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Vertical Distribution, Community and Population Structures of the Planktonic Chaetognatha in the Western Subarctic Pacific: Insights on the *Eukrohnia* Species Group

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Abstract: In the oceans, Chaetognatha can contribute significantly to the total zooplankton biomass (up to 10–30%). The genus *Eukrohnia*, the dominant Chaetognath genus in the western subarctic Pacific, includes *E. hamata* and *E. bathypelagica*. Although it has been pointed out that there is no genetic difference between the two species, no study has been made that treats them as the same species group. In this study, we investigated vertical distribution based on the eight vertical stratification samplings down to 1000 m depths conducted day/night at four seasons covering one year, community structure, and population structure of the three dominant Chaetognath species: *Parasagitta elegans*, *E. hamata*, and *E. bathypelagica* in the western subarctic Pacific. The population densities of each species at 0–1000 m water column were 0.04–0.36 ind. m^{-3} for *P. elegans*, 0.14–1.60 ind. m^{-3} for *E. hamata*, 0.24–1.54 ind. m^{-3} for *E. bathypelagica*, and 1.37–2.62 ind. m^{-3} for *Eukrohnia* juveniles. The vertical distributions were consistent both day and night, and no diel changes were observed for all species throughout the seasons. The vertical distribution of Chaetognaths evaluated by the distribution center was 61–169 m for *P. elegans*, 143–206 m for *Eukrohnia* juveniles, 134–279 m for *E. hamata*, and 253–612 m for *E. bathypelagica*. The body length of *P. elegans* ranged from 4 to 34 mm, and one to three cohorts were identified at each sampling occasion. While the presence of the eight stages has been reported for *Eukrohnia*, only one to five stages occurred, and specimens belonging to six to eight stages were not observed in the samples throughout the year. The body length of the whole *Eukrohnia* species ranged from 2 to 14 mm. The body length histograms of the *Eukrohnia* species group, including *E. hamata* and *E. bathypelagica*, and their juveniles showed the presence of two to four cohorts at each sampling date. Within the *Eukrohnia* species group, vertical changes in body length were present, which were characterized by the smaller specimens occurring at shallower depths, followed by an increase in body length with increasing depths. From the vertical distribution and population structure of the *Eukrohnia* species group (*Eukrohnia* juvenile + *E. hamata* + *E. bathypelagica*) in this study, there was no difficulty in treating them as one species. It may suggest that *E. hamata* and *E. bathypelagica* in the western subarctic Pacific could be treated as one species group. To clarify this point, a detailed genetic analysis of the *Eukrohnia* species group will be needed for future studies.

Keywords: vertical distribution; population structure; Chaetognatha; *Eukrohnia* species group

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1. Introduction

Chaetognatha is a marine phylum that has a wide distribution from the sea surface to the bottom of the worldwide oceans. In the oceans, Chaetognatha can contribute significantly to the total zooplankton biomass (up to 10–30%) [1]. Chaetognatha is carnivorous and preys on mainly small-sized copepods [2–4]. On the other hand, Chaetognatha is eaten by various fish: salmon [5], walleye pollock [6], and mesopelagic myctophids [7]. Thus, Chaetognatha plays an important role in transporting copepod secondary production to higher trophic-level organisms [8].

The life history of the pelagic Chaetognatha has been reported from various areas, including the North Atlantic [9–11], the Arctic Ocean [12,13], and the North Pacific [14–16]. On the other hand, the mtDNA COI analysis of the genus *Eukrohnia*, which has a worldwide distribution, shows that there is no genetic difference between *E. hamata* and *E. bathypelagica* of the same region, and *E. bathypelagica* is suggested to be a post-spawning individual of *E. hamata* [17]. From this point of view, it has been pointed out that it is necessary to re-analyze the life history of Chaetognatha, including the existence of cryptic species [18].

In the western subarctic Pacific, St. K2 has been set up as a long-term time-series observation station, and various biogeochemical studies, including plankton, have been conducted [19]. At St. K2, Chaetognatha has been reported to dominate in the 50–200 m depth range, accounting for 14–36% of total zooplankton biomass [20]. The dominance of Chaetognatha in zooplankton biomass at the mesopelagic layer of St. K2 has also been reported [21]. Regarding the vertical distribution of Chaetognatha at St. K2, they showed bimodal vertical distribution showing peaks at 0–50 m and 150–300 m, and few individuals distributed for 50–150 m depth both day and night [22]. Based on the sediment trap moored at 150 m of St. K2 collected at two-day intervals from June to July, *P. elegans* was collected as a zooplankton swimmer, and the body length of *P. elegans* showed a uni-modal cohort with peaks at 29.2–31.9 mm, showing the significant growth rate at 0.21 mm day^{-1} [23]. Although these findings are important, population structure has been observed only at certain depths and for a limited season. Thus, knowledge of the life cycle of Chaetognatha at St. K2 is scarce.

An oblique tow of a Bongo net from 0 to 200 m was conducted in the Oyashio region at 2–5 day intervals from March to April [24]. Data acquired revealed that *E. hamata* and *P. elegans* composed 95% of the Chaetognath abundance and showed three peaks in body length [24]. The growth rates of *E. hamata* and *P. elegans* were 0.039–0.050 mm day^{-1} and 0.042–0.101 mm day^{-1}, respectively [24]. For vertical distribution based on the vertical stratification samplings down to 5000 m, the distribution centers of *P. elegans*, *E. hamata*, and *E. bathypelagica* were at 26–187 m, 169–308 m, and 583–728 m, respectively; thus, distribution depth varied for the species [25]. For the life cycle of Chaetognatha, it has been reported that the generation time of *P. elegans* is one or two years based on the time-series samples collected from 150 m off Kushiro for four years [16]. In addition, based on the time series sampling by Bongo net from 0 to 1000 m depth in the Oyashio region at 2 to 3 month intervals, the recruitment of *E. hamata* juveniles occurs in spring and summer, and their growth rates show seasonality: fast in summer and autumn, slow in winter and spring, and having two-year generation lengths [18]. While these findings are important, as mentioned above, there is a possibility that *E. hamata* and *E. bathypelagica* are the same species within the *Eukrohnia* species [17,26]. These facts suggest that an analysis that treats both species as the same species group is needed, but such a study has not been conducted yet.

This study conducted day/night vertical distribution, seasonal changes in body length, and population structure studies of three dominant Chaetognath species (*P. elegans*, *E. hamata*, and *E. bathypelagica*) at St. K2 in the western subarctic Pacific based on day/night vertical stratification samples down to 1000 m at four seasons covering one year. For two *Eukrohnia* species considered to be the same species [17,26], the hypothetical species group "*Eukrohnia* species group", including *Eukrohnia* juvenile, *E. hamata*, and *E. bathypelagica,* was set. Then the body length, developmental stage composition, and vertical distribution of the *Eukrohnia* species group were analyzed. Through such analyses, the consistency of the treatment of both species as the same species was considered from an ecological perspective.

