Plankton Benthos Res 2(4): 184–197, 2007

Plankton & Benthos Research

Abundance and community structure of chaetognaths from the epipelagic through abyssopelagic zones in the western North Pacific and its adjacent seas

MIHO OZAWA[1], ATSUSHI YAMAGUCHI[1]*, TSUTOMU IKEDA[1], YUJI WATANABE[2] & JOJI ISHIZAKA[3]

[1] *Laboratory of Marine Biodiversity, Graduate School of Fisheries Sciences, Hokkaido University, 3–1–1 Minatomachi, Hakodate, Hokkaido 041–8611, Japan*
[2] *The General Environmental Technos Co. Ltd., 1–3–5 Azuchimachi, Chuo-ku, Osaka 541–0052, Japan*
[3] *Graduate School of Marine Science and Engineering, Nagasaki University, 1–14 Bunkyo, Nagasaki 852–8521, Japan*

Received 9 February 2007; Accepted 18 September 2007

Abstract: Abundance and community structure of chaetognaths were studied based on the vertical stratified zooplankton samples from the epipelagic through abyssopelagic zones (maximum: 5,000–5,800 m) at four stations in the western North Pacific (44°N, 39°N, 30°N, and 25°N) and one station each in the Japan Sea, Okhotsk Sea, and Bering Sea. Chaetognath standing stocks (indiv. m^{-2}) were greatest at subarctic stations (44°N, Okhotsk Sea, and Bering Sea). Vertically, chaetognath density (indiv. m^{-3}) was the greatest in the shallowest depths, and decreased with increasing depth. Chaetognaths occurred down to 4,000–5,000 m at subarctic stations, while chaetognaths were not found below 3,000 m at subtropical stations (30°N and 25°N). The number of chaetognath species was the greatest (22 representing 14 genera) at the transition station (39°N), and the least (1 species) at the station in the Japan Sea. Species diversity indices (H') were low at subarctic stations, but high at subtropical stations. Vertical profiles of H' varied also between these stations; it peaked at the mesopelagic zone at subarctic stations, and at the epipelagic zone at subtropical stations. Cluster analysis separated chaetognath communities of the study region into 5 groups (A–E) characterized by discrete spatial distribution: group A; the mesopelagic zone at subtropical and transition areas, group B; the epipelagic zone at subtropical and transition areas, group C; the bathy- and abyssopelagic zone (except the Japan Sea), group D; all depths in the Japan Sea, and group E; the epi- and mesopelagic zones in the subarctic area. For the four most abundant species at the subarctic stations, allometric data showed greater head width to total length ratios, and greater hook length to total length ratios for deeper-dwelling species. Relatively larger head width (i.e. large mouth) and longer hooks of deep-sea chaetognaths are considered to be an adaptation significant to the successful capture of prey zooplankton in resource limited deep-sea environments.

Key words: abyssopelagic, bathypelagic, chaetognaths, deep-sea, vertical distribution

Introduction

In terms of biomass, chaetognaths are known to be the second most dominant taxon in oceanic zooplankton communities worldwide, with biomasses 10–30% those of copepods, the most dominant taxon (Ryther 1969, Reeve 1970). Chaetognaths are primarily carnivores, feeding mainly on copepods, but euphausiids, amphipods, larvae of crustaceans, appendicularians, fish larvae, and other chaetognaths (i.e. cannibalism) are also reported in their diet (Feigenbaum 1991). In turn, chaetognaths are reported to be important prey for a variety of pelagic fishes (Moku et al. 2000, Yamamura et al. 2002). Thus, chaetognaths are considered to be an important mediator between animals at lower trophic levels and those at higher trophic levels in marine ecosystems.

In the waters around Japan, 30 species of chaetognaths have been recorded to date (Terazaki 1996). Community structure of chaetognaths in the North Pacific and its adjacent seas has been studied by Kotori (1976), Terazaki & Miller (1986), Terazaki (1993a), and Matsuda & Taniguchi (2001) based on the samples from the epipelagic (0–200 m) to mesopelagic (200–1,000 m) zones. For chaetognaths living below 1,000 m, abundance and vertical distribution have been reported by Kitou (1966a, b, 1967) and Vinogradov (1968) in the western North Pacific. Nevertheless, comprehensive analysis on the spatial variations of commu-

---

* Corresponding author: Atsushi Yamaguchi; E-mail, a-yama@fish.hokudai.ac.jp

nity structures of chaetognaths in the western North Pacific and its adjacent seas is still lacking.

To clarify this issue, we studied the abundance, vertical distribution and community structure of chaetognaths down to the abyssopelagic zone (~5,800 m) at four stations located from the subarctic to the subtropical western North Pacific Ocean. Additional sampling down to the lower bathypelagic zone (~3,000 m) was carried out in seas adjacent to the western North Pacific (Japan Sea, Okhotsk Sea, and Bering Sea), and these results are discussed in the light of spatial variations in the community structure. Based on allometric data of the feeding apparatus, the possible adaptive significance of the morphology of bathypelagic and abyssopelagic chaetognaths is noted.

Materials and Methods

Sampling

Deep plankton sampling was conducted at four stations (Sts. 44N [44°N, 155°E], 39N [39°N, 147°E], 30N [30°N, 147°E], and 25N [25°N, 137°E]) in the western North Pacific Ocean during the period of September 1999 through August 2001 (Fig. 1, Table 1). Zooplankton was collected from discrete depths with a modified NORPAC net (mesh size 90 μm, mouth opening 0.16 m^2, cf. Motoda 1957) from 0–100 and 100–200 m, and with a VMPS (Vertical Multiple Plankton Sampler, mesh size 90 μm, mouth opening 1.0 m^2, Tsurumi Seiki Co. Ltd., Yokohama, cf. Terazaki & Tomatsu 1997) for depths below 200 m. The total number of discrete sampling strata was 9 between 0–5,000 m (Sts. 44N, 39N, and 25N) or 10 between 0–5,800 m (St. 30N) (Table 1).

Sampling was also done in the Japan Sea, Okhotsk Sea, and Bering Sea (Fig. 1, Table 1). In the Japan Sea, vertical sampling of 5 strata with closing nets (mesh size 90 μm, mouth opening 0.28 m^2, cf. Kawamura 1989) down to 3,000 m was carried out at 42°30′N, 137°30′E on January 10, 1997. In the Okhotsk Sea, vertical sampling of 5 strata with the same closing net down to 2,000 m was carried out at 44°40′N, 145°20′E on September 30, 1997. In the oceanic Bering Sea (north of the Aleutian Islands), vertical sampling of 6 strata with a small mouth VMPS (mesh size 90 μm, mouth opening 0.25 m^2) was done at 53°30′N, 177°00′E on July 12, 2003.

All zooplankton sampling was done during nighttime. Samples were preserved in 5% borax-buffered formalin immediately on board. At each sampling station, CTD (Neil Brown or Sea Bird) casts were carried out to determine temperature and salinity profiles. Dissolved oxygen (DO) was measured by the Winkler titration method on water samples collected from Niskin bottles rosette-mounted on the CTD system.

Enumeration, identification and size measurements

From whole or 1/2 aliquots of the zooplankton samples, chaetognaths were sorted out and species identification was done under a stereomicroscope. For species identification, we referred to the descriptions of Terazaki (1996) and Nagasawa & Marumo (1976), the latter was useful for identification of smaller specimens. Smaller specimens of *Eukrohnia hamata and E. bathypelagica* without ovaries (Stage I) were difficult to distinguish from each other, so they were lumped as "*E. hamata*/*E. bathypelagica* Stage I" in the present study.

