ORIGINAL ARTICLE

Vertical changes in abundance, biomass and community structure of pelagic polychaetes down to 1000 m depths at Station K2 in the western subarctic Pacific Ocean covering the four seasons and day–night

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Pelagic polychaetes are distributed from the sea surface to greater depths of the oceans worldwide, but little information is available regarding their ecology. This study investigated the vertical distribution of abundance, biomass and community structure of pelagic polychaetes at a single station in the western subarctic Pacific based on day–night vertical stratified samples collected from a 0 to 1000 m water column during four seasons covering 1 year. The polychaete abundance and biomass ranged from 0 to 757 ind. 1000 m^{-3} and 0–6.1 mg WW m^{-3}, respectively. Ten pelagic polychaete species belonging to nine genera and six families were identified. From cluster analysis based on abundance, the polychaete community was divided into five communities. Each community occurred at different depth layers. Two surface groups seen at 0–200 m were dominated by two carnivorous species: *Tomopteris septentrionalis* and *Typhloscolex muelleri*. The deepest group, dominated by the particle feeder *Pelagobia longicirrata*, was seen at 500–1000 m. Two transition groups occurred in the intermediate depths. These vertical distributions of the pelagic polychaete

communities were common throughout the season and day. Water mass, food availability and the oxygen minimum layer are put forth as environmental factors that affect the pelagic polychaete community.

INTRODUCTION

Pelagic polychaetes are known to be distributed from the sea surface to the deep sea in the oceans worldwide (Ushakov 1974; Halanych *et al.* 2007). The feeding modes of pelagic polychaetes vary with species, including herbivores (Day 1967; Hopkins and Torres 1989) and carnivores (Lebour 1922; Rakusa-Suszczewski 1968; Feigenbaum 1979). For feeding modes of the cosmopolitan pelagic polychaete family (Typhloscolecidae), the presence of specialized prey–predator linkages in carnivorous zooplankton taxa (chaetognaths) is reported in oceans globally (Feigenbaum 1979; Øresland and Pleijel 1991; Øresland and Bray 2005). The numerically dominant species of pelagic polychaetes [*Pelagobia longicirrata (P. longicirrata)*] is an important prey of various pelagic organisms, including copepods, chaetognaths and fishes (Hopkins 1985, 1987; Hopkins and Torres 1989; Øresland 1990). The pelagic polychaete species dominating the mesopelagic layer (*Poeobius meseres*) are known to feed on sinking particles by extending a mucus web (Uttal and Buck 1996; Robison *et al.* 2010) and have an important role in determining the amount of vertical material flux (Christiansen *et al.* 2018). These facts indicate that pelagic polychaetes may have important roles in marine ecosystems for both the food web and vertical material flux of oceans worldwide.

Concerning the ecology of pelagic polychaetes, horizontal distributions (Fernández-Álamo 1991, 2006; Fernández-Álamo *et al.* 2003) and seasonal changes (Peter 1975; Batistić *et al.* 2004, 2007) of the community structure have been reported. Some pelagic polychaetes are known to have bioluminescence ability (Francis *et al.* 2016; Gouveneaux *et al.* 2017, 2018) and feed on sinking particles via the deployment of a mucus web and tentacles (Uttal and Buck 1996; Robison *et al.* 2010; Christiansen *et al.* 2018). Bioluminescence and feeding on sinking particles are considered to be adaptations of zooplankton for deep-sea environments (Vinogradov 1968; Haddock *et al.* 2010).

From the viewpoint of the deep-sea adaptation of pelagic polychaetes, information on their vertical distribution is important. However, little information is available on the vertical distribution of pelagic polychaetes. Although several studies have investigated vertical distributions of pelagic polychaetes down to greater depths (∼1000 m) in the Scotia Front (Siciński 1988), the Strait of Magellan (Guglielmo *et al.* 2014) and the South Adriatic Sea (Guglielmo *et al.* 2019), these studies are based on only one cruise (limited season), and no diel differences have been identified. Thus, it remains unknown whether the pelagic polychaete community structure varies with depth, showing seasonal and diel changes.

Regionally, information on pelagic polychaete ecology is scarce for the western subarctic Pacific, although they have been reported to occur throughout the year (Kitamura *et al.* 2016; Amei *et al.* 2020). Regarding the physical oceanographic characteristics of the western subarctic Pacific, the presence of cold dichothermal water (DTW) (Dodimead *et al.* 1963; Miura *et al.* 2002) and warm mesothermal water (MTW) (Dodimead *et al.* 1963; Ueno and Yasuda 2000, 2005) is prominent. DTW (1–3°C) is observed at 100–120 m in the western subarctic Pacific. This water is derived from the Bering Sea, where water is cooled by winter mixing and transported into the western subarctic Pacific through the East Kamchatka Current (Dodimead *et al.* 1963; Miura *et al.* 2002). MTW (3–4°C) is observed at 200–400 m in the western subarctic Pacific and is suggested to originate from the mixed water region between the subarctic and subtropical areas (Ueno and Yasuda 2000). The water in the mixed water region is transported to the Gulf of Alaska and the Bering Sea, then into the western subarctic Pacific through the East Kamchatka Current (Dodimead *et al.* 1963; Ueno and Yasuda 2000, 2005). These complex physical oceanographic conditions may affect the pelagic polychaete community, but no information is currently available.

In the western subarctic gyre of the North Pacific, a time-series observation station, Station K2, was set from 1999 to the present (cf. Wakita *et al.* 2016). The observations at St. K2 were mainly made by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), and various international programmes, such as VERTIGO (Buesseler *et al.* 2007; Steinberg *et al.* 2008a) and K2/S1 (Honda *et al.* 2016, 2017), were conducted. Through such research programmes, various biological aspects, such as primary productivity (Elskens *et al.* 2008; Matsumoto *et al.* 2014, 2016), phytoplankton (Boyd *et al.* 2008; Fujiki *et al.* 2014), archaea (Kaneko *et al.* 2016), zooplankton community (Steinberg *et al.* 2008b; Kitamura *et al.* 2016; Kobari *et al.* 2016), quantification of zooplankton egested fecal pellets (Wilson *et al.* 2008; Wilson and Steinberg 2010), sinking organic material flux (Honda *et al.* 2016,
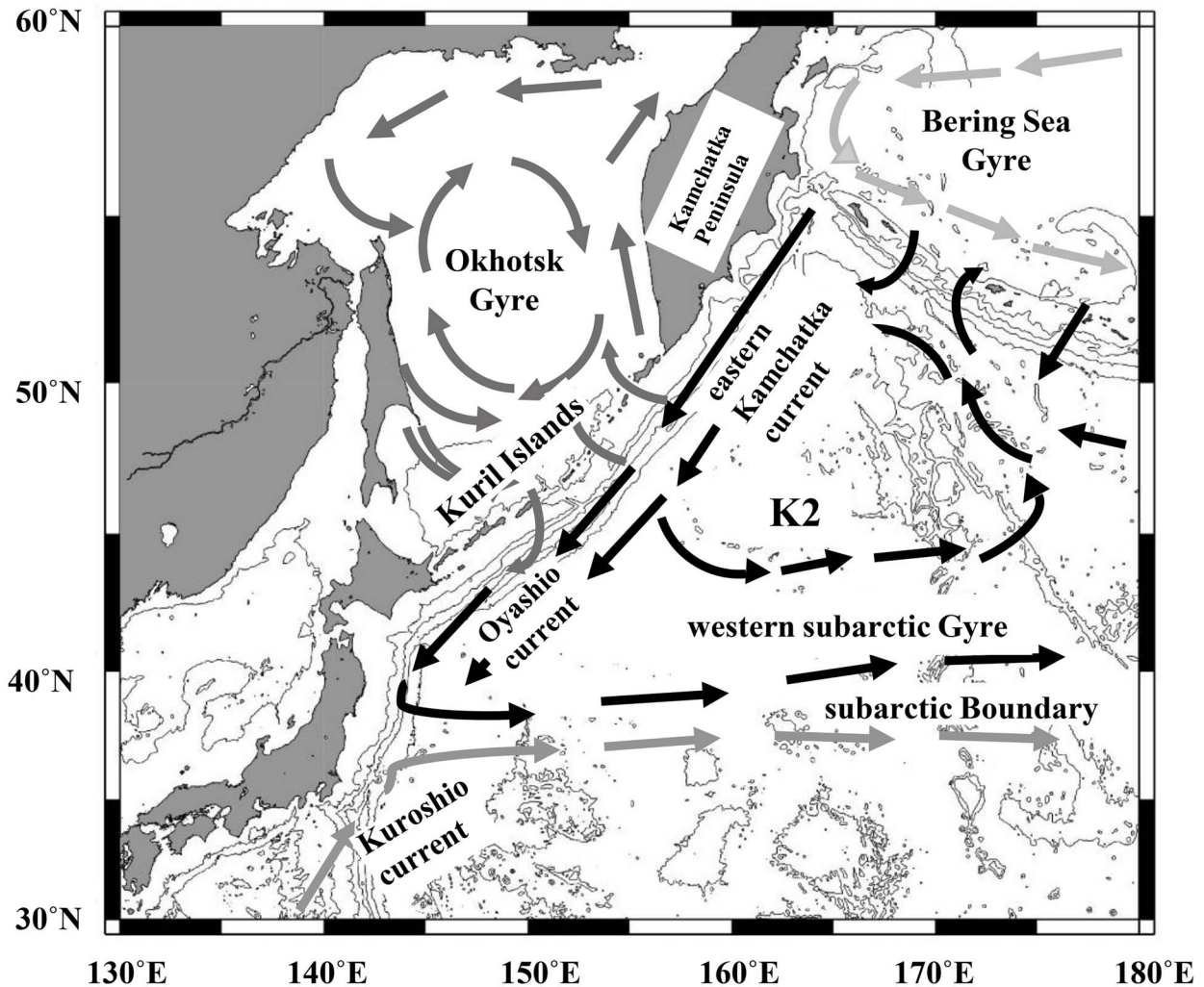
Fig. 1. Location of sampling station (K2) at the centre of the western subarctic gyre in the Pacific Ocean. Depth contours (1000, 3000 and 6000 m) and approximate positions of the currents (Okazaki *et al.* 2005) are superimposed.

