

Vertical distribution and seasonal variation of pelagic chaetognaths in Sagami Bay, central Japan

HIROOMI MIYAMOTO^{1,2,*}, SHUHEI NISHIDA², KAZUNORI KURODA² & YUJI TANAKA¹

¹Graduate School of Marine Science and Technology, Tokyo University of Marine Science and Technology, 4–5–7 Konan, Minato-ku, Tokyo 108–8477, Japan

²Atmosphere and Ocean Research Institute, University of Tokyo, 5–1–5 Kashiwanoha, Kashiwa, Chiba 277–8564, Japan

Received 22 November 2011; Accepted 24 February 2012

Abstract: The vertical distribution and seasonal variation of pelagic chaetognaths was investigated in Sagami Bay, based on stratified zooplankton samples from the upper 1,400 m. The chaetognaths were most abundant in the 100–150 m layer in January and May 2005, whereas they were concentrated in the upper 50 m in the other months. Among the 28 species identified, *Zonosagitta nage* had the highest mean standing stock, followed by *Flaccisagitta enflata* and *Eukrohnia hamata*. Cluster analysis based on species composition and density separated chaetognath communities into four groups (Groups A–D). While the distribution of Group C was unclear due to their rare occurrence, the other groups were more closely associated with depth than with season. The epipelagic group (Group A) was further divided into four sub-groups, which were related to seasonal hydrographic variation. The mesopelagic group (Group B) was mainly composed of samples from the 150–400 m layer, although Group A, in which the epipelagic species *Z. nage* dominated, was distributed in this layer from May to July. Below 400 m, all samples were included in the bathypelagic group (Group D). In this group, *Eukrohnia hamata* was dominant with larger standing stocks than in other tropical-temperate waters, suggesting that intrusions of subarctic water drive the large standing stock of this species. Combined, these observations suggest that the seasonal and vertical patterns of the chaetognath community in Sagami Bay are influenced by hydrographic changes in the epipelagic layer and the submerged subarctic water in the mesopelagic layer.

Key words: arrow worm, bathypelagic layer, cluster analysis, diversity, zooplankton

Introduction

Chaetognatha is a phylum of small marine carnivorous invertebrates, commonly called arrow worms. The phylum encompasses approximately 130 species, of which about 90 species are holoplankton (Thuesen 2012). Planktonic chaetognaths are distributed throughout pelagic ecosystems, often dominating mesozooplankton next to copepods (Bone et al. 1991, Ball & Miller 2006), and are important secondary consumers (Reeve 1970). In addition, chaetognaths have species-specific ranges in the ocean environment and are regarded as important indicators of water masses (Bieri et al. 1959, Nagai et al. 2006). Because of their importance in the pelagic food web, the distribution of pelagic chaetognaths around Japan has been reported by

several researchers (e.g. Furuhashi 1961, Tokioka 1959). Nagasawa & Marumo (1975, 1982), Terazaki & Marumo (1979), Terazaki (1992), and Kotori (1987) investigated the vertical distributions of epipelagic chaetognaths. Although studies on meso- and bathypelagic layers (>400 m) are much fewer, chaetognath abundances and distribution have been reported by Kitou (1966a, b, 1967a), Marumo & Nagasawa (1973), Johnson & Terazaki (2003), and Ozawa et al. (2007). While a large body of knowledge has accumulated on the distribution of chaetognaths, little is known of the seasonal variation in vertical distribution throughout the water column from epipelagic to bathypelagic depths.

Sagami Bay faces the western North Pacific and is located in the central part of Honshu, Japan. Toward the centre of the bay, there is an approximately 1,500 m deep submarine canyon called the Sagami Trough. The bay opens widely to the Pacific Ocean and bay water is influenced by the Kuroshio (Iwata 1979, Kawabe & Yoneno 1987), which

*Corresponding author: H. Miyamoto; E-mail, miyamoto@aori.u-tokyo.ac.jp

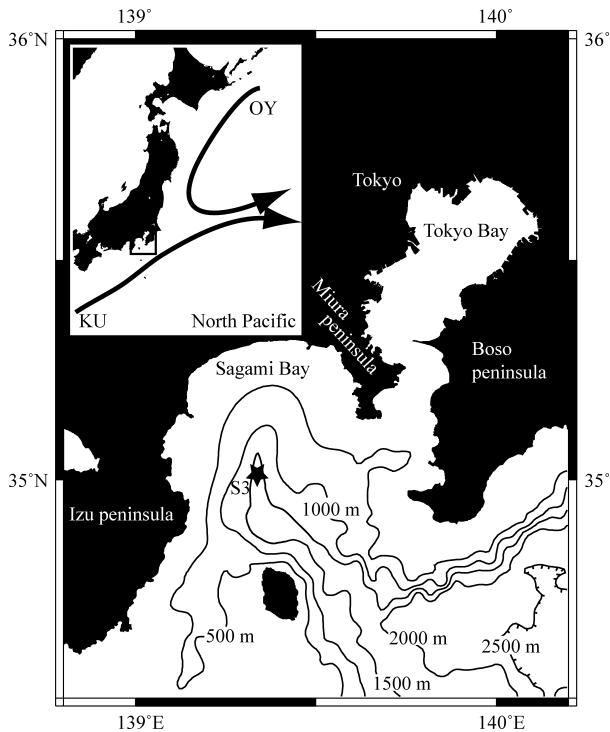


Fig. 1. Map of the study site and location of the sampling station S3. Arrows indicate the Kuroshio (KU) and Oyashio (OY) currents.

flows along the southern coast of Honshu (Fig. 1). The bay is also influenced by river inflow as well as outflowing water from Tokyo Bay (Kinoshita & Hiromi 2005). The North Pacific Intermediate Water (NPIW), which originates from the subarctic region, enters the bay within the meso- and bathypelagic zones. The salinity of the mesopelagic water fluctuates according to the strength of the intrusions (Senjyu et al. 1998, Yasuda 2003). These characteristics, along with its easy access for repeated sampling, make Sagami Bay an ideal site for examining the seasonal variation of zooplankton and its relationships with oceanographic conditions throughout the water column, including meso- and bathypelagic zones.

Extensive research has been conducted on the spatio-temporal variation of zooplankton in Sagami Bay, including studies of euphausiids (Hirota et al. 1982), copepods (Shimode et al. 2006, Kuriyama & Nishida 2006), amphipods (Nomura et al. 2003), and chaetognaths (Marumo & Nagasawa 1973, Nagasawa & Marumo 1977, 1982), with recent observations on the gelatinous fauna being conducted using underwater vehicles and video cameras (Hunt & Lindsay 1999, Lindsay & Hunt 2005). However, previous studies often suffered from limitations of sampling coverage, with respect to season, depth, and/or equipment. To address such limitations, we used an opening-closing net appropriate for chaetognath sampling, covering almost the entire depth range (0–1,400 m) and during all seasons. Specifically, this study aimed to (1) revise the existing in-

ventory of species, (2) examine the depth and seasonal variation of total chaetognath standing stock and species composition, and (3) examine the relationships between the observed patterns and oceanographic conditions and water masses. The distributional patterns of each species in relation to their size will be addressed in a companion paper.