2. Materials and Methods

2.1. Field Sampling

Day/night vertical stratified oblique tow of Intelligent Operative Net Sampling System (IONESS, SEA, Co. Ltd., Chiba, Japan) equipped 335 µm with 1.5 m^2 mouth area was made from eight layers (0–50, 50–100, 100–150, 150–200, 200–300, 300–500, 500–750, and

750–1000 m) at St. K2 (47° N, 160° E, Figure 1, Table 1) during four occasions: 29 October 2010, 26 February, 22–23 April, and 3–4 July 2011. The filtering volume of each sample was monitored by a flowmeter. Samples were preserved by 4% (v/v) borax-buffered formalin. Temperature, salinity, dissolved oxygen (DO), and fluorescence were measured by CTD (SBE 911plus; Sea-Bird Scientific) at each sampling occasion. For the zooplankton samples used in this study, data on the abundance and biomass of zooplankton taxa have already been published [20]. In this study, data on the abundance of copepods, the primary prey of Chaetognatha, were quoted from [20].

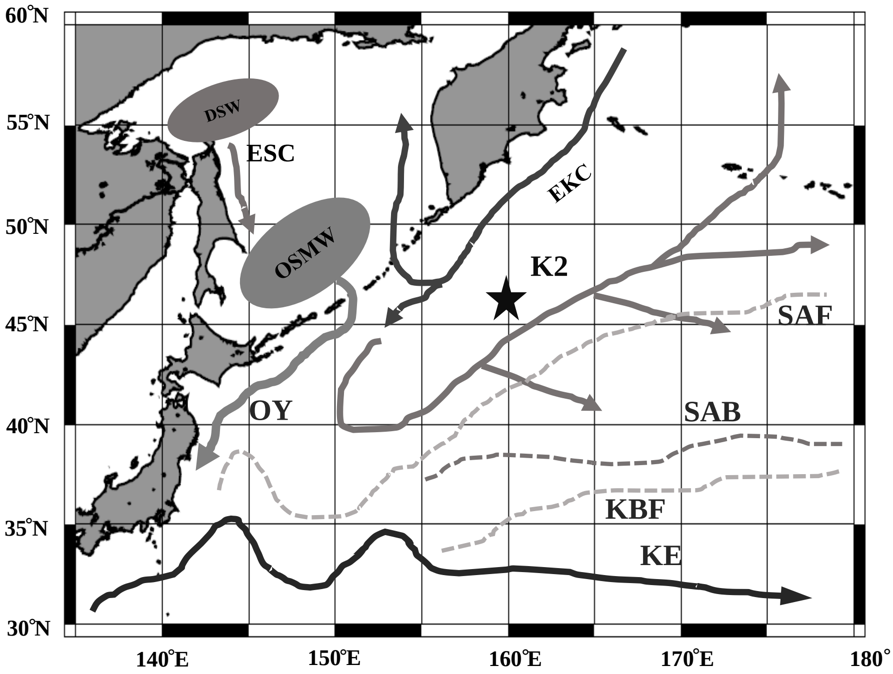

Figure 1. Location of the sampling station (K2) in the western subarctic Pacific gyre. Arrows represent the approximate positions and directions of the currents. EKC: East Kamchatka Current, OY: Oyashio, KE: Kuroshio Extension, TC: Tsushima Warm Current, SAF: Subarctic Front, SAB: Subarctic Boundary, KBF: Kuroshio Bifurcation Front, OSMW: Okhotsk Sea Mode Water, DSW: Dense Shelf Water, and OSMW: Okhotsk Sea Mode Water.

Table 1. Sampling data of the samples used in the present study collected at St. K2 in the western subarctic Pacific gyre from October 2010 to July 2021. All the samples were collected from eight discrete depths between 0 and 1000 m by oblique tow of IONESS.

Sampling Date	Local Time (Day/Night)
29 October 2010	12:09–13:52 (D)
29 October 2010	22:09–23:38 (N)
26 February 2011	12:35–14:41 (D)
26 February 2011	22:01–23:44 (N)
22 April 2011	21:59–23:56 (N)
22 April 2011	12:45–14:37 (D)
3 July 2011	12:05–13:55 (D)
3–4 July 2011	22:51–0:55 (N)

2.2. Abundance, Body Size, and Biomass

In the land laboratory, sorting of Chaetognatha was made on the sub-samples at a division rate of 1/2–1/64, which varied with the number of samples. Under a stereomicroscope, species identification and enumeration were made. Body length was measured with a precision of 0.1 mm using vernier calipers. For each individual, the developmental condition of the gonads was observed. Based on gonad development, *P. elegans* is classified into three developmental stages: stages 1, 2, and 3 [23]. Stage 1 is an individual without ovaries; stage 2 is an individual with a developing egg but no mature egg; and stage 3 is an individual with a mature egg [23]. *Eukrohnia* were classified into stages I to VIII using the criteria of [27]. The Chaetognatha were sorted by species and placed on a pre-weighed 100 µm mesh, removed water, and measured wet weight (WW) with a precision of 0.01 mg using an electronic balance (Mettler Toledo AT261). Calculation of the abundance and biomass data from per cubic meter (m^{-3}) to per square meter (m^{-2}) was made by multiplying the towed depth (m) with the value per cubic meter.

2.3. Vertical Distribution

The vertical distribution of the three dominant species (*P. elegans*, *E. hamata*, and *E. bathypelagica*) and *Eukrohnia* juvenile was analyzed with day/night for the four seasons. The vertical distribution core ($D_{50\%}$), where 50% of the population was distributed, was calculated based on abundances (ind. m^{-2}) in each sampling layer [28]:

$$D_{50\%} = d_1 + d_2 \times \frac{50 - p_1}{p_2}$$

where d_1 is the depth (m) of the upper depth of the 50% individual occurrence layer, d_2 is the maximum depth (m) of the 50% individual occurrence layer, p_1 is the cumulative individual percentage (%) that occurred at depths shallower than the 50% individual occurrence layer, and p_2 is the individual percentage (%) at the 50% individual occurrence layer.

2.4. Population Structure (Cohort Analyses)

Population structure analyses were made for the three dominant species: *P. elegans*, *E. hamata*, *and E. bathypelagica*, and one combined species group: the *Eukrohnia* species group (*E. hamata* + *E. bathypelagica*). Thus, we treated four taxonomic categories in this study. Based on the total number of the water column (ind. m^{-2}) at 0–1000 m, histograms on body length were made, and cohort analyses were performed using the aid of the MSExcel solver function [29]. In addition, depth distribution composition was also calculated for each body length at a 1 mm interval. The number of *Eukrohnia* juveniles was estimated by multiplying the composition of *E. hamata* and *E. bathypelagica* species that occurred in the same sample. In addition, since *E. hamata* and *E. bathypelagica* are genetically identical [17,26], one species group, the *Eukrohnia* species group (*Eukrohnia* juveniles + *E. hamata* + *E. bathypelagica*), was also set, and their body length histogram and distribution depth composition were analyzed.

