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Comparative ecology of three dominant pelagic chaetognaths (*Eukrohnia hamata*, *Parasagitta elegans*, *Pseudosagitta scrippsae*) in the Oyashio region during the spring phytoplankton bloom

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HIGHLIGHTS

- Various ecological parameters were studied for the three sympatric chaetognath species.
- Inter-species comparison showed clear species-specific pattern.
- The most important food organisms (25.1%) of *P. scrippsae* were the copepod *Metridia spp.*
- *M. pacifica* was not observed for the food items of the smaller body-sized *E. hamata* and *P. elegans*.
- The large body size of *P. scrippsae* may allow them to feed on *Metridia spp.* as prey.

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ABSTRACT

In the Oyashio region, the dominant water masses are switched at the surface layer within a short period during spring. Simultaneously, a large phytoplankton bloom is known to occur at the surface layer, and nearly half of the annual primary production is concentrated during spring. These drastic changes in the water mass and food condition are expected to strongly affect the macrozooplankton population dynamics. However, their effects on the chaetognath population remain unknown. To evaluate the effects of the water mass exchange and spring phytoplankton bloom, we analysed short-term changes in the population structure, growth rate, gut contents and predation impact of the three dominant chaetognaths (*Eukrohnia hamata*, *Parasagitta elegans*and *Pseudosagitta scrippsae*) in the Oyashio region during March–April 2007. Eleven samples were collected by a 0–200 m oblique tow of a Bongo net at night during 9 March to 30 April, 2007. The effects of the water mass exchange were significant for all three chaetognath species. During the sampling period, significant growth was observed for the two dominant species (*E. hamata* and *P. elegans*). The daily growth rate was 39–50 μm day^{-1} for *E. hamata* and 42–101 μm day^{-1} for *P. elegans*. The mean predation impact of *P. elegans* at 0–200 m was 0.194 no. prey consumed m^{-3} day^{-1} and that of *P. scrippsae* was 0.028 no. prey consumed m^{-3} day^{-1}. These values corresponded with 0–0.097% (*P. elegans*) or 0–0.043% (*P. scrippsae*) of the total zooplankton abundance during the spring.

1. Introduction

Following copepods, chaetognaths are known to be the dominant taxa in terms of zooplankton abundance and biomass in the Earth's oceans, and they are composed 5%–15% of mesozooplankton biomass (Longhurst, 1985). It has been reported that chaetognaths are typical carnivores and feed mainly on copepods

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and other taxa: euphausiids, amphipods, appendicularians, crustaceans, chaetognaths (cannibalism), and the eggs and larvae of fishes (Feigenbaum, 1991; Brodeur and Terazaki, 1999; Albaina et al., 2015). Chaetognaths are known to be prey organisms of the higher trophic predators, such as walleye pollock and pelagic fishes (Beamish et al., 1999; Yamamura et al., 2002). Thus, in marine ecosystems, pelagic chaetognaths play an important role as a vital link connecting between the secondary producers and higher trophic predators (Hopkins and Torres, 1989; Kruse et al., 2010a,b).

In the Oyashio region during spring, dominant water masses characterized by different temperatures are known to change drastically at the surface layer within a short period (Kono and Sato, 2010). Simultaneously, a large phytoplankton bloom is known to occur at the surface layer, and approximately half of the annual primary production is concentrated during the spring (Saito et al., 2002; Liu et al., 2004; Ikeda et al., 2008). Because chaetognaths reportedly undergo reproduction and growth during the spring bloom in the Oyashio region (Terazaki, 1998; Kotori, 1999), evaluation of the effects of the water mass exchange and primary production on the chaetognath community and population dynamics is of special interest.

To evaluate the biological responses to the spring phytoplankton bloom, high-frequency samplings were conducted during March–April 2007 at a fixed station in the Oyashio region. This project, known as the "Ocean Ecodynamics Comparison in the Subarctic Pacific" (OECOS), is endorsed by the North Pacific Marine Science Organizations (PICES) (Ikeda et al., 2010). Through the OECOS project, short-term changes in population structures have been evaluated for various taxa: e.g., epi- and mesopelagic copepods (Yamaguchi et al., 2010a,b; Abe et al., 2012), euphausiids (Kim et al., 2010a,b), amphipods (Abe et al., 2016) and cnidarians (Abe et al., 2014). However, no information is available for the dynamics of chaetognaths during the same period.

In the present study, as part of the OECOS project, we studied short-term changes in the population structure, food items, feeding impacts and growth rates of the three dominant chaetognaths (*Eukrohnia hamata, Parasagitta elegans* and *Pseudosagitta scrippsae*) in the Oyashio region during the spring phytoplankton bloom. In addition, for these three chaetognaths species, we evaluated the factors that control the inter-specific differences for the following three topics: (1) the effects of water mass exchange on the chaetognath population, (2) the food items and feeding impacts, and (3) the growth rate of each cohort.

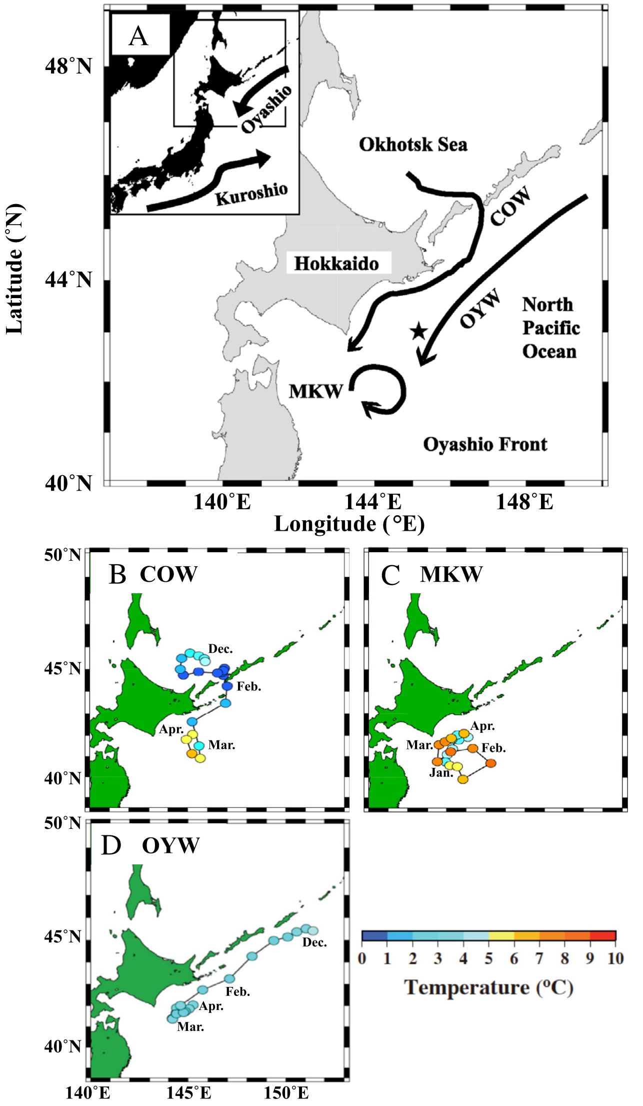


Fig. 1. Location of the Oyashio region and sampling station (star) in the Oyashio region (A). For A, the approximate current flows are shown. The remaining three panels are the results of FRA-ROMS analyses, which back-calculated the origin of each water mass at each sampling date. (B) COW; coastal Oyashio water (25 April), (C) MKW; modified Kuroshio water (12 April), (D) OYW; Oyashio water (6 April).

