pellet quantification by ZooScan (C), microscopic observation of faecal pellets egested by each dominant zooplankton species reared onboard (D), and microscopic quantification of macrozooplankton (E).

Date	Station	Local time	Sampling gear	Depth strata (m)	Water volume quantified (m^3)	Data collection				
						A	B	C	D	E
29 June 2019 (Night)	D2	20:20–22:17	CTD-RMS	0, 10	0.001	●				
		22:47–22:48	VMPS	0–100	19.29		●	●	●	
		22:41–22:47	VMPS	100–500	94.83		●	●	●	
		22:32–22:41	VMPS	500–1000	98.97		●	●	●	
30 June 2019 (Day)	E1	18:02–18:03	VMPS	0–100	19.98		●	●		
		17:55–18:02	VMPS	100–500	81.05		●	●		
		17:47–17:55	VMPS	500–1000	108.20		●	●		
29 June 2019 (Night)	D2	23:41–00:11	MOHT	52.6–69.4 (Horizontal haul)	21032					●

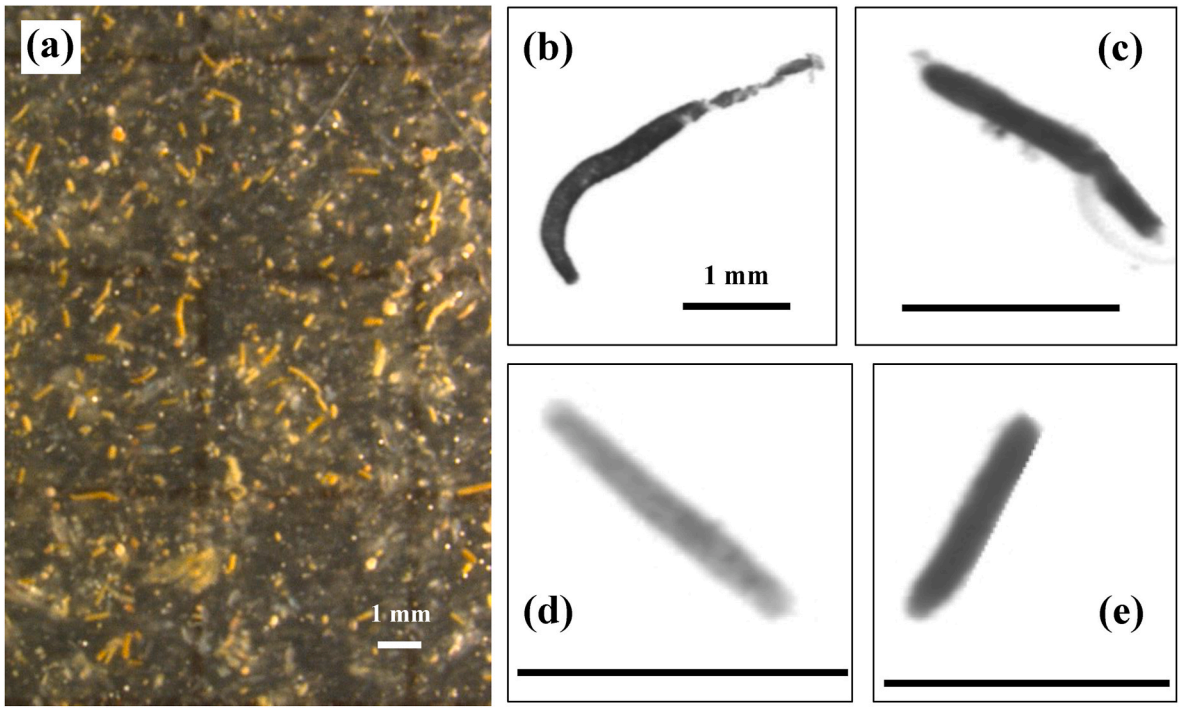

Fig. 2. (a) Example photographs of zooplankton samples collected by a vertical multiple plankton sampler (VMPS) at depths of 0–100 m in the daytime. Fresh samples were placed under the stereomicroscope. Note that brown-coloured faecal pellets were abundant. (b)–(e) Example images of formalin-preserved faecal pellet samples captured by ZooScan. Scale bars are 1 mm.

$$E = \frac{R}{1000} \times 0.97 \times \frac{12}{22.4} \times \frac{0.4}{0.3} \times Abu \times 8.52$$

where *Abu* is the abundance of each species (ind. m^{-3}), 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), 1/0.3 is the F/R, 0.4/0.3 is the E/R, 1/1000 is a unit conversion from μg to mg, and × 8.52 is the time of night hours of the study region/period.

While some copepods in this region (*Neocalanus* spp. and *Eucalanus bungii*) are known to have life cycles with diapause (Kobari et al., 2003), they were active during the studied season (early summer), although they had low abundance and biomass (see Section 3.2.). For these reasons, we included these copepod species in the ingestion and egestion estimates.

For comparative reference, the carbon mass of microplankton was calculated to evaluate the impacts of the feeding of these zooplankton (copepods and euphausiids) on *in-situ* microplankton. For this estimation, we applied the C:Chl. *a* ratio (30) that was previously used for the region around the Oyashio current (Taguchi and Saino, 1998). The integrated standing stocks (mg C m^{-2}) of microplankton were calculated by multiplying the C:Chl. *a* ratio by the Chl. *a* data for 1-m intervals through the 0–100 m depth layer (Fig. 3). The standing stocks of microplankton, mesozooplankton (copepods), macrozooplankton (euphausiids), and faecal pellets were all expressed in carbon units per square meter (mg C m^{-2}) for their quantitative comparison. The units of fluxes (ingestion and egestion rates) by mesozooplankton (copepods) and macrozooplankton (euphausiids) were standardised as mg C m^{-2} day^{-1}. For egestion rate determination, the daily impacts of meso- and

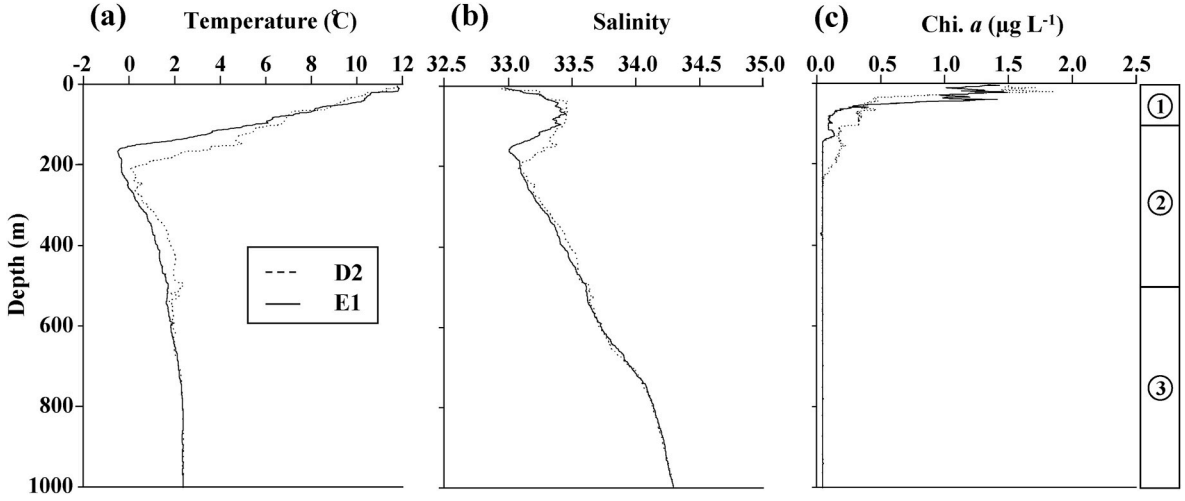

Fig. 3. Vertical changes in temperature (a), salinity (b), and chlorophyll *a* (c) at two stations (D2 and E1) in the southern Okhotsk Sea during 29–30 June 2019. Circled numbers in the right column indicate sampling layers of the Vertical Multiple Plankton Sampler (VMPS).

macrozooplankton feeding on microplankton stocks, as well as a quantitative comparison with the faecal pellet stocks, were evaluated.

3. Results

3.1. Hydrography

The water temperature, salinity, and Chl. *a* showed similar vertical distributions at both stations (Fig. 3). The water temperature at 0–1000 m depths ranged from −0.5–11.7 °C. The temperature was high at the surface, but it decreased rapidly with increasing depth. The temperature reached a minimum at depths of 180–200 m, where it had negative values at St. E1. The temperature at depths below this minima layer increased gradually to 2 °C at a 1000 m depth. The salinity was in the range of 33.0–34.6 and was low at the surface. It reached a maximum at depths of 50–60 m and a minimum at 180–200 m, where the temperature was also at a minimum. The maximum salinity was observed at a 1000 m depth. The Chl. *a* was in the range of 0.02–1.70 mg m^{-3} and the maximum was located at a depth of 20 m of St. E1. The Chl. *a* was high only at depths <100 m.