To examine possible morphological changes in the feed-

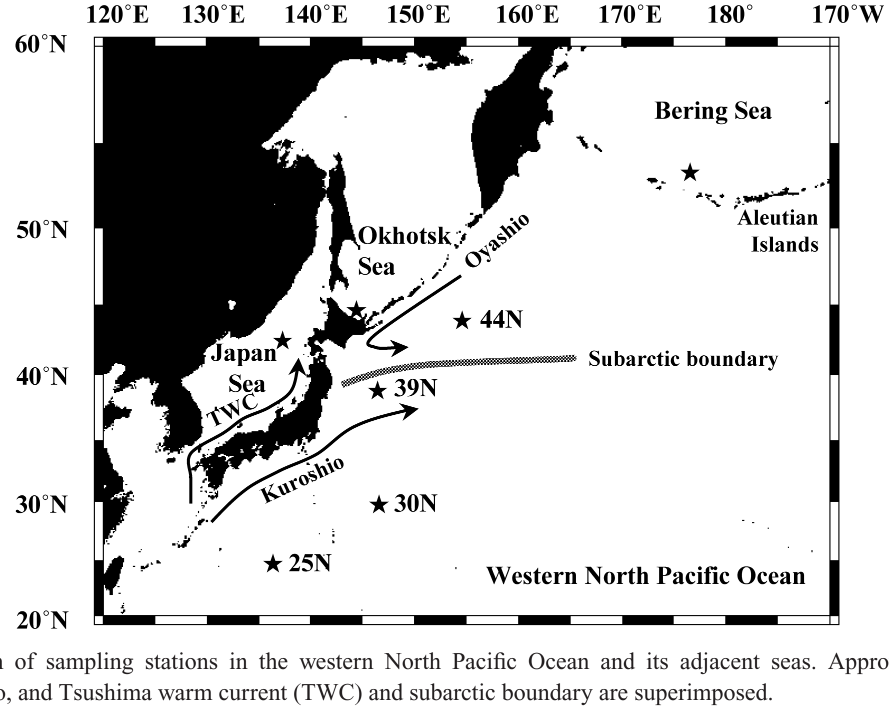

Fig. 1. Location of sampling stations in the western North Pacific Ocean and its adjacent seas. Approximate position of Kuroshio, Oyashio, and Tsushima warm current (TWC) and subarctic boundary are superimposed.

Table 1. Zooplankton sampling data in the western North Pacific and its adjacent seas. Bottom depth at each station shown in the parentheses. Abbreviations of ship names are Hr: RV "*Hakurei-Maru No. 2*", Ky: RV "*Kaiyo-Maru*", Ho: TS "*Hokusei-Maru*", Os: TS "*Oshoro-Maru*".

Area	Station code	Position	Sampling date	D/N	Ship	Net	Depth strata (m)
Western North Pacific	44N	44°00′N, 155°00′E	Sep. 25, 2000	Night	Hr	Closing NORPAC	0–100, 100–200
		(5,322 m)	Sep. 25, 2000	Night	Hr	VMPS 6000D	200–300, 300–500, 500–1,000, 1,000–2,000, 2,000–3,000, 3,000–4,000, 4,000–5,000
	39N	39°00′N, 147°00′E	Aug. 15, 2001	Night	Hr	Closing NORPAC	0–100, 100–200
		(5,340 m)	Aug. 17, 2001	Night	Hr	VMPS 6000D	200–300, 300–500, 500–1,000, 1,000–2,000, 2,000–3,000, 3,000–4,000, 4,000–5,000
	30N	30°00′N, 147°00′E	Oct. 4, 1999	Night	Hr	Closing NORPAC	0–100, 100–200
		(6,213 m)	Oct. 5, 1999	Night	Hr	VMPS 6000D	200–300, 300–500, 500–1,000, 1,000–2,000, 2,000–3,000, 3,000–4,000, 4,000–5,000, 5,000–5,800
	25N	25°00′N, 137°00′E	Sep. 20, 1999	Night	Hr	Closing NORPAC	0–100, 100–200
		(5,713 m)	Sep. 21, 1999	Night	Hr	VMPS 6000D	200–300, 300–500, 500–1,000, 1,000–2,000, 2,000–3,000, 3,000–4,000, 4,000–5,000
Japan Sea	Japan Sea	42°30′N, 137°30′E (3,650 m)	Jan. 10, 1997	Night	Ky	Closing net	0–100, 100–500, 500–1,000, 1,000–2,000, 2,000–3,000
Okhotsk Sea	Okhotsk Sea	44°40′N, 145°20′E (2,195 m)	Sep. 30, 1997	Night	Ho	Closing net	0–50, 50–250, 250–500, 500–1,000, 1,000–2,000
Bering Sea	Bering Sea	53°30′N, 177°00′E (3,779 m)	Jul. 12, 2003	Night	Os	VMPS 3000D	0–50, 50–250, 250–500, 500–1,000, 1,000–2,000, 2,000–3,000

ing apparatus of chaetognaths with an increase in habitat depth, we measured the ratios of the head width to the total length (an index of mouth size), and the hook length to the total length (an index of hook length) for the four abundant species (*Parasagitta elegans*, *Eukrohnia hamata*, *E. bathypelagica*, and *E. fowleri*) at the subarctic stations (44N, Bering Sea, and the Okhotsk Sea). The hook length was represented by the longest hook on each specimen (Terazaki 1993b). The head width, hook length and total length ($<$10 mm) were measured to the nearest 0.01 mm under a dissecting microscope with an eyepiece micrometer. For the specimens with a total length larger than 10 mm, total length was measured to the nearest 0.05 mm with a slide gauge.

Analysis of data

To evaluate species-specific vertical distributions, we calculated the depth where 50% of the population resides ($D_{50\%}$: Pennak 1943), $D_{25\%}$, and $D_{75\%}$ were also calculated. A species diversity index (H') was calculated using the equation: $H' = -\sum p_i \ln p_i$, where p_i is the composition (*proportion*) of *i*th species to the total abundance (indiv. m^{-2}) in the layer/station (Shannon & Weaver 1963).

For community structure analysis, we conducted a cluster analysis and non-metric multidimensional scaling (NMDS) ordination. Abundance data (X: indiv. m^{-2}) for each species was transformed to $\log_{10}(X+1)$ prior to analysis in order to reduce the bias of abundant species. Similarities between samples were examined by the Bray-Curtis index (Bray & Curtis 1957) according to the differences in species composition. For grouping the samples, the similarity indices were coupled with hierarchical agglomerative clustering with a complete linkage method. The NMDS ordination was carried out to delineate the sample groups on the two-dimensional map. All of these analyses were carried out using BIO$\sum$TAT II software (Sigma Soft).

Results

Hydrography

In the western North Pacific, the sea surface temperature was 13°C at St. 44N, and was about 29°C at Sts. 39N, 30N, and 25N (Fig. 2). Intermediate cold water ($<$2.0°C) was observed between 60 and 120 m at St. 44N. At the other stations, temperature decreased with increasing depth and was 1.5–2.0°C below 1,000 m depth. The surface salinity at St. 44N was 32.5, increased with increasing depth and stabilized finally at 34.6 (Fig. 2). At St. 39N, salinity fluctuated between 33.9 and 34.6 between 0–1,000 m depth, and stabilized to 34.6 below 1,000 m depth. Salinity profiles