2. Materials and methods

2.1. Field sampling

Macrozooplankton samples were collected at a single station (42°00′N, 145°15′E, depth ca. 4000 m) in the Oyashio region of the western subarctic Pacific at night (20:00–21:00 local time) on 9 and 14 March and 6, 8, 10, 12, 15, 17, 20, 25 and 30 April 2007 (Fig. 1). Bongo nets (70-cm mouth diameter, 335-μm mesh size) were obliquely towed from a 200-m depth to the surface (400-m wire with 60° wire angle) at a speed of 2 knots. Because of the limitation of ship time, only one net tow was made on each occasion. After collection, the samples were immediately preserved with v/v 5% borax-buffered formalin–seawater. The filtered water volumes were estimated from the readings of a flowmeter (Rigosha Co. Ltd., Tokyo) mounted on a net ring.

The environmental parameters of the temperature, salinity and chlorophyll *a* (Chl. *a*) fluorescence were measured with a CTD (SBE-9 plus, Sea Bird Electronics, Washington) cast at each sampling. Based on the temperature and salinity data, the mixture ratios of the three water masses (Coastal Oyashio Water: COW; Oyashio Water: OYW; modified Kuroshio Water: MKW) in the 0–50 m water column were calculated (Kono and Sato, 2010). Regarding food conditions, the mesozooplankton wet mass (g WM m^{-2}) data, collected with twin-NORPAC nets (100- and 335-μm mesh sizes, 45-cm diameter) from 0–150 m during the nights of 9–14 March and 6 April to 1 May, were analysed (Yamaguchi et al., 2010a). The samples collected by two mesh sizes were used for different purposes—species identification for the fine-mesh samples and wet mass estimation for the coarse-mesh samples. Because the results of both mesh sizes (WM in the coarse-mesh samples and biovolume in the fine-mesh samples) were highly correlated ($r^2 = 0.92, p < 0.0001$), the temporal changes in both mesh net samples were confirmed to be similar (Yamaguchi et al., 2010a).

2.2. Enumeration and measurement

In the land laboratory, all of the chaetognaths from the Bongo net samples were sorted and enumerated by species under a stereomicroscope. For species identification, we referred to Nagasawa and Marumo (1976) and Terazaki (1996). For *E. hamata*, second dominant chaetognath species, there is a possibility of including *E. bathypelagica*. However, because of their vertical distribution (deeper than *E. hamata*) (Terazaki and Miller, 1986), and recent molecular analysis suggests possibility of that they (*E. hamata* and *E. bathypelagica*) are actually large one-species group (Miyamoto et al., 2012), we treated them as *E. hamata* in this study. Concerning the third dominant chaetognath species (*P. scrippsae*), although the possibility of synonymy of *P. lyla* was previously noted (Tokioka, 1974), we followed the taxonomic systematics of Alvariño (1962). For the three dominant chaetognaths (*E. hamata, P. elegans* and *P. scrippsae*), the body length (BL, mm) was measured using a micrometre calliper or eye-piece micrometre mounted in a stereomicroscope with a precision of 0.05–0.10 mm. For the two most abundant species, *E. hamata* and *P. elegans,* specimens were classified into five maturation stages (juvenile, stage I, II, III and IV) according to Thomson (1947), Terazaki and Miller (1986) and Johnson and Terazaki (2003) (Table 1). The dry mass (DM, μg ind.$^{-1}$) was estimated from the BL (mm) by the following equations varied with species:

E. hamata: $\text{Log}_{10}\ \text{DM} = 3.80\ \text{Log}_{10}\ \text{BL} - 0.79$ (Matsumoto, 2008)
P. elegans: $\text{Log}_{10}\ \text{DM} = 2.91\ \text{Log}_{10}\ \text{BL} - 0.79$ (Imao, 2005)
P. scrippsae: $\text{Log}_{10}\ \text{DM} = 3.24\ \text{Log}_{10}\ \text{BL} - 0.98$ (Uye, 1982).

The gut contents of the three dominant chaetognaths were identified by species and enumerated under a dissecting microscope. To avoid the effect of cod-end feeding, the food items observed at the forward 1/4 of the gut were not enumerated (Øresland, 1987). For the copepods in the gut contents of the chaetognaths, identification of the copepodid stage was made, if possible. When the swimming legs or urosome of the copepods were damaged, their stages were estimated from the prosome length (PL) of the dominant copepods in the Oyashio region (Ueda et al., 2008). The number of prey per chaetognath (NPC, no. of prey ind.$^{-1}$, Nagasawa and Marumo, 1972) was calculated for each species for each sampling date.

Considered from their vertical distribution in the Oyashio region (Ozawa et al., 2007), entire populations used in the two species (*P. elegans* and *P. scrippsae*) may be collected by the sampling method of this study (oblique tow of Bongo net from 0 to 200 m). For these two species, the feeding rates (FR : no. of prey consumed ind.$^{-1}$ day^{-1}) were calculated by the following formula:

$$\text{FR} = \text{NPC} \times 24/\text{DT}$$

where DT is digestion time (hour) (Nagasawa and Marumo, 1972). DT was estimated from the following formula:

$$\text{DT} = 10.24\text{e}^{-0.095T}$$

where T is the integrated mean temperature (°C) at 0–200 m (Sameoto, 1987). The daily feeding impact (no. of prey m^{-3} day^{-1}) was estimated by multiplying with FR and abundance (ind. m^{-3}). Using the mesozooplankton abundance data (ind. m^{-3}) quantified by the NORPAC net, the daily feeding impact of the chaetognaths, in terms of the percentage removal of the mesozooplankton abundance (%, day^{-1}), was also calculated.

2.3. Data analysis

2.3.1. FRA-ROMS

To clarify the origin of the water mass at the surface layer of each sampling date, re-analyses of the hydrographic data (temperature, salinity, sea surface height and geostrophic velocity) were performed using a 1/10° grid high-resolution ocean model known as the Fisheries Research Agency Regional Ocean Model (FRA-ROMS; Fisheries Research Agency of Japan, 2014, http://fm.dc.affrc.go.jp/fra-roms/index.html). Details of the methods were presented elsewhere (Abe et al., 2016). We initially released particles at the surface layers (depths of 10, 20, 30, 50, 75, 100, 125, 150 and 200 m) of the sampling station (42°00′N, 145°15′E) and conducted a particle backtracking experiment for the previous six months. We examined the temporal change in the locations of the released particles to determine the origin of the water and evaluated the experienced water temperature changes.

2.3.2. Cohort analysis on body length

For the two most dominant chaetognaths (*E. hamata* and *P. elegans*), the cohorts were analysed based on the BL frequency distribution data at each sampling date fitted to the normal distribution curves. The length–frequency data were separated into multiple normal distribution curves with the aid of the free software "R" with an add-on package "mclust" (Fraley et al., 2012).

2.3.3. Correlation analysis with environmental parameters

For the three dominant chaetognath species (*E. hamata P. elegans* and *P. scrippsae*), the abundance (ind. m^{-2}) and biomass (mg DM m^{-2}) of each species were quantified for each sampling date. Then, correlation analyses with the environmental parameters (e.g., Julian day from 1 March, integrated mean temperature, salinity, Chl. *a*, water mass mixing ratio at 0–50 m water column and zooplankton biomass in the 0–150 m water column) were performed.