3. Results

3.1. Hydrography

Vertical changes in temperature, salinity, dissolved oxygen, and copepod abundance during day and night in four seasons are shown in Figure 2. Temperatures ranged from 1.2 to 8.5 °C in October, 1.8 to 3.6 °C in February, 1.4 to 3.7 °C in April, and 1.5 to 6.5 °C in July. The near-surface layer was warmer in October and July and cooler in February and April. For all seasons, the temperature decreased to 100 m, had a minimum, then increased to 200 m with the subsurface small maximum, and decreased below 200 m. Salinity ranged from 32.6–34.4 in October, 32.9–34.4 in February, 33.0–34.4 in April, and 32.8–34.4 in June. Salinity was low near the surface, especially in October, then gradually increased with increasing depth for all seasons. Dissolved oxygen was at 0.3–7.4 mL L^{-1} in October, 0.3–7.4 mL L^{-1} in February, 0.3–7.5 mL L^{-1} in April, and 0.3–7.5 mL L^{-1} in July. For all seasons, dissolved oxygen showed high values near the surface layer and decreased rapidly with increasing depth to 200 m, then stabilized around <1.4 mL L^{-1} below 200 m depths. The abundance of copepods was 14–732 ind. m^{-3} in October, 10–145 ind. m^{-3} in February, 8–174 ind. m^{-3} in April, and 5–190 ind. m^{-3} in June. The copepod abundance was high near the surface layer, especially in October. Common for all seasons, copepod abundance had a minimum at 150–200 m, formed a small maximum below, then decreased with increasing depth. There were few changes in copepod abundance and vertical distribution between day and night.

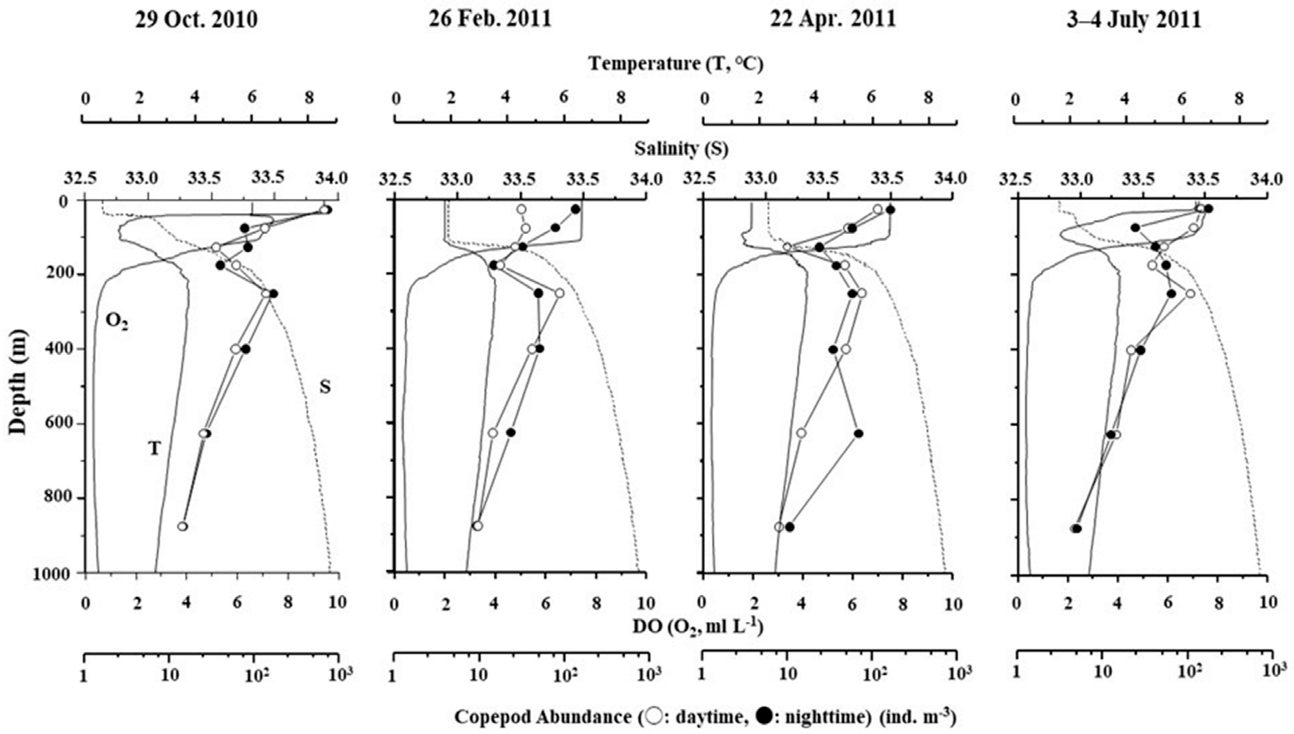

Figure 2. Vertical distribution of temperature, salinity, dissolved oxygen (DO), and copepod abundance (day and night) at St.K2 in the western subarctic Pacific gyre from October 2010 to July 2011. Note that scales of copepod abundance are in log scales.

3.2. Abundance and Biomass of Chaetognaths

In this study, Chaetognatha belonging to two genera and three species were identified (Table 2). Abundances of Chaetognaths at the water column (0–1000 m) were 0.04–0.36 ind. m^{-3} for *P. elegans*, 0.14–1.60 ind. m^{-3} for *E. hamata*, 0.24–1.54 ind. m^{-3} in *E. bathypelagica*, and *Eukrohnia* juveniles were 1.37–2.62 ind. m^{-3}. *Eukrohnia* juveniles accounted for nearly half of the total Chaetognath abundance. The next dominant species were *E. hamata* and *E. bathypelagica*. Both species accounted for about 20% of the total Chaetognath abundance. The abundance of *P. elegans* was around 5% of the population.

Table 2. Annual mean abundance and biomass at 0–1000 m water column at St. K2 in the western subarctic Pacific gyre during October 2010 to July 2021.

Species	**Abundance**		**Biomass**	
	(ind. m^{-3})	**(%)**	**(mg WW m^{-3})**	**(%)**
Parasagitta elegans	0.20 ± 0.03 (0.04–0.36)	5.3	13.29 ± 2.39 (4.89–26.16)	40.0
Eukrohnia hamata	0.80 ± 0.17 (0.14–1.60)	21.3	5.09 ± 1.41 (1.00–10.55)	15.3
Eukrohnia bathypelagica	0.87 ± 0.13 (0.24–1.54)	23.2	12.76 ± 2.67 (3.45–25.32)	38.4
Eukrohnia juvenile	1.88 ± 0.15 (1.37–2.62)	50.2	1.84 ± 0.39 (0.37–3.63)	5.5
Others	0.001 ± 0 (0–0.001)	0.03	0.24 ± 0.04 (0.15–0.42)	0.7

Biomasses at 0 to 1000 m water column were 4.89–26.16 mg WW m^{-3} for *P. elegans*, 1.00–10.55 mg WW m^{-3} for *E. hamata*, juveniles 3.45–25.32 mg WW m^{-3} for *E. bathypelagica*, and 0.37–3.63 mg WW m^{-3} for *Eukrohnia* juveniles (Table 2). Regarding species composition, *Eukrohnia* juvenile, which had a high composition in abundance, had a low composition of 5.5% in biomass due to the smaller body size. On the other hand, the numerical minor *P. elegans* had the highest composition of biomass, accounting for 40% of total Chaetognath biomass due to its large body size.

