Seasonal changes in the community structure of chaetognaths and the life cycle of the dominant chaetognath *Eukrohnia hamata* in the Oyashio region, western subarctic Pacific

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Abstract: The community structure and life cycle of dominant chaetognath species were studied in a 0–1000–m water column in the Oyashio region, western subarctic Pacific, six times during the year from March 2003 to February 2004. The abundance of chaetognaths ranged from 3235 to 6691 inds. m^{-2}. Throughout the study period, ten chaetognath species belonging to nine genera were identified. Among the chaetognaths, *Eukrohnia hamata* accounted for 39–62% of the abundance, followed by *E. hamata*/*Eukrohnia bathypelagica* juveniles, *Parasagitta elegans*, and *E. bathypelagica*. The species diversity (*H'*) of chaetognaths varied between 1.12 and 1.50. For *E. hamata*, individuals had a body length ranging from 2.3–23.8 mm. The abundance of juveniles fluctuated from 22.0–48.3% and was higher in June 2003. Based on cohort analysis, recruitment of *E. hamata* juveniles occurred from spring to summer, and they reached a body length of 8 mm in one year. The overwintered population showed rapid growth from June to October, when they reached 15 mm in body length. *Eukrohnia hamata* showed little growth in winter and reproduced the subsequent spring. Thus, a two–year life cycle of *E. hamata* is proposed for the population in the Oyashio region. For comparable information about the life cycle of *E. hamata*, an eight to ten–month generation length was reported for the population in the eastern subarctic Pacific. These regional differences in the generation length of *E. hamata* are attributed to differences in habitat temperature, with much higher temperatures in the eastern (3.8–6.0℃) than the western (2.3–2.9℃) subarctic Pacific.

Key words: chaetognaths, *Eukrohnia hamata*, life cycle, mesopelagic, Oyashio region

Introduction

Chaetognaths occur only in marine environments, having adapted to pelagic, benthic, coastal, and oceanic environments. For pelagic chaetognaths, 115 species have been reported globally (Bieri 1991), with more than 40 species occurring in the Pacific (Pierrot–Bults & Nair 1991) and 32 species present in the neighbouring waters of Japan (Terazaki 1996). Since each species prefers certain thermal and haline ranges, pelagic chaetognaths are used as water–mass indicator species (Bieri 1959). For most oceans,

the chaetognath biomass is large, following copepods, and it accounts for 10–30% of the copepod wet weight biomass (Ryther 1969, Reeve 1970). Planktonic chaetognaths are carnivores, feeding mainly on copepods, with protozooplankton, euphausiids, amphipods, crustacean larvae, and fish eggs and larvae having been reported as other food organisms (Feigenbaum 1991). Chaetognaths feed upon higher trophic levels such as fish (David 1955, Reeve 1966), which suggests that they have an important role in the material transfer that connects secondary producers and higher trophic levels.

Many studies of chaetognaths have reported the life cycles (Hirota 1959, Murakami 1959, 1966, Nagasawa & Marumo 1972, 1977, 1978, Nagasawa 1991, Kotori 1999)

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and food organisms (Nagasawa & Marumo 1972, King 1979) of neritic and epipelagic species of the family Sagittidae in the North Pacific, however, ecological information on mesopelagic species is scarce. The life cycle of mesopelagic chaetognaths has been reported in the Gulf of Alaska (Terazaki & Miller 1986) and the Oyashio region (Nishiuchi 1999). Regarding food items for mesopelagic chaetognaths, several studies have been published (Sullivan 1980, Terazaki & Marumo 1982). Despite their numerical dominance, information on the life cycles of mesopelagic chaetognaths is scarce.

In the present study, we analysed seasonal changes in the community structure of epi– and mesopelagic chaetognaths in the Oyashio region. The life cycle of the dominant mesopelagic chaetognath *Eukrohnia hamata* (Möbius, 1875), was evaluated by cohort analysis of body length and gonad maturation. These life cycle data were compared with those in the Gulf of Alaska, and specialized characteristics in the Oyashio region were evaluated.

Materials and Methods

Field sampling

Sampling was conducted at Site H (41°30′N, 145°50′E) in the Oyashio region during cruises of the T/S *Oshoro–Maru* and *Ushio–Maru* on six occasions with two–three–month intervals from 13 March 2003 to 8 February 2004 (Fig. 1, Table 1). Zooplankton samples were collected by oblique hauls of a flowmeter–incorporating Bongo net (70-cm mouth diameter, 335-μm mesh size) from 0–1000-m depths and preserved in borax–buffered 5% (v/v) formalin seawater. On each occasion, the temperature and salinity were measured by CTD (Sea–Bird Electronics, SBE911Plus).

Sample analyses

After measuring the weights of whole samples immersed in formalin–seawater, the samples were stirred well with the aid of a glass bar. Then, 500 ml of seawater containing zooplankton was injected into a jar to generate the subsample. The volumetric split ratio of such subsamples were 14.8–23.8% (Table 1). Based on the subsamples, sorting, species identification, and counting of

chaetognaths were performed under a stereomicroscope. For species identification, we referred to Yamaji (1984) and Terazaki (1996).