3. Results

3.1. Hydrography

The temporal changes in the temperature, salinity, Chl. *a*, water mass mixing ratio and mesozooplankton biomass from 9 March to 1 May in 2007 during OECOS period are shown in Fig. 2. Throughout the study period, the temperature and salinity ranged from 2–6 °C and 33.2–34.2, respectively (Fig. 2(A), (B)). Chl. *a* had three peaks (2–6 mg m^{-3}) in 7, 11 and 23 April (Fig. 2(C)). For the water mass mixing ratio at 0–50 m water column, the OYW and MKW composed approximately half of the water mass during March. Cold COW occurred in early April, and the observed timing of the COW corresponded with the Chl. *a* peaks mentioned above. For the eleven Bongo net sampling dates, the dominant water masses varied: i.e., COW for 20 and 25 April, OYW for 14 March and 6 April and MKW for 9 March and 8, 10, 12, 15, 17 and 30 April (Fig. 2(D)).

From the FRA-ROMS analyses, the various origins of the water masses were estimated. The origin of COW was in the Okhotsk Sea, while the origin of OYW was at the east Kamchatka current, which flows along the southern edge of the Kurile chain (Fig. 1(C)). During 2006–2007, clockwise warm water eddies were observed around the Oyashio region, and the origin of MKW was associated with this warm water eddy (Fig. 1(C)). The experienced water temperatures during the past six months also varied significantly with the water masses ($p < 0.001$, one-way ANOVA) (Fig. 1(C)). The experienced temperatures of the COW, MKW and OYW were 1.5–6.0 °C (4.0 ± 1.4 °C : mean ± 1 sd), 3.6–8.1 °C (5.8 ± 1.4 °C) and 2.2–4.9 °C (3.3±0.6 °C), respectively. During the study period, the mesozooplankton biomass varied between 13.2 (9 March) and 93.9 (16 April) g WM m^{-2}, was low during March, and showed high values with ca. 7 times increase after 10 April (Fig. 2(E)).

3.2. Abundance and biomass

Throughout sampling period, three chaetognath species belonging to three genera were found (*E. hamata*, *P. elegans* and

Table 1
Classification of maturation stages for *Eukrohnia hamata* and *Parasagitta elegans* in the Oyashio region, western subarctic Pacific. These criteria were made by referring to Thomson (1947), Terazaki and Miller (1986) and Johnson and Terazaki (2003).

Stage	Species	
	Eukrohnia hamata	*Parasagitta elegans*
Juvenile	Primitive germ cells have not commenced to develop	Primitive germ cells have not commenced to develop
Stage I	Ovaries and testes as fine tubes	Ovaries are formed
Stage II	Ovaries longer	Ovaries longer and only small ova are present
Stage III	Ova developing	A few large ova visible and seminal vesicles present
Stage IV	Ovaries stretching two-thirds of the distance to ventral ganglion	All ova are large and seminal vesicles filled

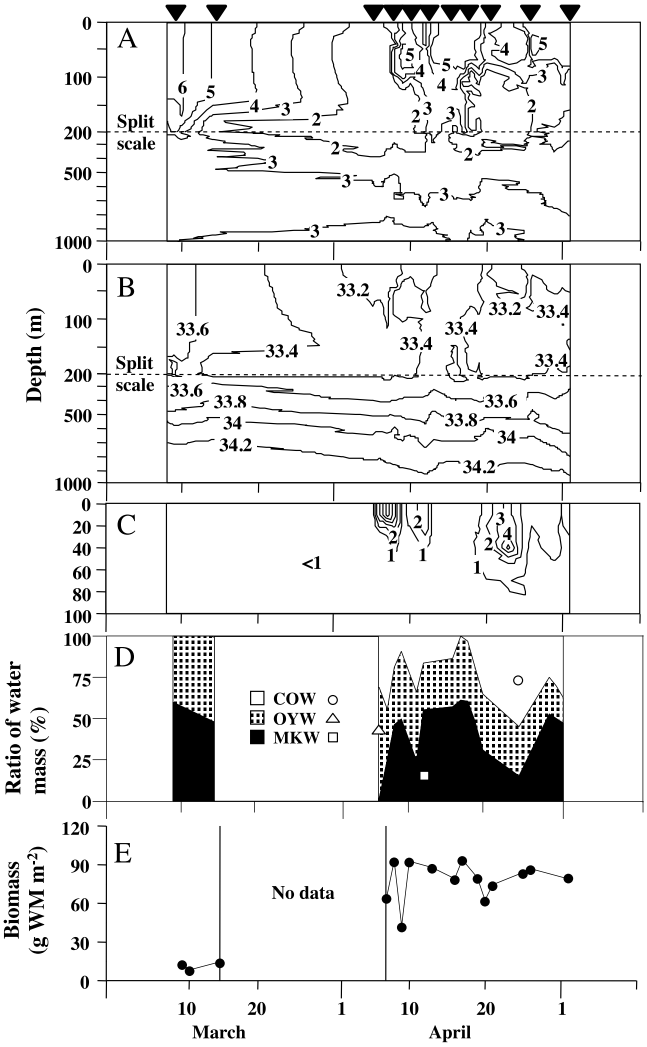


Fig. 2. Temporal changes in the temperature (A, °C), salinity (B), chlorophyll *a* (C, mg m^{-3}), the ratio of water mass at 0–50 m (D, %) and mesozooplankton wet mass at 0–150 m (E, mg WM m^{-2}) in the Oyashio region during 9 March to 1 May 2007. The data in D and E are from Kono and Sato (2010) and Yamaguchi et al. (2010a), respectively. The solid triangles on top abscissa in A indicate periods of the Bongo net samplings. The symbols in D indicate dates of FRA-ROMS analysis were made for each water mass (cf. Fig. 1(B)–(D)). COW; coastal Oyashio water, OYW; Oyashio water, MKW; mixed Kuroshio water.