2017 and references therein), biological pump estimation (Steinberg *et al.* 2008a; Wakita *et al.* 2016) and biological pump modelling (Bianchi *et al.* 2013), have been reported. Based on long-term observation data, the presence of the ocean acidification trend has also been reported (Wakita *et al.* 2017). Although this information is valuable, comparable data are not available for the pelagic polychaetes at St. K2.

This study revealed diel, seasonal and vertical changes in pelagic polychaete community structure based on day–night vertical stratification samples collected from a 0 to 1000 m water column at St. K2 in the western subarctic Pacific during four seasons covering 1 year. The pelagic polychaete abundance, biomass and community structure results were compared with the complex physical oceanographic conditions of the station. The results were also compared with the results of previous studies on

pelagic polychaetes conducted down to greater depths in oceans worldwide, as mentioned above (Siciński 1988; Guglielmo *et al.* 2014, 2019). Through this comparison, we aimed to evaluate the factors that determine the vertical distribution and community structure of pelagic polychaetes down to greater depths.

MATERIALS AND METHODS

Zooplankton samples were collected by day and night vertical stratified sampling from eight layers (0–50, 50–100, 100–150, 150–200, 200–300, 300–500, 500–750, 750–1000 m) by oblique towing of the Intelligent Operative Net Sampling System (IONESS, SEA Corporation) (mesh size: 335 μm; mouth area: 1.5 m²) at Station K2 (47°00′N, 160°00′E, bottom depth: 5200 m, Fig. 1) in

Table I: Zooplankton samplings (eight vertical stratification samplings between 0 and 1000 m) at St. K2 in the western subarctic Pacific from October 2010 to July 2011. D: day, N: night

Sampling date	Local time	D/N
29 Oct. 2010	12:09–13:52	D
29 Oct. 2010	22:09–23:38	N
26 Feb. 2011	12:35–14:41	D
26 Feb. 2011	22:01–23:44	N
22 Apr. 2011	21:59–23:56	N
23 Apr. 2011	12:45–14:37	D
3 July 2011	12:05–13:55	D
3–4 July 2011	22:51–0:55	N

the western subarctic Pacific on 29 October 2010, 26 February, 22–23 April and 3–4 July 2011 (Table I). The depths and volumes of the filtered water (m³) of the nets were monitored on deck. Data on filtered volume are available from the Supplementary Material. Collected samples were preserved by adding 4% (v/v) borax-buffered formalin. Temperature, salinity, dissolved oxygen (DO) and fluorescence were measured by CTD (SBE 911 plus; Sea-Bird Scientific) at each sampling occasion. For details about samplings, see Kitamura *et al.* (2016).

Based on temperature and salinity, water masses were identified for each depth and sampling date. We classified five water masses, seasonal pycnocline water (SPW), DTW, transition water (TW), MTW and deep water (DW), from the T–S characteristics at each sampling layer (Dodimead *et al.* 1963; Ueno and Yasuda 2000, 2005; Miura *et al.* 2002).

In the land laboratory, pelagic polychaetes were sorted from the 1/2 to 1/64 subsamples according to the quantity of the samples. For data on aliquots and the counted individual number of each sample, see the Supplementary Material 1. Specimens were identified and counted under a stereomicroscope. Species identification was made down to the lowest level possible, following Dales (1957) and Tebble (1962). For each genus or species, a batch of specimens in each sample was placed on preweighed mesh, and then water was removed with the aid of wipe paper. The wet weight was measured by an electronic balance (Mettler Toledo AT261) with a precision of 0.01 mg. Then, the vertical distributions of total abundance (ind. 1000 m⁻³) and total WW (mg WW m⁻³) were quantified.

For the community structure of the pelagic polychaetes, the similarity of samples based on abundance was calculated by the Bray–Curtis method (Bray and Curtis 1957). Abundance data of pelagic polychaete species (X: ind. 1000 m⁻³) were log-transformed (log $[X + 1]$) before analysis. Cluster analysis connected with complete linkage methods was performed for the grouping of the samples. Through nonmetric multidimensional scaling (NMDS; Minchin 1987) and Pearson's correlation coefficient, relationships between environmental variables (depth, temperature, salinity, DO, fluorescence) and polychaete sample ordinations were analysed. To evaluate the effects of season, day–night and depth on similarities between samples, PERMANOVA was performed. These analyses were carried out using PRIMER v7 (PRIMER-E Ltd). Intercommunity and water mass differences in the abundance of each species were tested by one-way ANOVA and post hoc test (Tukey–Kramer test). These analyses were performed using STAT-View.

RESULTS

Hydrography

Vertical distributions of temperature, salinity, DO and fluorescence at each sampling date are shown in Fig. 2. Throughout the sampling dates, the temperature, salinity, DO and fluorescence were 0.7–8.5°C, 32.5–34.5, 0.30–7.49 mL L⁻¹ and 0.02–2.32, respectively. Regarding temperature, the seasonalthermocline developed at 50 m in October and June, whereas the temperature was uniform at <100 m in February and April. Common to all seasons, temperature formed a sub-minimum (1–2°C) at ~100 m depth and a sub-maximum (ca. 3.5°C) at ~200 m. Then, the temperature decreased with increasing depth below 200 m. Salinity increased with increasing depth for all seasons. At shallower depths, salinity was uniform at 0–100 m in February and April, whereas it was low (32.6–32.8) at 0–50 m in June and October. DO decreased with increasing depth. DO was high above 200 m, whereas it was extremely low (<1.4 mL L⁻¹) below 200 m depth. High fluorescence was observed only above the thermocline. Since thermocline depths varied with season, high fluorescence was seen at 0–50 m in October and June and at 0–100 m in February and April. Fluorescence was higher in October and June than in February and April.

T–S diagrams throughout the study period are shown in Fig. 3. Except for the seasonal pycnocline observed above 50 m in October and July, water mass formation showed little seasonal change. The formation of the water masses greatly varied with depth. Thus, from shallow to deep, SPW (0–50 m only October and July), DTW (50–100 m), TW (100–150 m), MTW (150–500 m) and DW (500–1000 m) occurred.
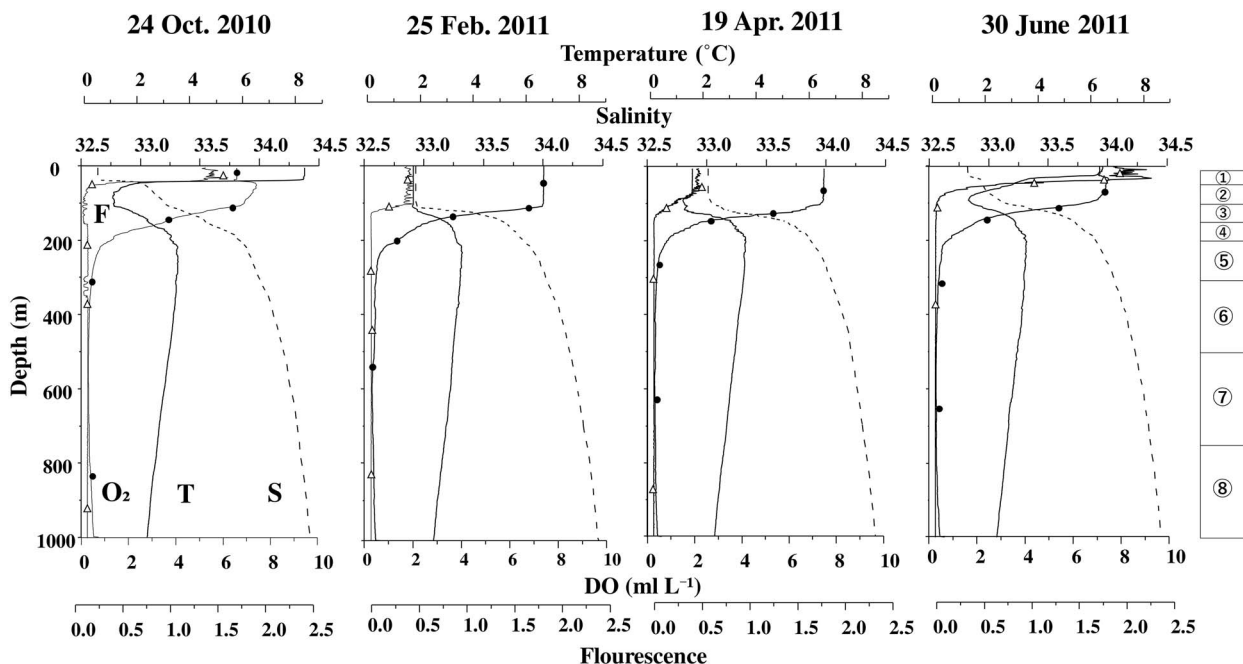
Fig. 2. Vertical changes in temperature (T), salinity (S), dissolved oxygen (DO, O_2) and fluorescence (F) at St. K2 in the western subarctic Pacific from October 2010 to June 2011. Circled numbers in the right column indicate the depth strata of the zooplankton sampling.