Materials and Methods

Sampling and sample processing

Zooplankton samples were collected in the daytime (ca. three hours during 9:07–16:52) in January, May, July, September, and November 2005 as well as in January and May 2006 at a fixed station (Stn S3; 35° 00'N, 139° 30'E) in central Sagami Bay using an Intelligent Operative Net Sampling System (IONESS: mesh aperture, 0.33 mm; effective mouth area, 1 m²), which is a modified open/closing net system based on the MOCNESS (Wiebe et al. 1985), during cruises of the T/S *Seiyo-Maru* (Fig. 1). The IONESS was towed obliquely in discrete layers. In January 2005, samples were collected only from eight layers in the upper 200 m (200–150, 150–100, 100–75, 75–50, 50–25, 25–10, 10–5, 5–0 m) bay a single tow, while in May 2005, 15 layers in the upper 1,100 m (deep tow: 1,100–1,000, 1,000–800, 800–600, 600–500, 500–400, 400–300, 300–200; shallow tow: 200–150, 150–100, 100–75, 75–50, 50–25, 25–10, 10–5, 5–0 m) were sampled by two tows. The 0–1,400 m layer was covered in all the other months. In September 2005, sampling for shallow (0–200 m) and deep (200 m–1,400 m) layers was conducted four days apart for logistical purposes, while the collections in July, November 2005, and May 2006 were made by consecutive shallow and deep tows (deep tow: 1,400–1,200, 1,200–1,000, 1,000–800, 800–600, 600–400, 400–300, 300–200; shallow tow: 200–150, 150–100, 100–75, 75–50, 50–25, 25–10, 10–5, 5–0 m). In January 2006, the IONESS sampled eight discrete layers from 1,400 m to the surface (1,400–1,000, 1,000–600, 600–400, 400–200, 200–150, 150–100, 100–50, 50–0 m) by a single tow. The volume of water filtered was estimated with a flow meter (Tsurumi-seiki Co. Ltd.) attached in the mouth of the net. The volume of water filtered by each net ranged from 130–940 m³ (mean: 434 m³). The samples were immediately fixed and preserved in ~5% formaldehyde/seawater solution buffered with sodium tetraborate.

Chaetognaths were separated from the zooplankton samples or aliquots were taken with a box-type or a cylinder-type splitter (Motoda 1959). More than 600 individuals per sample were counted and identified under a stereo- or compound microscope following Kitou (1967b) and applying Bieri's (1991) system for generic names. As for the taxonomic status of *Eukrohnia bathypelagica* Alvarino, 1962, we followed Aurich (1970) and Tokioka (1974) who assigned it as a junior synonym of *E. hamata* (Möbius, 1875). The classification of these two species was also not sup-

ported by a genetic marker (Miyamoto 2010).

Vertical profiles of temperature and salinity were obtained using a conductivity, temperature, depth (CTD) sensor (Falmouth Scientific, Inc.) attached in the mouth of the IONESS during each sampling cruise. A monthly CTD (Falmouth Scientific, Inc.) cast from 1,000 m to the surface was also carried out during other cruises of the *Seiyo-Maru* at Stn S3. The average values of temperature and salinity in the stratum were calculated from this CTD data.

Data analysis

The species composition comparisons between samples were compared by applying the Bray-Curtis similarity index (Bray & Curtis 1957). The density (ind. m^{-3}) was square-root transformed prior to the analysis to reduce bias caused by extremely abundant species. An inverse analysis was performed to examine species associations (Field et al. 1982). To avoid spurious associations among rare species, i.e. *Sagitta bipunctata* Quoy and Gaimard, 1827, *Zonosagitta bedoti* (Beraneck, 1895), and *Z. pulchra* (Doncaster, 1902), were excluded from the analysis since they were collected in only one series of tows. The unweighted pair-group method using arithmetic averages was applied to classify samples and species based on the similarity matrix.

The core of the vertical distribution of each species was estimated applying the weighted mean depth (WMD; Pearre 1973). The weighted mean temperature (WMT) and salinity (WMS) of dominant species were also calculated to show the core of distribution in relationship to temperature and salinity (Matsuzaki 1975).

Results

Hydrography

The surface water was well mixed in the upper 200 m during December 2004–April 2005, with a temperature of 14–15°C in the upper 80 m in April (Fig. 2). The thermocline started to form in May and continued to develop in the upper 40 m in August and September. Also, the isopleth of 13°C and 34.5 salinity were shallower in August and September than in the other seasons. In October, the depth of the thermocline increased to 150 m accompanied by vertical mixing, followed by weakened stratification due to enhanced mixing by cooling of the surface water from November. The mixed layer reached approximately 120 m in February 2006 and existed until April when the surface temperature started to increase. While the salinity in the upper 200 m was mostly higher than 34.4, low-salinity water (<34.2) occurred in the upper 30 m from June to September 2005. Whereas the water temperature below 200 m showed little seasonal variation, there were marked depressions in salinity (<34.25) in the 300–700 m layer during August 2005–April 2006.

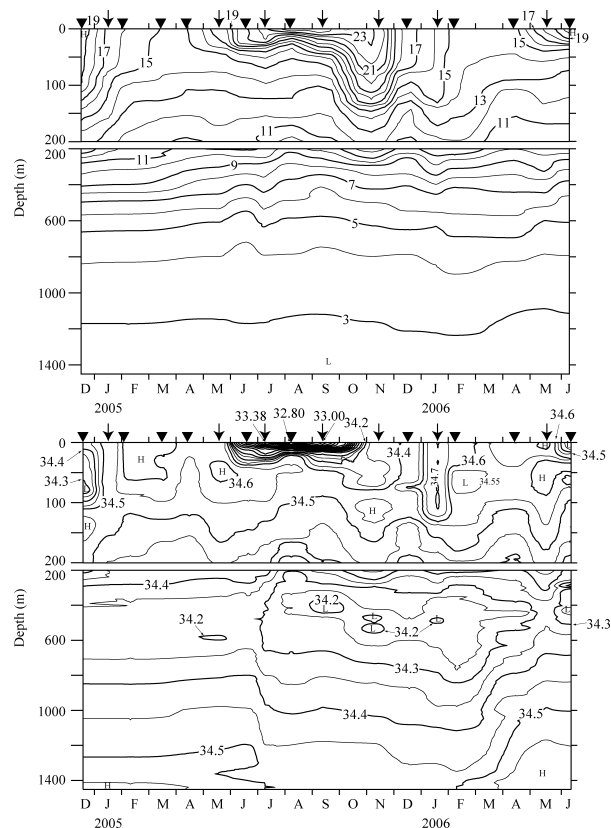


Fig. 2. Seasonal and vertical distribution of temperature and salinity at Stn. S3. Arrows show the days of zooplankton sampling with IONESS and CTD observations. Triangles indicate days of CTD observation only. Below 200 m, depth ranges are 200 m intervals.

Standing stock

The standing stock of chaetognaths in the upper 200 m ranged from 252 (January 2006) to 4,960 ind. m^{-2} (May 2006), with an average of $1,920 \pm 1,970$ (SD) ind. m^{-2} (Fig. 3). In the 200–1,000 m layer, the average was 524 ± 358 ind. m^{-2} with peaks in May 2006 and November 2005. The average stocks within the 0–1,000 m and 0–1,400 m layers from July 2005 to May 2006 were $2,970 \pm 2,360$ and $3,020 \pm 2,330$ ind. m^{-2} , respectively, and those in January 2005 and 2006 were lower than in the other months in the upper 200 m.

The density was mostly highest in the 0–50 m range (average 31 ± 40 ind. m^{-3}), with the exception of January and May 2005, and decreased roughly with depth (Fig. 3) to the minimum of 0.02 ind. m^{-3} in the 1,200–1,400 m layer.