Gonad maturation and body lengths were measured for the most abundant species, *Eukrohnia hamata*. *Eukrohnia hamata* is reported to be difficult to distinguish from *Eukrohnia bathypelagica* according to phylogenetic (mtDNA) analyses (Miyamoto et al. 2012). Notwithstanding, the abundance of *E. bathypelagica* was low enough in this study (cf. Table 1) that we discounted. Thus, if any contamination with *E. bathypelagica* occurred, the effect on the results was considered to be small, and we have treated the *E. hamata*/*bathypelagica* species group as *E. hamata* in this study. Gonad maturation was separated into five stages following Thomson (1947) and Terazaki & Miller (1986):

Juvenile: the ovary is not visible
Stage I: the ovary is developed
Stage II: small eggs are visible in the ovary
Stage III: some large eggs are visible in the ovary
Stage IV: all the eggs in the ovary are large
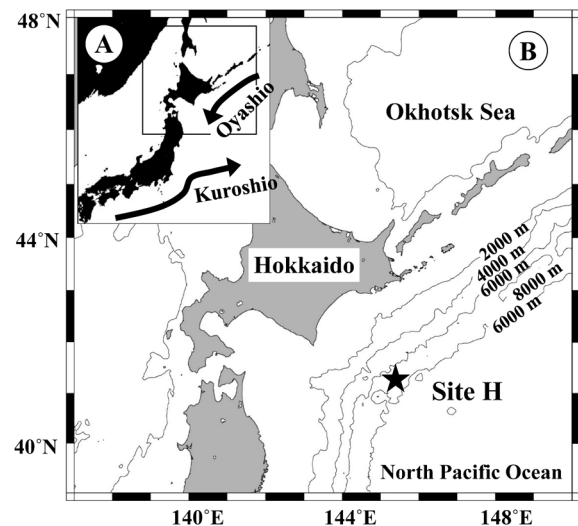For juveniles, species identification between *E. hamata*

Fig. 1. Location of the Oyashio region in the western subarctic Pacific (A) and sampling site (Site H) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in (B).

Table 1. Sampling information for chaetognaths collected by Bongo nets (335-μm mesh) in the Oyashio region. Abbreviations of the ship's names are Os: T/S *Oshoro Maru*, Us: T/S *Ushio Maru*.

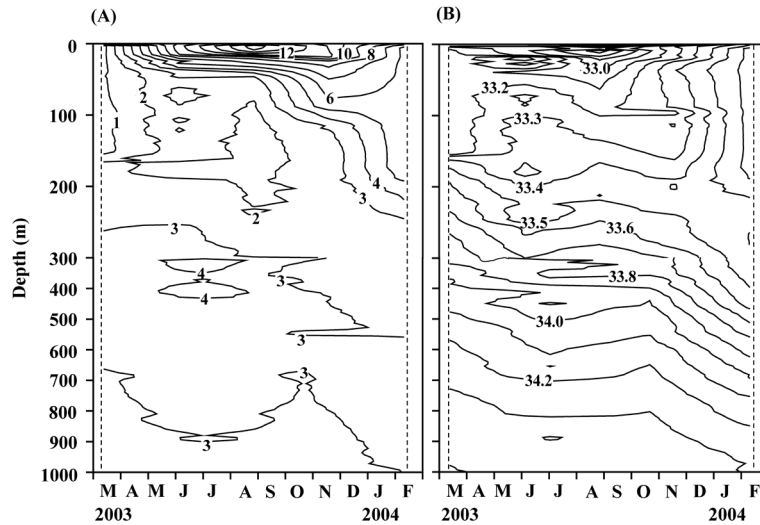| Sampling date	Sampling Day/Night	Ship	Volume of water filtered (m^3)	Subsample examined (%)
13 Mar. 2003	Night	Os	1736	23.6
4 June 2003	Day	Os	1726	12.9
23 Aug. 2003	Night	Os	1691	16.9
5 Oct. 2003	Day	Us	1323	21.4
17 Dec. 2003	Day	Os	2525	22.2
8 Feb. 2004	Day	Os	2149	14.8

Fig. 2. Seasonal changes in vertical profiles of temperature (A) and salinity (B) in the Oyashio region, western subarctic Pacific.

and *E. bathypelagica* was difficult, and they were treated as *E. hamata/E. bathypelagica* juveniles in this study. For small specimens (<10 mm), body length was measured with an eye–piece micrometre with a precision of 0.01 mm. For large specimens (≥10 mm), body length was measured using a slide calliper with a precision of 0.1 mm.

Community structure

The number of chaetognath individuals (*n*) was converted to abundance for the 0–1000 m water–column standing stock (*N*: inds. m^{-2}) using the following equation:

$$N = \frac{(n \times D)}{(s \times F)}$$

where *D* is the depth (m) to which the net was lowered, *s* is the split ratio of each sample, and *F* is the volume of filtered water (m^3). We applied *D*=1000 for all samples used in this study.