Polychaete community

In this study, 8200 polychaete specimens were counted in total, and 8149 polychaetes were identified at the genus or species level. For details of quantified numbers in each sample, see the Supplementary Material 1. Throughout the year, 10 pelagic polychaete species belonging to nine genera and six families were identified (Table II). For population density through the 0–1000 m water column, pelagic polychaetes occurred 235.3 ± 27.8 ind. 1000 m^{-3} (annual mean $\pm$ SE). The most numerically abundant species was *P. longicirrata* (annual mean: 176.2 ind. 1000 m^{-3}, 73.7% of total), followed by *Typhloscolex muelleri* (*T. muelleri*) (33.6 ind. 1000 m^{-3}, 14.0%), *Tomopteris septentrionalis* (*T. septentrionalis*) (17.3 ind. 1000 m^{-3}, 7.2%) and *Poeobius meseres* (4.9 ind. 1000 m^{-3}, 2.1%). These four numerically dominant species accounted for 97.0% of the annual mean pelagic polychaete abundance.

In terms of population density in each sampling layer, the abundance of pelagic polychaetes ranged from 0 to 757 ind. 1000 m^{-3} (Fig. 4). For daytime, the maximum abundances of the four seasons were seen at 150–500 m, especially at 300–500 m. For night-time, the maximum abundance was seen at 0–500 m, especially at the sea surface (0–50 m) in February and April.

For biomass, the annual mean standing stock of the pelagic polychaetes was 517.5 mg WW 1000 m^{-3} (Table II). Within the annual mean biomass, the proportion of large Tomopteridae was in the order of 52% while their numerical abundances were low.

In terms of density, the pelagic polychaete biomass ranged from 0 to 6.1 mg WW m^{-3} (Fig. 5). For the daytime, biomass peaks were seen at 150–500 m depths, especially at ~200 m. For the night-time, the maximum biomass was at 0–200 m, especially at the sea surface (0–50 m) in February and July.

Regarding the effect of water masses, three species (*P. longicirrata*, *T. muelleri* and *T. septentrionalis*) had significantly different abundances between the water masses (Table III). Within them, *P. longicirrata* was abundant in the water masses in the deep layer (DW and MTW). On the other hand, *T. mulleri* and *T. septentrionalis* showed high abundances for the shallowest SPW. Thus, these differences in pelagic polychaete abundances with the water masses were related to the vertical distribution of each species.

From cluster analysis based on abundance, the pelagic polychaete community was divided into five groups (A–E) at 58% dissimilarity (Fig. 6a). Each group contained 5–20 samples. Each group was also clearly separated in the NMDS plot (Fig. 6b). The environmental variables except for temperature (depth, salinity, DO and fluorescence) had significant directions in the NMDS ordination (Fig. 6b). According to the species composition, the predominant species were present for groups A, B and E
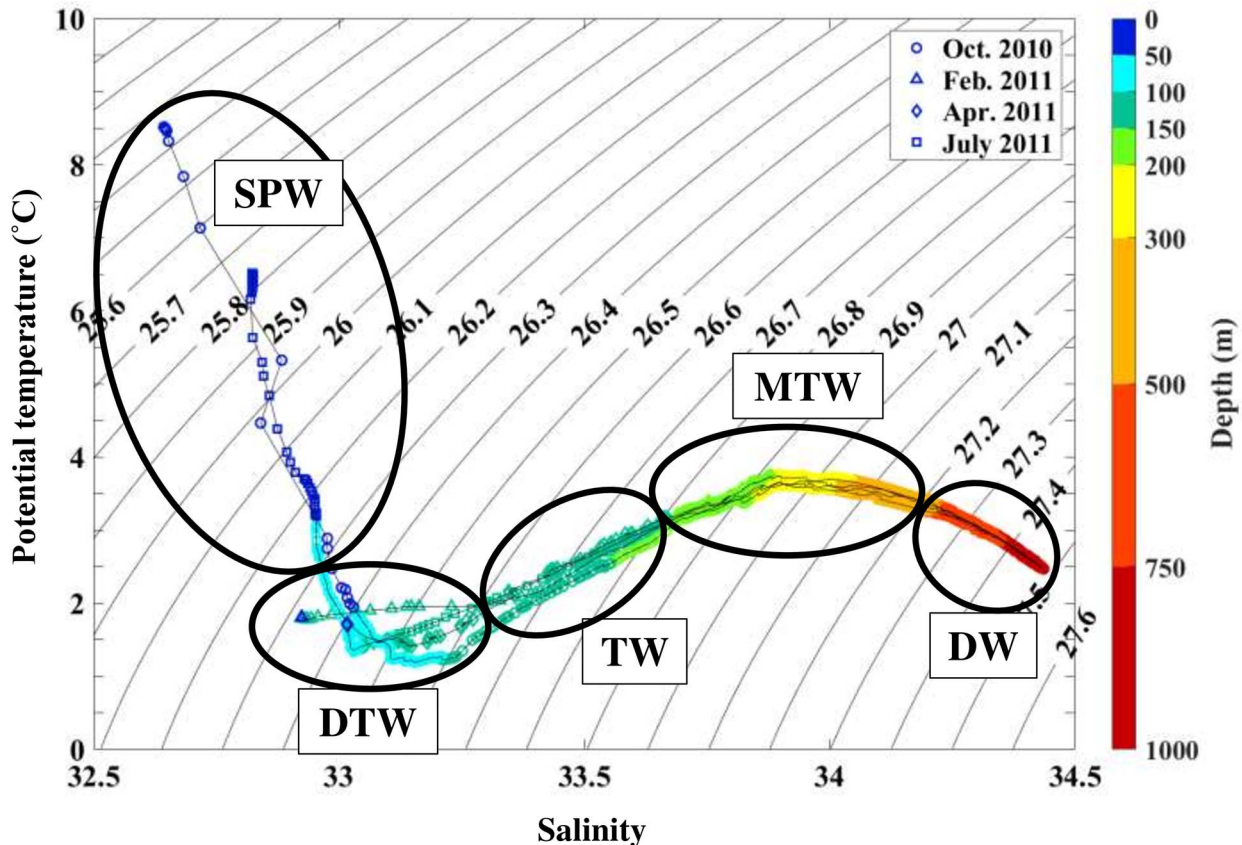
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Fig. 3. T–S diagram for the 0–1000 m water column at St. K2 during October 2010, February, April and July 2011. Five water masses were identified: seasonal pycnocline water (SPW), dichothermal water (DTW), transition water (TW), mesothermal water (MTW) and deep water (DW). Differences in colour for the symbols denote differences in the zooplankton sampling layers.

(Fig. 6c). Thus, *T. muelleri* was abundant in group A, *T. septentrionalis* was abundant in group B and *P. longicirrata* predominated in group E. Groups C and D were composed of various species, and the dominant species in the deep layer varied from each other. Thus, groups C and D consisted of *P. meseres* (group C) and *P. longicirrata* (group D), respectively.

The seven polychaete species showed significantly different abundances between the groups (one-way ANOVA, Table IV). Within them, the four numerically dominant species mentioned above constituted a species-specific abundant group. Thus, the most abundant groups of *P. longicirrata*, *T. muelleri*, *T. septentrionalis* and *P. meseres* were groups D, A, B and C, respectively (Table IV).

Diel, seasonal and vertical distributions of the pelagic polychaete community are shown in Fig. 7. The occurrence of each group varied vertically. Thus, group E was observed at the deepest layer (500–1000 m) throughout the year. Groups C and D were observed at 100–300 m and 150–500 m, respectively. In the sea surface layer (0–50 m), only groups A and B were observed. From the

viewpoint of seasonality, group C was observed in limited seasons (April and July), but the other groups occurred throughout the year. Although the vertical distribution of each group was similar for October, February and April, it was notable that the occurrence depths of each group became shallower for July (Fig. 7). There were no clear day–night difference patterns in the group distribution. According to the results of PERMANOVA, depth had the most prominent effect on polychaete grouping ($P < 0.001$) (Table V). The season and interaction of day–night × depth also had significant effects ($P < 0.05$).

DISCUSSION

Sampling design

This study was based on day–night vertical stratified samples collected from a 0 to 1000 m water column at a single station (K2) during four seasons covering 1 year. It should be noted that this sampling design includes some disadvantages in revealing pelagic polychaete ecology. First,

Table II: List of pelagic polychaete species identified for the 0–1000 m water column at St. K2 in the western subarctic Pacific from October 2010 to July 2011

Family	Species	Abundance (ind. 1000 m^{-3})	(%)	Biomass (mg WW 1000 m^{-3})	(%)
Lopadorrhynchidae					
	Maupasia coeca Viguier, 1886	0.81 ± 0.18	0.34	2.67 ± 1.28	0.45
	Pelagobia longicirrata Greeff, 1879	176.16 ± 24.81	73.65	141.64 ± 20.61	23.74
Iospilidae					
	Phalacrophorus spp.	2.28 ± 0	0.95	2.62 ± 0	0.44
Typhloscolecidae					
	Sagitella kowalewskii Wagner, 1872	0.35 ± 0	0.15	0.04 ± 0	0.01
	Typhloscolex muelleri Busch, 1851	33.56 ± 3.87	14.03	56.66 ± 6.96	9.50
Alciopidae					
	Plotohelmis capitata (Greeff, 1876)	0.17 ± 0	0.07	0.10 ± 0	0.02
	Rhynchonereella angelini (Kinberg, 1866)	0.12 ± 0	0.05	22.46 ± 0	3.76
Tomopteridae					
	Tomopteris septentrionalis Steenstrup, 1849	17.30 ± 3.15	7.23	234.89 ± 44.45	39.37
	Tomopteris (Johnstonella) pacifica (Izuka, 1914)	0.70 ± 0.29	0.29	74.80 ± 1.67	12.54
Flabelligeridae					
	Poeobius meseres Heath, 1930	4.90 ± 1.93	2.05	58.11 ± 28.02	9.74
Others		32.84 ± 1.33	1.19	2.65 ± 1.31	0.44