3.3. Vertical Distribution of the Three Dominant Chaetognath Species

The day/night vertical distribution of Chaetognath species (*P. elegans*, *E. hamata*, *E. bathypelagica*, and *Eukrohnia* juvenile) at each season is shown in Figure 3. The vertical distribution of Chaetognaths was consistent with day and night for all species, and no day and night differences were detected for any species or season ($p > 0.05$, Kolmogorov–Smirnov test) (Table 3).

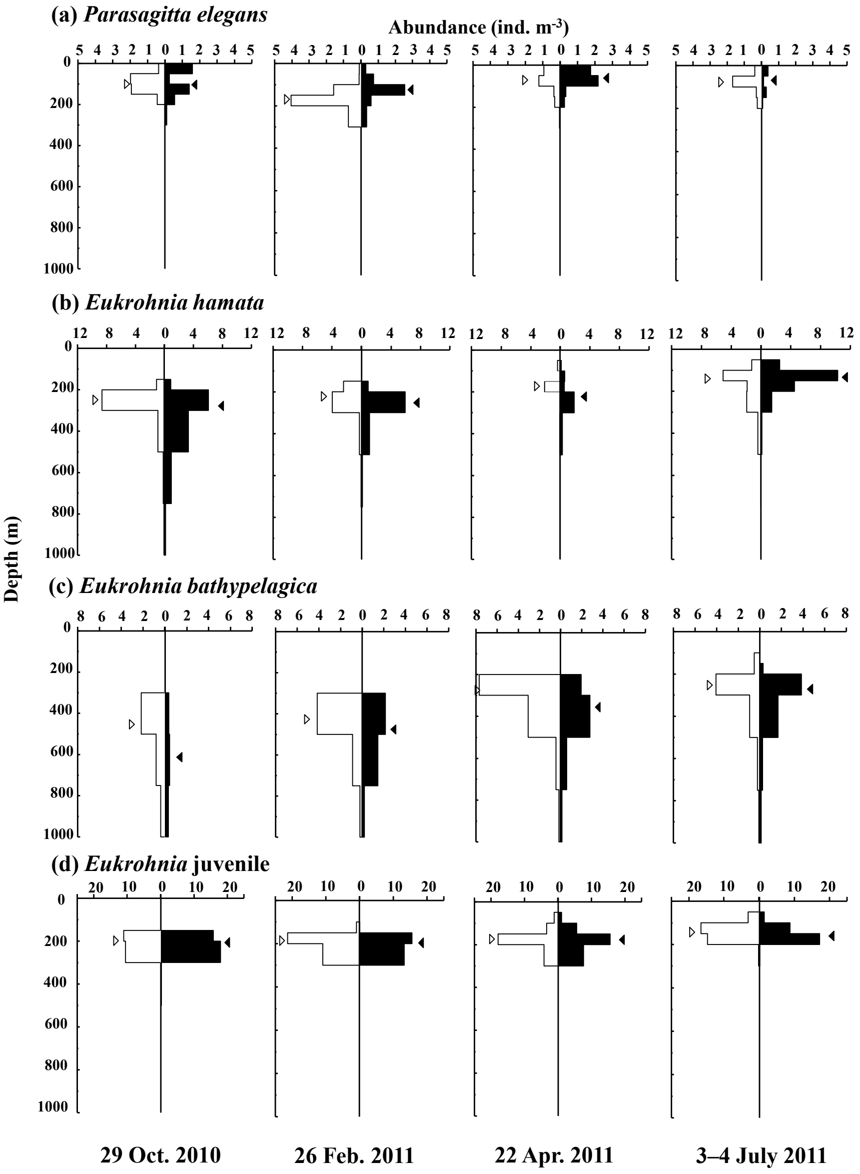

Figure 3. Day (open) and night (solid) vertical distribution of the four dominant Chaetognaths: *Parasagitta elegans* (**a**), *Eukrohnia hamata* (**b**), *Eukrohnia bathypelagica* (**c**), and *Eukrohnia* juvenile (**d**) at St. K2 in the western subarctic Pacific gyre during October 2010 to July 2011. Distribution cores ($D_{50\%}$) were calculated for each sample series and shown with triangles (open: day, solid: night).

Table 3. Summary of the vertical distribution cores ($D_{50\%}$, m) of each dominant chaetognath species in the western subarctic Pacific gyre during October 2010 to July 2011. (D): day, (N): night.

Species	29 October 2010		26 February 2011		22 April 2011		3–4 July 2011	
	(D)	**(N)**	**(D)**	**(N)**	**(D)**	**(N)**	**(D)**	**(N)**
Parasagitta elegans	100	104	169	124	71	62	77	69
Eukrohnia hamata	250	279	223	253	172	222	140	134
Eukrohnia bathypelagica	453	612	427	477	274	356	253	273
Eukrohnia juvenile	199	206	187	196	175	177	143	161

The vertical distribution of *P. elegans* was the shallowest among the species and was concentrated at 200 m depth. The vertical distribution of *P. elegans* was slightly deep in October and February ($D_{50\%}$: 100–169 m) and shallow in April and July ($D_{50\%}$: 62–77 m). The vertical distribution of *E. hamata* was deeper than that of *P. elegans*, which frequently occurred at 100–500 m. The vertical distribution of *E. hamata* was shallower in July ($D_{50\%}$: 134–140 m) than in October and February ($D_{50\%}$: 223–279 m). *Eukrohnia* juvenile was distributed at the same depth as *E. hamata* and abundant at 100–400 m. Like *E. hamata*, *Eukrohnia* juveniles mainly distributed shallower depths in July ($D_{50\%}$: 143–161 m) than in the other seasons ($D_{50\%}$: 175–206 m). The deepest-distributed species was *E. bathypelagica*, which occurred at 200–1000 m. Similar to the other species, the vertical distribution of *E. bathypelagica* was relatively deep in October and February ($D_{50\%}$: 253–356 m) and shallow in April and July ($D_{50\%}$: 253–356 m).

3.4. Population Structure

Body length histograms and depth distributions of the three dominant Chaetognath species (*P. elegans*, *E. hamata, and E. bathypelagica*) and *Eukrohnia* species group (*E. hamata* + *E. bathypelagica*) are shown in Figures 4–7. The body length of *P. elegans* ranged from 4 to 34 mm (Figure 4). There were one to three cohorts for the body length of *P. elegans* at each sampling date. For example, in July, the large body length, having a mean of 25–26 mm, was observed as one cohort both day and night. For the vertical distribution at each body length, the smaller individuals tended to be distributed at shallower depths, and the larger individuals were distributed at deeper layers, which was prominent, especially in October.

The body length of *E. hamata* ranged from 10 to 22 mm (Figure 5). There were two to four cohorts in body length of *E. hamata* at each sampling date. Within the eight developmental stages based on the criteria of [27], only stage 1–5 individuals have occurred for *E. hamata*, and stage 6–8 individuals were not present throughout the samples in this study. Commonly, for all seasons, the smaller individuals occurred at the shallower depths, and the larger individuals were distributed at the deeper layer.