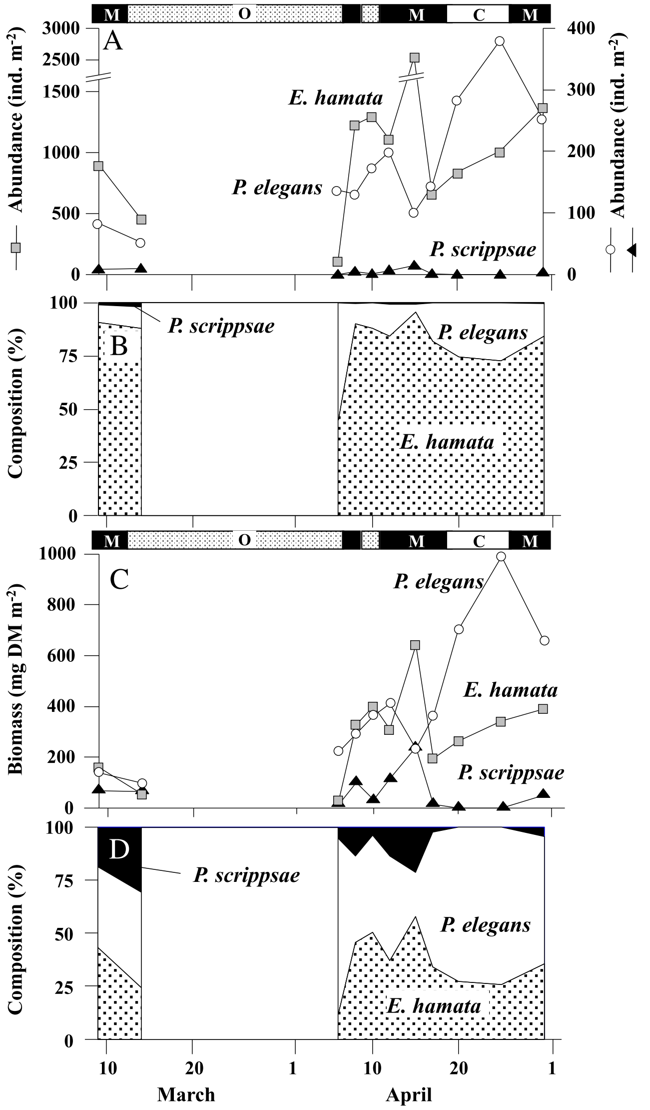


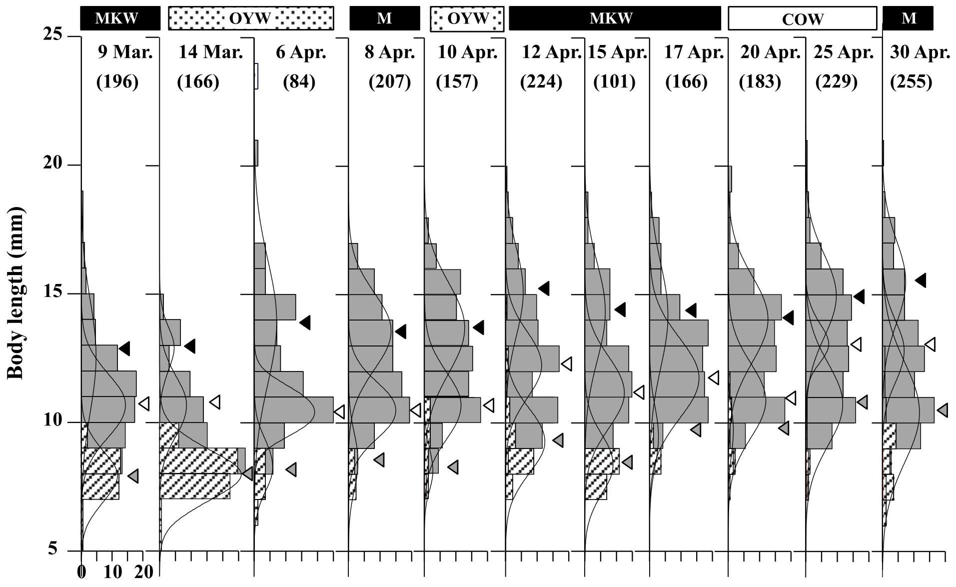
Fig. 3. Temporal changes in abundance (A), species composition in abundance (B), biomass (C) and species composition in biomass (D) of three chaetognaths (*Eukrohnia hamata*, *Parasagitta elegans* and *Pseudosagitta scrippsae*) in the Oyashio region during March–April 2007. C; coastal Oyashio water (COW), M; mixed Kuroshio water (MKW), O; Oyashio water (OYW).

P. scrippsae). Numerically, *E. hamata* and *P. elegans* dominated the chaetognath abundance (>95% total chaetognaths, Fig. 3(B)). While the abundance of *P. scrippsae* was less; because of the large body size of this species, the composition of *P. scrippsae* was increased in terms of biomass (Fig. 3(D)).

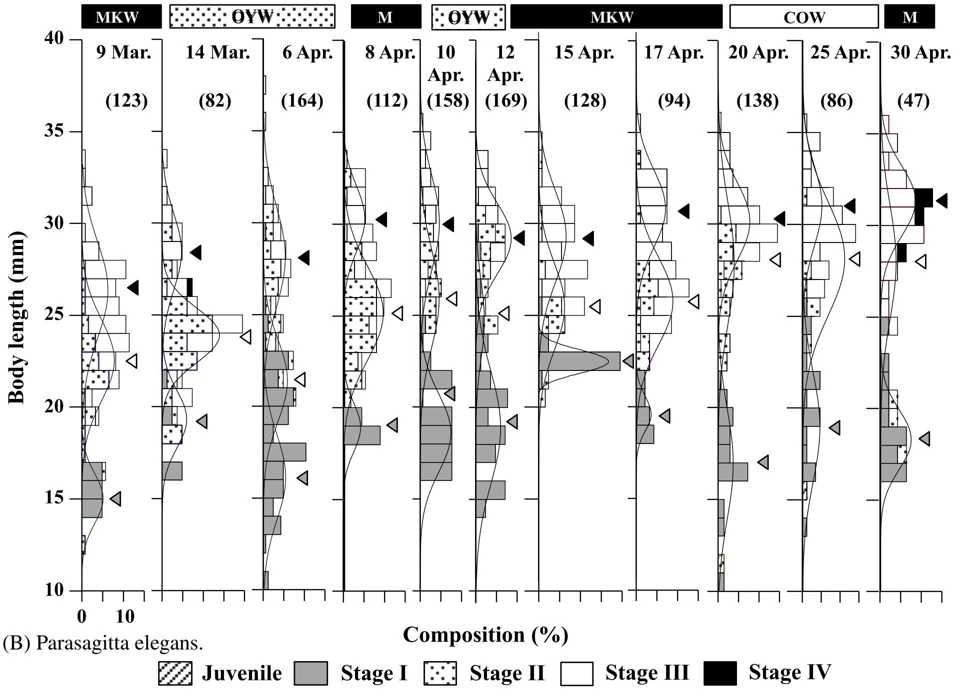
The abundance of *E. hamata* ranged between 113 and 2543 ind. m^{-2} (mean ± 1 sd : 1050 ± 594 ind. m^{-2}) during the study period (Fig. 3(A)). The biomass of *E. hamata* ranged between 31.2 and 640.8 mg DM m^{-2} (282.7 ± 165.0 mg DM m^{-2}). Both the abundance and the biomass of *E. hamata* were higher after 8 April 2007.

The abundance of *P. elegans* ranged between 52.4 and 380.4 ind. m^{-2} (176.0±92.4 ind. m^{-2}) during the sampling period (Fig. 3(A)). The biomass of *P. elegans* was at 95.8–988.8 mg DM m^{-2} (405.8 ± 258.9 mg DM m^{-2}) (Fig. 3(C)). Both the abundance and the biomass of *P. elegans* were higher after 20 April 2007.

The abundance of *P. scrippsae* ranged between 0 and 92.4 ind. m^{-2} (4.65 ± 4.72 ind. m^{-2}) during the sampling period (Fig. 3(A)). The biomass of *P. scrippsae* was at



(A) Eukurohnia hamata.



(B) Parasagitta elegans.

Fig. 4. Histograms showing the temporal changes in the body length of *Eukrohnia hamata* (A) and *Parasagitta elegans* (B) in the Oyashio region during 9 March to 30 April 2007. The numbers in the parentheses represent the number of individuals measured. Smooth curves indicate the results of cohort analysis. The mean body lengths of each cohort are shown with the triangles. COW; coastal Oyashio water, MKW; mixed Kuroshio water (M), OYW; Oyashio water.