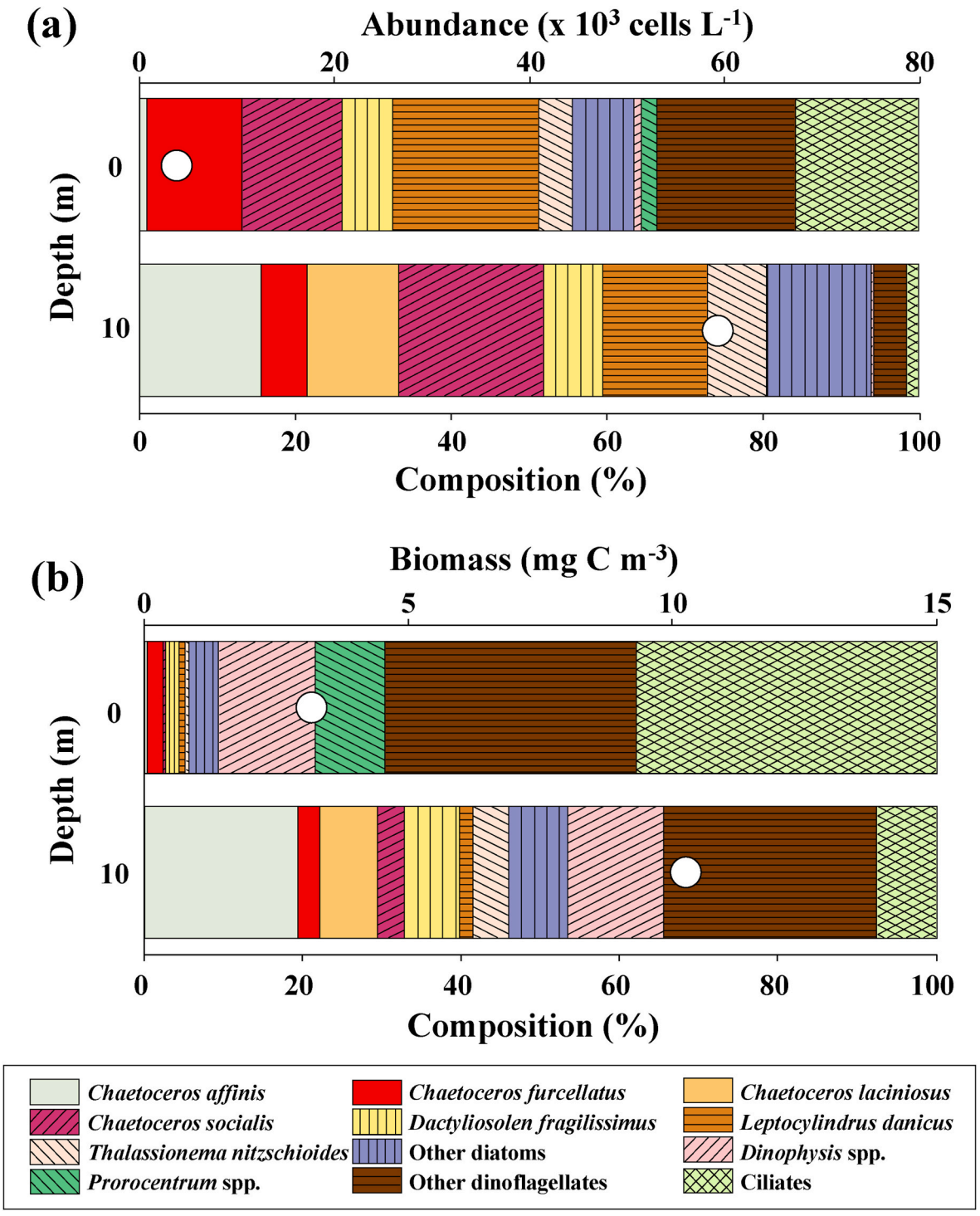

Fig. 4. Abundance (a) and biomass (b) of microplankton based on water sampling at the sea surface (0 m) and the depth of maximum chlorophyll *a* content (10 m) at St. D2 in the southern Okhotsk Sea during the night of 29 June 2019.

3.2. Plankton stock, taxonomic accounts, and flux

Since the hydrography was similar at the two sampling stations, the plankton results at the two stations were not distinguishable, and only distinctions between day and night were noted. Microplankton abundance was 3.7×10^3 cells L^{-1} at the sea surface and 59.3×10^3 cells L^{-1} at a depth of 10 m (Fig. 4a). In relation to their cell counts, the various taxa occurred evenly, but the diatoms *Chaetoceros socialis* and *Leptocylindrus danicus* were dominant taxa at both 0 and 10 m. The microplankton biomass was calculated as 3.2 mg C m^{-3} at the surface and 10.2 mg C m^{-3} at a 10 m depth (Fig. 4b). At the surface, the dominant taxa in the biomass were dinoflagellates and ciliates, whereas a high abundance of the diatom *Chaetoceros affinis* was observed at a 10 m depth. This was also where the maximum fluorescence was observed.

For mesozooplankton, the copepods were the predominant taxa (>95% both in abundance and biomass). The copepod abundance ranged from 205 to 7454 ind. m^{-3} and was highest at depths of 0–100 m during both day and night (Fig. 5a). The dominant taxa were small copepods, specifically *Oithona* spp. (Cyclopoida) and *Pseudocalanus* spp. (Calanoida). *Microsetella* spp. (Harpacticoida) were also abundant at depths of 0–100 m during the daytime. The biomass of copepods ranged from 8.9 to 66.5 mg C m^{-3} and was highest at 100–500 m depths during the daytime and 0–100 m depths at night (Fig. 5b). The large calanoid copepod *M. okhotensis* had high biomass throughout most of the layer, but the species did not occur at 0–100 m depths during the day. Instead, *Pseudocalanus* spp. were abundant there. At night, copepod feeding in each layer was in the range 0.13–2.7 mg C m^{-3} day^{-1}, and it was highest at depths of 0–100 m (Fig. 5c). The copepod egestion rate was in the range 0.05–1.1 mg C m^{-3} day^{-1} and was highest at 0–100 m depths (Fig. 5d).

For macrozooplankton, the euphausiids were the predominant taxa (>95% both in abundance and biomass). The total length of euphausiids collected by MOHT ranged from 6.5 to 25 mm and had a bimodal distribution consisting of different species (Fig. 6a). Smaller individuals (<13 mm) were dominated by *Thysanoessa inermis,* and larger individuals (>14 mm) were mostly comprised of *Euphausia pacifica*. The smaller euphausiid *T. inermis* was numerous in terms of abundance, but the larger euphausiid *E. pacifica* dominated in terms of biomass (Fig. 6b). The euphausiid ingestion rate was 0.27 mg C m^{-3} day^{-1} and was dominated by the large euphausiid *E. pacifica*. The euphausiid egestion rate was 0.11 mg C m^{-3} day^{-1} and was also dominated by *E. pacifica* (Fig. 6c).

3.3. Faecal pellet abundance, mass, and size

The abundance of faecal pellets ranged from 67.7 to 1888.2 faecal pellets m^{-3} and was the highest at 0–100 m depths during the daytime (Fig. 7a). The faecal pellet mass was in the range 0.13–2.96 mg C m^{-3} and was also the highest at 0–100 m depths during the daytime (Fig. 7b).

The individual volume of faecal pellets was in the range 0.005–0.6 mm^3 (Fig. 8). Differences between day and night and the sampling depths showed that large faecal pellets (>0.2 mm^3) were observed in all sampling layers at night, whereas such faecal pellets were not observed during the day. Small faecal pellets (0.005–0.03 mm^3) were the most abundant in all depth layers during both day and night. No significant differences were detected for the faecal pellet volumes between layers or between day and night ($p > 0.05$, one-way ANOVA). Common peaks in faecal pellet volume (0.010–0.015 mm^3) were observed in all of the layers during both day and night (Fig. 8). The smallest faecal pellet width was 131 μm and the largest was 722 μm. The sinking rate estimated from the faecal pellet volume was 189–1885 m day^{-1}.

3.4. Microscopic observations of egested faecal pellets

Faecal pellets egested during the rearing experiment were observed and photographed using a fluorescence microscope (Fig. 9). The contents of the faecal pellets were cyanobacteria, eukaryotic phytoplankton, diatoms, tintinnids, and faecal pellets from other zooplankton (repacked).

The mean volume and contents of faecal pellets collected during the rearing experiments of four copepod species and one euphausiid species collected from the three depth layers at night are shown in Fig. 10. The mean faecal pellet volume was 0.006–0.015 mm^3. The number of cells such as cyanobacteria, eukaryotic phytoplankton, diatoms, and tintinnids per faecal pellet volume was in the range 3.38–16.0 $\times 10^3$ cells mm^{-3}. For all examined zooplankton species, the dominant taxa in the faecal pellets, as cells per faecal pellet volume, were cyanobacteria (26.3–65.2%). Heterotrophic flagellates were the second-most abundant taxa, with a composition ranging from 9.6 to 55.3%. The highest number of cells per volume was found at 0–100 m depths for all species. Repacking was found for the calanoid copepod *G. variabilis* C5M, C6F at depths of 500–1000 m.

3.5. Carbon mass stocks and fluxes within the plankton community

Table 2 shows the standing stocks (mg C m^{-2}) of microplankton, copepods, euphausiids, and faecal pellets in the 0–100 m water column of the southern Okhotsk Sea, as well as the fluxes (ingestion and egestion rates in mg C m^{-2} day^{-1}) by copepods and euphausiids. The standing stock of microplankton was calculated to be 1412 mg C m^{-2}. The ingestion rates of copepods and euphausiids were 266 mg C m^{-2} day^{-1} and 27.1 mg C m^{-2} day^{-1}, respectively. The ingestion rates of euphausiids were approximately 1/10th that of copepods. The daily ingestion by these zooplankton taxa corresponded to 21% of the standing stock of microplankton. The carbon stocks of faecal pellets at 0–100 m depths ranged from 105 to 296 mg C m^{-2}. In contrast, the egestion rates by copepods and euphausiids were 107 mg C m^{-2} day^{-1} and 10.9 mg C m^{-2} day^{-1}, respectively (totalling 118 mg C m^{-2} day^{-1}). The calculations based on the whole ranges of faecal pellets corresponded to 40–112% of the observed faecal pellet stocks.