Species diversity

A total of 28 species belonging to 16 genera were identified, of which 16 species were collected on every of the sampling occasion (Table 1). *Heterokrohnia* specimens were counted as a single species; a detailed examination of the *Heterokrohnia* specimens is still in progress, but it in-

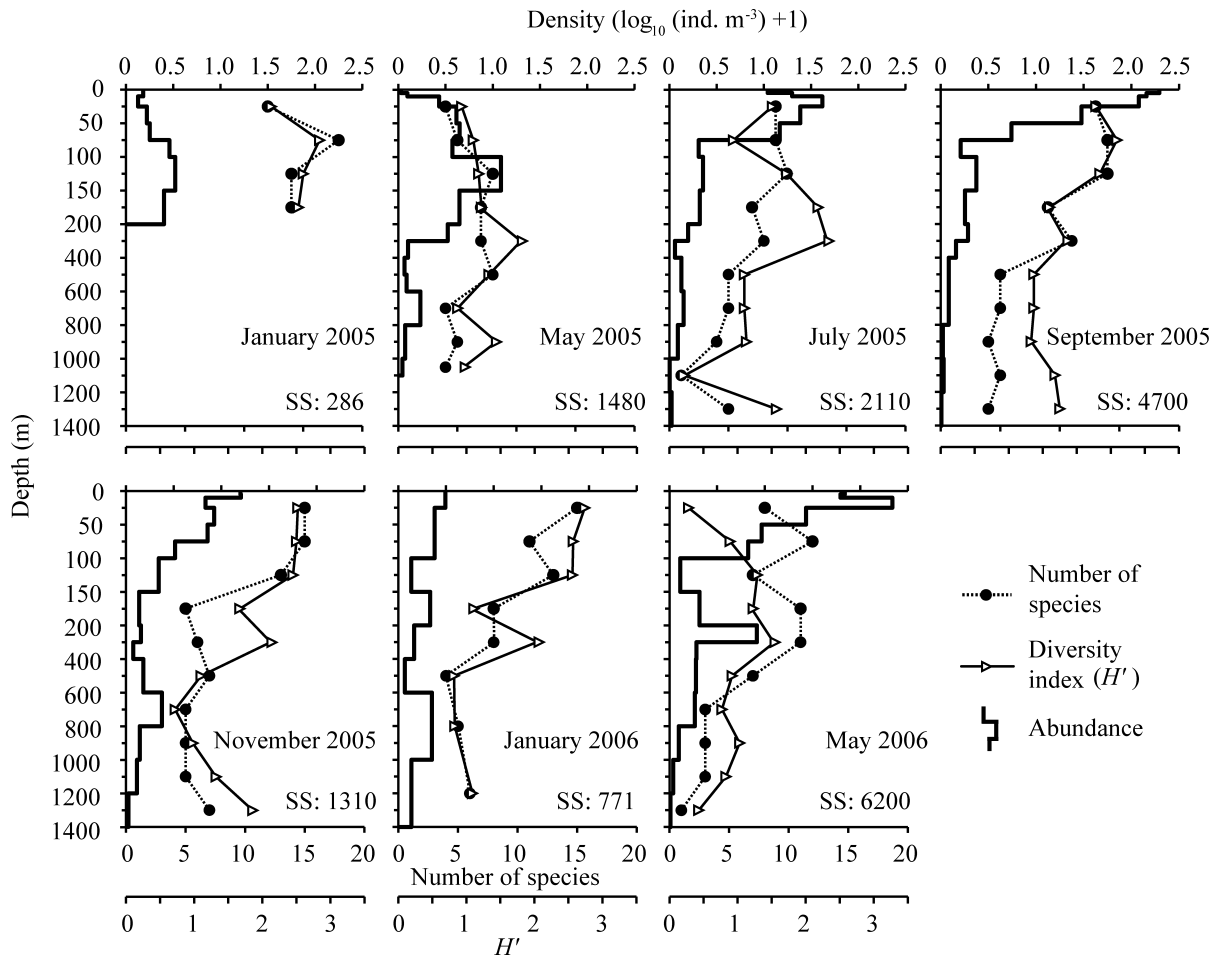


Fig. 3. Vertical distribution of density, the number of species, and diversity index (H'). SS represents standing stock (ind. m^{-2}) of the entire water column. The diversity indices at the same depth range (Upper 200 m, 50 m intervals; Lower 200 m, 200 m intervals) are shown except for on three sampling occasions.

indicates that they contain two or more undescribed species. The number of species from each vertical series ranged from 16 (May 2006) to 26 (November 2005) and tended to be smaller in May and July. This seasonal pattern in the water column was consistent with that in the upper 200 m (Fig. 3). The species number and diversity index were the highest in the upper 400 m and decreased with depth. Below 400 m, the species number was generally less than six species in each layer. Within the upper 200 m, the peaks in both the species number and the diversity index in each layer tended to shift to shallower depths from May to January.

Species composition

Zonosagitta naga (Alvariño 1967) comprised an average of 48% of standing stock of total chaetognaths in the whole integrated water column between May 2005 and May 2006 (Table 1), with particularly high values in July 2005 (53%) and May 2006 (84%), while it constituted less than 5% in November 2005 and January 2006. The other species that occupied more than 3% were *Aidosagitta*

regularis (Aida, 1897), *Eukrohnia hamata*, *Flaccisagitta enflata* (Grassi, 1881), and *Serratosagitta pacifica* (Tokioaka, 1940). *Eukrohnia hamata* accounted for more than 4.8% of the total chaetognath standing stock within the entire water column between May 2005 and 2006, except in September 2005. In September, *Fl. enflata* and *Mesosagitta minima* (Grassi, 1981) comprised more than 20% and were more abundant than *Z. naga*. In November 2005 and January 2006, because the standing stocks of epipelagic chaetognaths were low, *E. hamata* accounted for more than 30%.

The cluster analysis based on the Bray-Curtis similarity indices between samples identified four major groups (A–D) among the 91 samples at an 85% dissimilarity level (Fig. 4A). Group A mainly included samples from the upper 150 m (Fig. 4B) and was further classified into four sub-groups that appear to correspond with the seasonal pattern of hydrographic conditions. Group A₁ was composed of samples from 75–150 m in November 2005 and from 0–150 m in January 2005 and 2006, in which *Se. pacifica* and *Fl. enflata* comprised approximately 50% of the

Table 1. Standing stock (SS; ind. m⁻²) and weighted mean depth (WMD). Average values of SS were calculated from the data from May 2005 to May 2006. Average WMD was calculated from all data. *¹, *², *³, indicate sampling range of 0–200, 0–1,100, and 0–1,400 m respectively.