0.0–237.9 mg DM m^{-2} (63.2 ± 66.4 mg DM m^{-2}) (Fig. 3(C)). The timing of the high biomass of *P. scrippsae* corresponded with the timing of MKW as dominant (Fig. 3(C), (D)).

3.3. Body size and growth rate

Throughout the study period, the BL of *E. hamata* and *P. elegans*, the two dominant chaetognath species, ranged from 5.8–23.7 mm and 11.0–41.3 mm, respectively (Fig. 4). Small specimens of *P. elegans* (<10 mm) were not observed during the study period. From cohort analyses, the BL histograms of both *E. hamata* and *P. elegans* could be divided into 3 cohorts throughout the study period. Temporally, all three cohorts of *E. hamata* showed significant growth of BL during spring, and their growth rates ranged from 39 to 50 μm day^{-1} (Fig. 5(A)). Additionally, for *P. elegans*, significant growth of BL was observed for all three cohorts and their growth rates ranged between 42 and 101 μm day^{-1} (Fig. 5(B)).

3.4. Food items and feeding impact

The most numerous food items of *P. elegans* were copepods (78.4%) (Table 2). Within the food items, the copepod *Eucalanus bungii* composed 23.8% followed by *Neocalanus* spp. (4.5%).

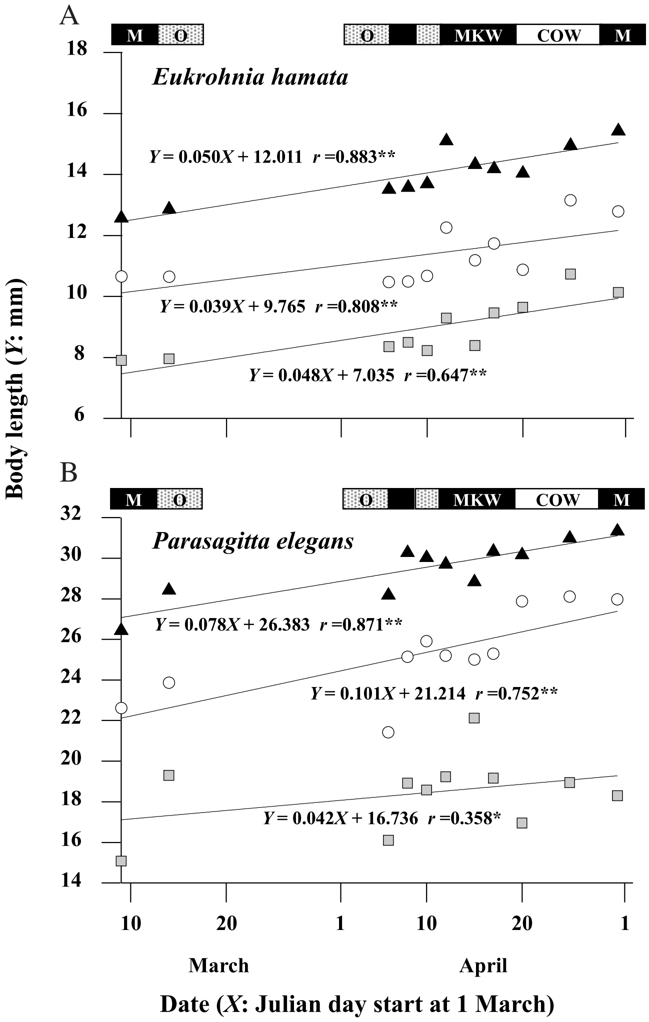


Fig. 5. Temporal changes in mean body length of each cohort of *Eukrohnia hamata* (A) and *Parasagitta elegans* (B), as identified in Fig. 4, in the Oyashio region during March–April 2007. Regressions between mean body length (Y: mm) and Julian day (X: March 1 as 1) are calculated for each cohort. *: $p < 0.05$, **: $p < 0.01$. COW; coastal Oyashio water, MKW or M; mixed Kuroshio water, O; Oyashio water.

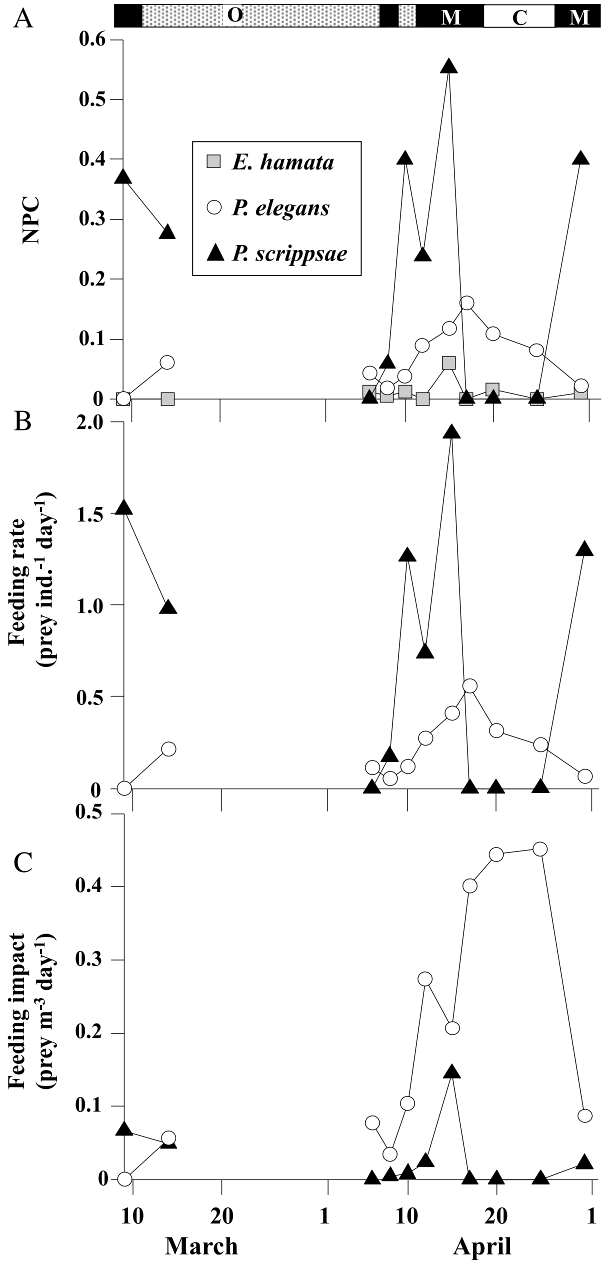


Fig. 6. Temporal changes in the number of prey per chaetognaths (NPC) for *Eukrohnia hamata*, *Parasagitta elegans* and *Pseudosagitta scrippsae* (A), feeding rate (B) and daily feeding impact (C) of *P. elegans* and *P. scrippsae* in the Oyashio region during March–April 2007. C; coastal Oyashio water, M; mixed Kuroshio water, O; Oyashio water.

The food items of *P. scrippsae* were also mainly composed of copepods (56.5%), while the prey copepod species varied with those of *P. elegans*. Thus, within the food items of *P. scrippsae*, *Metridia* spp. were dominant (25.1%), followed by *E. bungii* (10.5%). Because *E. hamata* was dominated by smaller BL specimens, amorphous items were dominant (60.0%) in their food items.