4. Discussion

4.1. Methodology

In this study, we quantified microplankton, the day and night vertical distribution of copepods at 0–1000 m depths, macrozooplankton (euphausiid) abundance and biomass, the number and mass of faecal pellets, the ingredients in the faecal pellets that were obtained through rearing experiments, and fluxes within the plankton community in the southern Okhotsk Sea during the summer. Though this study surveyed most of the planktonic and abiotic (faecal pellet) particles in the water column, several considerations regarding the methodology were made in the study. These considerations included the following: (i) the location of the day and night samplings, (ii) the methods for estimating zooplankton ingestion and egestion rates, and (iii) the quantification methods of *in-situ* faecal pellets. These are discussed in detail in the following paragraphs.

Between the day and night sampling stations, temperature, salinity, and fluorescence were similar (Fig. 3). Intrusions of the Soya Warm Current, which is characterised by high salinity (>33.6), on the southern Okhotsk Sea have been reported (Takizawa, 1982; Sakai et al., 2008; Sato et al., 2008). However, such high salinity was not observed for the surface layers in this study, and dichothermal waters (<0 °C) were observed at a depth of 180–200 m at each station (Fig. 3). These observations suggest that at both stations, the water structure consisted of Okhotsk Sea surface water placed above dichothermal waters (Takizawa, 1982). This may be attributed to the seasonal occurrence of the Soya Warm Current in this region—the current begins in late August and rarely occurs in April–June (Yamaguchi, 1993). Thus, though day and night samples were collected from different stations in this study, this methodology is expected to have a minor effect on the results, and the

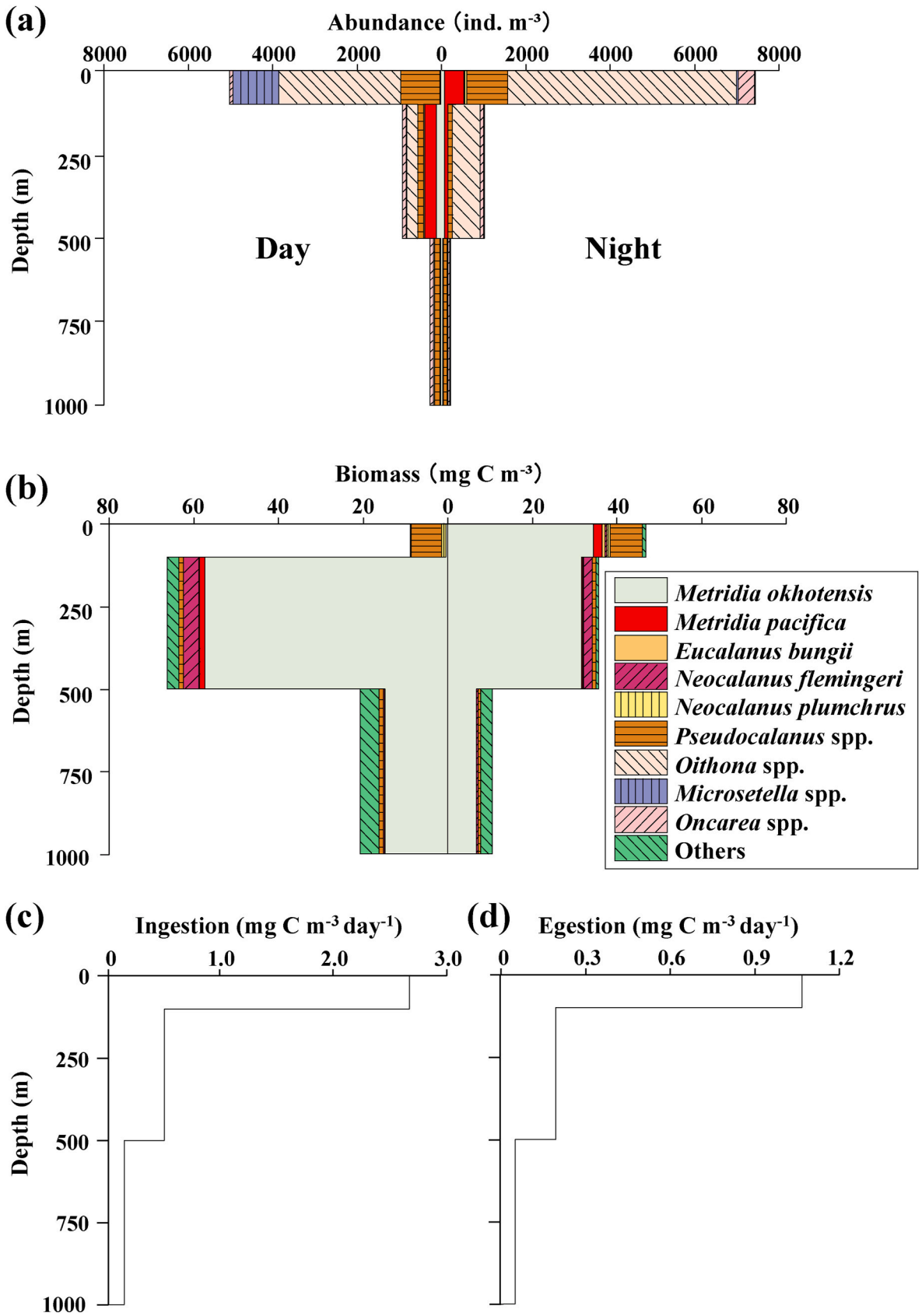

Fig. 5. Vertical changes in copepod abundance (a) and biomass (b) and their taxonomic contents in the southern Okhotsk Sea during the day and night of 29–30 June 2019. Ingestion (c) and egestion (d) were estimated for the night-time data by applying an empirical model for the respiration rate (Ikeda, 2014), with the habitat temperature and body weight as independent variables and the assumption of assimilation and net growth efficiencies (Steinberg et al., 2008). For details, see the text.

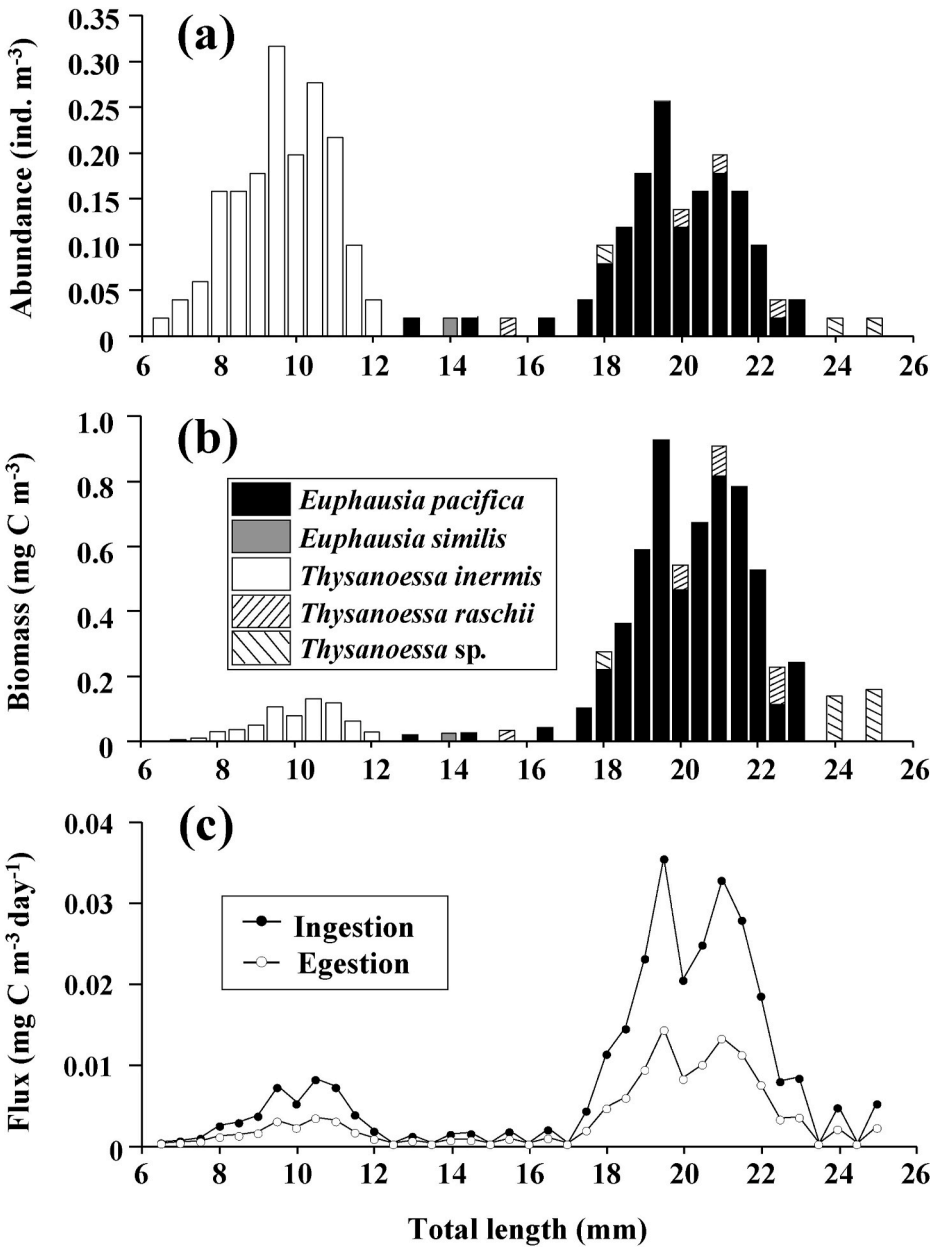

Fig. 6. Abundance (a) and biomass (b) of euphausiid species in relation to the total length of the horizontal tow of the Matsuda-Oozeki-Hu trawl (MOHT) at 50–70 m depths at St. D2 in the southern Okhotsk Sea during the night of 29 June 2019. Ingestion and egestion (c) were estimated for the night-time data by applying an empirical model for respiration rate (Ikeda, 2014) with habitat temperature and body weight as independent variables and the assumption of assimilation and net growth efficiencies (Steinberg et al., 2008). For details, see the text.

water samples can be assumed to have the same water mass conditions and biological settings.