	2005												2006											
	January* ¹		May* ²		July* ³		September* ³		November* ³		January* ³		May* ³		Average									
	SS	WMD	SS	WMD	SS	WMD	SS	WMD	SS	WMD	SS	WMD	SS	WMD	SS	WMD								
SAGITTIDAE Claus and Gaimard, 1987																								
<i>Aidanosagitta crassa</i>	0.459	24	10.4	71	106	15	23.6	13	10.8	21	0.914	40	52.4	13	34.0	28								
<i>A. neglecta</i>	0.0167	3	–	–	21.2	10	60.3	3	13.5	5	0.258	25	–	–	15.9	9								
<i>A. regularis</i>	4.35	32	–	–	–	–	564	6	46.4	7	10.3	28	11.4	14	105	17								
<i>Caecosagitta macrocephala</i>	–	–	21.7	698	17.0	727	15.3	692	25.3	805	8.46	1,020	21.9	708	18.3	775								
<i>Ferosagitta ferox</i>	0.0831	40	–	–	–	–	4.09	6	3.45	6	–	–	–	–	1.26	17								
<i>Fe. robusta</i>	–	–	–	–	–	–	2.66	3	20.2	22	0.52	25	–	–	3.90	17								
<i>Flaccisagitta enflata</i>	46.5	59	3.30	62	14.8	13	1,370	9	210	20	10.3	49	6.07	18	269	33								
<i>Fl. hexaptera</i>	7.50	–	16.0	154	4.37	77	6.48	93	10.1	79	2.45	78	3.79	89	7.20	95								
<i>Mesosagitta decipiens</i>	43.1	–	57.2	216	32.9	167	100	135	23.0	206	78.1	185	99.8	206	65.2	186								
<i>M. minima</i>	16.9	61	44.2	75	402	38	976	19	26.2	47	31.7	50	31.7	40	25.2	47								
<i>M. neodecipiens</i>	16.7	–	6.00	241	14.3	214	22.4	228	24.7	237	17.4	119	25.6	209	18.4	221								
<i>Parasagitta elegans</i>	–	–	0.675	900	–	–	0.970	700	10.6	769	1.05	963	–	–	2.22	833								
<i>Pseudosagitta lyra</i>	6.39	–	22.3	324	25.8	338	17.7	200	16.2	187	15.7	114	24.1	187	20.3	225								
<i>Ps. scrippsae</i>	–	–	0.433	550	–	–	–	–	4.97	700	11.6	763	–	–	2.83	671								
<i>Sagitta bipunctata</i>	–	–	–	–	–	–	–	–	0.821	20	–	–	–	–	0.137	20								
<i>Serratosagitta pacifica</i>	60.1	126	37.2	135	60.5	82	141	15	201	32	56.9	45	86.0	63	97.1	71								
<i>Se. pseudo-serratodentata</i>	1.12	–	8.99	149	10.9	80	3.20	56	3.07	72	4.14	59	4.54	67	5.81	80								
<i>Solidosagitta zetesios</i>	3.67	–	4.60	530	10.8	475	13.9	260	10.2	579	7.00	391	13.2	306	9.96	423								
<i>Zonosagitta bedoti</i>	3.88	100	–	–	–	–	–	–	–	–	–	–	–	–	–	100								
<i>Z. nagae</i>	18.1	78	687	111	1,120	25	853	11	25.7	25	23.4	52	5,180	20	1,310	46								
<i>Z. pulchra</i>	0.0663	88	–	–	–	–	–	–	–	–	–	–	–	–	–	88								
KROHNITTIDAE Tokioka, 1965																								
<i>Krohnitta pacifica</i>	1.18	34	–	–	–	–	24.6	5	6.18	6	0.134	75	–	–	5.15	30								
<i>K. subtilis</i>	5.76	–	14.1	307	4.86	163	18.0	81	5.79	115	11.7	224	26.8	227	13.5	194								
EUKROHNIDAE Tokioka, 1965																								
<i>Eukrohnia hamata</i>	0.716	–	162	619	102	727	36.8	678	395	703	175	709	296	556	194	665								
<i>E. fowleri</i>	–	–	6.93	923	4.67	938	5.33	1,113	11.6	1,075	–	–	–	–	4.76	1,012								
<i>Heterokrohnia sp.</i>	–	–	–	–	0.32	1,300	–	–	1.78	1,300	1.28	1,200	–	–	0.563	1,213								
PTEROSAGITTIDAE Tokioka, 1965																								
<i>Pterosagitta draco</i>	17.4	74	7.50	112	12.8	65	50.4	15	81.9	48	27.4	49	2.36	101	30.4	66								
SPAPELLIDAE Tokioka, 1965																								
<i>Bathyspadella oxydentata</i>	–	–	0.33	1,050	0.96	1,300	–	–	1.07	1,300	–	–	–	–	0.393	1,216								

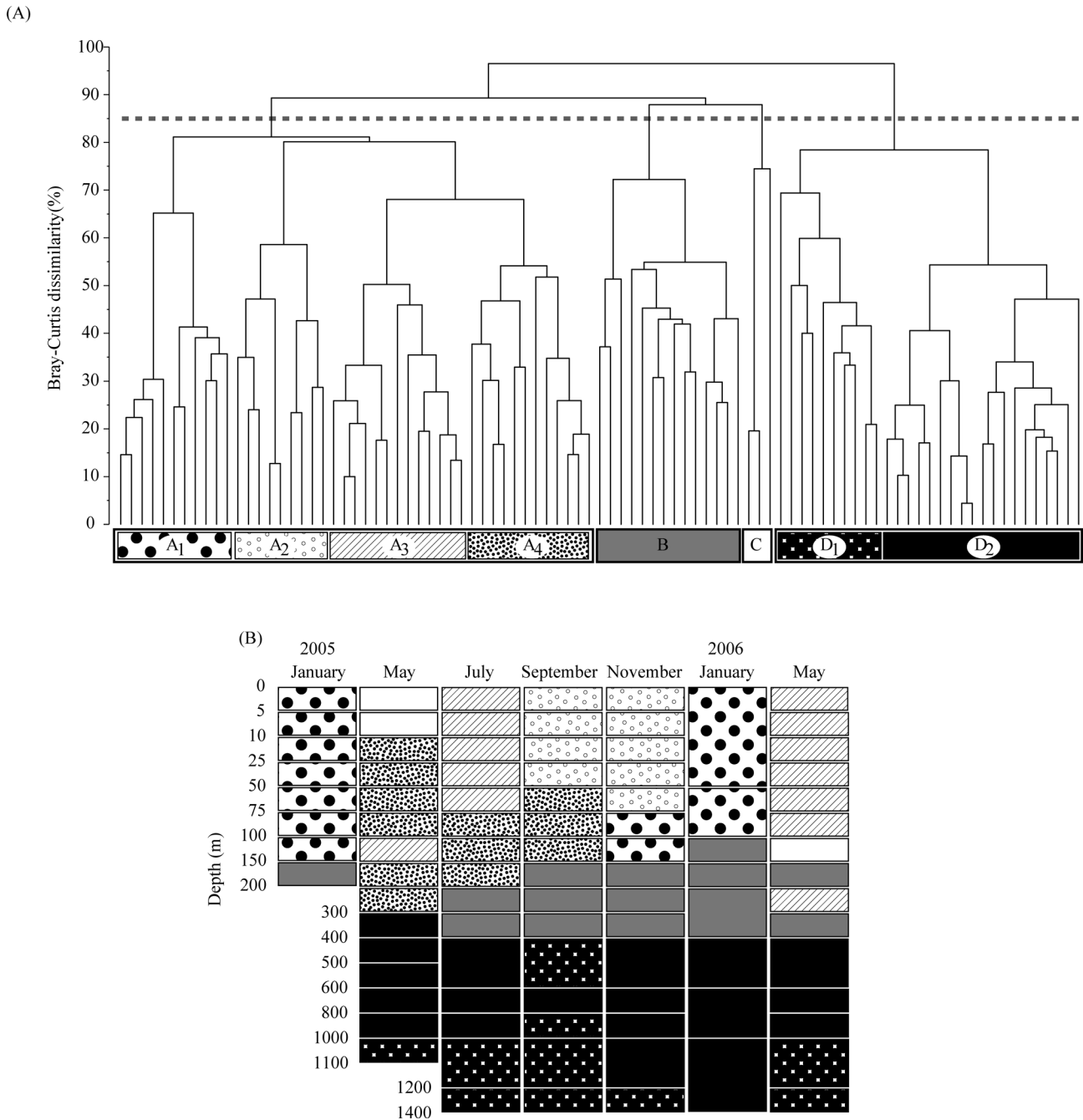


Fig. 4. Dendrogram of cluster analysis based on species composition and density (A), and vertical distribution of each group (B). The pattern of each cell in (B) corresponds to that in (A).