The temporal changes in the number of food items per chaetognath (NPC) are shown in Fig. 6(A). Throughout the study period, the NPC of *E. hamata* ranged between 0 and 0.0594 prey ind.$^{-1}$ (mean ± 1 sd : 0.0077 ± 0.0011), and the values remained low. NPC of *P. elegans* was 0–0.1590 prey ind.$^{-1}$ (0.0676 ± 0.0079) and peaked on 17 April. The NPC of *P. scrippsae* ranged between 0 and 0.5526 prey ind.$^{-1}$ (0.3357 ± 0.0253) and showed large variability with a high mean value. The timing of the high NPC values of *P. scrippsae* corresponded with the timing of the dominance of MKW in the water column (Fig. 6(A)).

The feeding rates of the chaetognaths ranged from 0 to 0.56 prey ind.$^{-1}$ day^{-1} (mean±1 sd : 0.22±0.16) for *P. elegans* and 0–1.94 prey ind.$^{-1}$ day^{-1} (mean±1 sd : 0.72±0.69) for *P. scrippsae* during the sampling period (Fig. 6(B)). The daily feeding impact (0–200 m) was 0–0.452 prey m^{-3} day^{-1} (mean ± 1 sd : 0.194 ± 0.163) for *P. elegans* and 0–0.145 prey m^{-3} day^{-1} (0.029 ± 0.042) for *P. scrippsae* (Fig. 6(C)). These values corresponded with the daily removal percentage on the total mesozooplankton abundance 0%–0.097% day^{-1} (*P. elegans*) and 0%–0.043% day^{-1} (*P. scrippsae*).

3.5. *Correlations with environmental parameters*

Ten environmental parameters had significant correlations with the abundance and biomass of the three dominant chaetognaths in the Oyashio region during the spring bloom (Table 3). Positive correlations were observed for six parameters: Julian day and *P. elegans* abundance or biomass, COW and *P. elegans* abundance or biomass, MKW and *P. scrippsae* abundance, and Chl. *a* and *P. elegans* abundance. Negative correlations were observed for four parameters: COW and *P. scrippsae* abundance, OYW and *E. hamata* abundance or biomass, and Chl. *a* and *P. scrippsae* abundance (Table 3).

Table 2
Food items observed in the gut of chaetognaths (*Eukrohnia hamata*, *Parasagitta elegans* and *Pseudosagitta scrippsae*) in the Oyashio region during March–April 2007. NPC: number of prey per chaetognath.

	Chaetognaths		
	E. hamata	*P. elegans*	*P. scrippsae*
Food item (%)			
Copepods			
Eucalanus bungii	–	12.5	–
Eucalanus bungii C2	–	–	2.1
Eucalanus bungii C3	–	–	2.1
Eucalanus bungii C5F	–	1.1	4.2
Eucalanus bungii C6F	–	10.2	2.1
Neocalanus cristatus	–	1.1	–
Neocalanus cristatus C4	–	2.3	–
Neocalanus sp.	–	1.1	–
Metridia pacifica	–	–	6.3
Metridia pacifica C5F	–	–	6.3
Metridia pacifica C6F	–	–	12.5
Pleuromamma scutullata C6F	–	–	2.1
Pseudocalanus sp.	–	–	2.1
Unidentified copepods	26.7	50.0	16.7
Chaetognaths			
Eukrohnia hamata	6.7	–	8.3
Parasagitta elegans	–	–	4.2
Appendicularians	6.7	–	–
Unidentified organisms	60.0	21.6	31.3
Number of individual food containing (n)	15	88	48
Number of total individual (n)	1938	1301	143
Grand mean of NPC	0.008	0.068	0.336

Table 3
Correlation coefficient (r) between environmental parameters (Julian day, integrated mean temperature, salinity, mixing ratio of water mass, chlorophyll *a* and mesozooplankton wet weight) and the abundance and biomass of the three dominant chaetognaths—*Eukrohnia hamata* (Eh), *Parasagitta elegans* (Pe) and *Pseudosagitta scrippsae* (Ps)—in the Oyashio region during March–April 2007. For details of the mixing ratio of the water masses, see Kono and Sato (2010). COW: coastal Oyashio water, MKW: modified Kuroshio water, OYW: Oyashio water.

Environmental parameter	Abundance (0–200 m)			Biomass (0–200 m)		
	Eh	Pe	Ps	Eh	Pe	Ps
Julian day	0.329	0.751^{**}	−0.469	0.545	0.767^{**}	−0.120
Temperature (0–50 m)	0.340	−0.402	0.465	0.198	−0.305	0.258
Salinity (0–50 m)	0.173	−0.542	0.473	0.005	−0.462	0.212
COW ratio of water mass (0–50 m)	0.041	0.848^{**}	-0.600^{*}	0.266	0.801^{**}	−0.392
MKW ratio of water mass (0–50 m)	0.395	−0.447	0.623^{*}	0.232	−0.362	0.538
OYW ratio of water mass (0–50 m)	-0.678^{*}	−0.476	−0.145	-0.732^{*}	−0.543	−0.300
Chl. *a* (0–150 m)	−0.168	0.609^{*}	-0.607^{*}	0.032	0.536	−0.326
Mesozooplankton wet weight (0–150 m)	0.059	0.494	−0.486	0.253	0.419	−0.141

* $p < 0.05$.
** $p < 0.01$.

4. Discussion

4.1. Effect of water mass exchange

The water mass exchanges that are characteristic of the Oyashio region during the spring, provide large variability in environmental conditions. Thus, high Chl. *a* was observed for the COW dominated timings (Kono and Sato, 2010). The size and taxonomic compositions of the pico- and nano-phytoplankton also varied with the water masses (Sato and Furuya, 2010). For the zooplankton taxa, the euphausiids showed high abundance under low temperature conditions (Kim et al., 2010a), and both the abundance and biomass of the hydromedusa *Aglantha digitale* were high during the COW-dominated timings (Abe et al., 2014). For amphipods, the taxa that perform strong diel vertical migration (DVM) showed little impact from the water mass exchanges at the surface layer (Abe et al., 2016).

In this study, positive correlations were observed between COW and *P. elegans* abundance or biomass, and between MKW and *P. scrippsae* abundance, while a negative correlation was observed between COW and *P. scrippsae* abundance (Table 3). Thus, the effects of the water mass exchange may be greater for chaetognaths than for other macrozooplankton taxa. The comparable case was amphipods. This taxon showed no or only extremely limited effects of the water mass exchange on species abundance and biomass (Abe et al., 2016). For the chaetognaths, it has been well known that each species has species-specific temperature and salinity ranges of occurrence. Because of these characteristics, chaetognaths are treated as water mass indicator organisms (Russell, 1935; Bieri, 1959).

Among the three species, *P. elegans* is known to occur at the shallowest depth (<250 m, Ozawa et al., 2007), to distribute in cold and less saline water masses and could not adapt and would die off under the warm core formed in the Oyashio region (Terazaki, 1992). These facts correspond with the positive correlation of the abundance and biomass of *P. elegans* with the COW originated in the Okhotsk Sea (Table 3). The Okhotsk Sea is the southernmost ice-covered ocean in the Northern Hemisphere (Zenkevitch, 1963). The cold and less saline water mass that is formed by melting ice in the Okhotsk Sea (Kono and Kawasaki, 1997) corresponds well the preferred hydrographic conditions of *P. elegans*,—as mentioned above (low temperature and low salinity, Terazaki, 1992).