In the present study, zooplankton ingestion and egestion rates were estimated using respiration rates (Ikeda, 2014). Some previous studies have applied a similar respiration rate by Ikeda (1985), but this method does not include depth as an independent variable (Steinberg et al., 2008). The differences in the outcomes of the two methods are at factors of 1.36–1.60 fold for deep layers (Kojima, unpublished data). This may be attributed to the fact that the independent variables in the respiration estimates included habitat depth (Ikeda, 2014). To estimate the physiological rates of deep-sea metazoans, selection of the applied empirical model that includes depth as an independent variable may be better for flux estimations targeting the deep layer, as shown in this study.

The first objective of this study was to quantify faecal pellets using fine-mesh (63 μm) plankton net samples (Figs. 7 and 8). In general, faecal pellets are collected by mooring of the DST (Trull et al., 2008; Wilson et al., 2008; Laurenceau-Cornec et al., 2015). Since the shape of the DST is cylindrical, the small-diameter collection mouth area is reported to be a problem (Emerson and Roff, 1987). Alternatively, the mass filtration method can be used. In this method, a large volume of seawater (200–1000 L) is collected at a given depth and then filtered through a 10–53 μm mesh filter for the quantitative collection of faecal pellets (Lomas and Moran, 2011; Stukel et al., 2011). Alternatively, a small amount of water (5–9.2 L) is also filtered through a 20–60 μm mesh net (Pasternak et al., 2000; Dagg et al., 2014). In this study, a large volume of seawater (19–108 m^3; which is a 2–540 times larger volume than that used in the mass filtration method) was filtered through fine mesh (63 μm) without clogging (Table 1).

The highest abundance of faecal pellets was observed for 0–100 m depths during the daytime. At this depth, the abundance of faecal pellets was comparable to that of copepods (Figs. 5 and 7). The collection of faecal pellets using a plankton net may result in the loss of pellets, as they can slip through the mesh (Tranter and Heron, 1967; Tranter and Smith, 1968; Smith et al., 1968). Moreover, this method can cause the physical destruction of faecal pellets (Omori and Ikeda, 1984). Despite such shortcomings, sufficient faecal pellets were collected using net meshes in the present study (Fig. 2a). The filtration efficiency of the VMPS ranged from 77.2 to 94.8% (mean ± standard deviation: 83.1 ±

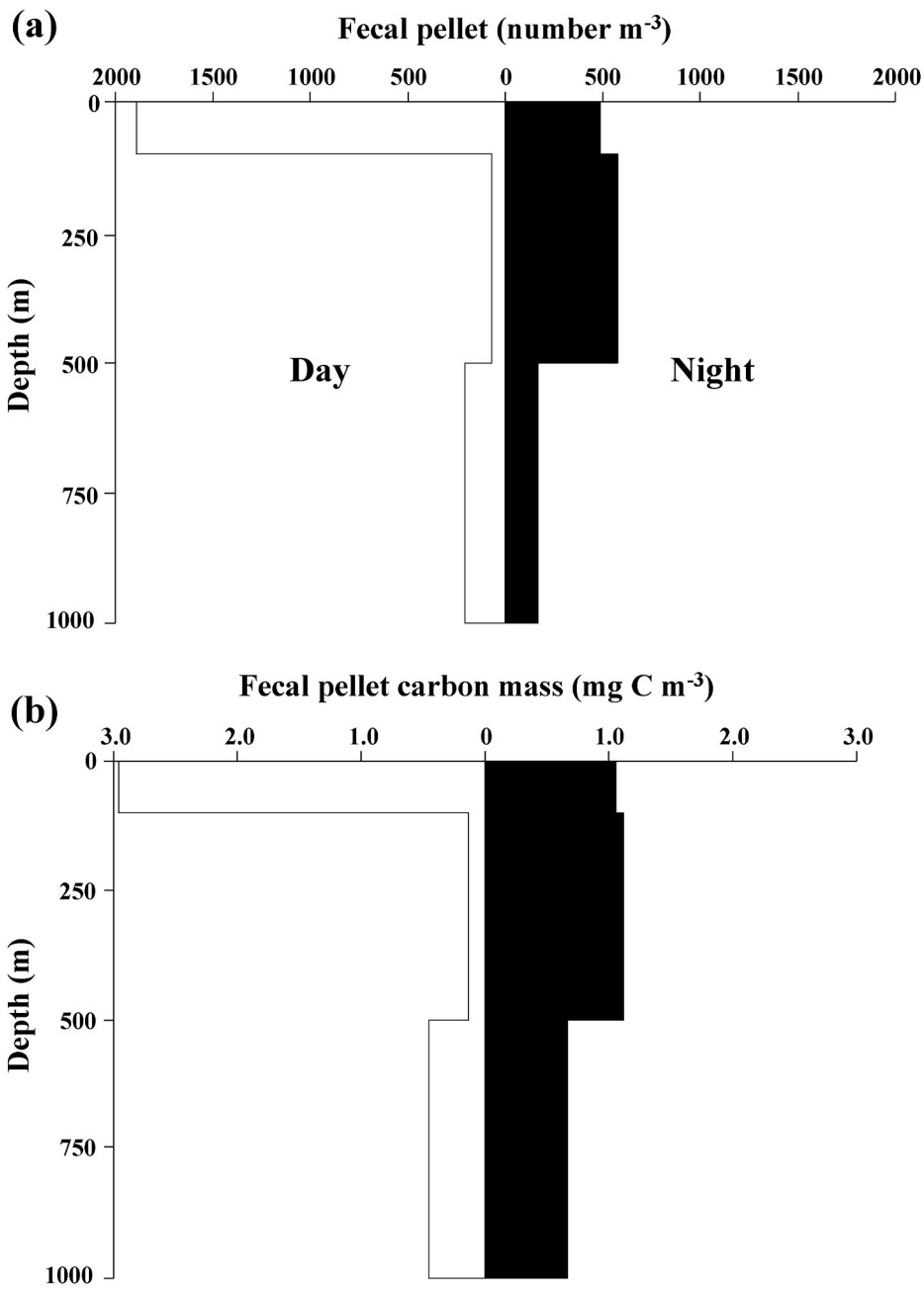

Fig. 7. Vertical changes in the faecal pellet number (a) and their carbon mass (b) during the day and night in the southern Okhotsk Sea during 29–30 June 2019.

6.6%), which was comparable to that of common quantitative collection nets (Omori and Ikeda, 1984). Because a large number of faecal pellets were collected, we were able to identify and conduct accurate size measurements of the faecal pellets through imaging analysis with Zoo-Scan (Fig. 2b–e). Hence, it was possible to calculate the day and night vertical distribution and to semi-quantitatively evaluate the faecal pellets based on the plankton samples. The observed faecal pellet volumes collected by fine-mesh nets in the field (peaked at 0.010–0.015 mm^3, Fig. 8) corresponded well with the pellets egested by various zooplankton species during on-board rearing (peaked at 0.010–0.015 mm^3, Fig. 10). The faecal pellet volumes quantified by the two methods showed no significant differences ($p > 0.05$, Mann-Whitney U test). This suggests that the underestimation of fragmented pellets smaller than the mesh openings might be minor. For quantitative evaluation or validation of faecal pellet collection by a fine mesh net, a comparison study on the collection of faecal pellets by two methods, namely DST and fine-mesh nets, is required in the future.

In conclusion, although some considerations are required, this study provides information on *in-situ* and laboratory-reared egested faecal pellets, the standing stocks of the whole plankton community (microplankton, mesozooplankton, and macrozooplankton), and the fluxes through meso- and macrozooplankton. The findings of this study are valuable and can be used to estimate the carbon budget in the pelagic zone of the southern Okhotsk Sea during summer.