Annual mean abundance and biomass (mean ± 1 SE: ind. 1000 m^{-3} or mg WW 1000 m^{-3} at 0–1000 m water column) and the species composition (%) are also shown.
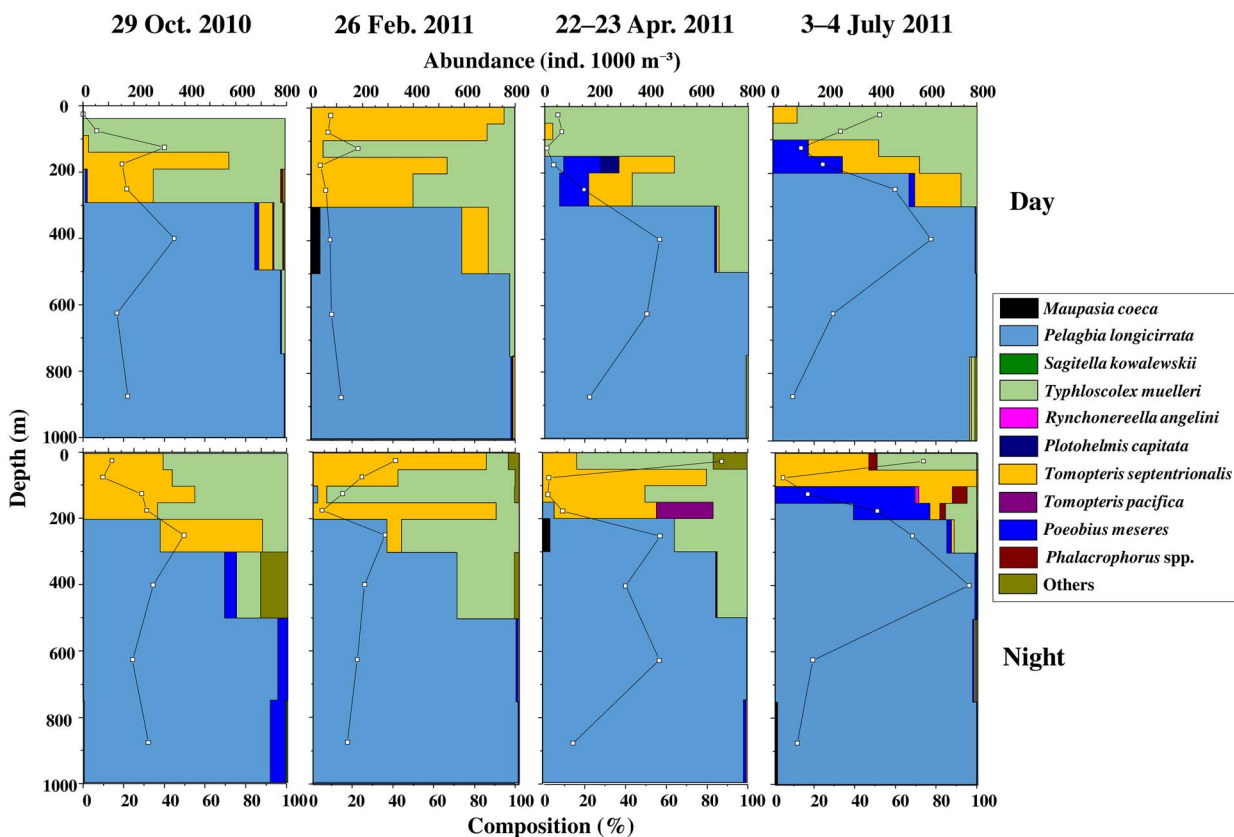

Fig. 4. Vertical changes in polychaete abundance and species composition for the 0–1000 m water column at St. K2 in the western subarctic Pacific from October 2010 to July 2011. The white symbols and black lines show the total abundance in each layer. The composition of each species is shown in a different colour.

Fig. 5. Vertical changes in polychaete biomass (wet weight: WW) and species composition for the 0–1000 m water column at St. K2 in the western subarctic Pacific from October 2010 to July 2011. The white symbols and black lines show the total abundance in each layer. The composition of each species is shown in a different colour.
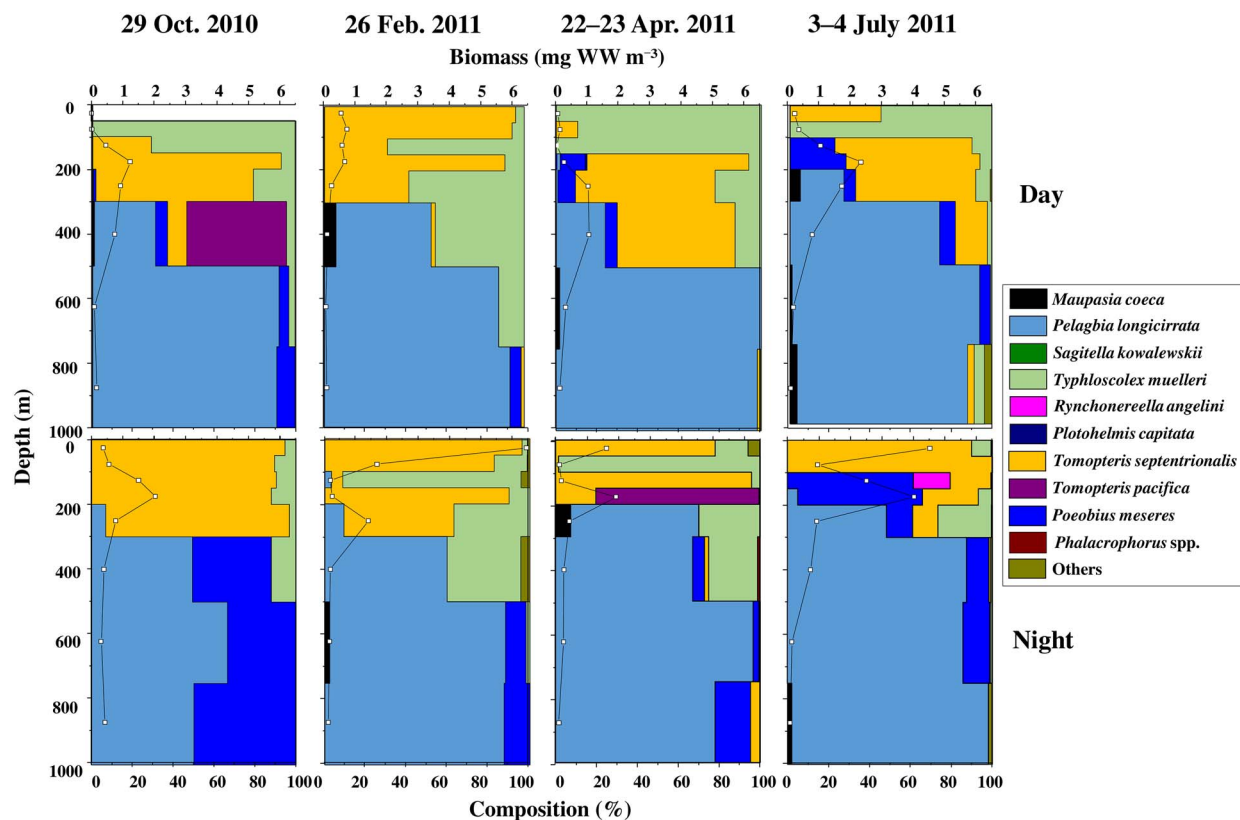
Table III: Comparison of polychaete abundances at five water masses: seasonal pycnocline water (SPW), dichothermal water (DTW), transition water (TW), mesothermal water (MTW) and deep water (DW) identified by the T–S diagram (cf. Fig. 3)

Species	Abundance (ind. 1000 m^{-3})					One-way ANOVA
	SPW (5)	DTW (21)	TW (10)	MTW (24)	DW (16)	
Maupasia coeca	0	0	0	1.35	0.370	NS
Pelagobia longicirrata	0[a]	0.125[b]	0.262[b]	174[c]	182[c]	**
Sagitella kowalewskii	0	0	0	0	0.087	NS
Typhloscolex muelleri	199[c]	93.0[b,c]	97.7[b,c]	54.2[a,b]	0.643[a]	*
Plotohelmis capitata	0	0	0	0.138	0	NS
Rhynchonereella angelini	0	0.117	0.245	0	0	NS
Tomopteris septentrionalis	80.7[b]	45.3[a,b]	41.7[a,b]	37.2[a,b]	0.284[a]	*
Tomopteris pacifica	0	0	0	0.915	0	NS
Poeobius meseres	0	5.32	11.2	13.1	2.43	NS