Based on the abundance data for each sampling period, the species diversity (*H'*) was calculated using the following equation (Shannon & Weaver 1949):

$$H' = -\sum p_i \ln p_i$$

where p_i indicates the proportion of the *i*th species in total abundance.

Life cycle of *Eukrohnia hamata*

For *E. hamata* and *E. hamazta/E. bathypelagica* juveniles, cohort analyses of body length histogram data were performed using Microsoft Excel Solver (Aizawa & Takiguchi 1999). To evaluate the growth of *E. hamata* and *E. hamata/E. bathypelagica* juveniles, the body length growth curve was expressed using the von Bertalanffy equation:

$$l_t = l_{max}(1 - e^{-K[t-t_0]})$$

where *t* is the age (year), l_t is the estimated body length at time *t* (mm), *K* is the growth coefficient, t_0 is the age when the body length is zero, and l_{max} is the asymptotic size. For analysis of the von Bertalanffy equation, we used the Microsoft Excel Solver function (Gorie 2001).

Results

Hydrography

Throughout the study period, the sea surface temperature ranged between 0.7°C (March 2003) and 14.5°C (August 2003), and the temperature below 250 m ranged from 2.5–3.5°C (Fig. 2A). Salinity at the sea surface ranged from 31.4 (June 2003) to 33.5 (February 2004). Salinity increased with increasing depth and reached 34.4 at 1000 m (Fig. 2B). T–S diagrams at each sampling date are shown in Fig. 3. Based on the water mass classification by Ohtani (1971), cold (≤3°C) and fresh (33.0–33.3) Oyashio water was observed at depths above 200 m, except in February 2004. The effect of a warm core ring (temperature ≥4°C and salinity ≥33.5) was detected for the surface layer in December 2003 (0–50 m) and February 2004 (0–200 m) (Fig. 3).

Chaetognath community structure

The chaetognath standing stock in the 0–1000 m water column ranged from 3235 inds.m^{-2} (December 2003) to 6591 inds.m^{-2} (June 2003) (mean: 4722 inds.m^{-2}, Table 2). Throughout the study period, ten species belonging to nine genera were observed: *Caecosagitta macrocephala* (Fowler, 1904); *Eukrohnia bathypelagica* Alvariño, 1962; *Eukrohnia hamata* (Möbius, 1875); *Krohnitta subtilis* (Grassi, 1881); *Mesosagitta minima* (Grassi, 1881); *Parasagitta elegans* (Verrill, 1873); *Pseudosagitta lyra* (Krohn, 1853); *Sagitta bipunctata* Quoy & Gaimard, 1827; *Solidosagitta zetesios* (Fowler, 1905); *Zonosagitta nagae* (Alvariño, 1967).
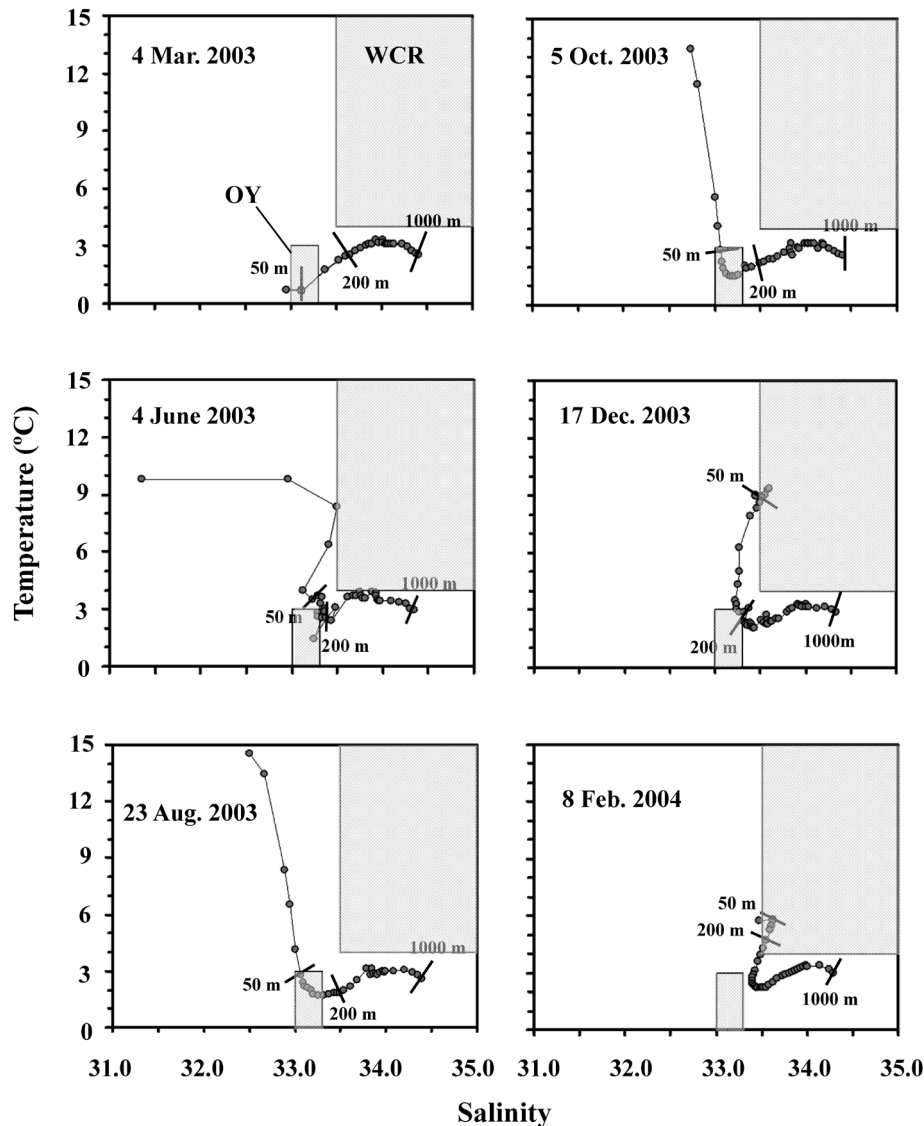
Fig. 3. Seasonal changes in the T–S diagram in the Oyashio region. T–S ranges of Oyashio (OY) and the Warm Core Ring (WCR) are presented as shaded rectangles (cf. Ohtani 1971).