4.2. Plankton community

Information on the microplankton in the southern Okhotsk Sea is limited to chlorophyll data. It has been reported that the chlorophyll density during the spring phytoplankton bloom (March–April) is above 2 mg Chl. a m^{-3} (Mustapha and Saitoh, 2008; Shimizu, 2009; Kasai et al., 2010). During June–August, the sub-surface maximum number of

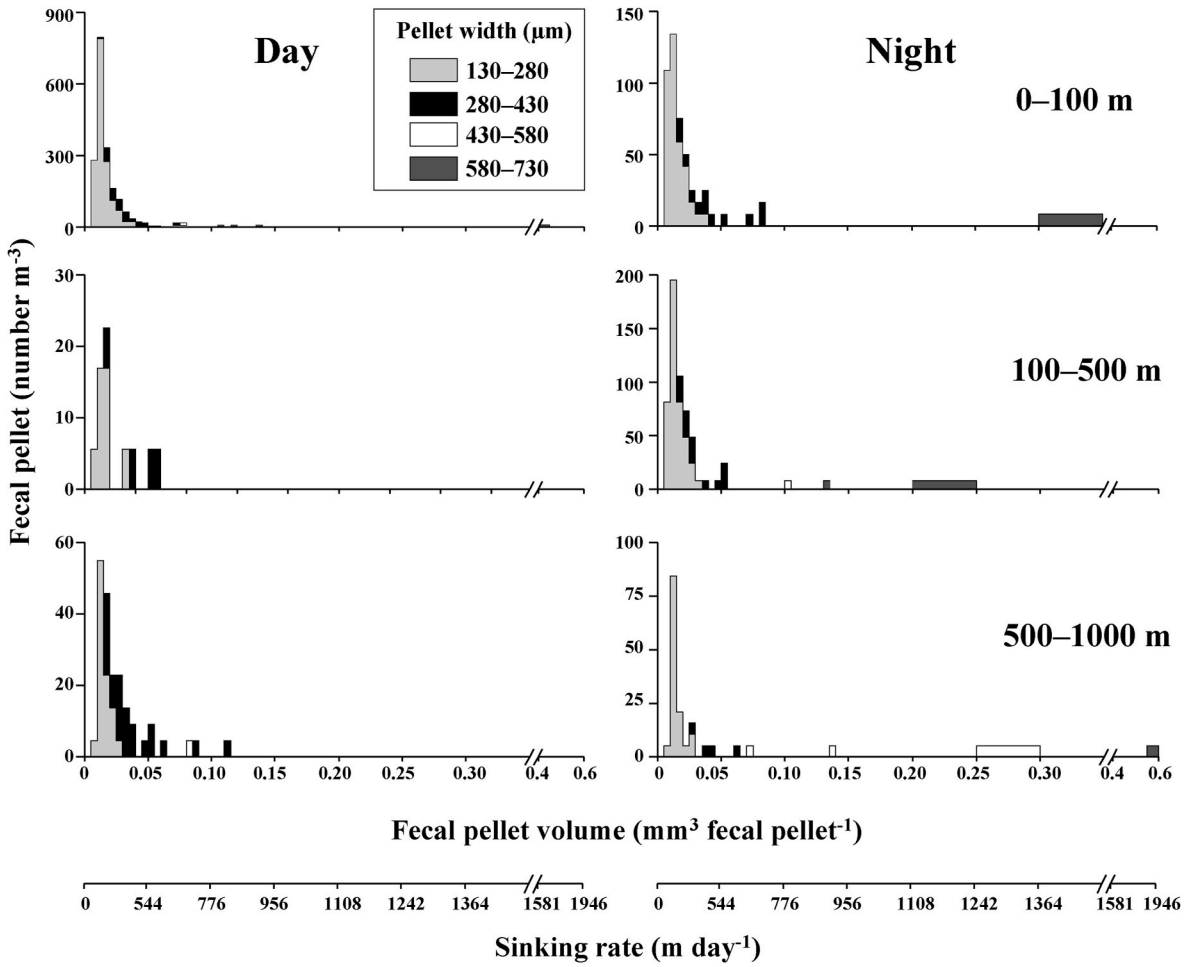

Fig. 8. Histograms showing the faecal pellet volume at each depth layer in the southern Okhotsk Sea during 29–30 June 2019. Differences in the histogram patterns represent pellet width (= minor axis of length). Based on faecal pellet volume, the sinking rate (m day^{-1}) was estimated using the empirical equation described by Small et al. (1979).

phytoplankton can be observed at a depth of approximately 20 m (Kasai et al., 2010), and the chlorophyll concentration is approximately 1 mg Chl. *a* m^{-3} (Mustapha and Saitoh, 2008; Shimizu, 2009). The surface water of the Okhotsk Sea is reported to contain a higher nutrient content and more Chl. *a* than that of the Soya Warm Current (Hamasaki et al., 1998). In the present study, the surface water of the Okhotsk Sea was dominant in the water mass and had a maximum concentration (1.7 mg m^{-3}) near the surface layer (20 m); these results corresponded well with those of previous reports (Fig. 3). Further, small-sized phytoplankton (<2 μm) contributed the most to overall primary productivity owing to the heavy grazing pressure of copepods on large-sized phytoplankton (Shiomoto, 2011). The three diatom species that were dominant at the study site (*C. socialis*, *C. affinis*, and *L. danicus*) are all cosmopolitan, and their dominance is well documented in various regions of the Northern Hemisphere (Marshall et al., 2005; Guo et al., 2014; Righetti et al., 2020). However, the dominance of dinoflagellates and ciliates, especially in biomass (Fig. 4b), has not been previously reported in the Okhotsk Sea. This might be a new finding of the present study.

Regarding mesozooplankton, it is well known that the zooplankton fauna during summer in the southern Okhotsk Sea are dominated by copepods and that *M. okhotensis* dominates the biomass (Yamaguchi, 2015; Arima et al., 2016; Hiragi and Yamaguchi, 2019). The present study reported that *M. okhotensis* dominated the copepod biomass during both the day and night (Fig. 5b), whereas cyclopoid copepod *Oithona* spp. were dominant with respect to abundance (Fig. 5a). *Oithona* spp. are omnivores that can consume a wide range of food items; they are dominant in the oceans worldwide (Turner, 2004). In the Okhotsk Sea, *Oithona similis* has four generations per year, with a peak spawning season during the spring phytoplankton bloom (Shebanova et al., 2011). The life cycle of *O. similis* may contribute to the numerical dominance of *Oithona* spp. during the post-phytoplankton bloom in June. However, the contribution of *Oithona* spp. to overall biomass was small due to its small body size. The large-sized calanoid copepod *M. okhotensis,* which is known to perform nocturnal ascent diel vertical migration (DVM) (Padmavati et al., 2004; Takahashi et al., 2009), dominated the biomass. The DVM behaviour of *M. okhotensis* was clearly observed in the present study (Fig. 5b). Small-sized calanoid copepod *Pseudocalanus* spp. are known to dwell on the surface layer during both daytime and night-time during early summer (Yamaguchi and Shiga, 1997); this habit allows *Pseudocalanus* spp. to dominate the biomass at depths of 0–100 m during the daytime. Furthermore, harpacticoid copepod *Microsetella* spp. were found to be abundant in the 0–100 m depth layer during the daytime (Fig. 5a). *Microsetella* species are known to feed on detritus and marine snow (Uye et al., 2002). Hence, the high density of *Microsetella* spp. in the 0–100 m layer during the daytime may be attributed to the high density of faecal pellets in this layer (Fig. 7). Dominance of *Microsetella* spp. has not previously been reported in the Okhotsk Sea, and it thus may be a new finding of this study.

Among the macrozooplankton fauna of the southern Okhotsk Sea, euphausiids, especially *E. pacifica*, are known to be abundant (Tomiyama et al., 2017). In south-eastern Hokkaido, the biomass of *E. pacifica* reaches 381–833 mg C m^{-2} (Taki, 2006; Kim et al., 2009). The