Values are the mean abundance at each water mass. Differences between groups were tested by one-way ANOVA and post hoc Tukey–Kramer test. For the results of the Tukey–Kramer test, differences in superscript letters indicate significant differences ($P < 0.05$). Numbers in parentheses indicate the number of samples occupied by each water mass. $*P < 0.05$, $**P < 0.01$, NS: not significant.
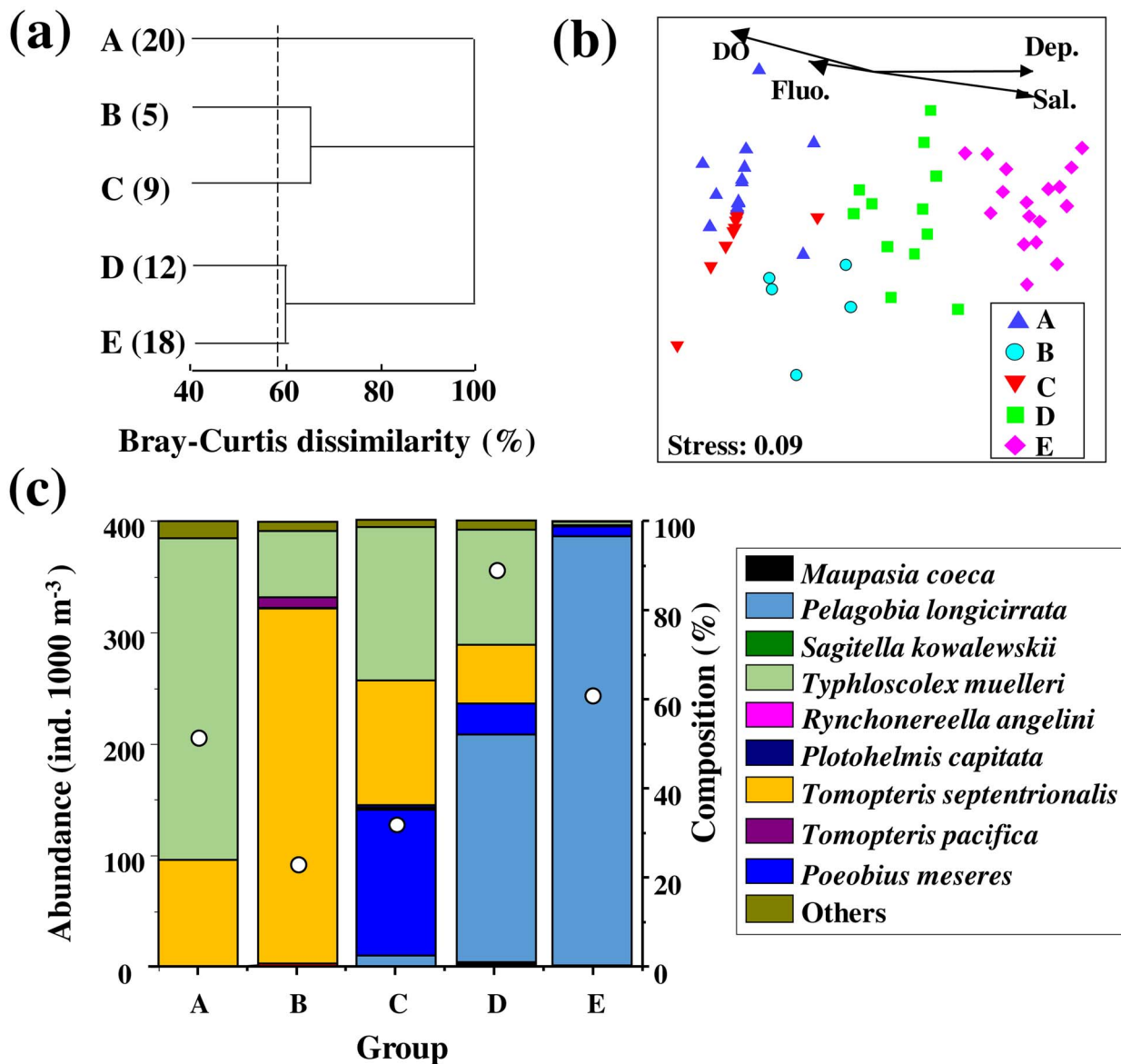
Fig. 6. (a) Results of cluster analysis based on pelagic polychaete abundance. Five groups (A–E) were identified at 58% Bray–Curtis dissimilarity connected with the complete linkage method. Numbers in parentheses indicate the number of samples each group contained. (b) NMDS plots of each group. Arrows indicate directions of significant environmental parameters. Dep.: depth, Temp.: temperature, Sal.: salinity, DO: dissolved oxygen, Fluo.: fluorescence. (c) Mean abundance (white circle) and species composition of each group.

since the samplings were conducted at one fixed station only, spatial patterns were not addressed in this study. Second, it should be noted that horizontal advection may inevitably be present. Third, since only one sample series was collected for each day–night sampling date (no repetition), it may inevitably be an effect of patchy distribution. Fourth, the long net-towing depths, especially the deep layer, may mask the small-sized distribution patterns of the pelagic polychaetes.

Of the four disadvantages described above, the effect of horizontal advection was probably the weakest. This is because clear seasonal changes in water mass were only present for the upper 50 m (Fig. 3), and the long-term horizontal velocity around K2 seems to be weak, which can be confirmed by the distribution of climatological sea surface height around K2 (*e.g.* Fig. 2a of Isoguchi *et al.* 2006). This fact is also confirmed by the results of Onodera *et al.* (2014), who conducted monitoring of

Table IV: Comparison of polychaete abundances in five groups (A–E) identified by Bray–Curtis dissimilarity (cf. Fig. 6)

Species	Abundance (ind.1000 m^{-3})					One-way ANOVA	Tukey–Kramer test				
	A (20)	B (5)	C (9)	D (12)	E (18)						
Maupasia coeca	0	0	0	2.61	0.389	∗	A	C	B	E	D
Pelagobia longicirrata	0.241	0.442	2.88	127	121	∗∗	A	B	C	E	D
Sagitella kowalewskii	0	0	0	0	0.077	NS					
Typhloscolex muelleri	147	13.5	43.3	64.1	0.918	∗∗	E	B	C	D	A
Plotohelmis capitata	0	0	0.663	0	0	∗	A	E	D	B	C
Rhynchonereella angelini	0	0	0.49	0	0	∗	A	E	D	B	C
Tomopteris septentrionalis	49	73.5	35.2	32.8	0.368	∗	E	D	C	A	B
Tomopteris pacifica	0	2.21	0	0.172	0	NS					
Poeobius meseres	0.103	0	41.3	17.4	2.69	∗∗	B	A	E	D	C

Values are the mean abundance in each group. Differences between groups were tested by one-way ANOVA and post hoc Tukey–Kramer test. For the results of the Tukey–Kramer test, any groups not connected by the underlines are significantly different ($P < 0.05$). Numbers in parentheses indicate the number of samples included in each group. ∗$P < 0.05$, ∗∗$P < 0.01$, NS: not significant.
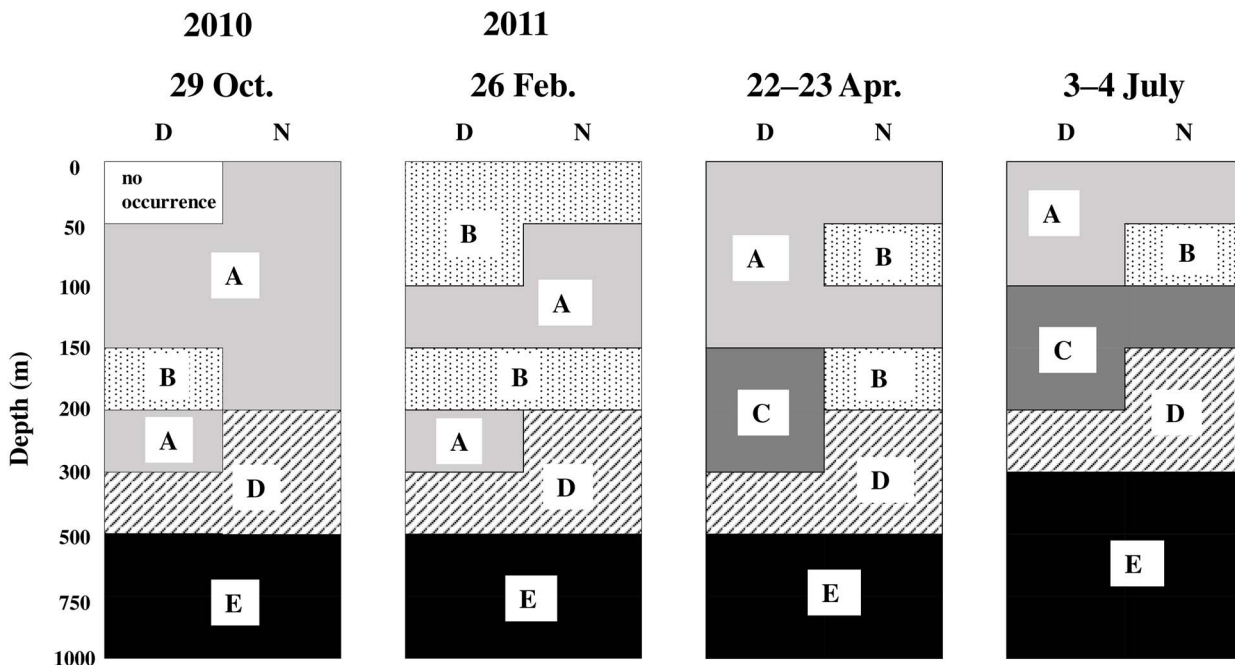

Fig. 7. Seasonal, vertical and diel changes in the occurrence of the five polychaete community groups (A–E) identified by Bray–Curtis dissimilarity based on their abundance (cf. Fig. 6a). D: day, N: night.