Eukrohnia hamata dominated throughout the year (39–62% of the abundance), followed by *E. hamata/E. bathypelagica* juveniles, *P. elegans,* and *E. bathypelagica*. The above three species composed 83–99% of the chaetognath abundance (Table 2). For each sampling date, five to seven chaetognath species were observed. For June 2003, *K. subtilis* and *S. bipunctata* were detected. From December 2003 to February 2004, *M. minima, S. zetesios,* and *Z. nagae* were identified. The species diversity (*H'*) ranged from 1.12 (October 2003) to 1.50 (December 2003) (Table 2).

Population structure of *Eukrohnia hamata*

For the dominant chaetognaths, the population structure of *Eukrohnia hamata* and *E. hamata/Eukrohnia bathypelagica* juveniles was analysed. The abundance of *E. hamata* and *E. hamata/E. bathypelagica* juveniles ranged from

2314 inds.m^{-2} (December 2003) to 5006 inds.m^{-2} (June 2003). Body length ranged from 2.3 to 23.8 mm (Fig. 4). Within the population, *E. hamata/E. bathypelagica* juveniles and stage I dominated for more than 60% of the year (Fig. 5). The composition of juveniles was high (45–48%) in March and June 2003 and low (22–25%) in October and December 2003. Reproductive individuals (stage IV) were abundant (3.3%) in February 2004 and did not occur in August 2003.

On each sampling date, two to three cohorts were observed for *E. hamata* (Fig. 6). The mean body length of each cohort varied from 4.7 mm to 15.6 mm. The cohorts with both the smallest and largest mean body length were observed in June 2003. The means and standard deviations of each cohort were determined using a time course beginning with the smallest cohort in June (Fig. 7). Based on this analysis, one cohort was found to reach a body length

Table 2. Abundance (inds. m^{-2}) and species composition (%) of chaetognaths in the Oyashio region (0–1000 m), western subarctic Pacific. The species diversity index (H') is also calculated.

Species	2003										2004	
	13 Mar.		4 June		23 Aug.		5 Oct.		17 Dec.		8 Feb.	
	inds.m^{-2}	%	inds.m^{-2}	%	inds.m^{-2}	%	inds.m^{-2}	%	inds.m^{-2}	%	inds.m^{-2}	%
Eukrohniidae												
Eukrohnia bathypelagica	365	7.8	383	5.8	299	7.2	220	5.2	144	4.5	282	5.1
Eukrohnia hamata	2063	44.3	2586	39.2	1941	46.9	2595	61.9	1738	53.7	3090	56.1
E. hamata/E. bathypelagica juveniles	1682	36.1	2414	36.6	1300	31.4	731	17.4	575	17.8	1616	29.3
Eukrohnia spp.	10	0.2	—	—	—	—	—	—	4	0.1	6	0.1
Sagittidae												
Caecosagitta macrocephala	5	0.1	—	—	10	0.3	—	—	4	0.1	9	0.2
Krohnitta subtilis	—	—	4	0.1	—	—	—	—	—	—	—	—
Mesosagitta minima	—	—	—	—	—	—	—	—	274	8.5	3	0.1
Parasagitta elegans	197	4.2	1154	17.5	577	13.9	576	13.7	209	6.5	127	2.3
Pseudosagitta lyra	5	0.1	36	0.5	3	0.1	7	0.2	70	2.2	115	2.1
Sagitta bipunctata	—	—	4	0.1	—	—	—	—	—	—	—	—
Solidosagitta zetesios	—	—	—	—	—	—	—	—	—	—	3	0.1
Zonosagitta nagae	—	—	—	—	—	—	22	0.5	83	2.6	—	—
Sagittidae spp.	2	0.1	—	—	7	0.2	11	0.3	5	0.2	—	—
Unidentified	334	7.2	9	0.1	3	0.1	32	0.8	130	4.1	257	4.7
Total	4662	100.0	6591	100.0	4142	100.0	4193	100.0	3235	100.0	5509	100.0
Number of species	5		6		5		5		7		7	
Diversity index (H')	1.28		1.25		1.22		1.12		1.50		1.17	