The body length of *E. bathypelagica* ranged from 10 to 22 mm (Figure 6). There were two to three cohorts in body length of *E. bathypelagica* at each sampling date. However, it should be noted that the small body length cohorts of this species were derived from the combination of *Eukrohnia* juveniles, as mentioned before. Also, for *E. bathypelagica*, within the eight developmental stages of maturation based on the *E. hamata* criteria [27], only stage 1–5 individuals have occurred, and stage 6–8 individuals did not occur throughout the samples. The vertical distribution of *E. bathypelagica* was shallower in April and July than in October and February, but ontogenetic changes in vertical distribution were not clear for this species.

The body length of *Eukrohnia* juveniles ranged from 2 to 14 mm (Figure 7). For the *Eukrohnia* species group (*Eukrohnia* juvenile + *E. hamata* + *E. bathypelagica*), the entire body length ranged from 2 to 22 mm. Within the eight developmental stages based on the *E. hamata* criteria [27], only stage 1–5 individuals occurred, and stage 6–8 individuals were not present throughout the samples. The *Eukrohnia* species group showed clear ontogenetic changes in vertical distribution depth. Seasonally, in April and July, the new adults at 8–12 mm body length were distributed at shallower depths than juveniles at 50–200 m.

Within adults, vertical distribution became deeper with growth. The largest individuals were found below 200 m. Seasonal changes in vertical distribution were evidenced by the shallowest distribution in July.

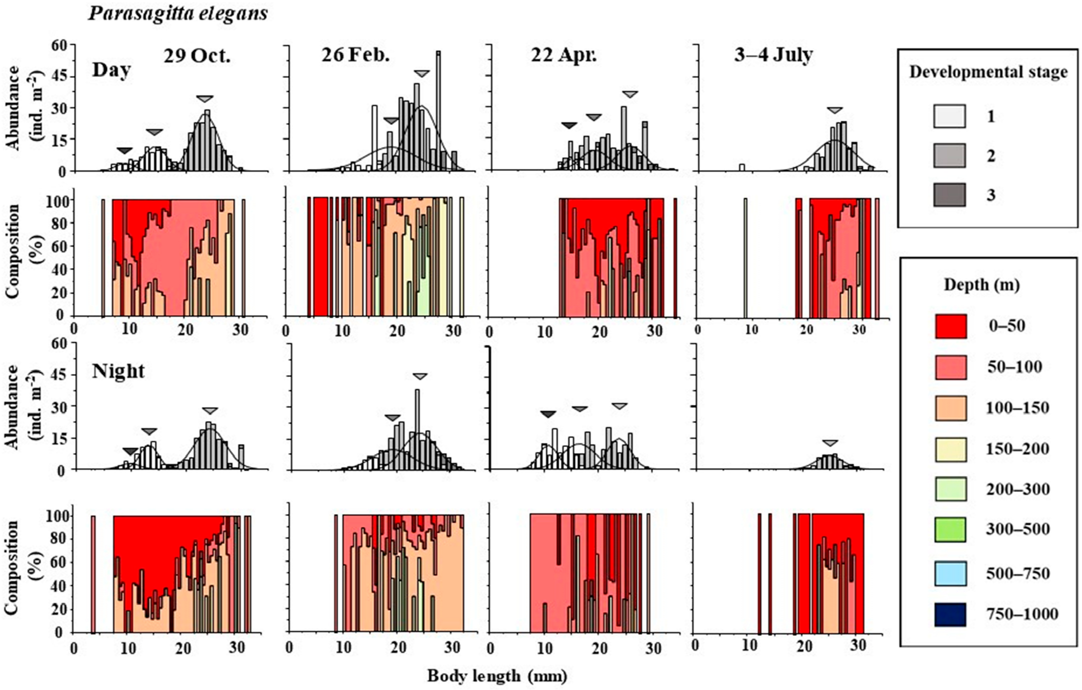

Figure 4. Seasonal changes in body length histograms and their distribution depths of *Parasagitta elagans* at St. K2 in the western subarctic Pacific gyre during the daytime (**upper**) and nighttime (**lower**) of the four sampling occasions (October 2010, February, April, and July 2011). Triangles denote the mean body lengths of each cohort.

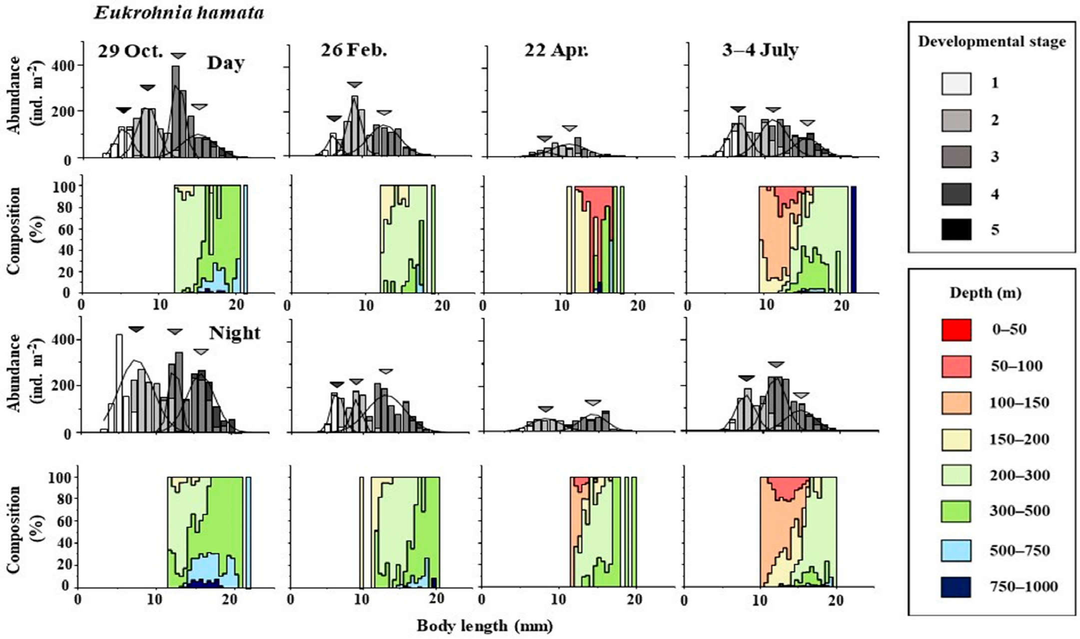

Figure 5. Seasonal changes in body length histograms and their distribution depths of *Eukrohnia hamata* at St. K2 in the western subarctic Pacific gyre during the daytime (**upper**) and nighttime (**lower**) of the four sampling occasions (October 2010, February, April, and July 2011). Triangles denote the mean body lengths of each cohort. Note that depth distribution data were not shown for the juveniles and were thus presented only for *E. hamata* at larger body sizes.