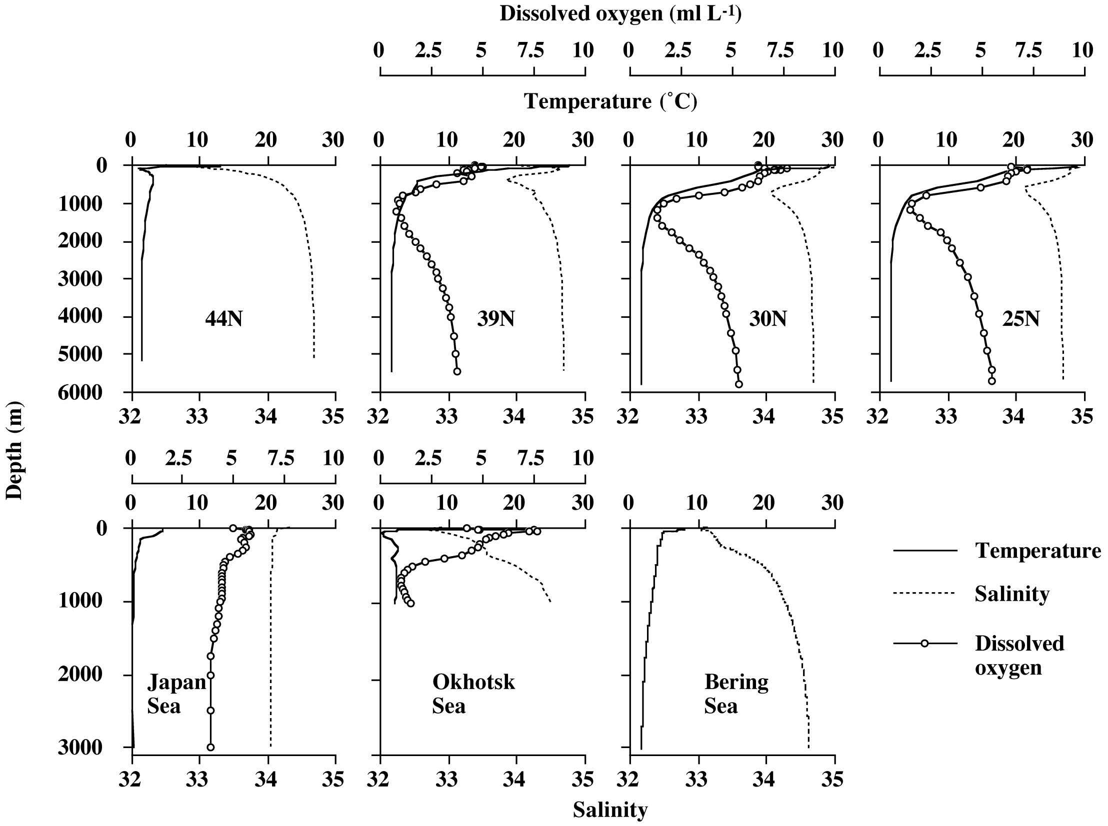

Fig. 2. Vertical profiles of temperature (°C), salinity, and dissolved oxygen (ml L^{-1}) in the western North Pacific Ocean (upper) and its adjacent seas (lower). Note that dissolved oxygen was not determined at St. 44N or in the Bering Sea. Depth scales are not the same between upper and lower panels.

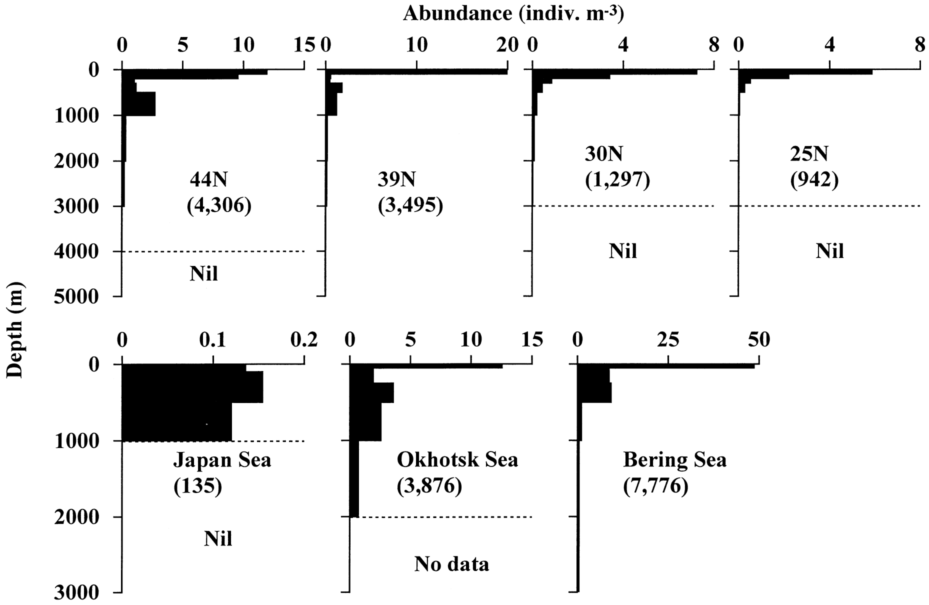

Fig. 3. Vertical distribution of the abundance of chaetognaths (indiv. m^{-3}) at four stations in the western North Pacific Ocean (upper) and at single stations in the Japan Sea, Okhotsk Sea, and Bering Sea (lower). Note that abundance scales vary between panels. Water column integrated standing stocks (indiv. m^{-2}) are shown in parentheses. Nil: no occurrence.

were similar at Sts. 30N and 25N, with a minimum at ca. 600 m depth. Dissolved oxygen profiles at Sts. 39N, 30N, and 25N were similar to each other, with an oxygen minimum layer (<2 ml L^{-1}) at ca. 1,000 m depth (no dissolved oxygen data at St. 44N) (Fig. 2).

The profiles of temperature and dissolved oxygen concentration at the Japan Sea station were characterized by the presence of extreme low temperature (<1.0°C) yet high oxygen concentration (3.9–4.5 ml L^{-1}) below 500 m depth (Fig. 2). This cold and oxygen-rich deep-water is known as "Japan Sea Proper Water" (Sudo 1987). Salinity in the Japan Sea was near homogenous (34.1) throughout the water column. A marked hydrographic characteristic of the Okhotsk Sea station was the presence of the intermediate cold water (<1°C) at 20–200 m depth. The salinity profile at the Okhotsk Sea station was similar to that at St. 44N in the western North Pacific. At the station in the Bering Sea, both temperature and salinity profiles were similar to those at St. 44N and the Okhotsk Sea station.

Hereafter, we refer to St. 44N, and the Okhotsk Sea and Bering Sea stations as "subarctic stations", St. 39N as the "transition station", and Sts. 30N and 25N as "subtropical stations".

Abundance and vertical distribution

In terms of abundance integrated over the extent of the water column that was studied, chaetognaths were most abundant at the station in the northernmost Bering Sea (7,776 indiv. m^{-2}) and least abundant at the station in the Japan Sea (135 indiv. m^{-2}) (Fig. 3). Within the western North Pacific, the abundance was greatest at St. 44N, and decreased gradually toward St. 25N. Sampling depths of the four stations in the western North Pacific were deep (0–5,000 m or 5,800 m) compared with those in the adjacent seas (0–2,000 m or 3,000 m, Table 1). However, these differences in sampling depth among stations are thought unimportant, since the abundance of chaetognaths below 2,000 or 3,000 m depth was extremely low (Fig. 3). In fact, the greatest abundance was observed at a shallower station (~3,000 m Bering Sea) and the lowest abundance was obtained at a deeper station (~5,000 m 25N).

A common feature seen in the vertical distribution patterns of chaetognaths was the incidence of a near-surface maximum, with the only exception being the Japan Sea station. The maximum density was 48.6 indiv. m^{-3} at 0–50 m depth at the Bering Sea station (Fig. 3). At St. 44N and 39N in the Pacific and at the Okhotsk Sea station, a secondary peak was also observed at mesopelagic depths of 250–1,000 m, thus showing bimodal vertical distribution patterns. In the western North Pacific, chaetognaths occurred down to the abyssopelagic zone (~4,000 or 5,000 m) at 44N and 39N, but they did not occur below 3,000 m depth at Sts. 30N or 25N. Chaetognaths did not occur below 1,000 m depth in the Japan Sea.

The vertical distribution of chaetognaths evaluated by $D_{50\%}$ varied not only according to species but also from one sampling station to the next within a species. For the most common chaetognath *Parasagitta elegans*, $D_{50\%}$ was 26–187 m at subarctic stations (44N, Okhotsk Sea, and Bering Sea), while it was 448–473 m at transition stations (39N and the Japan Sea) (Table 2). For the other chaetognaths at subarctic stations, $D_{50\%}$ was 169–308 m for *Eukrohnia hamata*, 583–728 m for *Eukrohnia bathypelagica*, and