of 15 mm in two years. These findings indicated that *E. hamata* had a two–year generation length in the Oyashio region. Growth in body length through time can be expressed by the von Bertalanffy equation:

$$l_t = 34.8(1 - e^{-0.25[t+0.37]})$$

where *t* is time (year) and l_t is the body length (mm) at time *t*. The mean body length in the cohort was larger than the von Bertalanffy equation during summer to autumn, while it was smaller than the von Bertalanffy equation during winter to spring (Fig. 7).

Discussion

Chaetognath community structure

The number of species was lower in our study (10 species) than in a previous study in the Oyashio region (15 species; Nishiuchi 1999). A deep–sea species, *Eukrohnia fowleri* (Ritter–Záhony, 1909), and four warm–water species, *Aidanosagitta regularis* (Aida, 1897), *Decipisagitta decipiens* (Fowler, 1905), *Flaccisagitta enflata* (Grassi, 1881) and *Serratosagitta pseudoserratodentata* (Tokioka, 1939), were reported by Nishiuchi (1999) but did not occur in our study. While the sampling frequency employed by Nishiuchi (1999) was high (fifteen times per year), these

warm–water species were collected on only one or two occasions. They were considered to be transported by a warm core ring (Terazaki 1992, Johnson & Terazaki 2003). Compared with Nishiuchi (1999), the low frequency of sampling (six vs fifteen times per year) in this study might have prevented the collection of these rare warm–water species.

Ozawa et al. (2007) reported that the species diversity varied greatly between the subarctic and the subtropical regions; the species diversity was lower (H'=1.22–1.38) in the subarctic region and higher (H'=2.17–2.35) in the subtropical region. The regional pattern corresponded well with that known on larger geographical scales (e.g. Indo–Pacific region) (Miyamoto et al. 2014). The species diversity in this study (H'=1.12–1.50; species number 5–7) corresponded well to the values in the subarctic region reported by Ozawa et al. (2007).

With regards to seasonal changes in the chaetognath community structure in the Oyashio region, interestingly, the timing of warm–water species occurrence varied with the species. Thus, *Krohnitta subtilis* and *Sagitta bipunctata* were observed in June 2003, while *Mesosagitta minima, Solidosagitta zetesios*, and *Zonosagitta nagae* were abundant from December 2003 to February 2004 (Table 2). These periods (June, December 2003, and February 2004) corresponded with the timing of the occurrence of the
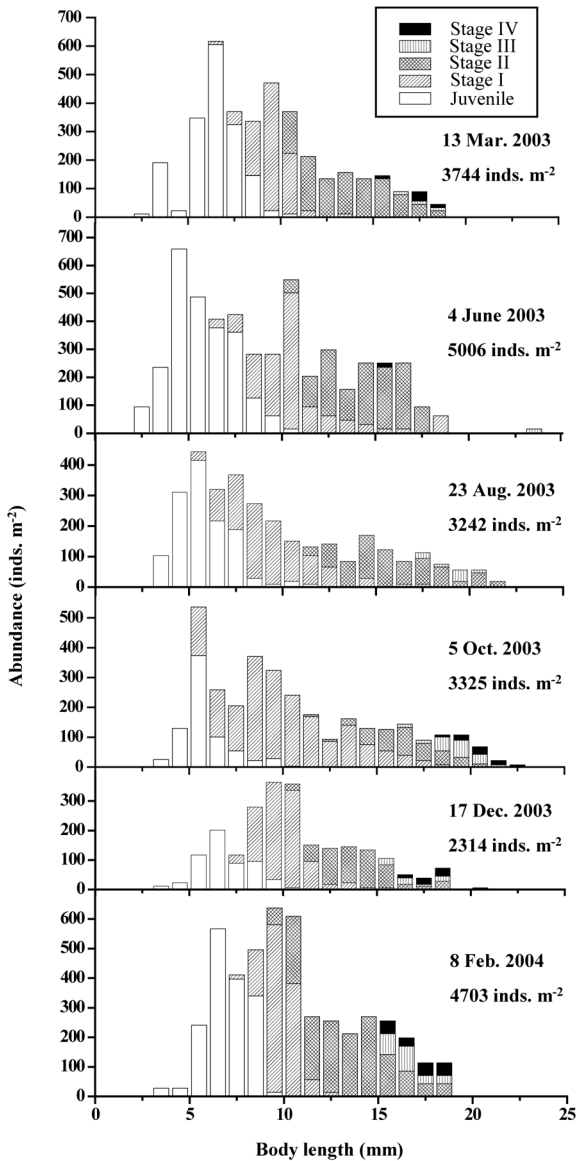
Fig. 4. Body length distribution and maturity stage composition of *Eukrohnia hamata* (Stage I–IV) and *E. hamata/E. bathypelagica* juveniles in the Oyashio region (0–1000 m), western subarctic Pacific.
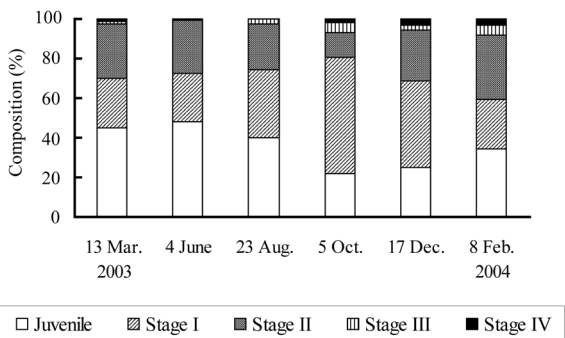