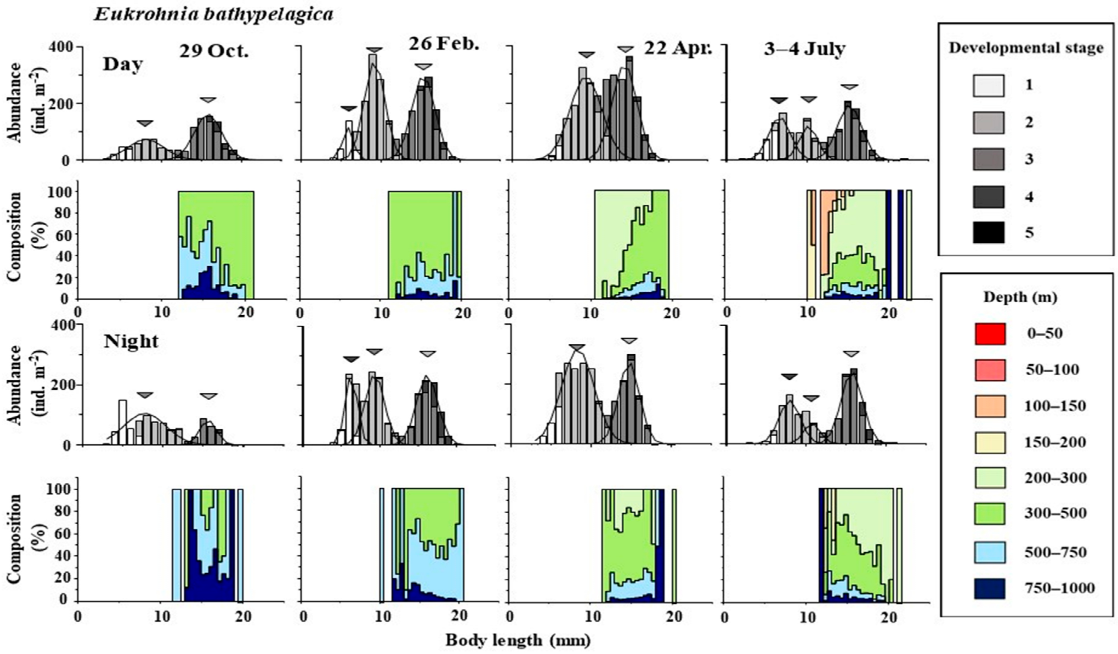

Figure 6. Seasonal changes in body length histograms and their distribution depths of *Eukrohnia bathypelagica* at St. K2 in the western subarctic Pacific gyre during the daytime (**upper**) and nighttime (**lower**) of the four sampling occasions (October 2010, February, April, and July 2011). Triangles denote the mean body lengths of each cohort. Note that the data for *Eukrohnia* juveniles were not included in the depth composition panels.

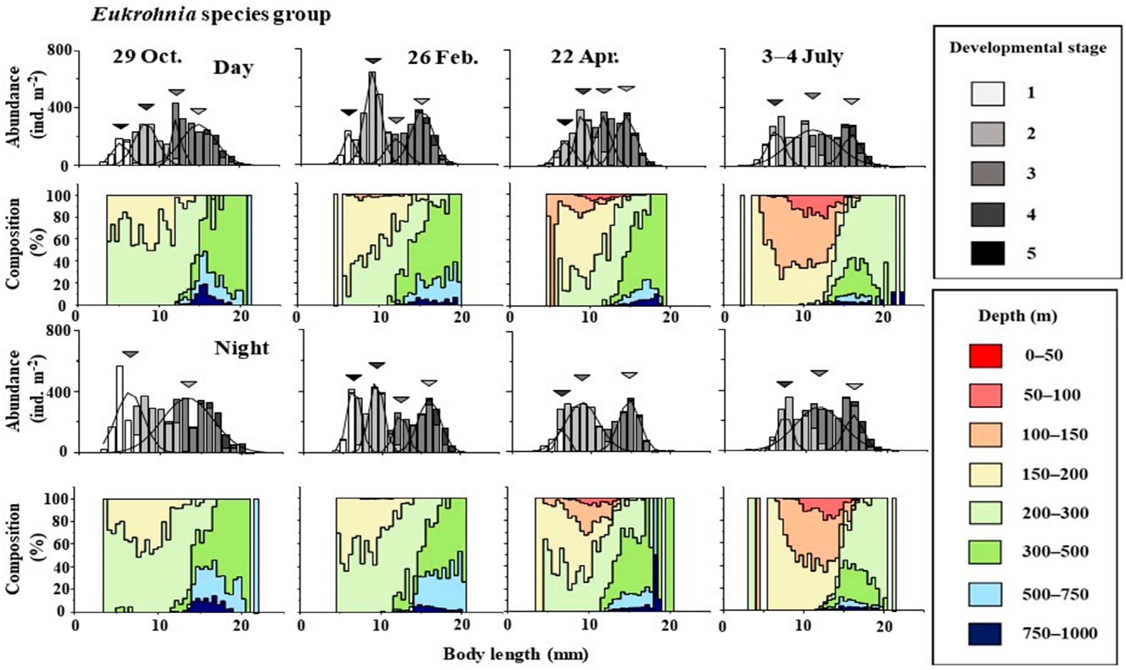

Figure 7. Seasonal changes in body length histograms and their distribution depths of the *Eukrohnia* species group (juveniles + *E. hamata* + *E. bathypelagica*) at St. K2 in the western subarctic Pacific gyre during the daytime (**upper**) and nighttime (**lower**) of the four sampling occasions (October 2010, February, April, and July 2011). Triangles denote the mean body lengths of each cohort.

The mean body length of each cohort and developmental stage composition of *P. elegans*, *E. hamata*, *E. bathypelagica*, and *Eukrohnia* species group (*Eukrohnia* juvenile + *E. hamata* + *E. bathypelagica*) are shown in Figure 8. The body lengths were classified into two to four cohorts at each sampling date. However, it should be noted that the number of cohorts varied between day and night, even at the same sampling date for the *E. hamata* and *Eukrohnia* species groups in October. Thus, some discrepancies were present. For *P. elegans* developmental stage composition, stage II dominated throughout the year, while in *Eukrohnia*, stages II and III dominated.