Table V: PERMANOVA results based on Bray–Curtis dissimilarities using polychaete abundance data in relation to environmental factors (season, day/night, depth). D: day, N: night

Factors	df	Pseudo F	P
Season	3	2.567	<0.05
D/N	1	1.7781	ns
Depth	7	29.349	<0.001
Season × D/N	3	1.8086	ns
Season × Depth	21	1.4893	ns
D/N × Depth	7	2.568	<0.05

diatom communities by a moored sediment trap at St. K2 during 2005–2006 and 2009–2010 and found that offshore species were commonly dominant for K2. Thus, the effect of horizontal advection in the water mass may be considered small in this study.

Regarding comparable information on pelagic polychaetes down to greater depths, several studies are available (Siciński 1988; Guglielmo et al. 2014, 2019). These studies were based on only one-time sampling (no repetition), no day and night samplings at the same station (no diel comparison) and snap-shot sampling at a single cruise (no seasonal examination). Considering these facts, although some disadvantages or flaws may be present, the sampling design of this study (day–night samplings from four seasons) may be sufficient to advance our knowledge of pelagic polychaete ecology.

Abundance and biomass

Comparable to this study, several studies have investigated pelagic polychaetes down to greater depths (Siciński 1988; Guglielmo et al. 2014, 2019). The abundance, biomass, depths of peak abundance and dominant family of pelagic polychaetes based on the vertically stratified samples collected down to greater depths (750–1400 m) are summarized in Table VI. All samplings were conducted by applying a 200–335 μm mesh net, which may allow us to make a somewhat quantitative comparison with other studies. The maximum abundance of this study (769 ind. 1000 m⁻³) is similar to that at Scotia Front in the Southern Ocean (249 ind. 1000 m⁻³) (Siciński 1988). On the other hand, the maximum abundances in the Strait of Magellan (34 000 ind. 1000 m⁻³, Guglielmo et al. 2014) and South Adriatic Sea (14 500 ind. 1000 m⁻³, Guglielmo et al. 2019) are much higher than those in the present study (Table VI). The high abundance of pelagic polychaetes in the Strait of Magellan and South Adriatic Sea might be related to the semi-enclosed locations of the study areas (Guglielmo et al. 2014, 2019).

At shallower depths, the mean abundances of pelagic polychaetes have been reported as 143–549 ind. 1000 m⁻³ at 0–200 m depths in the Gulf of Tehuantepec, eastern subtropical Pacific (Fernández-Álamo and Sanvicente-Añorve 2005), and 374 ind. 1000 m⁻³ at depths of 0–75 m along the eastern South Adriatic coast (Batistić et al. 2007). Thus, the mean abundance of this study (50–137 ind. 1000 m⁻³) is comparable to those in the Southern Ocean, eastern subtropical Pacific and South Adriatic coast.

In this study, the vertical distribution of wet weight biomass was also evaluated (Fig. 4). Information on comparable biomass is available from the Strait of Magellan

Table VI: Comparison of the maximum density mean abundance and biomass, depths of peak abundance and composition of family in abundance for polychaetes collected by vertical stratified sampling down to greater depths (ca. 1000 m) from worldwide oceans

Location	Temperature range (°C)	Sampling gear (mesh size: μm)	Depth (m)	Maximum density (ind. 1000 m⁻³)	Mean abundance (ind. 1000 m⁻³)	Mean biomass (mg WW 1000 m⁻³)	Depths of peak abundance (m)	Composition of family in abundance (%)	References
Scotia Front (Southern Ocean)	−1.5 to 1.7*	Nansen net (200 μm)	0-1400	249	40.7 ± 6.4	8.36 ± 1.9	100-300	Lopadorrhynchidae (86.0), Tomopteridae (6.3), Typhloscolecidae (4.8)	Siciński (1988), *Rakusa-Suszczewski (1988)
Strait of Magellan	7.4-10.7	BIONESS (230 μm)	0-750	34 000	1101.9 ± 176.9	55 378 ± 34 022	200-400	Lopadorrhynchidae (95.8), Tomopteridae (4.2)	Guglielmo et al. (2014)
South Adriatic Sea	12.5-20.3	BIONESS (230 μm)	0-1100	14 500	359.3 ± 55.8	-	0-200	Tomopteridae (67.2), Alciopidae (23.8), Typhloscolecidae (3.7), Lopadorrhynchidae (1.9)	Guglielmo et al. (2019)
Western subarctic Pacific	1.2-8.5	IONESS (335 μm)	0-1000	769	235.3 ± 27.8	517.5 ± 74.3	0-500	Lopadorrhynchidae (74.9), Typhloscolecidae (14.3), Tomopteridae (7.6), Flabelligeridae (2.1)	This study

Values are the mean ± SE.

(Siciński 1988) and the Scotia Front (Guglielmo *et al.* 2014). The annual mean of the total wet weight biomass in this study (517 mg WW 1000 m⁻³) was set between the two studies (Table VI). Although comparable data are scarce, from the viewpoint of material flux and energy flow within the ecosystem, information on biomass is needed for future study.

Regional comparison of community structure

In the present study, 10 pelagic polychaete species belonging to nine genera and six families were identified from the 0 to 1000 m water column (Table II). Concerning the species number of pelagic polychaetes, based on CalCOFI samples, the presence of a clear latitudinal pattern is reported for the 0–200 m water column between 21°N and 40°N latitudes off California, eastern North Pacific (Fernández-Álamo *et al.* 2003). According to Fernández-Álamo *et al.* (2003), the pelagic polychaete community has been divided into three groups: the north, south and transition groups. The north group is characterized by high abundance and relative divergence (11 species), the south group is characterized by low abundance but the most divergence (16 species) and the transition group has the lowest abundance and species diversity. The number of species in this study (10 species) is close to that of the northern group of Fernández-Álamo *et al.* (2003) (11 species). Similar latitudes of the northern group of Fernández-Álamo *et al.* (2003) and this study may explain the comparable species diversity of the two studies. Thus, the study region of this study is characterized by a high abundance of pelagic polychaetes, which may be related to the high productivity of the region (Fernández-Álamo *et al.* 2003).

Concerning dominant species, various studies conducted down to greater depths reported that *P. longicirrata* is the most numerically dominant species (Siciński 1988; Guglielmo *et al.* 2014). *P. longicirrata* was also the most numerically dominant species in this study (Table II). From the viewpoint of family composition, Lopadorrhynchidae, including *P. longicirrata*, comprised 75–96% in the Strait of Magellan, the Scotia Front and the western subarctic Pacific (Table VI). On the other hand, in the South Adriatic Sea, Lopadorrhynchidae occurred only at 2% and was replaced by Tomopteridae, comprising 67% (Guglielmo *et al.* 2019) (Table VI). These facts indicate that a large regional pattern is present for the pelagic polychaete community. In addition to the community structure, the vertical distribution of the same species also varies with the region. Thus, *P. longicirrata* is distributed at 100–400 m in the Strait of Magellan from March to April (Guglielmo *et al.* 2014) and the Southern

Ocean during October (Siciński 1988) and at 0–75 m in the Adriatic Sea throughout the year (Batistić *et al.* 2007). In the present study, *P. longicirrata* occurred from 300 to 1000 m throughout the year (Fig. 4). This suggests that seasonal or geographical changes are present in the depth ranges of the cosmopolitan pelagic polychaete species (*P. longicirrata*). Clearly, more study is needed for generalization of this concept.

Diel and seasonal change in community structure

For diel changes in the pelagic polychaete community, high density at the surface layer during the night was observed for abundance in February and April and for biomass in February and July (Figs. 4 and 5). These facts suggest that such diel changes in vertical distribution may be caused by the nocturnal ascent diel vertical migration (DVM) of pelagic polychaetes. In fact, nocturnal ascent DVM was detected for the shallower dwelling *T. septentrionalis* in April and July in this study (Amei unpublished data). Concerning the DVM of pelagic polychaetes, Guglielmo *et al.* (2011) reported that two epipelagic polychaete species (*P. longicirrata*, *Tomopteris planktonis*) showed high abundance at night, whereas their vertical distributions were stable throughout the day based on samplings at 0–190 m depths in the Strait of Magellan. These facts suggest that nocturnal ascent DVM was present for the epipelagic dwelling polychaetes. However, their diel changes may be limited for the species distributed more shallowly, and no diel changes were detected in terms of the community structure of the pelagic polychaetes (Fig. 7).

Concerning seasonal changes, polychaete community group C was observed only for in limited seasons (April and July) (Fig. 7). Group C was characterized by the dominance of *P. meseres* (Table IV). As a special ecological characteristic of *P. meseres,* this species feeds on sinking particles by extending the mucus web, which is not observed for other pelagic polychaete species (Uttal and Buck 1996; Robison *et al.* 2010). Seasonally, the amount of sinking particles at St. K2 evaluated by the sediment trap is known to be high during April and July (Honda *et al.* 2016, 2017). This season corresponds with the timing at which group C was observed for the pelagic polychaete community. The shallower shift in the vertical distribution of each pelagic polychaete community in July (Fig. 7) may be related to the high sinking particulate flux during that period (Honda *et al.* 2016, 2017). Thus, seasonal changes in the amount of passive sinking particle flux are suggested to affect seasonality in the pelagic polychaete community, especially the sinking particle feeder (*P. meseres*) at St. K2.

Vertical changes in community structure

For the grouping of the pelagic polychaete community, the temporal factors (diel and seasonal) had a relatively small effect ($P < 0.05$), and the most important factor in determining the grouping was the depth (vertical) ($P < 0.001$) (Table V). The most prominent vertical changes in the environmental parameters at St. K2 were at the occurrence of the five water masses vertically (Fig. 3) and the development of the exclusive oxygen minimum layer below 200 m depth (Fig. 2). Although other parameters (temperature, salinity and fluorescence) also showed vertical changes, these changing patterns are common for the worldwide ocean. Next, we argue for their effects on the pelagic polychaete community.