Fig. 5. Seasonal changes in maturity stage composition of *Eukrohnia hamata*, including *E. hamata/E. bathypelagica* juveniles, in the Oyashio region, western subarctic Pacific.
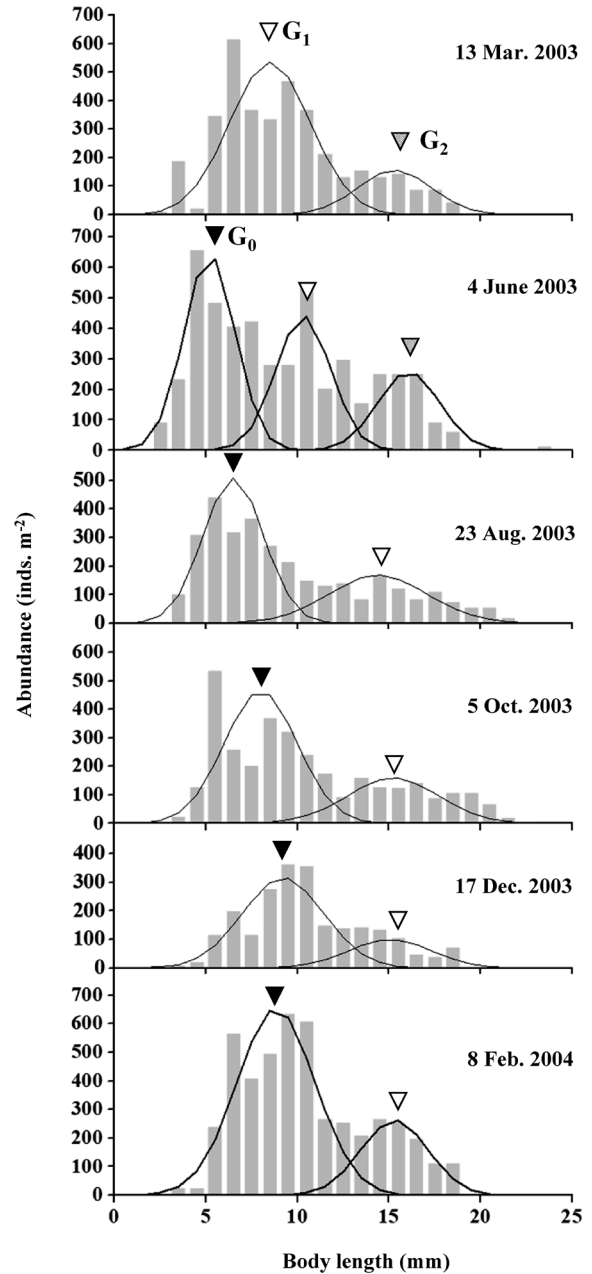

Fig. 6. Seasonal changes in the cohort composition of *Eukrohnia hamata* in the Oyashio region, western subarctic Pacific. G_0, G_1, and G_2 represent the cohort aged +0, +1 and +2 years old. Triangles indicate the peak length of each cohort.

warm–core ring observed in the T–S diagram (cf. Fig. 3).