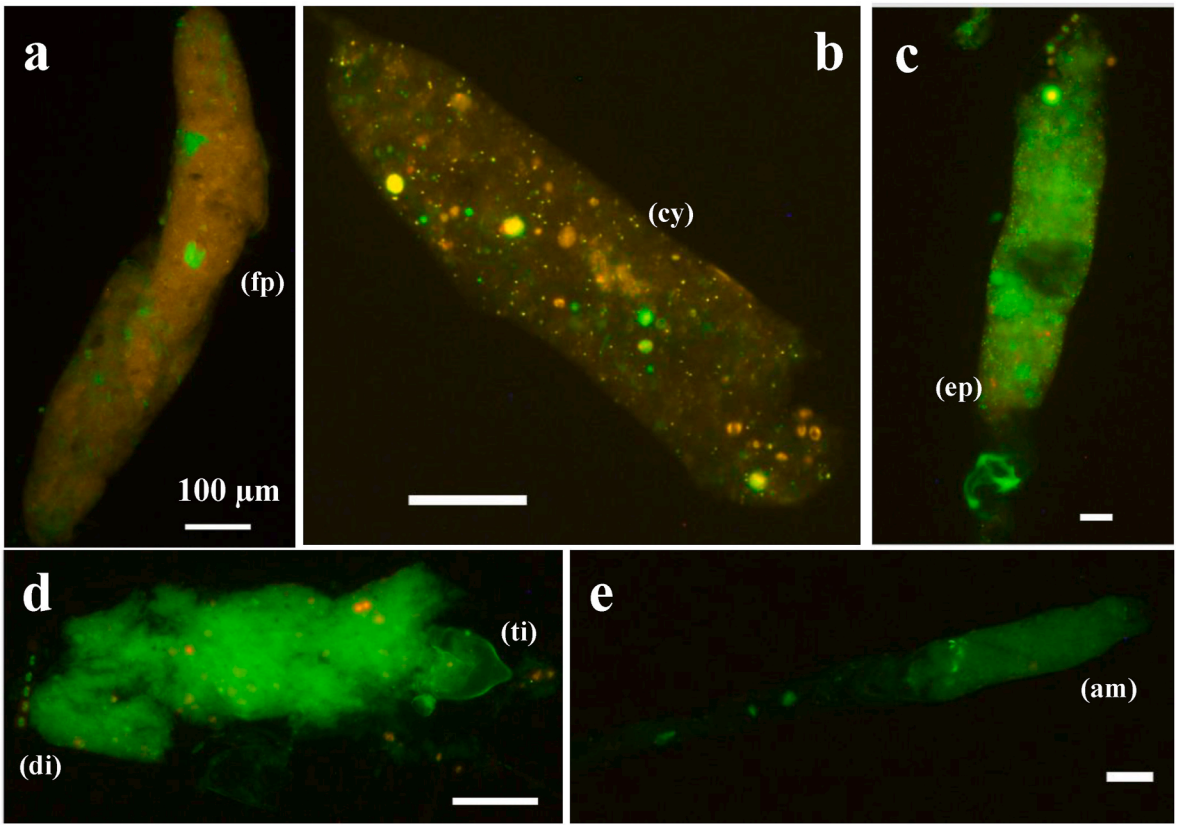

Fig. 9. Zooplankton faecal pellets as viewed under an epifluorescence microscope. (a) *Gaetanus variabilis* at 500–1000 m, (b) *Metridia okhotensis* at 0–100 m, (c) *Neocalanus plumchrus* at 0–100 m, (d) *Thysanoessa inermis* at 100–500 m, (e) *Neocalanus cristatus* at 100–500 m. (fp) faecal pellet, (cy) cyanobacteria, (ep) eukaryotic phytoplankton, (di) diatom, (ti) tintinnid lorica, (am) amorphous material. Scale bars are 100 µm.

standing stocks of euphausiids observed in the present study (726 mg C m^{-2}) corresponded well with previously reported values (Table 2). The small-sized euphausiid *T. inermis* (TL: 8–10 mm) and the large-sized *E. pacifica* (18–22 mm TL) were observed at the study sites (Fig. 6). The body sizes of *E. pacifica* corresponded with the maximum sizes of this species that have previously been reported in the adjacent Oyashio region (Kim et al., 2009), indicating that *E. pacifica* may have been in the reproduction phase during the study period. The daily growth rate of *T. inermis* along the weight base (0.0030) was similar to that of the sympatric *E. pacifica* (0.0025) in the Gulf of Alaska (Pinchuk and Hopcroft, 2007). The substantially different body sizes of the two dominant euphausiids (*E. pacifica* and *T. inermis*) in the southern Okhotsk Sea suggest that the timing of reproduction and life cycles varies among species in this region. As the $\delta^{15}N$ of euphausiids is higher than that of copepods in the southern Okhotsk Sea, euphausiids are expected to be more carnivorous than copepods (Gorbatenko et al., 2014). Furthermore, the presence of DVM is also characteristic of the euphausiids in this region (Mizukami et al., 2019).

4.3. Faecal pellets in the field

During net collection, any particles that are smaller than the diagonal distance of the mesh size are not collected (Tranter and Heron, 1967; Tranter and Smith, 1968; Smith et al., 1968). The diagonal distance of the 63-µm mesh in the VMPS used in the present study was 88.2 µm, and the smallest size of the collected faecal pellets was 131.2 µm (Fig. 8). Hence, it was assumed that particles with size <130 µm may not have been collected due to physical destruction during collection or the loss of small particles through the mesh. In contrast, faecal pellets with a width >130 µm were considered to be quantitatively collected.

The faecal pellet sizes collected using DST at 150–500 m depths during July–August at St. K2 in the adjacent western subarctic Pacific were reported to be 0.01–0.75 µg C $pellet^{-1}$ (see Fig. 4 in Wilson et al., 2008). Wilson et al. (2008) applied the carbon-to-volume conversion factor of 0.08 mg C mm^{-3}; using the same method, the above values are expressed as 0.000125–0.009375 mm^3 in volume. The equivalent spherical diameters of the faecal pellets collected at 60–200 m depths during July at St. K2 were reported to be 0.065–0.075 mm (see Fig. 5 in Kobari et al., 2016), which can be expressed in volume as 0.000144–0.000221 mm^3. The faecal pellets collected in the present study were larger (peaks, 0.010–0.015 mm^3) than the above-mentioned values (Fig. 8). This suggests that more large faecal particles can be collected using net towing methods than using the DST mooring method. As the two methods resulted in large differences in the faecal pellet volume, we suspect that the cause was the differences in the filtering volume of the two devices. Based on the mouth area of the DST cylinder (7.5–11 cm diameter; Valdes and Price, 2000) and the sinking velocity of the faecal pellets (−150 m day^{-1}; McDonnell and Buesseler, 2010), the observed volume of the DST per day can be estimated as 0.66–1.43 m^3. These values are much lower than the filtering volumes of the nets used in this study (19.3–108.2 m^3, Table 1). In addition to these differences in quantitative volume, the filtering by plankton net mesh (63 µm) used in this study may have caused inevitable fragmentation of small-sized faecal pellets. A combination of both effects (large quantitative volume and filtering through mesh) is considered to be a cause of the larger volume of the faecal pellets in this study than of those quantified by DST. In the future, quantitative evaluation or validation of faecal pellets using a combination of the two methods, DST and fine-mesh net collection, is needed.

For the faecal pellet volumes, log-log regressions are present from the zooplankton length (prosome or total length of copepods) (Uye and Kaname, 1994; Stamieszkin et al., 2015; Kobari et al., 2016). Using these

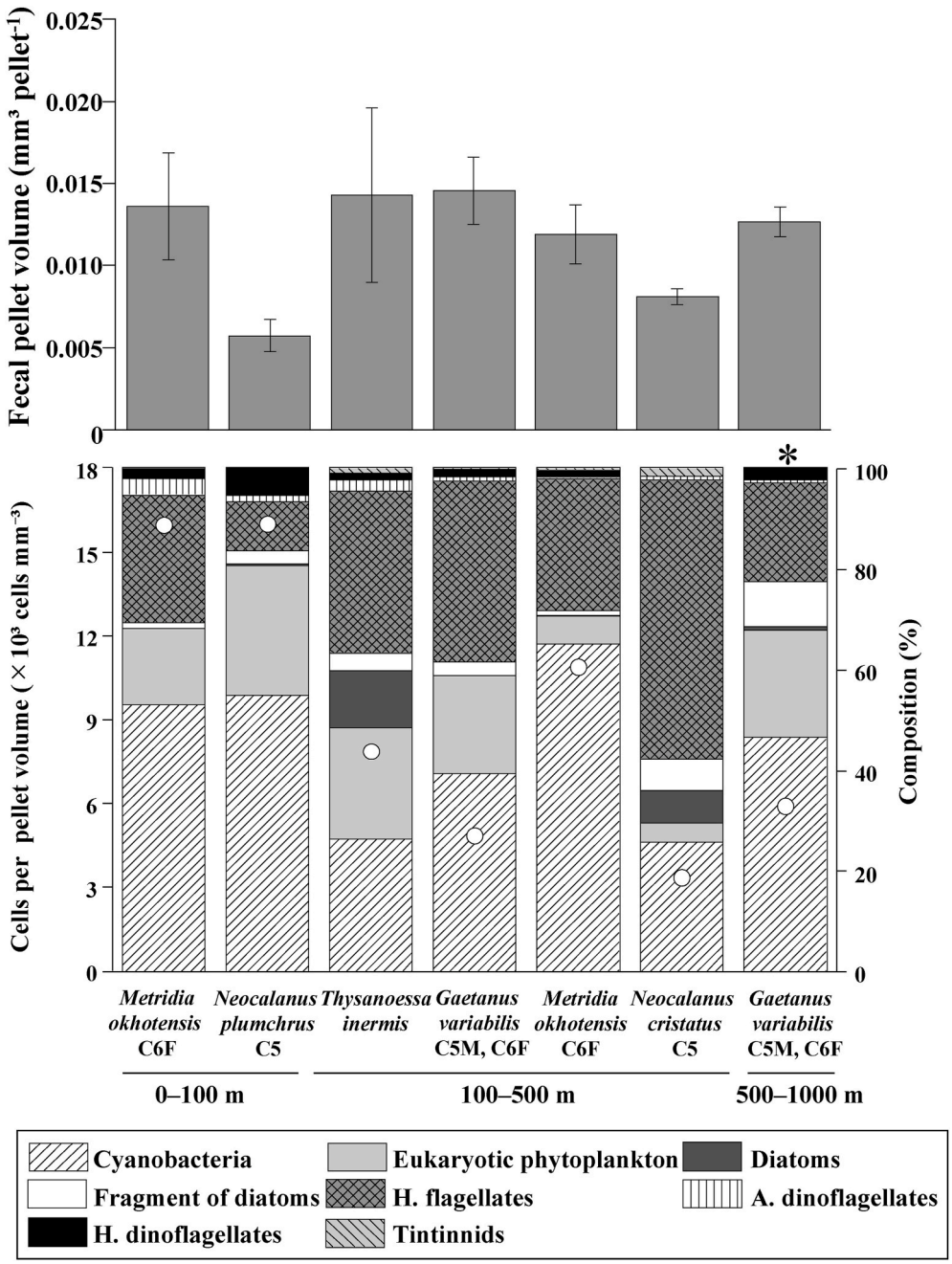

Fig. 10. Faecal pellet volume (upper) and the number and taxonomic composition of cells per faecal pellet volume (lower) egested by various zooplankton species based on on-board rearing experiments of specimens collected with a vertical multiple plankton sampler (VMPS) on the night of 29 June 2019. Bars in the upper panel represent standard errors. Asterisks denote that coprophagy was observed for the species.