On the other hand, *P. scrippsae* is known to occur at 0–300 m and is abundant in the warm core that separated from the Kuroshio Extension (Terazaki, 1992). *P. scrippsae* is also reported to be dominant in the southern transition domain along the 180°

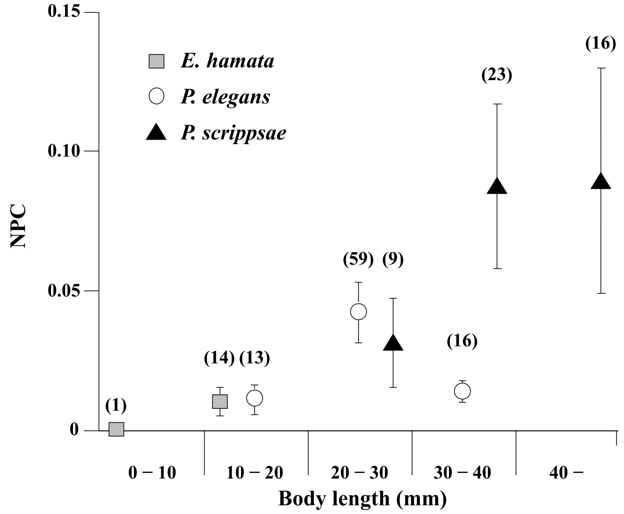


Fig. 7. Mean (symbols) and standard deviation (bars) of NPC presented for each 10 mm body length size class of three chaetognaths in the Oyashio region during March–April 2007. The numbers in the parentheses indicate the number of measured specimens.

meridian line in the central North Pacific (Nishiuchi et al., 1997). Thus, these facts suggest that *P. scrippsae* is a warmer-water species among the three species treated in this study. Because of these warm-water characteristics, the abundance of *P. scrippsae*may show a positive correlation with the MKW (originated from Kuroshio Extension), and a negative correlation with the COW (originated in the Okhotsk Sea) (Table 3).

The vertical distribution of *E. hamata,* is concentrated at 169–308 m depths (Ozawa et al., 2007), and their mature specimens are known to distribute below 250 m depths in the subarctic Pacific (Terazaki and Miller, 1986). These facts indicate that *E. hamata* is a mesopelagic species, while the other two species (*P. elegans* and *P. scrippsae*) are characterized as epipelagic species (Ozawa et al., 2007). Because *E. hamata* is characterized as a mesopelagic species, its abundance and biomass showed negative correlations with the OYW, the dominant water masses at the epipelagic layer in the Oyashio region (Table 3). Thus, the abundance and biomass of the mesopelagic *E. hamata* may decrease when the strengths of the epipelagic water masses are strong.

4.2. Food items and feeding impact

The mean NPC (no. prey ind.$^{-1}$) of the chaetognaths in this study was 0.336 for *P. scrippsae*, 0.068 for *P. elegans* and 0.008 for *E. hamata* (Table 2). These NPC values should be considered the differences of the BL by species. Thus, we compared the NPC values at each 10-mm BL interval (Fig. 7). From the comparison of the NPC, the NPC shows evidence of increasing with increasing BL, with the exception of the 30–40 mm BL of *P. elegans* (Fig. 7). Highly significant correlations were observed between the BL and head width (HW) for all of the chaetognath species (Fig. 8). These facts suggest that the wider body-size organisms are available as food for the larger BL chaetognath specimens. The increasing composition of large-sized food items with increasing BL has been reported for *P. elegans* in the North Sea and Gulf of Alaska (Brodeur and Terazaki, 1999; Saito and Kiørboe, 2001). The highest NPC of *P. scrippsae* in this study (Fig. 6(A)) might be caused by the largest BL of this species. The large BL may allow them to feed on wide-sized food items in the area and during the period of this study (Fig. 7). It also should be noted that gut passage-time of the large BL *P. scrippsae* is expected to be longer than the other species and thus may induce the high NPC of this species.

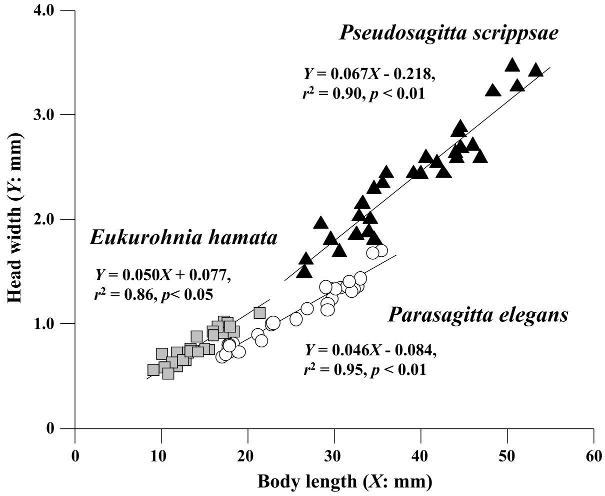


Fig. 8. Relationship between head width and body length of three chaetognaths in the Oyashio region during March–April 2007. Regressions are shown by species.

The mean feeding rates (FR, prey ind.$^{-1}$ day^{-1}) were 0.22 for *P. elegans* and 0.72 for *P. scrippsae* during the study period, (Fig. 6(B)). The FR of *P. elegans* has been reported from various locations. Thus, 0.7–0.9 for spring to summer and 0.2 for winter in the Swedish fjord (Øresland, 1987), 0.12 for the Arctic Ocean (Grigor et al., 2015) and 1.76–5.50 in the North Sea (Saito and Kiørboe, 2001) (Table 4). These FR values of *P. elegans* have a latitudinal pattern: thus, FR is low for high latitude oceans, while it is high for low latitude oceans (Table 4). This latitudinal pattern may reflect the differences in the habitat temperature (Feigenbaum, 1982; Grigor et al., 2015). Notably, that high FR have been reported for *P. elegans* in laboratory experiments (2.5 at 15 °C: Kuhlmann, 1977; 4.0 at 13 °C: Reeve, 1980).

The mean feeding impact of the chaetognaths in the Oyashio region were 0.194 no. prey consumed m^{-3} day^{-1} for *P. elegans* and 0.028 no. prey consumed m^{-3} day^{-1} for *P. scrippsae* (Fig. 6(C)). These values accounted for 0%–0.097% day^{-1} of the zooplankton abundance at 0–150 m for *P. elegans* and 0%–0.043% day^{-1} for *P. scrippsae* (Table 4). These values are lower than the values reported from other locations (0.08%–0.6% day^{-1}) (Table 4). In the Oyashio region during spring because various copepod species (*E. bungii*, *Metridia* spp., *Pseudocalanus* spp.) reproduce at a massive scale (Yamaguchi et al., 2014), the food organisms for chaetognaths may be sufficiently available. The abundant prey may decrease the feeding impact of the chaetognaths.

As notable characteristics of food items, the most important food organisms (25.1%) of *P. scrippsae* were the copepod *Metridia* spp. (Table 2). While for the sympatric chaetognath species, no *M. pacifica* was observed for the food items of the smaller body-sized *E. hamata* (BL: 5.8–23.7 mm) and *P. elegans* (11.0–41.3 mm) (Table 2). The swimming behaviour of *Metridia* spp. is reported to be a continuous cruising, and their swimming speed is reported to be 2.3–5.4 mm s^{-1} (Wong, 1988). *Metridia* spp. is known to have strong DVM (Takahashi et al., 2009; Yamaguchi et al., 2010b), and the speed of DVM behaviour is reported to be 6.4–9.2 mm s^{-1} (Hattori, 1989). While the swimming speed is faster for *Metridia* spp., the large body size of *P. scrippsae* (BL: 12.0–55.0 mm) may allow them to feed on *Metridia* spp. as prey.