Life cycle of *Eukrohnia hamata*

Eukrohnia hamata, the dominant chaetognath in the Oyashio region, is distributed worldwide in oceanic regions and is abundant and distributed in the near–surface layer in high–latitude oceans (Froneman & Pakhomov 1998, Kruse et al. 2010, Kosobokova & Isachenko 2017) but scarce in the meso– and bathypelagic layers of low–latitude oceans (Alvariño 1965). The life cycle of *E. hamata* varied among the regions: a two–year generation length
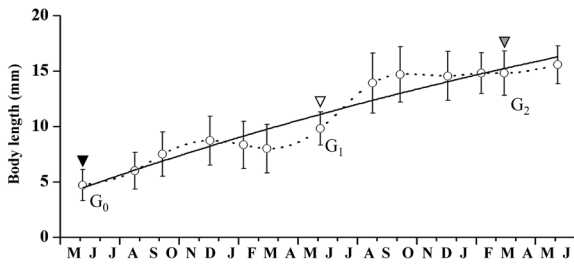
Fig. 7. Estimated growth curve of *Eukrohnia hamata* in the Oyashio region, western subarctic Pacific. Dots and bars indicate means and standard deviations of body length, respectively. Symbols of G_0, G_1, and G_2 (+0, +1 and +2 years old) correspond with those in Fig. 6. The solid line denotes the fitted von Bertalanffy's growth curve.

in a Nordic fjord (Korsfjorden), Barents Sea, Baffin Bay, and Beaufort Sea (Bogorov 1940, Sands 1980, Sameoto 1987, Grigor et al. 2017), eight to ten months with three discrete generations in a year in the Gulf of Alaska (Terazaki & Miller 1986), and a four–year generation length in the Oyashio region (Nishiuchi 1999). Our study showed a two–year generation length with reproduction occurring during October to March (Fig. 4).

For the studies in the Oyashio region, the filtered volumes in our study were higher (1,323–2,525 m³) compared to the other study (4–432 m³; Nishiuchi 1999). This difference was due to differences in the sampling methods, where Nishiuchi (1999) sampled much deeper (0–2000 m), owing to employing vertically stratified hauls of a smaller mouth ring (60-cm) and a smaller mesh size (100 μm). In this study, the sampling depth was shallow (0–1000 m), and samples were collected by oblique hauls of large mouth rings (70-cm) with a large mesh size (335 μm). Thus, because of the large filtered volumes, the number of chaetognath individuals collected was much greater in this study. Because the number of collected individuals was low, Nishiuchi (1999) combined data into two periods; December–May and June–October, and based analyses on these two periods, thereby assessing the life cycle of *E. hamata*. Conversely, since a sufficient number of individuals was collected at each sampling date during the present study, a cohort analysis could be performed at each sampling date with two–month intervals throughout the year.

As mentioned in Materials and methods, distinguishing the two species (*E. hamata* and *E. bathypelagica*) is difficult for juveniles without a visible ovary. In a molecular analysis, both *E. hamata* and *E. bathypelagica* are classified into a single–species group (Miyamoto et al. 2012). From the perspective of phylogenetic distance, regional differences in *E. hamata* have been detected, with differences between *E. hamata* and *E. bathypelagica* within a region therefore being inevitable (Miyamoto et al. 2012, Kulagin et al. 2014). These findings suggest that combining *E. hamata*/*E. bathypelagica* juveniles may be allowable for life cycle analysis of the single–species group of
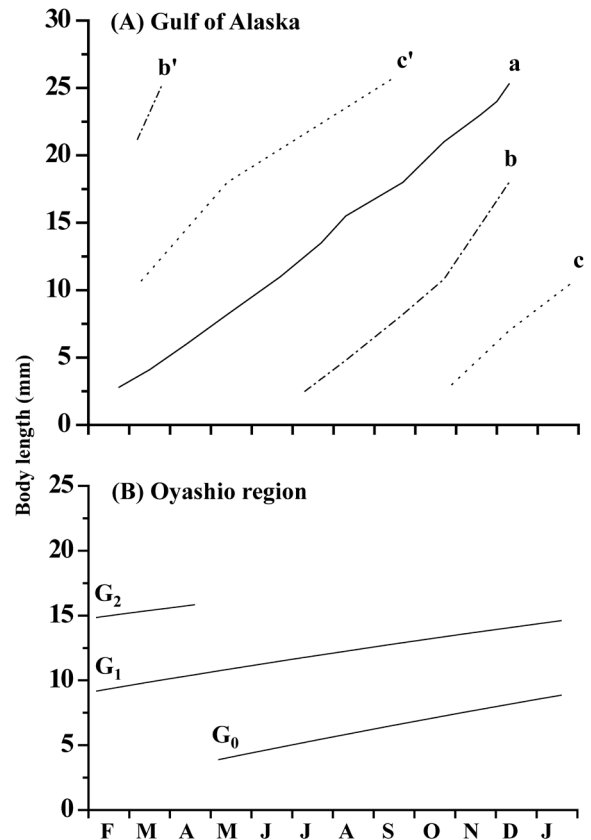

Fig. 8. Growth curves of *Eukrohnia hamata* in the Gulf of Alaska (Terazaki & Miller 1986) (A) and in the Oyashio region (B). Note that three discrete cohorts (shown as a, b–b′ and c–c′) are observed over the year in the Gulf of Alaska while only one cohort occurred in the Oyashio region.