Table 2
Comparison of the standing stock and fluxes (ingestion and egestion) in carbon units for the 0–100 m water column of the southern Okhotsk Sea during 29–30 June 2019. For details of each taxon and subject, see Fig. 4 (microplankton), 5 (copepods), 6 (euphausiids), and 7 (faecal pellets). Note that fluxes were estimated based on metabolic rates (Ikeda, 2014). (D): day, (N): night.

		Flux (mg C m^{-2} day^{-1})	
Taxa/subject	Standing stock (mg C m^{-2})	Ingestion	Egestion
Microplankton	1412		
Copepods	885 (D) - 4697 (N)	266	107
Euphausiids	726 (N)	27.1	10.9
Fecal pellet	105 (N) - 296 (D)		

regressions, the prosome lengths of copepods with egested faecal pellets with a volume of 0.010–0.015 mm^3 are estimated to be 4.2–4.3 mm. These values corresponded to those of *M. okhotensis* adult females, the predominant species in the mesozooplankton biomass in this study (Fig. 5b). The observed faecal pellet volumes from the net samples (0.010–0.015 mm^3) corresponded well with the faecal pellet volume egested by this species during the on-board laboratory rearing experiments (Fig. 10). These findings suggest that the faecal pellets observed in the present study net are not fragmented during the net collections.

The abundance of *M. okhotensis* in the 0–100 m layer during the night was found to be 33 ind. m^{-3} (Fig. 5b). For copepods, the daily egested faecal pellet number is 100–150 pellets $ind.^{-1}$ day^{-1} or 8–12 pellets $ind.^{-1}$ h^{-1} when feeding occurs only at night (Mauchline, 1998). As the night-time length during the study period was 8.52 h, the number of

faecal pellets egested by *M. okhotensis* at night was estimated to be 68–102 faecal pellets ind.$^{-1}$ (= [8 to 12] × 8.52). By multiplying the number of faecal pellets by the *M. okhotensis* abundance, the number of faecal pellets egested by *M. okhotensis* at 0–100 m depths during the night was found to be 2244–3366 faecal pellets m^{-3} (= 33 × [68 to 102]). The calculated values are 1.2–1.8 times higher than those for the observed faecal pellet density (1888 faecal pellets m^{-3}) in the 0–100 m layer during the daytime (Fig. 7). This discrepancy may be attributed to the loss of faecal pellets during net towing (Tranter and Heron, 1967; Tranter and Smith, 1968; Smith et al., 1968). Zooplankton feeding on the faecal pellets and the destruction of faecal pellets into small fragments may have also decreased the number of faecal pellets in field (Noji et al., 1991; Suzuki et al., 2003; Iversen and Poulsen, 2007). It should be noted that the faecal pellet density in the 0–100 m layer during the night (486 faecal pellet m^{-3}) was substantially lower than the estimated faecal pellet density during the daytime (Fig. 7).

The most prominent finding of this study was that the faecal pellet density at the surface layer during the daytime was much higher (four times) than that during the night (Fig. 7). In general, since DSTs are moored for a certain period (3–4 days) (Buesseler et al., 2007; Wilson et al., 2008; Kobari et al., 2016), it is difficult to evaluate the day/night differences of faecal pellets in the field. Therefore, the differences in the faecal pellet density during the day and night is a novel finding of the present study. Large-sized taxa with high swimming abilities, such as the copepod *M. okhotensis* and two euphausiid species, were abundant at night, whereas the small-sized copepods such as *Oithona* spp., *Microsetella* spp., and *Pseudocalanus* spp. were dominant during the daytime. The genera *Oithona* and *Microsetella* have been reported to attach to detritus and perform coprophagy or coprorhexy (Turner, 2002; Uye et al., 2002; Suzuki et al., 2003; Iversen and Poulsen, 2007). However, as they feed mainly on small-sized faecal pellets, large-sized faecal pellets (0.010–0.015 mm^3) may not be consumed during the daytime (Fig. 2) (Turner, 2004; Reigstad et al., 2005).

The sinking velocity of faecal pellets is correlated with their size and density; it exceeds 1000 m day^{-1} for large-sized faecal pellets (e.g. those of Salpida) (Paffenhöfer and Knowles, 1979; Small et al., 1979; Uye and Kaname, 1994; Trull et al., 2008). In the present study, the sinking velocities of the observed faecal pellets were estimated to be faster than 100 m day^{-1} (Fig. 8). This suggests that large-sized faecal pellets egested by *M. okhotensis* at 0–100 m depths rapidly sink to deep layers without being affected by coprophagy or coprorhexy by small copepods. Furthermore, bacterial decomposition can also result in the fragmentation of faecal pellets, but it takes 25 days for pellets to decompose (Cherry et al., 1978; Emerson and Roff, 1987; Turner, 2015).

Coprorhexy of faecal pellets may have been substantial at the cod end of the surface samples, where the large-sized zooplankton with high swimming ability were abundant at night. However, the effect of coprorhexy may have been minimal for the surface layer at daytime because of the lack of large-sized zooplankton taxa with high swimming ability in the sample. This could have caused the high density of faecal pellets at 0–100 m depths during the daytime, but this does not seem to be the case for the present study, as extremely large faecal pellets (>0.20 mm^3) were collected throughout the layer at night (Fig. 8). These large faecal pellets were clearly larger than those of the copepod *M. okhotensis* and the euphausiid *T. inermis* observed during the laboratory rearing experiments. This result suggests that such large-sized faecal pellets are egested by the large-sized euphausiid *E. pacifica* (Figs. 6 and 10). Such large-sized faecal pellets are expected to be more vulnerable to coprorhexy by large-sized zooplankton with high swimming ability. The presence of large-sized pellets at night suggests that coprorhexy by large-sized zooplankton with high swimming ability at the cod end may be minor. However, if coprorhexy was present, the faecal pellets affected by coprophagy and coprorhexy may have become fragmented because the sizes of the faecal pellets (peaked at 0.010–0.015 mm^3) were near the end of the collection limits of the applied mesh size (63 μm), which would have made it difficult to collect the faecal pellets using the plankton net method applied in this study. The sinking velocity of large faecal pellets observed only at night was estimated to be > 1000 m day^{-1} (Fig. 8). Hence, these large faecal pellets may not have been collected during the daytime in the present study.

The presence of a nocturnal active diel feeding rhythm without DVM has been reported for the dominant large-sized copepods *Gaetanus* spp. and *M. okhotensis* in the subarctic Pacific (Takahashi et al., 2008; Abe et al., 2012). These diel zooplankton feeding rhythms suggest that the change in faecal pellet egestion must also follow a diel pattern. In the present study, vertical stratified vertical tows of the fine-mesh plankton nets were used to filter large volumes of water. Consequently, day/night density and vertical distribution of faecal pellets were evaluated in the field. Hence, this new method can be used in future studies to evaluate the quantity of faecal pellets in the field.

4.4. Microscopic observation of faecal pellets

In this study, the constituents of faecal pellets that were egested by zooplankton during the on-board laboratory rearing experiments were examined and expressed as the number of cells per faecal pellet volume. In similar studies, items obtained from the hindgut digestive tracts of copepods were quantified (Arashkevich, 1969; Harding, 1974; Wilson and Steinberg, 2010; Abe et al., 2012). In these studies, only organisms with hard shells could be identified to the species level if formalin was used for preservation. In contrast, if the collected specimens were immediately frozen in liquid nitrogen and then thawed under cool and dark conditions, observations under a fluorescence microscope showed that the faecal pellets contained many pico-sized cyanobacteria cells that could not have been directly consumed by copepods; this is explained by the feeding of copepods on detritus aggregates (Wilson and Steinberg, 2010). In the present study, zooplankton individuals were reared under cold and dark conditions, and faecal pellets were preserved using 1% glutaraldehyde stored dark and cool conditions until microscopic observation. This allowed us to examine the faecal pellet samples in good condition, meaning that the cell-containing pigments could also be observed.

The presence of viable phytoplankton (diatoms and dinoflagellates) in the faecal pellets of copepods is well known (Fowler and Fisher, 1983; Maneiro et al., 2002; Kuwata and Tsuda, 2005). In fact, the low assimilation efficiency of copepods when diatoms are consumed (e.g., 45% in *Thalassiosira nordenskioeldii*; Abe et al., 2013) indicates that phytoplankton cells are not fully digested when passed through the digestive tract. In the present study, cyanobacteria were the most common taxa that contained the highest number of cells per faecal pellet volume compared to all other zooplankton species (Fig. 10). This indicates that the sinking of zooplankton faecal pellets is an efficient pathway for the vertical transport of phytoplankton cells from the surface layer to the deep sea, and they are also an important food source for deep-sea organisms (Trull et al., 2008; Wilson et al., 2008; Wilson and Steinberg, 2010).