total number of chaetognaths (Fig. 5). Group A₁ was distributed in high-salinity water (>34.5) (Fig. 2). Group A₂ consisted of samples from the upper 75 m, which was characterized by low-salinity and high-temperature waters in September and November. The top three species, *Fl. enflata*, *Se. pacifica*, and *A. regularis* in Group A₂ comprised 76.5% of the total number of chaetognaths. Group A₃ mainly included samples from July 2005 and May 2006, and Group A₄ occurred in May, July, and September 2005. Although the most dominant species was *Z. nageae* in both

Groups A₃ and A₄, the next dominant species differed between the groups (Group A₃, *M. minima*; A₄, *M. decipiens* (Fowler, 1905)). The species diversity index was higher in Group A₄ than A₃. Group A₃ was distributed across a wider range of salinities than Group A₄. Group B contained samples collected from 100–400 m depth during all sampling occasions except in May 2005. This group mainly occurred in the transitional layer between high-salinity water at approximately 150 m and the salinity-minimum layer around 600 m. The typical species in this group were *M.*

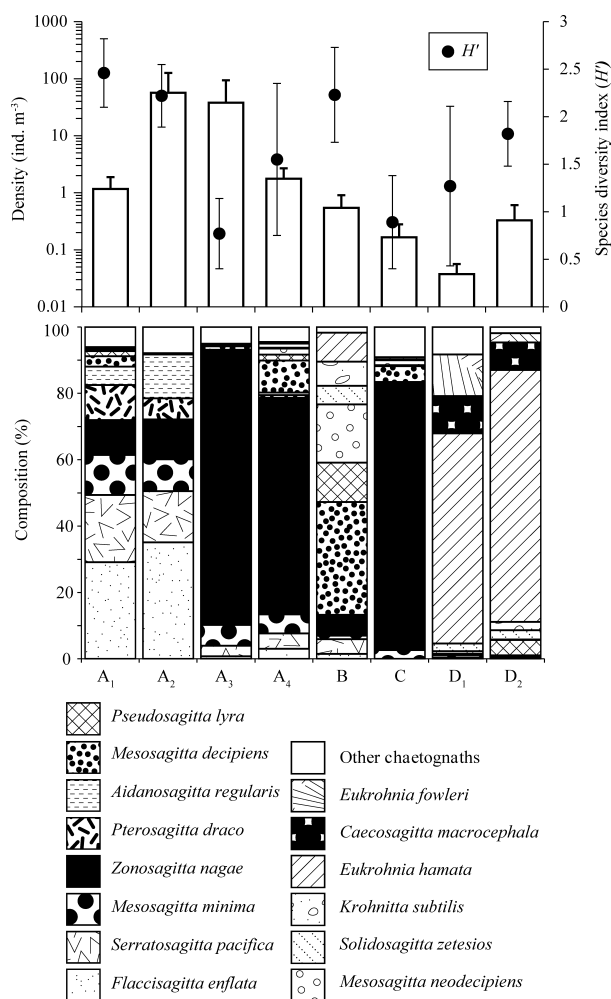


Fig. 5. Density, species diversity, and species composition of the groups shown in Fig. 4. Vertical bars in density and diversity indices indicate standard deviations.

decipiens, *M. neodecipiens* (Tokioka, 1959), and *Pseudosagitta lyra* (Krohn, 1853). Group C included three samples, two of which were from the upper 10 m in May 2005 and the other from 100–150 m in May 2006. *Zonosagitta nagae* was dominant in this group, and the densities were fewer than in Groups A and B. Group D contained 29 samples, all of which were collected below 400 m except for one sample from 300–400 m in May 2005. This group was further clustered into two sub-groups (Group D₁ and D₂). Group D₁ was mostly distributed in deeper layers than Group D₂. The dominant species in both groups was *E. hamata*, but it was much less abundant in Group D₂, resulting in higher percentages of *Caecosagitta macrocephala* (Fowler, 1904) and *E. fowleri* Ritter-Záhony, 1909 in this group. Group D₁ was mainly distributed in the layer that was influenced by the NPIW.

Assemblages of species

The inverse cluster analysis resulted in seven groups of species at a similarity level of 20% (Fig. 6). The species

belonging to Groups 1–4 were distributed below 500 m (Table 1). Group 1 was composed of *Caecosagitta macrocephala* and *Eukrohnia fowleri*. *Caecosagitta macrocephala* was the second most dominant species in Groups 1–4. These species mainly occurred below the NPIW (Fig. 7). The boreal species *Parasagitta elegans* (Verrill, 1873) and *Pseudosagitta scrippsae* (Alvarino, 1962) made up Group 2. *Parasagitta elegans* was distributed at 400–1,400 m and *Ps. scrippsae* was mainly distributed from 600–1,000 m (Fig. 8), although it was found at 200–400 m in January 2006. *Parasagitta elegans* and/or *Ps. scrippsae* were found in May and November 2005 and January 2006. The standing stocks of *Pa. elegans* and *Ps. scrippsae* were much larger in November and January 2006, respectively. *Bathyspadella oxydentata* Miyamoto & Nishida, 2011 and *Heterokrohnia* sp., which were collected by the net tows nearest to the bottom, formed Group 3. Group 4 had a single species, *E. hamata*. The average weighted mean depth (WMD) of *E. hamata* was 665 m from May 2005 to May 2006. The standing stock of this species in the whole water column was greatest in November, with the peak density (1.15 ind. m⁻³) at 600–800 m. *Parasagitta elegans*, *Ps. scrippsae*, and *E. hamata* were mainly found in the NPIW. Group 5 had seven species, *Flaccisagitta hexaptera* (d'Orbigny, 1836), *Krohnittia subtilis* (Grassi, 1881), *Mesosagitta decipiens*, *M. neodecipiens*, *Ps. lyra*, *Serratosagitta pseudoserratodentata* (Tokioka, 1939), and *Solidosagitta zetesios* (Fowler, 1905), which were distributed from 90–500 m. The WMDs of these species, with the exception of *So. zetesios*, were deepest in May 2005. Of the Group 5 species, the WMDs of *Se. pseudoserratodentata*, *K. subtilis*, *M. decipiens*, and *So. zetesios* were shallowest in September 2005 (Table 1). Although the species were mainly found in the transitional layer between the NPIW and the epipelagic water, *Fl. hexaptera*, *Se. pseudoserratodentata*, *Ps. lyra*, and *K. subtilis* also occurred in the Kuroshio water. Group 6 was dominated by *Zonosagitta nagae*, *Fl. enflata*, *M. minima*, and *Se. pacifica*, and all species, except *Aidanosagitta regularis*, were present on all sampling occasions. The WMDs of the Group 6 species were shallowest in September and deepest in May 2005. *Flaccisagitta enflata* and *A. regularis* were distributed across a wide range of salinities, but were mainly distributed in high-temperature water (>20°C). These species were found in higher temperature and lower salinity water compared to other species. *Zonosagitta nagae* was also distributed across a wide range of salinities. However, their temperature range was also wider than that of *Fl. enflata*. Conversely, the standing stock of this species in Kuroshio water was remarkably lower than that in the coastal area. *Serratosagitta pacifica*, *Pterosagitta draco* (Krohn, 1853), and *Z. nagae* were distributed across a wide temperature range (10–24°C), whereas the salinity range for these species was mostly high with the exception of one sample. Group 7 species [*A. crassa* (Tokioka, 1938), *A. neglecta* (Aida, 1897), *Ferosagitta ferox* (Doncaster, 1902), *Fe. ro-*