4.3. Growth rate and reproduction

For *P. elegans*, the mature stage IV specimens with a BL of approximately 30 mm, occurred on 30 April 2007 (Fig. 4(b)). This suggests that reproduction may have started for *P. elegans* at end of April. The reproduction peak of *P. elegans* is reported to be

Table 4
Feeding rate of *Parasagitta elegans* and *Pseudosagitta scrippsae* from various oceans.

Chaetognath species	Feeding rate		Predation impact on zooplankton	Location	Habitat temperature	Reference
	(prey ind.$^{-1}$ day^{-1})	(prey m^{-3} day^{-1})	(%, ind. day^{-1})		(°C)	
Parasagitta elegans	0.12	0.66		Arctic area	Close to 0	Grigor et al. (2015)
	0.07–0.27	0.032–0.743		North Pacific	3.5–5.1	Matsuda and Taniguchi (2001)
	0–0.56	0–0.452	0–0.097	Site H, Western North Pacific	1–6	This study
	0.34	0.368		Gulf of Alaska	4.7–5.6	Brodeur and Terazaki (1999)
	0.2–0.9			Gullmarsfjorden	3–20	Øresland (1987)
	0.30–1.05		0.08–0.22	Barents Sea	−1.8 to −1.2	Falkenhaug (1991)
	0.33–0.77	0.001–0.1		Baffin Bay, Greenland	−1–4	Sameoto (1987)
	0.53–1.33			Vineyard Sound, Massachusetts	0	Feigenbaum (1982)
	0.75–3.55	2.34–66.34		Irish Sea	6–14	Alvarez-Cadena (1993)
	1.76–5.50			North Sea	10.6	Saito and Kiørboe (2001)
	2.71	16.77	0.3–0.6	Kandalksha Bay and White Sea		Solov'ev and Kosobokova (2003)
Pseudosagitta scrippsae	0–1.94	0–0.145	0–0.043	Site H, Western North Pacific	1–6	This study

Table 5
Growth rate of *Eukrohnia hamata* and *Parasagitta elegans* form various oceans.

Chaetognath species	Growth rate (μm day^{-1})	Location	Habitat temperature (°C) and depth	Reference
Eukrohnia hamata	6–20	Site H, Western North Pacific	2–17	Nishiuchi (1999)
	15	Site H, Western North Pacific	2.3–2.9 (>250 m)	Matsumoto (2008)
	39–50	Site H, Western North Pacific	1–6 (0–200 m)	This study
	83–100	Station P, Eastern North Pacific	3.8–6.0 (100–500 m)	Terazaki and Miller (1986)
Parasagitta elegans	14–44	high-Arctic fjord, Svalbard	−1.7–4	Grigor et al. (2014)
	20–70	Site H, Western North Pacific	2–17	Nishiuchi (1999)
	30–290	Western North Pacific	1.25–3.44 (100 m)	Kotori (1999)
	40–70	North Sea	6–17	Saito and Kiørboe (2001)
	42–101	Site H, Western North Pacific	1–6 (0–200 m)	This study
	69	Conception Bay, Newfoundland	−1.0	Choe and Deibel (2000)
	117–150	Celtic Sea	7.8–17.1	Conway and Williams (1986)
	150	Oslofjord, southern Norway		Jakobsen (1971)
	167–200	Station P, Eastern North Pacific	6.0–13.8 (surface)	Terazaki and Miller (1986)

late spring to summer in the Oyashio region (Terazaki, 1998; Kotori, 1999). From cohort analysis, 3 cohorts were identified for the BL of *P. elegans*, and the growth rates of each cohort were 42–101 μm day^{-1} (Figs. 4, 5). The growth rates of *P. elegans* were reported from various oceans and ranged from 14–44 μm day^{-1} for the Arctic fjord (Grigor et al., 2014) to 167–200 μm day^{-1} for the eastern subarctic Pacific (Terazaki and Miller, 1986) (Table 5). The growth rates of *P. elegans* in this study were within the range of these reported values. For *P. elegans*, Sameoto (1971) reported that generation length (GL: day) is negatively correlated with the temperature (t : °C) and their relationships were expressed with $\mathrm{GL} = 611.51/t^{0.811}$. These facts well confirm that the growth rates found in this study were between those of the cold Arctic Ocean and the warm eastern subarctic Pacific.

For *E. hamata*, the deeper distribution (>250 m) of the mature specimens was well documented (Terazaki and Miller, 1986). The sampling depth of this study (0–200 m), may have resulted in the collection of only small-sized immature specimens. In the Oyashio region, the recruitment of new a generation is reported to be at spring to summer (Matsumoto, 2008). Juvenile specimens occurred in this study (Fig. 4(A)). The growth rates of each cohort of *E. hamata* ranged between 39–50 μm day^{-1} (Fig. 5(A)). These values were higher than the values based on the annual samples in the Oyashio region (6–20 μm day^{-1}, Nishiuchi, 1999; Matsumoto, 2008), while they were lower than the values in eastern subarctic Pacific (83–100 μm day^{-1}, Terazaki and Miller, 1986) (Table 5). An explanation of the higher growth rates in this study than the values found with annual-based observation, the growth rates in this study are based on small-sized specimens at shallower depths (0–200 m) (note that Matsumoto, 2008 collected samples from 0–1000 m depths). Seasonal changes in growth rate are also reported for *E. hamata* in the Oyashio region, and high growth rates were observed for spring to summer, while low growth rate was the case in winter (Matsumoto, 2008). Because this study treated only smaller specimens at shallower depths during the faster growing season in spring, the growth rates of this study might be faster than the previous study in same region (Matsumoto, 2008). The faster growth rates in the eastern subarctic Pacific (Terazaki and Miller, 1986) might be caused by the high habitat temperature (3.8–6.0 °C) compared with that in the Oyashio region western subarctic Pacific (0.9–6.1 °C) (Table 5).

The comparison of the growth rates of the two sympatric chaetognath species in this study showed that the growth rates of *P. elegans* (42–101 μm day^{-1}) were faster than those of *E. hamata* (39–50 μm day^{-1}) (Fig. 5). Because of the deeper vertical distribution of *E. hamata* than that of *P. elegans* in the Oyashio region (Ozawa et al., 2007), the habitat temperature of *E. hamata* is expected to be lower than that of *P. elegans*. Within the species (*P. elegans*), the growth rate is known to increase with increasing habitat temperature (Sameoto, 1971). In addition to the temperature, the abundance and biomass of the zooplankton and copepods, major prey of chaetognaths, were high at the surface layer and decreased exponentially with increasing depth in the Oyashio region (Yamaguchi et al., 2002, 2004). Considering habitat temperature and food density, the growth rates of the mesopelagic chaetognaths are expected to be slower than those of epipelagic species. In the eastern subarctic Pacific, the growth rate of mesopelagic *E. hamata* (83–100 μm day^{-1})

is reported to be slower than that of the sympatric epipelagic *P. elegans* (167–200 μm day^{-1}) (Terazaki and Miller, 1986). In the present study, this pattern (slower growth rate of *E. hamata* [39–50 μm day^{-1}] than that of *P. elegans* [42–101 μm day^{-1}]) was well documented (Table 5).

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