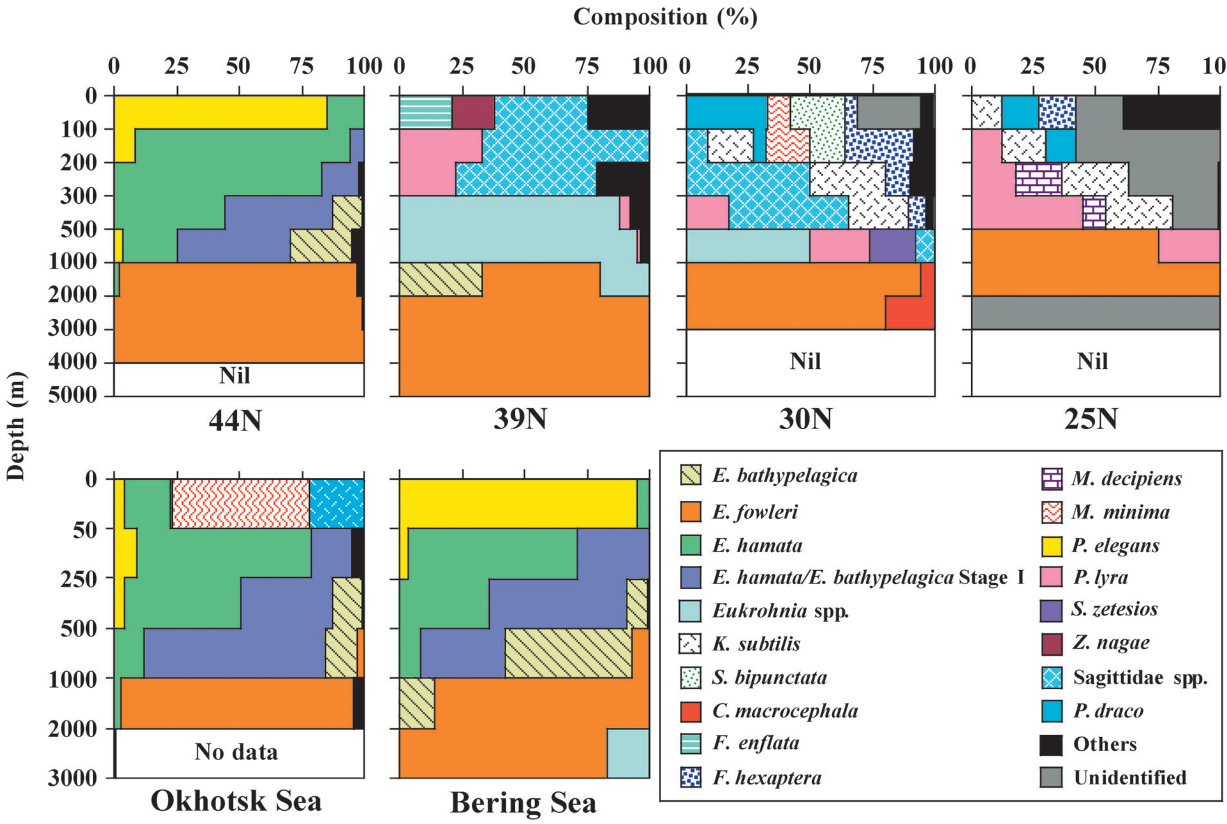

Fig. 4. Vertical changes in the species composition of chaetognath communities at four stations in the western North Pacific Ocean (upper) and at single stations in the Okhotsk Sea and Bering Sea (lower). Note that the Japan Sea data are not shown because of the presence of only one species (*Parasagitta elegans*). Nil: no occurrence.

1,474–1,918 m for *Eukrohnia fowleri*. Thus the vertical distributions of common chaetognaths were well separated at the subarctic stations (Table 2). At transition and subtropical stations (39N, 30N, and 25N), $D_{50\%}$s of most chaetognaths were 50 m (e.g., all specimens occurred in the 0–100 m sampling layer) except some Sagittidae species >200 m (e.g., *Mesosagitta decipiens*, *Pseudosagitta lyra*, *Caecosagitta macrocephala*, and *Solidosagitta zetesios*) (Table 2).

Community structure

Over the course of this study, 26 species from 14 genera of chaetognaths were identified (Table 2). The number of species per station was the greatest at 39N in the western North Pacific (14 genera 22 species) and the least in the Japan Sea (*P. elegans* only). At St. 44N in the western North Pacific, *P. elegans* contributed to 85% of the total number of chaetognaths at 0–100 m, *E. hamata* 44–86% of the total number at 100–500 m, and *E. bathypelagica* 25% of the total number at 500–1,000 m depths (Fig. 4). Species composition at stations in the Bering Sea and Okhotsk Sea were similar to those at St. 44N, with the exception of 0–50 m in the Okhotsk Sea, where warm-water *M. minima* dominated (55%, cf. Fig. 4). Species composition at Sts. 30N and 25N in the western North Pacific was identical, e.g., warm-water *Pterosagitta draco* and *Flaccisagitta hexaptera* dominated at 0–200 m, and *P. lyra* and *Krohnitta subtilis* at 200–1,000 m. At the transition St. 39N, both cold-water and warm-water species occurred together, thus making the number of species greatest at this station. Except for the Japan Sea station, where *P. elegans* was the only chaetognath (Table 2), *E. fowleri* was the predominant species among bathypelagic (1,000–3,000 m) and abyssopelagic (>3,000 m) chaetognaths across the stations (Fig. 4).

Species diversities of chaetognaths varied from one station to the next, and were high ($H'=2.2$–2.4) at the transition (39N) and subtropical stations (30N and 25N) and low ($H'=1.2$–1.4) at the subarctic stations (44N, Okhotsk Sea, and Bering Sea) (Fig. 5). Vertical distribution patterns of H' also differed from one station to the next: e.g., it peaked at near surface layers at transition and subtropical stations, and at 500–1,000 m depth at subarctic stations. It is noted that the sharp H' minimum at 100–300 m at Sts. 44N, 39N, and the Okhotsk Sea station (Fig. 5) corresponded to the depth stratum of low chaetognath abundance mentioned above (Fig. 3).

Cluster analysis based on the abundance of each species showed that chaetognath communities could be divided into five groups (A–E) at 26% Bray-Curtis similarity (Fig. 6A). Two-dimensional NMDS plots showed that these groups

Table 2. The abundance (indiv. m^{-2}) and percent contribution of each species to the total abundance of chaetognaths in the western North Pacific Ocean and its adjacent seas. $D_{50\%}$ indicates the depth (m) where 50% of the population resides.

Genus/species	44N			39N			30N			25N			Japan Sea			Okhotsk Sea			Bering Sea		
	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$
Eukrohnia																					
E. bathypelagica Alvariño, 1962	360	8.4	728	54	1.5	1,500	–	–		–	–		–	–		273	7.0	583	512	6.6	625
E. fowleri Ritter-Záhony, 1909	471	10.9	1,862	213	6.1	2,246	75	5.8	1,548	22	2.3	917	–	–		689	17.8	1,474	712	9.2	1,918
E. hamata (Möbius, 1875)	1,475	34.3	169	–	–		–	–		–	–		–	–		970	25.0	308	2,164	27.8	217
E. hamata/*E. bathypelagica* Stage I	784	18.2	673	–	–		–	–		–	–		–	–		1,315	33.9	643	1,945	25.0	342
Eukrohnia spp.	78	1.8	–	908	26.0	–	45	3.5	–	–	–		–	–		–	–		66	0.8	–
Krohnitta																					
K. pacifica (Aida, 1897)	–	–		–	–		48	3.7	91	–	–		–	–		–	–		–	–	
K. subtilis (Grassi, 1881)	–	–		26	0.7	65	88	6.8	207	134	14.2	100	–	–		–	–		–	–	
Krohnitta spp.	–	–		–	–		–	–		–	–		–	–		–	–		9	0.1	–
Sagitta																					
S. bipunctata Quoy and Gaimard, 1828	–	–		10	0.3	50	190	14.6	60	23	2.4	50	–	–		–	–		–	–	
Aidanosagitta																					
A. delicata (Tokioka, 1939)	–	–		10	0.3	50	–	–		–	–		–	–		–	–		–	–	
A. neglecta (Aida, 1897)	–	–		79	2.3	50	–	–		45	4.8	50	–	–		–	–		–	–	
A. regularis (Aida, 1897)	–	–		69	2.0	50	–	–		56	6.0	50	–	–		–	–		–	–	
Caecosagitta																					
C. macrocephala (Fowler, 1904)	8	0.2	1,600	6	0.2	750	7	0.5	1,758	–	–		–	–		–	–		–	–	
Ferosagitta																					
F. ferox (Doncaster, 1902)	–	–		49	1.4	50	–	–		–	–		–	–		–	–		–	–	
F. robusta (Doncaster, 1902)	–	–		30	0.8	50	–	–		–	–		–	–		–	–		–	–	
Flaccisagitta																					
F. enflata (Grassi, 1881)	–	–		443	12.7	50	–	–		68	7.2	50	–	–		–	–		–	–	
F. hexaptera (d'Orbigny, 1836)	–	–		–	–		117	9.0	130	90	9.6	50	–	–		–	–		–	–	
Mesosagitta																					