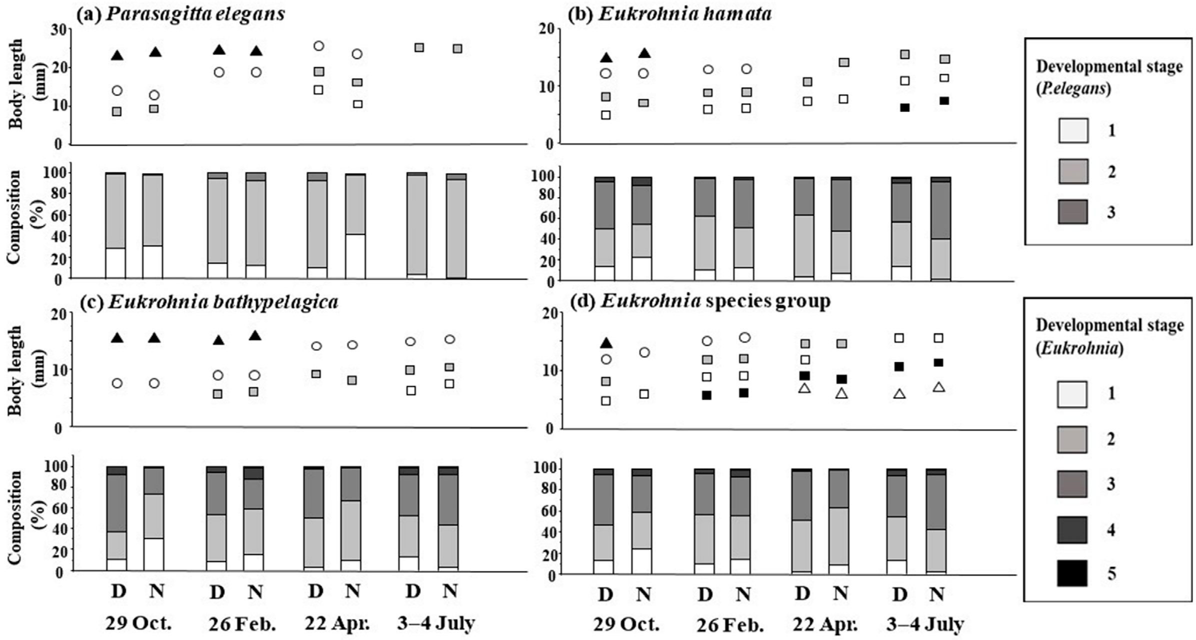

Figure 8. Seasonal changes in mean body lengths evaluated by cohort analyses for *Prasagitta elegans* (**a**), *Eukrohnia hamata* (**b**), *Eukrohnia bathypelagica* (**c**), and *Eukrohnia* species group (**d**) at St. K2 in the western subarctic Pacific gyre during the day (D) and night (N) of the four sampling occasions (October 2010, February, April, and July 2011). Symbols in the body length panels represent the mean body length values of each cohort. For details on each species, see Figures 4–7.

4. Discussion

4.1. Abundance and Biomass of Chaetognatha

The dominant Chaetognath species in the western Subarctic Pacific gyre were two species belonging to the genus *Eukrohnia* (*E. hamata* and *E. bathypelagica*) in abundance and *P. elegans* in terms of biomass (Table 2). These results well correspond with those in the Gulf of Alaska in the eastern subarctic Pacific [15]. To add to these species, *Pseudosagitta scrippsae* is also listed as the dominant species in the Oyashio region of the western subarctic Pacific [24]. This might be because the research area of [24] was at a lower latitude than this study and had a shallower sampling depth (200 m). In fact, the dominant species in the studies conducted at higher latitudes (basin of the Bering Sea) down to the depth of 3000 m corresponded with this study [25].

Within the three dominant species of this study, *P. elegans* is known to distribute mainly in the epipelagic zones of the high latitude areas of the Northern Hemisphere, such as the North Pacific, the North Atlantic, and the Arctic Ocean [1,8,30]. On the other hand, the two species of *Eukrohnia* are thought to have a worldwide distribution, distributed in the epipelagic zones of both the Arctic and Southern Oceans and the deep sea of the lower latitudes [3,4,31,32]. However, such a global distribution of *Eukrohnia* species has been doubted, and no genetic differences in *E. bathypelagica* and *E. hamata* within the same region, geographically four classifications, and the possibility that *E. bathypelagica* would be a post-spawning individual of *E. hamata* have been proposed by the mtDNA COI region analyses [17,26]. Furthermore, a genetic study on *E. hamata* has also been made for the geographic distribution, and the results of [17] have been confirmed to be correct by [33]. Unfortunately, since the genetic analysis of *E. bathypelagica* has not been made in [33], the genetic correspondence between *E. hamata* and *E. bathypelagica* reported in [17,26] has not been tested yet. Thus, this study is the first attempt to treat *E. hamata* and *E. bathypelagica* as a single "species group" based on field sampling.

A comparison of the abundance and biomass of the three dominant Chaetognath species in this study with those of the other regions is shown in Table 4. Abundances of *P. elegans* and *E. hamata* in this study were similar to or slightly higher than those in the adjacent Oyashio region. The highest abundance of *P. elegans* (2483–3922 ind. m^{-2}) has been reported in the Celtic Sea and central Long Island Sound in the North Atlantic, where the water depths are shallow (0–37 or 0–90 m) [34,35]. These facts suggest that the abundance of the epipelagic species *P. elegans* is high in the neritic areas, which are characterized by high primary productivity.

On the other hand, the vertical distribution of *E. hamata* has been reported to be deeper than that of *P. elegans* in various oceans, including the Arctic Ocean [36,37], the subarctic Pacific [15,25], and the North Atlantic [38,39]. Since the distribution of *E. hamata* extended deeper than that of *P. elegans*, the abundance in the water column (ind. m^{-2}) would be higher for the former than the latter [13,18,24,36,37]. The vertical distribution of *E. bathypelagica* has been reported to be deeper than that of *E. hamata* [15,25]. Such restriction of the occurrence depths of *E. bathypelagica* implies that the abundance of this species remains similar to or slightly lower than that of *E. hamata* [18,31]. The *Eukrohnia* is carnivorous, and their primary diet has been reported to be small copepods [2,4,25,36,37,40]. The abundance of the small copepods was high in the shallower depths and low in the deep sea (Figure 2). These facts suggest that the competition for the prey animal (small copepods) would be high in the deep sea, and increasing sizes of head width and hook length of deep-sea *Eukrohnia* have been reported and interpreted to capture prey animals in the resource-limited deeper layers [25]. Considering these facts, *E. bathypelagica*, distributed in food-scarce environments, is thought to have a limited abundance due to a limited food supply, although its vertical distribution is wide.

4.2. Vertical Distribution

The vertical distribution of the same three dominant Chaetognath species in this study has been reported in the Gulf of Alaska in the eastern subarctic Pacific, and the distribution depths of *P. elegans*, *E. hamata*, and *E. bathypelagica* are reported to be 0–100 m, 100–500 m, and 250–1000 m, respectively [15]. The same vertical occurrence order of these three species, *P. elegans* < *E. hamata* < *E. bathypelagica*, has also been reported for the western subarctic Pacific and its marginal seas [25]. These facts suggest that this pattern is solid and is commonly observed throughout its occurrence areas.

For the whole zooplankton biomass, bimodal vertical distribution has been reported at St. K2, with peaks at the surface layer and 200–300 m [20,22]. This bimodal vertical distribution has also been observed even for Chaetognaths [22], and *P. elegans* formed the surface maximum, while a deeper maximum was composed by *Eukrohnia* species (Figure 3).

This study did not detect diel vertical migration (DVM) for any species (Figure 3). On the other hand, the presence of DVM, in which small specimens occur near the surface layer day and night while large individuals perform nocturnal ascent, has been reported for *P. elegans* in the Gulf of Alaska and Dabab Bay in Washington [14,41–43]. The magnitude of this DVM has been reported to be around 50 m [14]. These facts suggest that the sampling design of this study (minimum depth internal at 25 m) was too large to evaluate such a small DVM.

For the prominent characteristics of the vertical distribution of the *Eukrohnia* species group, juveniles occurred at the narrower, shallower depths of 150–300 m. *E. hamata* extended to a deeper layer than juveniles, and then *E. bathypelagica* extended further deeper than that of *E. hamata* (Figure 3c). Thus, within *Eukrohnia* species, their vertical distribution was seen in the order of *Eukrohnia* juveniles < *E. hamata* < *E. bathypelagica*. Such a phenomenon as *Eukrohnia* (developmental descent) has been reported in the North Pacific [42,44], Arctic Ocean [13,38], and South Ocean [31,40,45]. Thus, such ontogenetic vertical distribution is considered to be a feature of this genus.