Concerning water masses, the pelagic polychaete community has been reported to be strongly affected by water masses in the South Adriatic Sea (Guglielmo *et al.* 2019). The effect of water masses on the polychaete community was also present in this study (Table III). It should be noted that although both water mass and polychaete community separated into the same numbers: five groups, their species-specific corresponding pattern (i.e. each water mass has a different polychaete community) was not the case. In this study, the water masses separated and varied vertically, and the distribution showed limited seasonal change only in the near-surface layer (Fig. 3). These stable hydrographic characteristics may allow adaptation of each pelagic polychaete species for suitable conditions that may vary with species. In addition to the changes in water masses, other environmental characteristics, such as DO (Fig. 2) and the quality and quantity of the sinking particles (Wilson *et al.* 2008), may also vary vertically. However, since these vertical changes in environmental parameters occur sympatrically, it is difficult to identify, distinguish or separate the effect of each parameter on the pelagic polychaete community.

Interestingly, the four dominant species in this study had species-specific abundant communities (Table IV), and their feeding modes varied with species. For the shallower depths (0–150 m) characterized with the three water masses (SPW, DTW and TW), the dominant species of the pelagic polychaete community groups A and B were both carnivorous: *T. muelleri* and *T. septentrionalis* (Figs. 6 and 7). This may be related to the biomass of their prey (other zooplankton) being high at the surface layer, which was quantified by the same vertical stratified net samples used in this study (Kitamura *et al.* 2016).

For the middle layer (150–500 m) characterized by the two water masses (TW and MTW), the dominant species *P. meseres* is known to feed on sinking particles such as fecal pellets via the deployment of a mucus web or grasping with ciliated tentacles (Uttal and Buck 1996). These facts suggest that *P. meseres* is adapted for life in the deep realm. Adding to such feeding modes, the weight-specific oxygen consumption rate of *P. meseres* is reported to be extremely low (1.7–6.8% of that of the other pelagic polychaete species) (Thuesen and Childress 1993). In the present study region, the development of the oxygen minimum layer, which was characterized by extremely low DO (<2 mL L^{-1}), occurred below 200 m depth (Fig. 2). For the vertical distribution of *Poeobius* sp., it has been reported that they form prominent peaks just below the thermocline (Christiansen *et al.* 2018). These ecological characteristics of *P. meseres* corresponded well to the environmental characteristics of the depths (150–500 m) of their abundance groups, C and D, *e.g.* below the thermocline and extremely low DO (Fig. 7).

For the deepest layer (500–1000 m) characterized by the one water mass (DW), group E was predominated by *P. longicirrata* throughout the year (Figs. 6 and 7). In terms of feeding modes, *P. longicirrata* is reported to be an herbivore feeding on phytoplankton (Hopkins and Torres 1989). However, considering their vertical distribution (500–1000 m), it is difficult to assume that fresh phytoplankton are the main food items of *P. longicirrata* in the study region. Notably, within Lopadrynchidae, only the genus *Pelagobia* has a pair of diminutive mandibles or two hooks at the pharynx (Uschakov 1974; Fauchald and Jumars 1979; Jumars *et al.* 2015). From the presence of such feeding apparatuses (fangs), Jumars *et al.* (2015) suggest that *Pelagobia* species feed on gelatinous prey or skin and mucus from fish (as in the case of *Lopadorrhynchus*), obtaining the observed diatoms secondarily from the gut or surface of their prey. To clarify the feeding modes of *Pelagobia* species, the application of stable isotopes to their bodies and molecular analysis of their gut content may provide new insights in the future.

CONCLUSION

Through observations in four seasons covering day–night down to 1000 m depth in the western subarctic Pacific, the pelagic polychaete community was separated into five groups. The distributions of each group separated vertically and showed little diel and seasonal change. Three factors are considered causes of these vertically different communities of pelagic polychaetes. The first is the differences in feeding modes (*e.g.* food availability): carnivores were abundant at the surface. The second is the adaptation for the oxygen minimum layer: the vertical distribution of the low weight-specific metabolic rate species corresponded with the oxygen minimum layer. The third is the water mass: the water mass and pelagic polychaete

community varied vertically. Since these vertical changes in environmental factors occurred sympatrically, it is difficult to identify, distinguish or separate their effects on the polychaete community. To clarify the importance of each environmental parameter on the pelagic polychaete community, regional comparison, which is characterized by highly different environmental conditions and/or laboratory experiments for adaptation to low DO conditions, may be interesting for future study.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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REFERENCES

Amei, K., Jimi, N., Kitamura, M., Yokoi, N. and Yamaguchi, A. (2020) Community structure and seasonal changes in population structure of pelagic polychaetes collected by sediment traps moored in the subarctic and subtropical western North Pacific Ocean. *Zoosymposia*, **19**, 41–50.

Batistić, M., Kršinić, F., Jasprica, N., Carić, M., Viličić, D. and Lučić, D. (2004) Gelatinous invertebrate zooplankton of the South Adriatic: species composition and vertical distribution. *J. Plankton Res.*, **26**, 459–474.

Batistić, M., Jasprica, N., Carić, M. and Lučić, D. (2007) Annual cycle of the gelatinous invertebrate zooplankton of the eastern South Adriatic coast (NE Mediterranean). *J. Plankton Res.*, **29**, 671–686.

Bianchi, D., Stock, C., Galbraith, E. D. and Sarmiento, J. L. (2013) Diel vertical migration: ecological controls and impacts on the biological pump in a one-dimensional ocean model. *Global Biogeochem. Cycles*, **27**, 478–491.

Boyd, P. W., Gall, M. P., Silver, M. W., Coale, S. L., Bidigare, R. R. and Bishop, J. (2008) Quantifying the surface-subsurface biogeochemical coupling during the VERTIGO ALOHA and K2 studies. *Deep-Sea Res. II*, **55**, 1578–1593.

Bray, J. R. and Curtis, J. T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, **27**, 325–349.

Buesseler, K. O., Lamborg, C. H., Boyd, P. W., Lam, P. J., Trull, T. W., Bidigare, R. R., Bishop, J. K. B., Casciotti, K. L. *et al.* (2007) Revisiting carbon flux through the ocean's twilight zone. *Science*, **316**, 567–570.

Christiansen, S., Hoving, H., Schütte, F., Hauss, H., Karstensen, J., Körtzinger, A., Schröder, S., Stemmann, L. *et al.* (2018) Particulate matter flux interception in oceanic mesoscale eddies by the polychaete *Poeobius* sp. *Limnol. Oceanogr.*, **63**, 2093–2109.

Dales, K. P. (1957) *Pelagic Polychaetes of the Pacific Ocean*, University of California Press, Berkeley and Los Angeles.

Day, J. H. (1967) *A Monograph on the Polychaeta of Southern Africa*, Vol. **656**, Trustees of the British Museum, London, pp. 1–878.

Dodimead, A. J., Favorite, F. and Hirano, T. (1963) Salmon of the North Pacific Ocean, part II. *Bull. Int. North Pacific Fish. Comm.*, **13**, 1–195.

Elskens, M., Brion, N., Buesseler, K., Van Mooy, B. A. S., Boyd, P., Dehairs, F., Savoye, N. and Baeyens, W. (2008) Primary, new and export production in the NW pacific subarctic gyre during the vertigo K2 experiments. *Deep-Sea Res. II*, **55**, 1594–1604.

Fauchald, K. and Jumars, P. A. (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.*, **17**, 193–284.

Feigenbaum, D. (1979) Predation on chaetognaths by Typhloscolecid polychaetes: one explanation for headless specimens. *J. Mar. Biol. Assoc. UK*, **59**, 631–633.

Fernández-Álamo, M. A. (1991) Holoplanktonic polychaetes from the Gulf of California: August–September 1977. *ColCOFI Rep.*, **32**, 97–104.

Fernández-Álamo, M. A. (2006) Composition, abundance and distribution of holoplanktonic polychaetes from the expedition "El Golfo 6311-12" of Scripps Institution of Oceanography. *Sci. Mar.*, **70**, 209–215.

Fernández-Álamo, M. A., Sanvicente-Añorve, L. and Alatorre-Mendieta, M. A. (2003) Changes in pelagic polychaete assemblages along the California current system. *Hydrobiologia*, **496**, 329–336.

Fernández-Álamo, M. A. and Sanvicente-Añorve, L. (2005) Holoplanktonic polychaetes from the Gulf of Tehuantepec. *Mexico. Cah. Biol. Mar.*, **46**, 227–239.

Francis, W. R., Powers, M. L. and Haddock, S. H. D. (2016) Bioluminescence spectra from three deep-sea polychaete worms. *Mar. Biol.*, **163**, 255.

Fujiki, T., Matsumoto, K., Mino, Y., Sasaoka, K., Wakita, M., Kawakami, H., Honda, M. C., Watanabe, S. *et al.* (2014) Seasonal cycle of phytoplankton community structure and photophysiological state in the western subarctic gyre of the North Pacific. *Limnol. Oceanogr.*, **59**, 887–900.

Gouveneaux, A., Flood, P. R., Erichsen, E. S., Olsson, C., Lindström, J. and Mallefet, J. (2017) Morphology and fluorescence of the parapodial light glands in *Tomopteris helgolandica* and allies (Phyllodocida: Tomopteridae). *Zool. Anz.*, **268**, 112–125.