According to Wilson and Steinberg (2010), the number of phytoplankton cells contained in the copepod digestive tract was higher at the near-surface layer at night at St. K2 in the western subarctic Pacific. This was assumed to be a reflection of the high feeding activity that occurred at night and the high number of phytoplankton cells in the near-surface layer. In the present study, the highest number of cells per faecal pellet volume was also observed at the surface layer (0–100 m) for all species (Fig. 10). This suggests that the surface-dwelling specimens may have fed on fresh phytoplankton cells. In addition to common cyanobacteria and heterotrophic flagellates, microplankton such as diatoms and tintinnid loricae were found in the zooplankton faecal pellets. These results corresponded well with those of previous reports, and they may reflect the feeding modes of different species (Arashkevich, 1969; Wilson and Steinberg, 2010; Abe et al., 2012). It was observed that *G. variabilis* fed on faecal pellets (coprophagy) at 500–1000 m depths (Fig. 9a). The family Aetideidae, which includes *Gaetanus*, is reported to be

mesopelagic and has been observed to feed on sinking particles from the overlying layer (Yamaguchi et al., 2007; Abe et al., 2012). Concerning coprophagy, most information is derived from indirect counting under laboratory rearing. Therefore, direct evidence of coprophagy is lacking. However, the findings of the present study provide direct evidence of coprophagy by *G. variabilis*.

4.5. Carbon mass fluxes within the planktonic community

Information on standing stocks, taxonomic accounts, and fluxes via the planktonic community in the Okhotsk Sea (i.e. this study) and at St. K2 in the subarctic Pacific (Kobari et al., 2008, 2016; Wilson et al., 2008) are summarised in Table 3. The primary productivity in the western subarctic Pacific is reported to be 315–592 mg C m^{-2} day^{-1} (Wilson et al., 2008; Takahashi et al., 2009; Kobari et al., 2016). In the present study, primary productivity was not measured, but the microplankton biomass was quantified as 1412 mg C m^{-2} (Table 2). Although the standing stock varies with phytoplankton production, zooplankton grazing, sinking, and phytoplankton death, the values calculated in the present study are consistent with values obtained in the adjacent western subarctic Pacific (Boyd et al., 2008).

The standing stocks and ingestion rates of copepods at St. K2 in the western subarctic Pacific during July–August are 1733–3370 mg C m^{-2} and 192–367 mg C m^{-2} day^{-1}, respectively (Kobari et al., 2008, 2016). The results of the present study [standing stocks were 885 (day)–4697 (night) mg C m^{-2} and the ingestion rate was 266 mg C m^{-2} day^{-1}] correspond well with previously reported values (Table 3). These findings suggest that the observed standing stocks and ingestion rates of copepods in the present study are typical for the southern Okhotsk Sea and western subarctic Pacific during summer.

However, the taxonomic composition of the copepod community varies greatly between these regions. Large copepod *Neocalanus* spp. are dominant at St. K2 in the western subarctic Pacific (Kobari et al., 2008), and *M. okhotensis* dominates the southern Okhotsk Sea; these are special characteristics of this region (Fig. 5b) (Yamaguchi, 2015; Arima et al., 2016; Hiragi and Yamaguchi, 2019). As *M. okhotensis* follows a clear DVM pattern, the active flux due to DVM (respiration and death at deep layers during the daytime) has been reported to be large (Takahashi et al., 2009). The most prominent differences in the plankton stocks between the Okhotsk Sea and St. K2 were regarding the diel migrant biomass. That of the former (3812 mg C m^{-2}) was approximately three times larger than that of the latter (1100 mg C m^{-2}) (Table 3). While this discrepancy is available for the migrant biomass, it is interesting that the copepod ingestion (266 and 192–367 mg C m^{-2} day^{-1}) and egestion (107 and 77–147 mg C m^{-2} day^{-1}) at each region were at the similar value (Table 3). It may due to the regional differences in the body sizes of the dominant copepods at each region. Thus, the body size of *M. okhotensis* dominated in the Okhostk Sea is much smaller than those of *Neocalanus* spp. dominated at K2 in the western subarctic Pacific. Thus, while the migrant biomass was varied with region, the taxonomic accounts of the migrant biomass may determine the quantity of the ingestion and egestion rates from the upper layer. In the future, it is important to estimate the active flux that occurs due to the DVM of *M. okhotensis* in the southern Okhotsk Sea. Moreover, little information is available on standing stocks and ingestion rates of macrozooplankton (euphausiids) in this region. Studies at St. K2 have not adequately considered such macrozooplankton. Therefore, more research is needed on the standing stocks and fluxes associated with macrozooplankton; midwater trawling (MOHT) combined with acoustic surveys can be used for this purpose (Mizukami et al., 2019).

Table 3
Regional comparison on standing stocks and fluxes of copepods in the 0–100 m layer of the Okhotsk Sea (this study) and in the 0–150 m layer at St. K2 in the western subarctic Pacific. Data for St. K2 are from Kobari et al. (2008, 2016) and Wilson et al. (2008).

Parameters	Okhotsk Sea	K2
	(0–100 m)	(0–150 m)
Standing stock (mg C m^{-2})		
Copepods	885-4697	1733–3370
Diel migrants	3812	1100
Dominant copepod species	*Metridia okhotensis*	*Neocalanus* spp.
Flux (mg C m^{-2} day^{-1})		
Primary production	–	315–592
Copepod ingestion	266	192–367
Copepod egestion	107	77–147

Faecal pellet fluxes in the western North Pacific (mainly from the subarctic region) are 7–28.5 mg C m^{-2} day^{-1} at 50–150 m depths (Taguchi and Saino, 1998; Wilson et al., 2008; Takahashi et al., 2009; Kobari et al., 2016). Although this study only considered the standing stock of faecal pellets, the above-mentioned daily fluxes corresponded with 2.4–27.1% of the carbon mass of faecal pellets (105–296 mg C m^{-2}) at 0–100 m depths in this study (Table 2). This suggests that a great portion of the faecal pellets were disintegrated (consumed, destroyed, or decomposed) in the 0–100 m portion of the surface layer. In contrast, a previous study has reported that most (82%) of the faecal pellets egested by large copepods and euphausiids are disintegrated in the euphotic layer (Ayukai and Hattori, 1992). Additionally, the faecal pellet density can also decrease due to coprophagy during pellet sedimentation (Suzuki et al., 2003; Kobari et al., 2016). Thus, most of the faecal pellets egested in the near-surface layer may be consumed by other zooplankton and decomposed within the near-surface layer (Urban-Rich et al., 1999; Maar et al., 2004). Furthermore, faecal pellets can be destroyed by the swimming behaviour of zooplankton, which can break the pellets into small particles (coprorhexy) (Suzuki et al., 2003; Iversen and Poulsen, 2007). Through the destruction of faecal pellets into small particles, their sinking velocity is reduced by more than 50%, and their decomposition is enhanced (Noji et al., 1991; Poulsen and Kiørboe, 2005; Iversen and Poulsen, 2007). The resulting small organic particles can then be consumed by various zooplankton (Paffenhöfer and Knowles, 1979; Poulsen and Kiørboe, 2005). Thus, the intensity of coprophagy, as observed for *G. variabilis* in this study, may be a key factor for determining the vertical material flux via faecal pellets in the ocean.

5. Conclusion

To evaluate differences in the stocks and vertical distribution of faecal pellets between daytime and night-time, we conducted imaging analysis using ZooScan on faecal pellets collected by a VMPS equipped with fine mesh (63 μm) through three depth layers between 0 and 1000 m in the southern Okhotsk Sea. Additionally, observations of the whole plankton community, ranging from microplankton to meso- and macrozooplankton, as well as direct observations of the faecal pellets egested during on-board laboratory rearing were made. The faecal pellets showed diel changes, and both their numbers and carbon mass were high in the daytime; in contrast, only large-sized faecal pellets (>0.20 mm^3) were observed at night. Based on empirical equations that considered faecal pellet volumes and zooplankton body sizes, the most common faecal pellets observed (approximately 0.010–0.015 mm^3) were considered to be egested by the dominant copepod *M. okhotensis*; this was confirmed by independent laboratory rearing experiments. The standing stocks of faecal pellets at the surface layer (0–100 m) were clearly higher than the faecal pellet fluxes reported for the adjacent western subarctic Pacific. These facts suggest that most of the faecal pellets disintegrated in the surface layer before sinking. Since large-sized faecal pellets were only observed at night, they may be transported to a deeper layer (>1000 m) within a day, which would correspond with their estimated sinking velocity. Through the laboratory rearing experiment, direct evidence of coprophagy was observed for the mesopelagic copepod *G. variabilis*. This suggests that sinking faecal pellets may be important food items for deep-sea organisms. To collect faecal pellets, two main quantitative methods are available: DST moorings and large-

volume (200–1000 L) filtration with fine mesh (0–60 μm). The filtration volume of VMPS is 2–540 times larger than that of the large-volume filtration method, and the mesh size of the net is as fine as 63 μm. Although losses through the mesh and destruction of the faecal pellets during net sampling are inevitable, gently towing fine-mesh and non-filtered cod ends may allow us to quasi-quantitatively collect faecal pellets, as demonstrated in this study. Applying imaging analysis (Zoo-Scan) allows us to easily identify faecal pellets and obtain accurate size measurements. To evaluate the differences of faecal pellets between day and night in the field, the combination of the vertical towing of fine mesh equipped non-filtered cod ends and imaging analyses on the collected samples may be a new method that can be utilised in the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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