Table 2. Continued

Genus/species	44N			39N			30N			25N			Japan Sea			Okhotsk Sea			Bering Sea		
	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$	indiv. m^{-2}	%	$D_{50\%}$
M. decipiens (Fowler, 1905)	–	–		8	0.2	268	11	0.9	268	14	1.5	275	–	–		–	–		–	–	
M. minima (Grassi, 1881)	–	–		138	3.9	82	108	8.3	50	23	2.4	25	–	–		346	8.9	25	–	–	
M. neodecipiens (Tokioka, 1959)	–	–		6	0.2	50	–	–		11	1.2	50	–	–		–	–		–	–	
Parasagitta																					
P. elegans (Verrill, 1873)	1,123	26.1	56	21	0.6	473	–	–		–	–		135	100	448	94	2.4	187	2,359	30.3	26
Pseudosagitta																					
P. lyra (Krohn, 1853)	–	–		49	1.4	274	36	2.8	583	62	6.6	260	–	–		–	–		–	–	
Serratosagitta																					
S. pacifica (Tokioka, 1940)	–	–		30	0.8	50	–	–		–	–		–	–		–	–		–	–	
S. pseudoserratodentata (Tokioka, 1939)	–	–		–	–		13	1.0	50	–	–		–	–		–	–		–	–	
Solidosagitta																					
S. zetesios (Fowler, 1905)	–	–		10	0.3	467	17	1.3	750	–	–		–	–		–	–		–	–	
Zonosagitta																					
Z. bedoti (Beraneck, 1895)	–	–		49	1.4	50	–	–		–	–		–	–		–	–		–	–	
Z. nagae (Alvariño, 1967)	–	–		374	10.7	50	–	–		–	–		–	–		–	–		–	–	
Z. pulchra (Doncaster, 1902)	–	–		10	0.3	50	–	–		–	–		–	–		–	–		–	–	
Sagittidae spp.	–	–		867	24.8	–	111	8.5	–	–	–		–	–		136	3.5	–	9	0.1	–
Pterosagitta																					
P. draco (Krohn, 1853)	–	–		39	1.1	50	247	19.1	52	116	12.3	64	–	–		–	–		–	–	
Unidentified (Damaged specimens)	8	0.2	–	–	–		184	14.2	–	278	29.5	–	–	–		53	1.4	–	–	–	
Total	4,306	100		3,495	100		1,297	100		942	100		135	100		3,876	100		7,776	100	

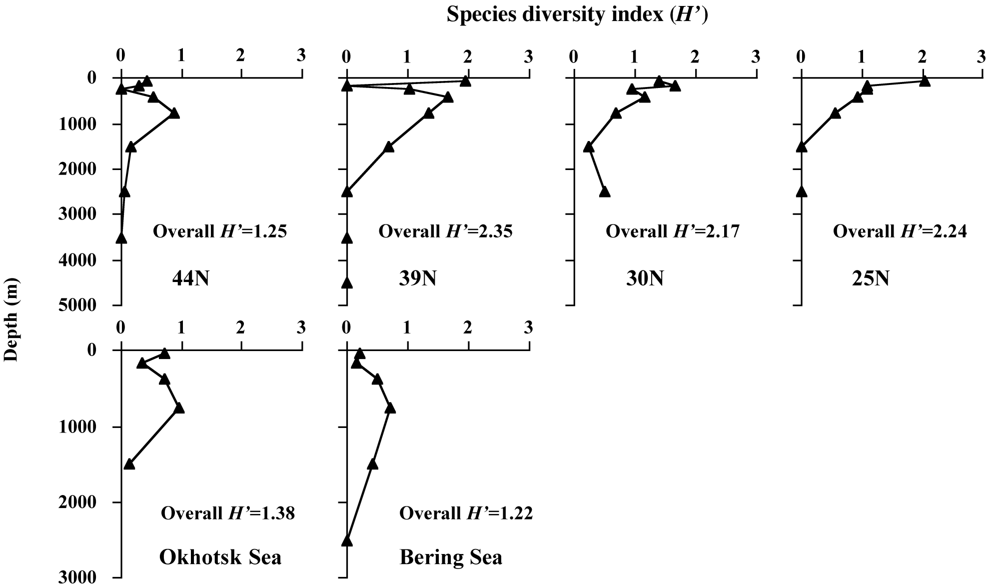

Fig. 5. Vertical changes in the species diversity index (H') of chaetognath communities at four stations in the western North Pacific (upper) and at single stations in the Okhotsk Sea and Bering Sea (lower). Overall H' at each station was calculated based on the standing stock data.

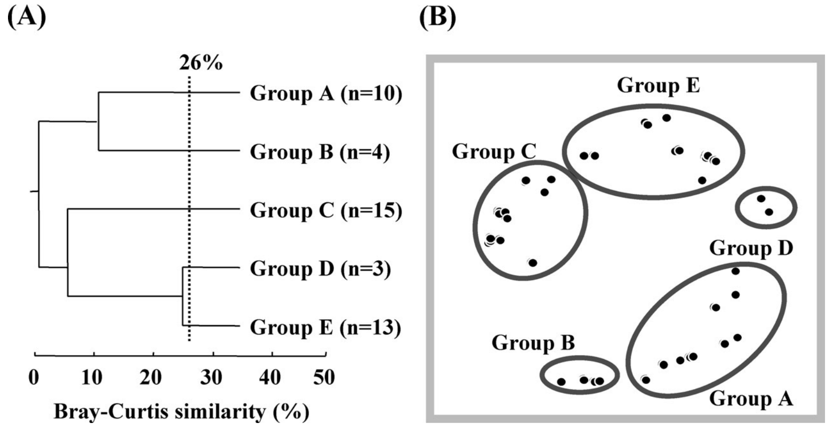

Fig. 6. (A): Community structure of chaetognaths according to station/depth complex data, and the results of cluster analyses based on the Bray-Curtis similarity index (%). Five groups were identified at 26% similarity (broken line). The numbers of samples included are shown in parentheses. (B): Two-dimensional map by NMDS (non-metric multidimensional scaling methods) of chaetognath communities specified by the depth-station complex data. Five groups (group A–E) that clustered according to the Bray-Curtis similarity index (Fig. 6A) are circled in the panel.

were well separated from each other (Fig. 6B). Spatially, the mesopelagic and epipelagic zones of lower latitudes were characterized by the incidences of groups A and B, respectively (Fig. 7). Group C occurred below 1,000 m depth (excepting the Japan Sea). Group D was seen only in the Japan Sea, and group E in the epi- to mesopelagic zones of the subarctic stations. Chaetognath species representing each group were identified by one-way ANOVA and Sheffe's post-hoc test on the abundance data (indiv. m^{-2}). The analysis showed that group A was represented by *P. lyra*, group B by *K. subtilis*, *P. draco*, *S. bipunctata*, and *F. hexaptera*, group C by *E. fowleri*, and group E by *E. hamata* (Table 3). Group D was not represented by any species, indicating that the basis of this discrimination of the groups was the relative abundance of common species but not the abundance of a given species.