Table 4. Regional comparison in abundance of the three dominant chaetognath species (*Eukrohnia bathypelagica*, *E. hamata* and *Parasagitta elegans*) from worldwide oceans.

Region	Season	Gear	Mesh (µm)	Depth (m)	Abundance (ind. m^{-2})									Reference
					E. bathypelagica			*E. hamata*			*P. elegans*			
					Min	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**	
Oyashio	Spring	Bongo	335	0–200	-	-	-	113	2543	1050	52	380	176	Abe et al. (2016) [24]
Celtic Sea	Annual	LHPR	280	0–90	-	-	-	-	-	-	22	2483	-	Conway and Williams (1986) [34]
Arctic Ocean	Annual	Multi-net	200	0–520	-	-	-	56	894	-	16	462	-	Grigor et al. (2017) [36]
Arctic Ocean	Annual	Multi-net	200	0–580	-	-	-	158	894	468	16	204	71	Grigor et al. (2020) [37]
Arctic Ocean	Summer	Multi-net	150	0–3000	-	-	-	804	1773	1087	0	16	3	Kosobokova and Hopcroft (2021) [13]
Oyashio	Annual	NORPAC	335	0–150	-	-	-	-	-	-	90	795	-	Kotori (1999) [16]
Oyashio	Annual	Bongo	335	0–1000	220	383	-	1738	3090	-	127	1154	-	Matsumoto and Yamaguchi (2020) [18]
Bering Sea	Summer	VMPS	90	0–5000	-	-	512	-	-	2164	-	-	2359	Ozawa et al. (2007) [25]
Okhotsk Sea	Summer	VMPS	90	0–5000	-	-	273	-	-	970	-	-	94	Ozawa et al. (2007) [25]
western subarctic Pacific	Summer	VMPS	90	0–5000	-	-	360	-	-	1475	-	-	1123	Ozawa et al. (2007) [25]
Japan Sea	Summer	VMPS	90	0–5000	-	-	0	-	-	0	-	-	135	Ozawa et al. (2007) [25]
Buffin Bay	Summer	BIONESS	243	0–500	-	-	-	130	444	-	0	405	-	Sameoto (1987) [38]
Long Island Sound	Annual	Ring net	202	0–37	-	-	-	-	-	-	-	3922	-	Tiselius and Peterson (1986) [35]
Southern Ocean	Summer/Winter	Multi-net	100	0–3000	27	82	-	81	224	-	-	-	-	Kruse et al. (2009) [31]
K2	Annual	IONESS	335	0–1000	240	1540	870	140	1600	800	40	360	200	This study

Ontogenetic vertical distribution changes in Chaetognaths: deeper occurrences of large-sized specimens have been reported for *P. elegans* and *E. hamata* in the Gulf of Alaska [42]. In this study, both *P. elegans* and *E. hamata* showed this developmental descent ontogenetic vertical distribution clearly (Figures 4 and 5). Since Chaetognatha are large in body size, they are important as food for various fish [46–48]. Therefore, to avoid predation by visual predators such as fish, large-sized specimens may perform a deeper distribution, which would induce ontogenetic vertical distribution.

4.3. Population Structure of Chaetognaths

This study observed two to four cohorts for the body length histograms of *P. elegans*, *E. hamata*, and *E. bathypelagica* (Figure 8). Based on the time-series trace of the body length cohort, life histories of Chaetognaths in the subarctic Pacific were conducted for *P. elegans* [16,24,49] and *E. hamata* [18,49] by tracing their cohorts over time. The daily growth rates in body length have been reported as 14–290 µm day^{-1} in *P. elegans* and 6–100 µm day^{-1} in *E. hamata* (see Table 3 of [31]). Considering these values, maturation of the specimens is possible within three months. However, since the sampling interval of this study is three months (four times in one year), it is difficult to analyze their life cycles by tracing the body length of each cohort.

The most prominent finding of this study is that both *Eukrohnia* species (*E. hamata* and *E. bathypelagica*) had no large mature specimens reported for *E. hamata* in the Arctic Ocean (Figures 5–7). Thus, in the Arctic Ocean, the maturation stages of *E. hamata* have been classified into eight stages [27]. While only stages belonging to 1 to 5 occurred and no individuals belonging to 6 to 8 stages were observed throughout this study, it is also mentioned that there is a scarce occurrence of mature individuals of *E. hamata* and *E. bathypelagica* in the Southern Ocean [3,31]. As the causes of such a low abundance of mature specimens, it is suggested that the deeper occurrence of mature individuals and the long time interval (low time resolution) in sampling design may prevent the appropriate collection of the mature specimens [31].

These two factors (deeper occurrence of mature specimens and failure to collect mature specimens due to insufficient time resolution) are also inevitable in this study; however, considering their vertical distributions (Figure 3), it is hard to assume that only mature *E. hamata* and *E. bathypelagica* occur below 1000 m depth. Genetic analyses suggest that *E. hamata* and *E. bathypelagica* belong to the same species group and are geographically divided into four species groups [17,26]. The four species groups are reported to occur in different geographical regions: the northern North Pacific, the Southern Ocean, the tropical Pacific, and the Atlantic–Arctic Ocean [17,26]. From these geographical distributions of genetic groups of *Eukrohnia* species, it is suggested that the population in the northern North Pacific (this study) and that in the Arctic Ocean [27] belong to different cryptic species. If this hypothesis is correct, the cryptic species group of *Eukrohnia* in the arctic ocean (Ham-B in [17]) has eight stages of maturity. In contrast, the species of *E. hamata* in the northern North Pacific (Ham-D in [17]) has only five maturation stages.

In terms of the body length of *Eukrohnia* spp., there are substantial differences between the Arctic Ocean and the northern North Pacific. Thus, the body length of *E. hamata* (Ham-B) in the Arctic Ocean has been reported to be as large as 41 mm [13,27]. On the other hand, *E. hamata* (Ham-D) in the northern North Pacific has a maximum body length of 28 mm [15,24] (Figures 5–7). Such a large geographical variation in body length may reflect the genetic differences seen in the *Eukrohnia* species group.

As another point to consider, there are no genetic differences between *E. hamata* and *E. bathypelagica*, and they should be treated as one species, as pointed out by [17]. The vertical distribution and population structure of the *Eukrohnia* species group, which combines *Eukrohnia* juvenile, *E. hamata*, and *E. bathypelagica*, have no difficulty considering or treating one species group (Figure 7). This may suggest that *E. hamata* and *E. bathypelagica* are the same species in the western subarctic Pacific. To clarify this point, detailed genetic analysis of the *Eukrohnia* species group, including *Eukrohnia* juveniles, small to large individuals of *E. hamata,* and *E. bathypelagica,* will be required in future studies.

In conclusion, regional genetic segregation would be present considering the great regional differences in body size and mature stage of *Eukrohnia* species. Within the same region (especially in the western subarctic Pacific), *Eukrohnia* species, including *E. hamata* and *E. bathypelagica*, could be treated as one species group. Further molecular analysis will be required for the *Eukrohnia* species group to evaluate these issues.

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