E. hamata/*E. bathypelagica*.

Both the findings of Nishiuchi (1999) and the present study define *E. hamata*/*E. bathypelagica* juveniles. The vertical distribution of *E. bathypelagica* is known to be much deeper than that of *E. hamata* (distribution centre ranging from 583–1500 m for the former and 169–308 m for the latter, Ozawa et al. 2007). Since the sampling depth of Nishiuchi (1999) is much deeper than in this study (0–2000 m vs 0–1000 m), the contamination effect of *E. bathypelagica* may have been greater in his study. The smaller mesh size of Nishiuchi (1999) than in the present study (100 μm vs 335 μm) may have induced a much larger proportion of smaller *E. hamata*/*E. bathypelagica* juveniles. These features (deeper sampling depth with smaller mesh sizes) suggest a much more severe contamination effect due to the presence of *E. bathypelagica* juveniles, with regards to the life cycle analysis of *E. hamata* conducted by Nishiuchi (1999).

The generation lengths reported in the Gulf of Alaska (eight to ten months, Terazaki & Miller 1986) were much shorter than those in the Oyashio region (two years; 24 months) (Fig. 8). Comparative studies on zooplankton life cycles in the Gulf of Alaska and the Oyashio region have

been conducted mainly only for the dominant calanoid co-pepods. The generation length is longer in the Oyashio region for *Metridia pacifica* Brodsky, 1950 (Padmavati et al. 2004), which has been attributed to the habitat temperature. The habitat temperature for *E. hamata* ranges from 3.8–6.0°C at 100–500 m in the Gulf of Alaska (Miller et al. 1984), while it was 2.3–2.9°C at 250 m in the Oyashio region (Fig. 2). Thus, a colder habitat temperature is observed for *E. hamata* in the Oyashio region.

A negative relationship between generation length and habitat temperature is well known for the epipelagic chaetognath *Parasagitta elegans*. According to Sameoto (1971), the generation length (*GL*: day) is expressed by the habitat temperature (*T*: °C):

$$GL = 611.51/T^{0.811}.$$

As an example, inserting the habitat temperatures of *E. hamata* in the Gulf of Alaska and Oyashio region (5°C and 2.6°C) into the above equation, the generation length is predicted to be 166 days (Gulf of Alaska) and 282 days (Oyashio region), respectively. The difference in generation lengths of 1.7 times (=282/166) may be usable as a guide to extrapolate differences in the generation length of *E. hamata* in the two different locations, although the equation was derived for *P. elegans*.

The life cycle of *E. hamata* has been studied in several locations. A two–year generation length has been reported for *E. hamata* in a Nordic fjord (Korsfjorden), the Barents Sea, Baffin Bay, and the Beaufort Sea (Bogorov 1940, Sands 1980, Sameoto 1987, Grigor et al. 2017). The correspondence in the generation length of *E. hamata* in the Oyashio region with these locations may be due to the correspondence in habitat temperature (2–3°C) with those high–latitude oceans (Sameoto 1987).

Interestingly, *E. hamata* growth exhibits a clear seasonal pattern, i.e., their growth is much greater (above the von Bertalanffy curve) during summer to autumn, while it is poor (below the von Bertalanffy curve) during winter to spring (Fig. 7). The seasonal phenology of *E. hamata* is summarized as follows. The high proportion of juveniles that formed a new generation (G_0) occurred from March to August. The matured population was found in G_1 from October to March, suggesting that reproduction occurred mainly in this season. This gap between the occurrence of G_0 and the reproductive season was caused by the sampling efficiency of the 0.335 mm mesh net. Nagasawa & Marumo (1977) showed that small individuals (less than 5 mm in body length) were underestimated in numerical abundance by using 0.335 mm mesh net sampling. In one year, the G_0 reached a body length of ca. 8 mm (Fig. 6). During winter to spring, the growth of G_0 was slow and poor, and negative growth might have occurred between January and May (Fig. 7). From June to October, and during the next summer, *E. hamata* showed rapid growth, reaching a body length of ca. 15 mm, followed by slow and poor growth in the subsequent winter (Fig. 7). Thus,

the two-year population (G_1) may enter reproduction from October to March (Fig. 4). Some remains occurred as G_2 in March and June (Fig. 6).

Temperature has been reported as an environmental factor affecting the growth and generation length of chaetognaths (Sameoto 1971). However, the habitat temperature of *E. hamata* (2.3–2.9°C) is mostly stable throughout the year. These findings suggest that other environmental factors such as food may have important roles in governing the seasonal growth rate. In regards to the prey of *E. hamata*, the small calanoid copepod *Pseudocalanus minutus* (Krøyer, 1845) may be important. *Pseudocalanus minutus* was the only species detected in the gut contents of *E. hamata* in this study (Matsumoto, unpublished data). Since *P. minutus* undergo diapause at deeper depths around 250 m, and their descent occurs during summer to autumn (Yamaguchi & Shiga 1997), the greater growth of *E. hamata* than the von Bertalanffy curve during summer to autumn might be a reflection of the abundant availability of food (prey) for this species during that season.

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