Gouveneaux, A., Gielen, M. and Mallefet, J. (2018) Behavioural responses of the yellow emitting annelid *Tomopteris helgolandica* to photic stimuli. *Luminescence*, **33**, 511–520.

Guglielmo, L., Minutoli, R., Bergamasco, A., Granata, A., Zagami, G. and Antezana, T. (2011) Short-term changes in zooplankton community in Paso Ancho basin (Strait of Magellan): functional trophic structure and diel vertical migration. *Polar Biol.*, **34**, 1301–1317.

Guglielmo, R., Gambi, M. C., Guglielmo, L. and Minutoli, R. (2014) Composition, abundance and distribution of holoplanktonic polychaetes within the Strait of Magellan (southern America) in austral summer. *Polar Biol.*, **37**, 999–1015.

Guglielmo, R., Bergamasco, A., Minutoli, R., Patti, F. P., Belmonte, G., Spanò, N., Zagami, G., Bonanzinga, V. *et al.* (2019) The Otranto Channel (South Adriatic Sea), a hot-spot area of plankton biodiversity: pelagic polychaetes. *Sci. Rep.*, **9**, 19490.

Haddock, S. H. D., Moline, M. A. and Case, J. F. (2010) Bioluminescence in the sea. *Ann. Rev. Mar. Sci.*, **2**, 443–493.

Halanych, K. M., Cox, L. N. and Struck, T. H. (2007) A brief review of holopelagic annelids. *Integr. Comp. Biol.*, **47**, 872–879.

Honda, M. C., Kawakami, H., Matsumoto, K., Wakita, M., Fujiki, T., Mino, Y., Sukigara, C., Kobari, T. *et al.* (2016) Comparison of sinking particles in the upper 200 m between subarctic Station K2 and subtropical station S1 based on drifting sediment trap experiments. *J. Oceanogr.*, **72**, 373–386.

Honda, M. C., Wakita, M., Matsumoto, K., Fujiki, T., Siswanto, E., Sasaoka, K., Kawakami, H., Mino, Y. *et al.* (2017) Comparison of carbon cycle between the western Pacific subarctic and subtropical time-series stations: highlights of the K2S1 project. *J. Oceanogr.*, **73**, 647–667.

Hopkins, T. L. (1985) Food web of an Antarctic midwater ecosystem. *Mar. Biol.*, **89**, 197–212.

Hopkins, T. L. (1987) Midwater food web in McMurdo Sound, Ross Sea. *Antarctica. Mar. Biol.*, **96**, 93–106.

Hopkins, T. L. and Torres, J. J. (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep-Sea Res.*, **36A**, 543–560.

Isoguchi, O., Kawamura, H. and Oka, E. (2006) Quasi-stationary jets transporting surface warm waters across the transition zone between the subtropical and the subarctic gyres in the North Pacific. *J. Geophys. Res.*, **111**, C10003.

Jumars, P. A., Dorgan, K. M. and Lindsay, S. M. (2015) Diet of worms emended: an update of polychaete feeding guilds. *Ann. Rev. Mar. Sci.*, **7**, 497–520.

Kaneko, R., Nagata, T., Suzuki, S. and Hamasaki, K. (2016) Depth-dependent and seasonal variability in archaeal community structure in the subarctic and subtropical western North Pacific. *J. Oceanogr.*, **72**, 427–438.

Kitamura, M., Kobari, T., Honda, M. C., Matsumoto, K., Sasaoka, K., Nakamura, R. and Tanabe, K. (2016) Seasonal changes in the mesozooplankton biomass and community structure in subarctic and subtropical time-series stations in the western North Pacific. *J. Oceanogr.*, **72**, 387–402.

Kobari, T., Nakamura, R., Unno, K., Kitamura, M., Tanabe, K., Nagafuku, H., Niibo, A., Kawakami, H. *et al.* (2016) Seasonal variability in carbon demand and flux by mesozooplankton communities at subarctic and subtropical sites in the western North Pacific Ocean. *J. Oceanogr.*, **72**, 403–418.

Lebour, M. V. (1922) The food of plankton organisms. *J. Mar. Biol. Assoc. UK*, **12**, 644–677.

Matsumoto, K., Honda, M. C., Sasaoka, K., Wakita, M., Kawakami, H. and Watanabe, S. (2014) Seasonal variability of primary production and phytoplankton biomass in the western Pacific subarctic gyre: control by light availability within the mixed layer. *J. Geophys. Res.*, **119**, 6523–6534.

Matsumoto, K., Abe, O., Fujiki, T., Sukigara, C. and Mino, Y. (2016) Primary productivity at the time-series stations in the northwestern Pacific Ocean: is the subtropical station unproductive? *J. Oceanogr.*, **72**, 359–371.

Minchin, P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, **69**, 89–107.

Miura, T., Suga, T. and Hanawa, K. (2002) Winter mixed layer and formation of dichothermal water in the Bering Sea. *J. Oceanogr.*, **58**, 815–823.

Okazaki, Y., Takahashi, K., Onodera, J. and Honda, M. C. (2005) Temporal and spatial flux changes of radiolarians in the northwestern Pacific Ocean during 1997–2000. *Deep-Sea Res. II*, **52**, 2240–2274.

Onodera, J., Ohashi, A., Takahashi, K. and Honda, M. C. (2014) Time-series variation of diatom valve fluxes at Station K2 in the western Subarctic Pacific. *Diatom*, **30**, 104–121.

Øresland, V. (1990) Feeding and predation impact of the chaetognath *Eukrohnia hamata* in Gerlache Strait, Antarctic Peninsula. *Mar. Ecol. Prog. Ser.*, **63**, 201–209.

Øresland, V. and Pleijel, F. (1991) An ectoparasitic typhloscolecid polychaete on the chaetognath *Eukrohnia hamata* from the Antarctic Peninsula. *Mar. Biol.*, **108**, 429–432.

Øresland, V. and Bray, R. A. (2005) Parasites and headless chaetognaths in the Indian Ocean. *Mar. Biol.*, **147**, 725–734.

Peter, G. (1975) On the seasonal distribution of some polychaetes in the Indian Ocean area along 110° meridian. *Mahasagar*, **8**, 45–52.

Rakusa-Suszczewski, S. (1968) Predation of Chaetognatha by *Tomopteris helgolandica* Greef. *J. Cons. Int. Explor. Mer.*, **32**, 226–231.

Robison, B. H., Sherlock, R. E. and Reisenbichler, K. R. (2010) The bathypelagic community of Monterey Canyon. *Deep-Sea Res. II*, **57**, 1551–1556.

Siciński, J. (1988) Pelagic Polychaeta in the Scotia Front west of Elephant Island (BIOMASS III, October–November 1986). *Pol. Polar Res.*, **9**, 277–282.

Steinberg, D. K., Van Mooy, B. A. S., Buesseler, K. O., Boyd, P. W., Kobari, T. and Karl, D. M. (2008a) Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnol. Oceanogr.*, **53**, 1327–1338.

Steinberg, D. K., Cope, J. S., Wilson, S. E. and Kobari, T. (2008b) A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean. *Deep-Sea Res. II*, **55**, 1615–1635.

Tebble, N. (1962) The distribution of pelagic polychaetes across the North Pacific Ocean. *Bull. British Mus. Nat. History Zool.*, **7**, 371–492.

Thuesen, E. V. and Childress, J. J. (1993) Metabolic rates, enzyme activities and chemical compositions of some deep-sea pelagic worms, particularly *Nectonemertes mirabilis* (Nemertea; Hoplonemertinea) and *Poeobius meseres* (Annelida; Polychaeta). *Deep-Sea Res. I*, **40**, 937–951.

Ueno, H. and Yasuda, I. (2000) Distribution and formation of the mesothermal structure (temperature inversions) in the North Pacific subarctic region. *J. Geophys. Res.*, **105**, 16885–16897.

Ueno, H. and Yasuda, I. (2005) Temperature inversions in the subarctic North Pacific. *J. Phys. Oceanogr.*, **35**, 2444–2456.

Ushakov, P. V. (1974) *Fauna of the U.S.S.R.: Polychaetes*, Israel Program for Scientific Translations, Jerusalem.

Uttal, L. and Buck, K. R. (1996) Dietary study of the midwater polychaete *Poeobius meseres* in Monterey Bay, California. *Mar. Biol.*, **125**, 333–343.

Vinogradov, M. E. (1968) *Vertical Distribution of the Oceanic Zooplankton. Academy of Science of the USSR*, Israel Program for Scientific Translations, Jerusalem.

Wakita, M., Honda, M. C., Matsumoto, K., Fujiki, T., Kawakami, H., Yasunaka, S., Sasai, Y., Sukigara, C. *et al.* (2016) Biological organic carbon export estimated from the annual carbon budget observed in the surface waters of the western subarctic and subtropical North Pacific Ocean from 2004 to 2013. *J. Oceanogr.*, **72**, 665–685.

Wakita, M., Nagano, A., Fujiki, T. and Watanabe, S. (2017) Slow acidification of the winter mixed layer in the subarctic western North Pacific. *J. Geophys. Res.*, **122**, 6923–6935.

Wilson, S. E., Steinberg, D. K. and Buesseler, K. O. (2008) Changes in fecal pellet characteristics with depth as indicators of zooplankton repackaging of particles in the mesopelagic zone of the sub-tropical and subarctic North Pacific Ocean. *Deep-Sea Res. II*, **55**, 1636–1647.

Wilson, S. E. and Steinberg, D. K. (2010) Autotrophic picoplankton in mesozooplankton guts: evidence of aggregate feeding in the mesopelagic zone and export of small phytoplankton. *Mar. Ecol. Prog. Ser.*, **412**, 11–27.