Head width and hook length of chaetognaths

The ratios of head width to total body length, and hook length to total body length of the four most abundant chaetognaths at the subarctic stations (44N, Okhotsk Sea, and Bering Sea) increased with depth (Fig. 8). This was especially so for the bathypelagic species *E. fowleri* ($D_{50\%}$: 1,474–1,918 m), which had the largest ratios for both (Fig. 8). *P. elegans* exhibited a slightly shallower distribution

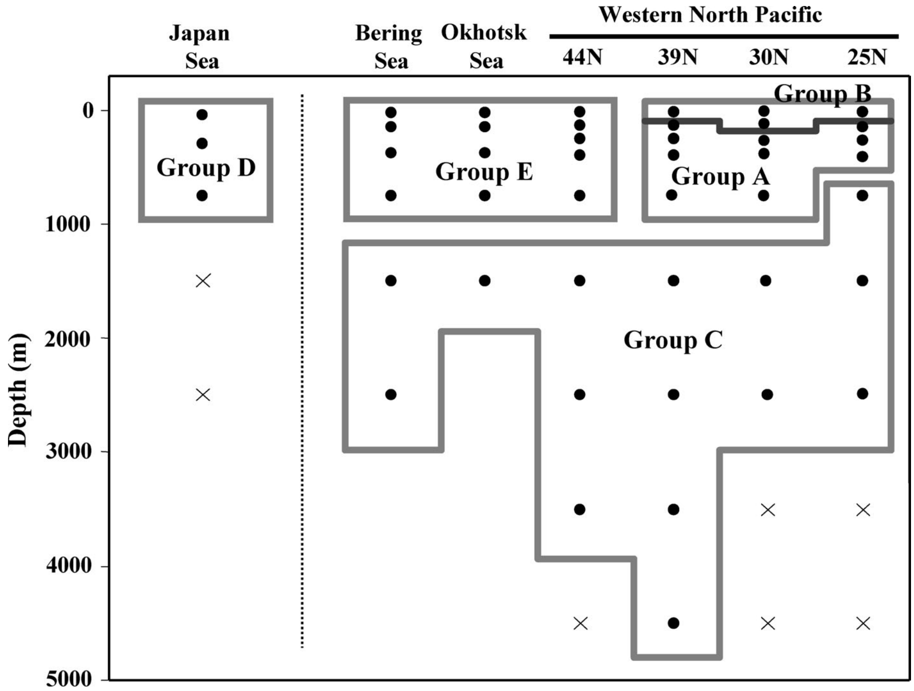

Fig. 7. Spatial separation of chaetognath community groups identified by Bray-Curtis similarity index data (cf. Fig. 6). Sampling depth is shown by closed circles (positive occurrence) and crosses (negative occurrence). Note that the 5,000–5,800 m data (negative occurrence) at St. 30N was omitted in this panel.

Table 3. Mean abundance (indiv. m^{-2}) of each chaetognath species in five clustered groups (A–E) identified by Bray-Curtis similarity analysis (cf. Fig. 6). The numbers in parentheses indicate the number of samples included in each group. Differences between groups were tested with one-way ANOVA. In each group, the mean abundances showed in bold letters were significantly greater than in other groups (Scheffe's post-hoc test, $p<0.05$).

	Mean abundance (indiv. m^{-2})					one-way ANOVA	
Species	A (n=10)	B (n=4)	C (n=15)	D (n=3)	E (n=13)	*F*	*p*
E. bathypelagica	0	0	8	0	84	3.39	0.02
E. fowleri	0	0	**151**	0	6	4.33	0.005
E. hamata	0	0	2	0	**353**	7.13	<0.001
K. subtilis	12	**32**	0	0	0	9.94	<0.001
S. bipunctata	0	**56**	0	0	0	7.68	<0.001
C. macrocephala	0.59	0	0.94	0	0.10	0.93	0.46 (NS)
F. hexaptera	1	**48**	0	0	0	18.24	<0.001
F. enflata	0	128	0	0	0	4.26	0.006
M. minima	0	67	0	0	27	1.54	0.21 (NS)
M. decipiens	3	0	0	0	0	7.08	<0.001
P. elegans	2	0	0	45	275	1.21	0.32 (NS)
P. lyra	**14**	0	0.31	0	0	25.86	<0.001
S. zetesios	3	0	0	0	0	2.05	0.11 (NS)
Z. nagae	0	94	0	0	0	2.96	0.03
P. draco	3	**94**	0	0	0	10.05	<0.001

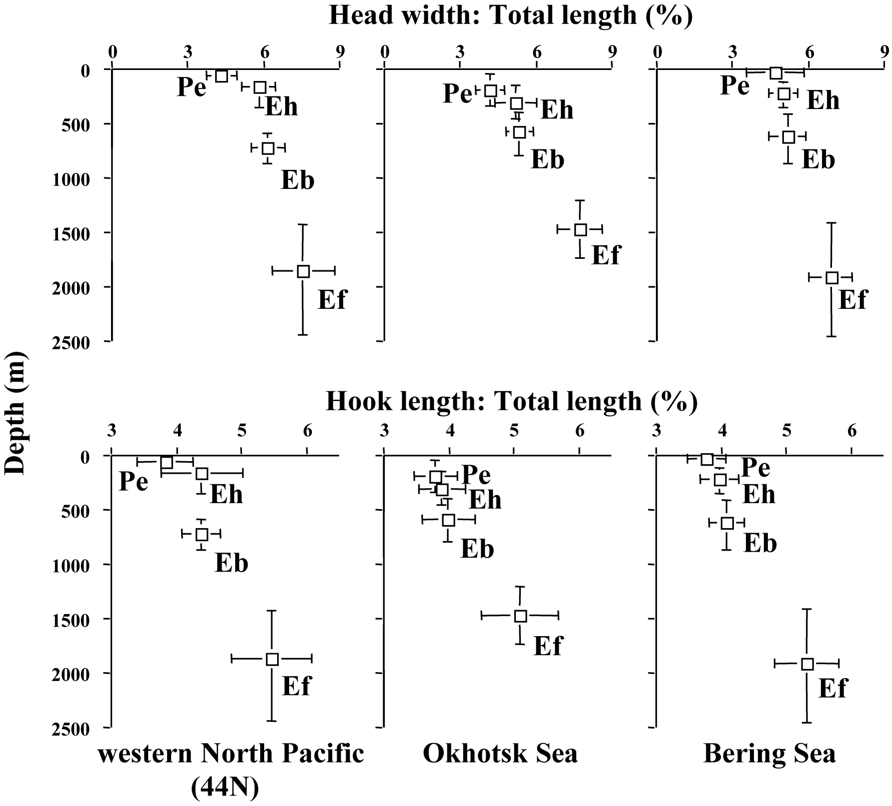

Fig. 8. Vertical profiles of the relationships between head width: total length ratio (upper), and hook length: total length ratio (lower) of chaetognaths. Horizontal/vertical bars across the means indicate standard deviations for the ratios and ranges of $D_{25\%}$–$D_{75\%}$, respectively. Pe: *Parasagitta elegans*, Eh: *Eukrohnia hamata*, Eb: *E. bathypelagica* and Ef: *E. fowleri*.

than *E. hamata*, and the head width and hook length relative to the total body length of *E. hamata* was consistently greater than *P. elegans* across the three stations (Fig. 8).

Discussion

Abundance and vertical distribution

At most sampling stations, the maximum sampling depths were well above the bottom (>200 m above bottom, Table 1). Since unique benthopelagic swarms of chaetogonaths have been observed only <100 m above the bottom (cf. Brodeur & Terazaki 1999, Choe & Deibel 2000), their effect, if any, would not be great on the present results.

Concerning the seven stations of this study, standing stocks of chaetognaths were greater at subarctic stations than subtropical stations (Fig. 3). At these stations, the same high to low latitude patterns have also been reported for copepod biomass (Yamaguchi et al. 2002a, 2004). Since copepods are the main food source of chaetognaths (Feigenbaum 1991), latitudinal changes in copepod biomass may be considered to be a cause of the latitudinal changes in chaetognath abundance.

Vertically, chaetognaths showed abundance maxima at 0–100 m and 500–1,000 m, or an abundance sub-minimum at 100–500 m, at Sts. 44N and 39N in the western subarctic Pacific and at the Okhotsk Sea station (Fig. 3). The depth of the abundance sub-minimum corresponds to the depth where the intermediate cold water was observed at St. 44N and Okhotsk Sea station but this was less marked at St. 39N (Fig. 2). This phenomenon (low chaetognath abundance in the intermediate cold water) has previously been reported by Vinogradov (1968) as "both zooplankton abundance and biomass decreased at intermediate cold waters". Since the intermediate cold water is formed by melting of sea ice in the previous year (Itoh et al. 2003), such a cold layer is considered to not be suitable as a habitat for oceanic chaetognaths.

The distribution of chaetognaths is known to be closely linked to hydrographic conditions (temperature and salinity) and for this reason chaetognaths have been used as biological tracers of water masses in the epi- and mesopelagic zone (cf. Pierrot-Bults & Nair 1991). The present study showed that chaetognaths were not found below 3,000 m at the subtropical stations (30N and 25N, Fig. 3). Despite the fact that hydrographic conditions at these depths are extremely similar between subarctic and subtropical stations (cf. Fig. 2), chaetognaths were found in the deepest samples (4,000–5,000 m) at the subarctic and transition stations (44N and 39N, Fig. 3). Kitou (1966a) studied the vertical distribution of chaetognaths down to 6,500 m at 34°N in the western North Pacific, and found no chaetognaths below 3,000 m.