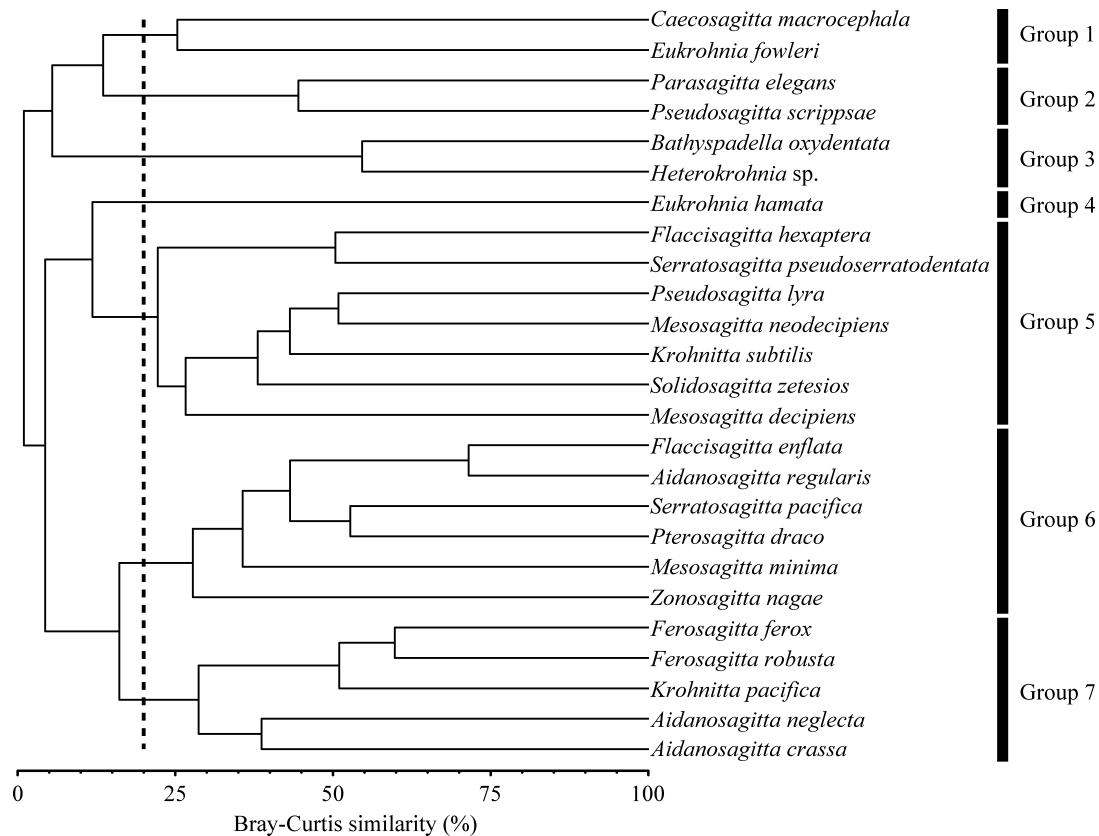


Fig. 6. Dendrogram of species association (inverse) analysis.

busta (Doncaster, 1902), and *K. pacifica* Aida, 1897] mostly occurred in the upper 30 m, and *A. crassa* was the only species that occurred on all sampling occasions (Table 1). All of the species in Group 7, except *A. crassa*, were found at high temperatures (24°C) from September to January.

Discussion

We recorded the occurrence of 28 species of pelagic chaetognaths in Sagami Bay, including the first record of *Heterokrohnia* specimens. The 27 species have already been reported by Tokioka (1939), Marumo & Nagasawa (1973), Nagasawa & Marumo (1977), and Miyamoto & Nishida (2011). This number represents approximately 30% of the global species richness of pelagic chaetognaths and is higher than that reported from other well-investigated regions such as the Sargasso Sea (17 species: Pierrot-Bults & Nair 2010), east Atlantic Ocean (20 species: Pierrot-Bults & Nair 2010), Arctic Ocean (seven species: Sameoto 1987), Sulu and Celebes seas (22 species: Johnson & Terazaki 2006), South China sea and Gulf of Thailand (27 species: Alvarino 1967, Rottman 1978), Indian Ocean (23 species: Nair et al. 2002), Antarctic Ocean (six species: Johnson et al. 2004), and off Chile (22 species: Fagetti 1972). These studies covered depth ranges of approximately 1,000 m to the surface, and thus are comparable

with the present study. The extremely high local diversity in Sagami Bay is attributable to the influence of a variety of water masses that may be responsible for the observed changes in species composition of chaetognaths, both in space and time, as discussed in the following paragraphs. The *Heterokrohnia* specimens occurred in the deepest samples, coinciding with several previous reports of their occurrence in near-bottom layers (Casanova & Chidgey 1987, 1990, Casanova 1992, 1994). *Heterokrohnia bathybia* Marumo & Kitou, 1966 was reported in the western north Pacific (Marumo & Kitou 1966). The *Heterokrohnia* specimens collected herein differ from *H. bathybia* in body length and the proportion of tail segment to body and appear to represent several undescribed species.

In the present study, high species diversity was found during summer and autumn, and was attributed to the occurrence of species regarded as tropical species (Marumo & Nagasawa 1973), and which are included in Group 7. This pattern is similar to the previous results of Nagasawa and Marumo (1977), and is consistent with the seasonal change of copepod diversity in the epipelagic layer of Sagami Bay (Shimode et al. 2006). In the meso- and bathypelagic layer (>400 m layer), the seasonal change in the diversity index was unclear in comparison with that in the epipelagic layer. The number of species and the diversity index decreased with depth, which is consistent with previous studies such as those from off Valparaíso, Chile (Ulloa

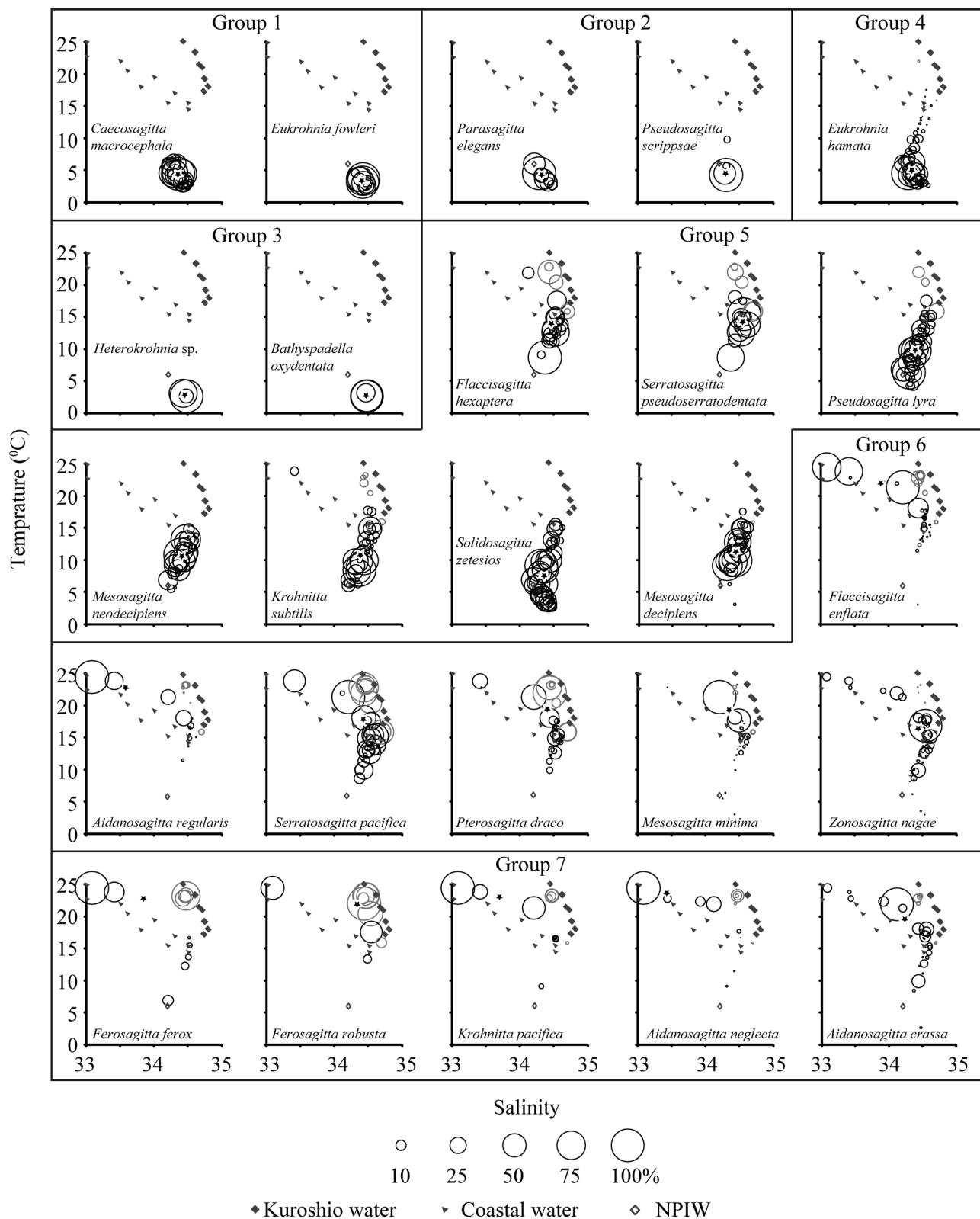


Fig. 7. Relative standing stock (ind. m⁻²) of chaetognaths in relation to temperature and salinity. The areas of the circles represent percentages; the maximum standing stock (ind. m⁻²) during the observation in the present study is defined as 100%. Gray circles represent the density in the water strongly influenced by the Kuroshio current. A star indicates the weighted mean temperature (WMT) and salinity (WMS) for each species. Temperature and salinity indicating Kuroshio water, coastal water, and North Pacific Intermediate Water (NPIW) are shown by the grey symbols; the values are referenced from Iwata (1979) and Senjyu et al. (1998).

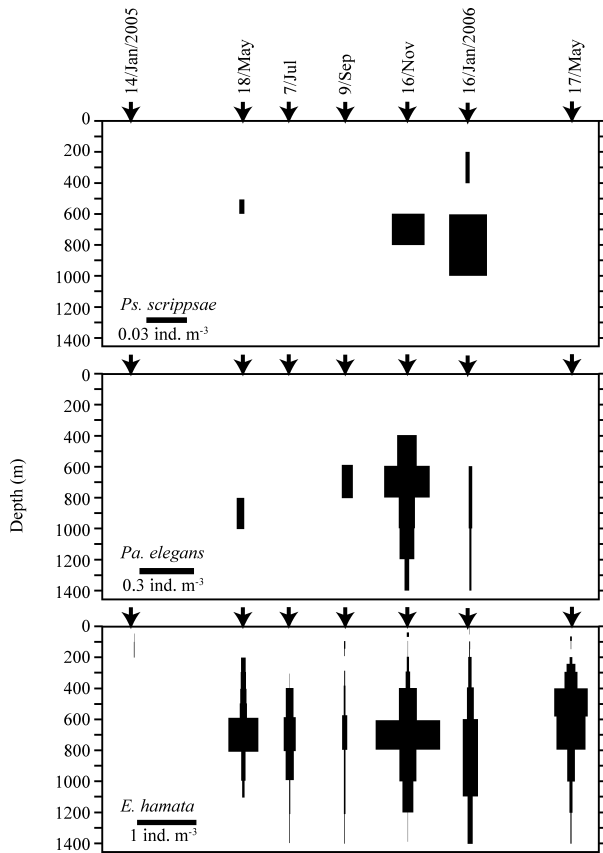


Fig. 8. Vertical distribution of *Pseudosagitta scrippsae*, *Parasagitta elegans* and *Eukrohnia hamata*.

et al. 2000), the Sulu and Celebes seas (Johnson et al. 2006), and the waters south of the Kuroshio (Ozawa et al. 2007). This pattern contrasts with that observed in many other pelagic animals, such as copepods and ostracods (Roe 1972, Angel 1993, Yamaguchi et al. 2002, Shimode et al. 2006, Kuriyama & Nishida 2006), in which species diversity peaks in the mesopelagic layer. In Sagami Bay, the copepod diversity in June 1996 tended to increase with depth in the upper 200 m, but reached a plateau below that layer (Shimode et al. 2006), which is considerably different to the pattern observed in the chaetognaths in the present study (July 2005). Shimode et al. (2006) reported that the community structure of copepods changed in the 200–300 m layer and that the copepods inhabiting below that depth consisted mainly of species with diverse feeding modes (carnivores, suspension feeders, and omnivores) and tactics such as the use of venom (Nishida & Ohtsuka 1996), ambush predation (Matsuura & Nishida 2000), detection of chemical cues (Nishida & Ohtsuka 1997), and specialized detritivory (Nishida et al. 2002). It has been suggested that food-resource partitioning is one of the major factors allowing the co-existence of many species at mesopelagic depths (Kuriyama & Nishida 2006, Matsuura et al. 2010). In contrast, pelagic chaetognaths are essentially carnivorous and are unable to utilize inactive organic particles

such as phytoplankton and detritus. They are highly efficient predators as they couple beating with their well-developed muscles (Feigenbaum 1991) and mechano-reception by ciliary fence receptors covering the whole body surface (Feigenbaum 1991, Bone & Goto 1991) in addition to the possible use of venom (Thuesen 1991). However, their feeding structures consist of a relatively simple assemblage of hooks, teeth, and mouth and they are devoid of complex feeding appendages such as those found in copepods and ostracods. This may prevent them from exploiting diverse feeding niches that are potentially available in the mesopelagic depths (see also Ozawa et al. 2007).

We identified four groups of samples based on their species composition. While the distribution of Group C was unclear due to the rarity occurrence of the species in the group, the distribution of the other groups was more closely related to depths than to seasons. The boundaries between these groups that were identified, i.e. 150 m and 400 m, coincide well with the 200 m and 500 m boundaries proposed by Marumo & Nagasawa (1973). The distribution of these groups corresponds with the vertical hydrographic structure in Sagami Bay. Group A was mainly distributed in the water mass formed by the mixing of Kuroshio and coastal waters, while Group D was mainly in the NPIW. Group B was found in the transitional layers between the mixed epipelagic water and the NPIW.

The seasonal change of the dominant species in the epipelagic layer (0–150 m) in Sagami Bay observed in the present study was also reported by Nagasawa & Marumo (1977: *Zonosagitta nagae* in March–August, *Flaccisagitta enflata* in August–November, *Serratosagitta pacifica* in December–February). We further observed that the community was not homogeneous but was structured vertically within the upper 150 m in July, September, and November 2005. The boundary between the different assemblages corresponded with the thermocline and halocline, suggesting that the species composition was influenced by temperature and salinity.

According to Nagai et al. (2006, 2008) the occurrence and abundance of chaetognath species is highly dependent on temperature, but only partially on salinity. In the present study, some species (e.g., *Fl. enflata* and *A. regularis*) were distributed across a wide range of salinities but over a narrow range of high temperatures. Conversely, *Pterosagitta draco* and *Se. pacifica*, as well as the species of Group 5, occurred over a wide range of temperatures but in a limited salinity range, while *Z. nagae* occurred within a wide spectrum of both temperature and salinity. It should be noted that these apparent differential influences of temperature and salinity according to the species distribution may not be due to a direct response of the species to these factors, but could rather reflect a complex mixing of waters and the ecological specificity of the population growth of any particular species in such waters.