From the viewpoint of feeding conditions for chaetognaths, prey (copepods) is abundant in the epipelagic region and decreases exponentially with increasing depth (cf. Yamaguchi et al. 2002b). Chaetognaths are not visual predators but ambush predators that detect water movements created by prey organisms using filaments on their body surface (Feigenbaum 1991). Their perception system for detecting prey, combined with the rapid decline in prey abundance with depth, suggests severe food limitation in the bathy- and abyssopelagic zones. The ratios of metazooplankton to total planktonic biomass at bathy- and abyssopelagic zones are known to be high at the subarctic station (4.3–39.3% at 44N), but extremely low at the subtropical station (0.05–0.3% at 25N) (Yamaguchi et al. 2004). This low biomass of chaetognath prey in the bathy- and abyssopelagic zones at subtropical stations may be the reason that chaetognaths were absent below 3,000 m in these regions (Fig. 3).

Community structure

The number of chaetognath species varied with region (Fig. 4, Table 2). The greatest number (22 species) was recorded at St. 39N and was due to the occurrence of both cold-water species and warm-water species. At the same station, the species numbers were greatest in the epipelagic layer from 0–100 m (14 species, Fig. 4). Station 39N is located in the transitional domain, characterized by a mixture of cold-water derived from the Oyashio current and warm-water from the Kuroshio current (Fig. 1). Chaetognath community structure in the transitional domain and warm core rings in this region have been studied by several authors (Kitou 1974, Terazaki 1989, Johnson & Terazaki 2003). Kitou (1974) conducted year-round sampling from 0–100 m depths and revealed seasonal changes in the chaetognath community. He reported 17 species of chaetognaths, of which 12 species were also observed in the present study. As abundant species, Kitou (1974) listed *Sagitta* (*=Zonosagitta*) *nagae*, *Sagitta* (*=Mesosagitta*) *minima, Sagitta* (*=Flaccisagitta*) *enflata and Sagitta* (*=Aidanosagitta*) *regularis*, which is in good agreement with the results of the present study (Fig. 4, Table 2).

An anomalous feature of the chaetognath fauna (and other zooplankton taxa) in the Japan Sea is the lack of meso- and bathypelagic species such as *Eukrohnia* as compared with the adjacent North Pacific Ocean (Zenkevitch 1963); despite the fact that the Japan Sea is deep enough (maximum: 3,700 m, average: 1,350 m) to accommodate meso- and bathypelagic species. As a possible cause, Terazaki (2001) noted that the depths of all straits connecting the Japan Sea to the North Pacific are too shallow (<130 m) to allow invasion of meso- and bathypelagic species from the adjacent North Pacific Ocean to the Japan Sea. While *Parasagitta elegans* is an epipelagic species in the North Pacific, they are known to extend their vertical distribution down to the mesopelagic zone in the Japan Sea, possibly because of the absence of competitors such as *Eukrohnia hamata* in the Japan Sea (Terazaki 1993b, Ozawa et al. 2004). Chaetognath species, other than *P. elegans*, recorded in the Japan Sea are all warm-water species, and are thought to be transported from the Pacific Ocean with the Tsushima warm-water current, a branch of the Kuroshio current (Kitou 1974). The absence of warm-water chaetognaths at the Japan Sea station in this study may be due to conditions being too cold for them because of the location of the station (northern Japan Sea, Fig. 1) and the sampling season (mid-winter, Table 1).

While species diversity (H') varied greatly with region (Fig. 5), there were two major trends; one was a high diversity (overall H'=2.2–2.4) at the transition and subtropical stations (39N, 30N, and 25N), and the other was low diversity (overall H'=1.2–1.4) at the subarctic stations (44N, Okhotsk Sea, and Bering Sea, Fig. 5). Vertical distribution patterns of H' were different between these two regions; i.e. H' peaked in the epipelagic 0–100 m at subtropical stations, but in the mesopelagic 500–1,000 m at subarctic stations (Fig. 5). This regional difference in the vertical distribution of H' is caused by the incidence of many species in the epipelagic zones at subtropical stations, and by the overlapping vertical distributions of the three *Eukrohnia* species (*E. hamata*, *E. bathypelagica*, and *E. fowleri*) in the mesopelagic zones at subarctic stations (Fig. 4). For zooplankton taxa other than chaetognaths, Yamaguchi et al. (2002b) computed H' of copepod communities down to 4,000 m at the same 44N station and found it peaked also at 500–1,000 m (peak H'=2.6 [day]–2.8 [night], Yamaguchi et al. 2002b). The species diversity values of chaetognaths calculated in this study at the same subarctic station (peak H'=0.9, Fig. 5) are much lower than those of copepods. For this reason, it is considered that copepods exhibited a variety of feeding modes (suspension, detritus and carnivorous feeding, cf. Mauchline 1998) in contrast to the monotonic feeding mode (carnivorous feeding) of chaetognaths. The variety of feeding modes in copepods is considered to be a cause of the high species diversity of copepods (Ohtsuka & Nishida 1997).

Our cluster analysis showed that the subtropical chaetognath communities in the top 1,000 m could be separated into group B (0–100 m) and group A (200–1,000 m) (Fig. 7). Group B was characterized by *Krohnitta subtilis*, *Pterosagitta draco*, *Sagitta bipunctata*, *F. enflata*, *Flaccisagitta hexaptera*, and *Zonosagitta nagae*, while group A was characterized by the dominance of *Pseudosagitta lyra* only (Table 3). A clear vertical separation of chaetognath communities has been reported in the top 500 m of the central Northwest Atlantic; e.g., *F. enflata* and *F. hexaptera* occur ≤300 m, and *P. lyra* is distributed below these species (Pierrot-Bults 1982). Within the subtropical stations (30N and 25N) in the western North Pacific, the prevalence of chaetognaths in the epipelagic zone (Fig. 3) and the order of the vertical distribution patterns of each chaetognath species (cf. Fig. 4, Table 2) seems to be similar to those reported in the central Northwest Atlantic. The overall abundance of chaetognaths in the top 2,000 m at a station near Bermuda (32°N, 64°W) was reported as 1,039 indiv. m^{-2} (Pierrot-Bults 1982) which is similar to the 942–1,297 indiv. m^{-2} observed at the two subtropical stations in this study (Table 2).

Deep-sea adaptation

Four of the abundant species at the subarctic stations (44N, Okhotsk Sea, and Bering Sea) exhibited a clear vertical separation in their distributions: *P. elegans* being in the epipelagic, *E. hamata* in the epi- to mesopelagic, *E. bathypelagica* in the meso- to bathypelagic and *E. fowleri* in the bathy- to abyssopelagic zones (Fig. 4). As noted above, the feeding mode (ambush predators) of chaetognaths may seriously limit their ability to thrive in the bathy- and abyssopelagic zone because of the extremely low prey abundance there. If this assumption is correct, how are bathy- and abyssopelagic *E. fowleri* coping with the low food abundance conditions in their habitats? For chaetognaths, mouth size is known to determine the size of ingestible prey (Feigenbaum 1991). The length of the hooks is also considered to be an important factor determining the success of their predatory attacks. The indices of both mouth size and hook length determined for the four chaetognaths in this study were smallest for epipelagic *P. elegans* and largest for bathy- and abyssopelagic *E. fowleri* (Fig. 8). Despite partial overlapping, *E. hamata* was mostly distributed deeper than *P. elegans* and exhibited larger mouth size and hook length indices. *E. hamata* and *E. bathypelagica* had similar mouth size and hook length indices, but the latter occurred deeper than the former (Fig. 8). These results may be interpreted to mean that *P. elegans* and *E. hamata* are reducing their competition for food by eating different sized prey, while *E. hamata* and *E. bathypelagica* may be eating prey of the same size, but avoiding competition by occupying non-overlapping habitat depths. In meso- and bathypelagic copepods, variation in body size and feeding appendages has been considered life history traits that reduce competition for food within the resource limited meso- and bathypelagic zones (Nishida & Nishikawa 2002). *E. fowleri*, inhabiting bathy- and abyssopelagic zones may have no chaetognath competitors for prey (Fig. 4) but their mouth size and hook lengths were significantly larger than in the other species (Fig. 8). The large mouth size and long hook length of *E. fowleri* may be indicative of greater predation ability, an adaptation to the resource-limited bathy- and abyssopelagic environments.

Shallow-living *P. elegans* release eggs directly into the water, while deep-living *E. bathypelagica* and *E. fowleri* carry egg sacs and egg hatching takes place within the sac (Terazaki & Miller 1982). Body sizes of newly hatched specimens of meso- and bathypelagic *Eukrohnia* species (*E. bathypelagica*: 2.5 mm and *E. fowleri*: 3.0–3.5 mm) are much greater than those of the epipelagic species (*P. elegans*: 1.2–1.4 mm) (Terazaki 2001). These reproductive features of deep-sea *Eukrohnia* species, combined with feeding apparatus features described in the present study, are considered to be specific adaptations to resource-limited deep-sea environments.

Acknowledgements

We are grateful to A. C. Pierrot-Bults and an anonymous reviewer for valuable comments, and to S. Chiba for kindly advice on cluster analysis. We thank the captains and crews of the R.V. *Hakurei-Maru No. 2*, *Kaiyo-Maru* and T.S. *Oshoro-Maru*, *Hokusei-Maru* for their cooperation during the field sampling. We also thank H. Ishida, T. Harimoto, S. Suzuki and Y. Sekido for their help during the field sampling. Part of the plankton samples used in the present study were those collected during the WEST-COSMIC (Western Pacific Environment Assessment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change) project, which was supported by the New Energy Industry Development Organization (NEDO).

References

Bray JB, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27: 325–349.

Brodeur RD, Terazaki M (1999) Springtime abundance of chaetognaths in the shelf region of the northern Gulf of Alaska, with observations on the vertical distribution and feeding of *Sagitta elegans*. Fish Oceanogr 8: 93–103.

Choe N, Deibel D (2000) Seasonal vertical distribution and population dynamics of the chaetognath *ParaSagitta elegans* in the water column and hyperbenthic zone of Conception Bay, Newfoundland. Mar Biol 137: 847–856.

Feigenbaum D (1991) Food and feeding behavior. In: The Biology of Chaetognaths (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 45–54.

Itoh M, Ohshima KI, Wakatsuchi M (2003) Distribution and formation of Okhotsk Sea Intermediate Water: An analysis of isopycnal climatological data. J Geophys Res 108 (C8), doi:10.1029/2002JC001590.

Johnson TB, Terazaki M (2003) Species composition and depth distribution of chaetognaths in a Kuroshio warm-core ring and Oyashio water. J Plankton Res 25: 1279–1289.

Kawamura A (1989) Fast sinking mouth ring for closing Norpac net. Bull Jap Soc Sci Fish 55: 1121.

Kitou M (1966a) Chaetognaths collected on the fifth cruise of the Japanese expedition of deep seas. La Mer 4: 15–23.

Kitou M (1966b) Chaetognaths collected on the sixth cruise of the Japanese expedition of deep seas. La Mer 4: 47–51.

Kitou M (1967) Chaetognaths collected on the eighth cruise of Japanese expedition of deep seas. La Mer 5: 33–36.

Kitou M (1974) Chaetognatha. In: Marine Plankton (ed Marumo R). University of Tokyo Press, Tokyo, pp. 65–85. (in Japanese)

Kotori M (1976) The biology of Chaetognatha in the Bering Sea and the northern North Pacific Ocean, with emphasis on *Sagitta* *elegans*. Mem Fac Fish Hokkaido Univ 23: 95–183.

Matsuda S, Taniguchi A (2001) Diel changes in vertical distribution and feeding conditions of the chaetognath *ParaSagitta elegans* (Verrill) in the subarctic Pacific in summer. J Oceanogr 57: 353–360.

Mauchline J (1998) The biology of calanoid copepods. Adv Mar Biol 33: 1–710.

Moku M, Kawaguchi K, Watanabe H, Ohno A (2000) Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. Mar Ecol Prog Ser 207: 129–140.

Motoda S (1957) North Pacific standard plankton net. Inform Bull Planktol Japan 4: 13–15.

Nagasawa S, Marumo R (1976) Identification of young chaetognaths based on the characteristics of eyes and pigmented regions. Bull Plankton Soc Japan 23: 96–106. (in Japanese with English abstract)

Nishida S, Nishikawa J (2002) Trophodynamics in the deep-sea. Kaiyo Monthly Extra 29: 96–106. (in Japanese)

Ohtsuka S, Nishida S (1997) Reconsideration on feeding habits of marine pelagic copepods (Crustacea). Oceanography in Japan 6: 299–320. (in Japanese with English abstract)

Ozawa M, Yamaguchi A, Kitamura M (2004) Small scale distribution of chaetognaths at Shiribeshi Seamount in the northern Japan Sea; an analysis of video records of submersible remotely operated vehicle. Bull Fish Sci Hokkaido Univ 55: 145–150. (in Japanese with English abstract)

Pennak RW (1943) An effective method of diagramming diurnal movements of zooplankton organisms. Ecology 24: 405–407.

Pierrot-Bults AC (1982) Vertical distribution of Chaetognatha in the central Northwest Atlantic near Bermuda. Biol Oceanogr 2: 31–61.

Pierrot-Bults AC, Nair VR (1991) Distribution patterns in Chaetognatha. In: The Biology of Chaetognaths (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 86–116.

Reeve MR (1970) The biology of Chaetognatha I. Quantitative aspects of growth and egg production in *Sagitta hispida*. In: Marine Food Chains (ed Steele JH). Oliver and Boyd, Edinburgh, pp. 168–189.

Ryther JH (1969) Photosynthesis and fish production in the sea. Science 166: 72–76.

Shannon CE, Weaver W (1963) The Mathematical Theory of Communication. University of Illinois Press, Urbana, 125 pp.

Sudo H (1987) A note on the Japan Sea proper water. Prog Oceanogr 17: 313–336.

Terazaki M (1989) Chaetognatha in the warm core eddy off Sanriku. Kaiyo Monthly 21: 711–716. (in Japanese)

Terazaki M (1993a) Seasonal variation and life history of the pelagic Chaetognatha, *Sagitta elegans* Verrill, in Toyama Bay, southern Japan Sea. J Plankton Res 15: 703–714.

Terazaki M (1993b) Deep-sea adaptation of the epipelagic chaetognath *Sagitta elegans* in the Japan Sea. Mar Ecol Prog Ser 98: 79–88.

Terazaki M (1996) Chaetognatha. In: An Illustrated Guide to Marine Plankton in Japan (eds Chihara M, Murano M). Tokai University Press, Tokyo, pp. 1271–1289. (in Japanese)

Terazaki M (2001) Ecological studies on carnivorous plankton, Chaetognatha. La Mer 39: 155–160. (in Japanese)

Terazaki M, Miller CB (1982) Reproduction of meso- and bathypelagic chaetognaths in the genus *Eukrohnia*. Mar Biol 71: 193–196.

Terazaki M, Miller CB (1986) Life history and vertical distribution of pelagic chaetognaths at Ocean Station P in the subarctic Pacific. Deep-Sea Res 33A: 323–337.

Terazaki M, Tomatsu C (1997) A vertical multiple opening and closing plankton sampler. J Adv Mar Sci Tec Soc 3: 127–132.

Vinogradov ME (1968) Vertical distribution of the oceanic zooplankton (English translation, I.P.S.T., Jerusalem, 1970), Keter Press, Jerusalem, 339 pp.

Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MM (2002a) Structure and size distribution of plankton communities down to the greater depths in the western North Pacific Ocean. Deep-Sea Res II 49: 5513–5529.

Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MM (2002b) Community and trophic structures of pelagic copepods down to the greater depths in the western subarctic Pacific (WEST-COSMIC). Deep-Sea Res I 49: 1007–1025.

Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MM (2004) Latitudinal differences in the planktonic biomass and community structure down to the greater depths in the western North Pacific. J Oceanogr 60: 773–787.

Yamamura O, Honda S, Shida O, Hamatsu T (2002) Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations. Mar Ecol Prog Ser 238: 187–198.

Zenkevitch L (1963) Biology of the Seas of the U.S.S.R. (English translation by Botcharkaya S). George Allen and Unwin Ltd., London, 955 pp.