Marumo & Nagasawa (1973) reported the dominance of *Mesosagitta decipiens*, *M. neodecipiens*, and *Pseudosa-*

Table 2. Standing stock (ind. m⁻²) of *Eukrohnia hamata* and species closely-related to *E. hamata* in each area.

Area	Sampling layer (m)	<i>E. hamata</i>	<i>E. bathypelagica</i>	<i>E. hamata</i> & <i>E. bathypelagica</i>	Juvenile of <i>E. hamata</i> & <i>E. macro-nuera</i>	Reference
Subpolar region						
Oyashio region	0–5,000	1,475	360	784	–	Ozawa et al. 2007
Okhotsk Sea	0–2,000	970	273	1,315	–	Ozawa et al. 2007
Bering Sea	0–3,000	2,164	512	1,945	–	Ozawa et al. 2007
Georges Bank, western North Atlantic	0–max 1,000	43.5	1.8	–	–	Cheney 1985
Buffin Bay, North Atlantic	0–max 1,043	130–626	–	–	–	Samemoto 1987
Australian sector, Southern Ocean	0–500	534–1,089	–	–	–	Johnson & Terazaki 2004
Tropical-temperate region						
Oyashio-Kuroshio mixing region	0–5,000	–	54	–	–	Ozawa et al. 2007
Northern Sargasso Sea (33°N)	0–1,000	4–6	–	–	–	Pierrot-Bults & Nair 2010
Northern Sargasso Sea (29°N)	0–1,000	1–5	–	–	–	Pierrot-Bults & Nair 2010
Northern Sargasso Sea	0–max 1,000	0.9	0.05	–	–	Cheney 1985
Southern Sargasso Sea (24°N)	0–1,000	0	–	–	–	Pierrot-Bults & Nair 2010
Southern Sargasso Sea (19°N)	0–1,000	4	–	–	–	Pierrot-Bults & Nair 2010
Southern Sargasso Sea (14°N)	0–1,000	4–20	–	–	–	Pierrot-Bults & Nair 2010
Eastern North Atlantic (11°N)	0–1,000	–	–	–	2	Pierrot-Bults & Nair 2010
Eastern North Atlantic (03°N)	0–1,000	–	–	–	18	Pierrot-Bults & Nair 2010
Eastern South Atlantic (13°S)	0–1,000	–	–	–	35	Pierrot-Bults & Nair 2010
Eastern South Atlantic (25°S)	0–1,000	–	–	–	16	Pierrot-Bults & Nair 2010
Off Varaiso, South Pacific	0–900	6.632	–	–	–	Ulloa et al. 2000
Sagami Bay	0–max 1,400	194±131	–	–	–	The present study

gitta lyra in the mesopelagic layer in Sagami Bay. These species coincide with the dominant species in Group B, which was distributed within 150–400 m in the present study. However, Groups A₃ and A₄, which were dominated by *Z. nagae*, occurred at 150–300 m in May 2005 and 2006. In particular, the density of *Z. nagae* at 150–300 m in May was highest among all samples. According to Nagasawa & Marumo (1977), *Z. nagae* actively reproduces from May to July in the bay and is abundant in the epipelagic layer. The present study clearly showed that *Z. nagae* was also abundant in the mesopelagic layer during their reproductive season.

It has been reported that meso- and bathypelagic chaetognaths move to epipelagic layers by upwelling (Alvarino 1965, Ulloa et al. 2000, 2004, Noblezada et al. 2008). During our observation, the occurrence of upwelling in the central part of the bay in September 2005 was suggested from an offshore meandering of the Kuroshio paths (information provided by the Japan Coast Guard; Kanagawa Prefectural Fisheries Station). Also, in the vertical profile of temperature and salinity in the present study, the isopleths of 13°C and 34.5 salinity in September were shallower than in the other seasons, suggesting the occurrence of upwelling. Of the Group 5 species, *Se. pseudoserratodentata*, *M. decipiens*, and *K. subtilis* were found in shallower layers in September compared to the other months, suggesting that the distributional range of the three species was pushed shallower by the upwelling. In contrast, the WMDs of all species except *Solidosagitta zetesios* that were distributed

in deeper layers than *K. subtilis*, *M. decipiens*, and *Se. pseudoserratodentata* were less shallow in September, suggesting that the species may have been less affected by the upwelling. However the WMD of *So. zetesios* was in the shallower range as for the other three species in September. Terazaki (1973) and Terazaki & Marumo (1982) reported that young individuals of *So. zetesios* were distributed in shallower layers (200–300 m) than adults, and were abundant in summer in Sagami Bay. In our other study, the young individuals without ovaries were also abundant in the 200–400 m layer in September (unpublished data), indicating that the shallow WMD of *So. zetesios* is due to an increase in number of young individuals.

Group D was mainly distributed below 400 m and contained two sub-groups with a boundary at around 1,000 m, which coincides with the boundary between the NPIW and the Pacific Deep Water (Iwata 1986). It has been suggested that *Parasagitta elegans* and *Ps. scrippsae*, which are distributed in the epipelagic layer of subarctic areas, inhabit areas below 600 m in Sagami Bay (Marumo 1966, Marumo & Nagasawa 1973). Marumo (1966) reported that these species occur in the mesopelagic layer due to the intrusion of subarctic water. In the present study, these species were distributed below 400 m and occurred in May, September, and November 2005 and January 2006 when low-salinity water (<34.2) was present at 400–800 m. According to Senjyu (1998) salinities of less than 34.2 indicate a strong intrusion of subarctic water in the mesopelagic layer of Sagami Bay, suggesting that the abundance

of the two boreal species is strongly influenced by subarctic water.

In regions north of 60°N *Eukrohnia hamata* occurs near the surface, whereas it lives in deeper waters at lower latitudes, e.g. below 100 m at 40°N and around 1,000 m near the equator (Angel 1997). This species was dominant in Groups D₁ and D₂. The standing stock of *E. hamata* in Sagami Bay was remarkably smaller than that of the epipelagic *E. hamata* reported in the Antarctic, Subarctic, and Arctic regions (Table 2), while it was larger than that in the tropical-temperate region where this species occurs in the meso- and bathypelagic layers. The standing stock of *E. hamata*, as well as that of other boreal species, peaked in November, when the intrusion of subarctic water was strong. Miyamoto (2010) reported that *E. hamata* comprises four genetically-distinct groups on the basis of mitochondrial DNA gene sequences. To the south of Honshu, the boreal group, which is dominant in the subarctic Pacific, occurred with the group distributed in temperate waters. This finding provides additional evidence that the occasionally high standing stock in Sagami Bay was probably caused by an intrusion of boreal *E. hamata*, which is abundant in northern epipelagic waters, as are *Pa. elegans* and *Ps. scrippsae*.

In conclusion, this study showed that vertical and seasonal patterns in the community structure of the pelagic chaetognaths in Sagami Bay correspond with the dynamics of the oceanic environment, including the vertical structure of water masses, upwelling, and intrusions of subarctic water. The relationship between chaetognath community and the environment shown by this fine-scale investigative study will contribute to future studies, such as those on long-term changes in their community structure and spatial distributions.

Acknowledgments

We thank Drs. Takashi Ishimaru, Naho Horimoto and Masato Moteki (Tokyo University of Marine Science and Technology) who provided helpful comments and advice. We also thank the captain and crew members of the T/S *Seiyo-Maru* (Tokyo University of Marine Science and Technology) for their cooperation at sea. Thanks are also due to Dr. Shinji Shimode (The University of Tokyo) for his advice in the statistical analyses, and to the members of the Plankton Laboratory, Tokyo University of Marine Science and Technology for their advice and discussion. Dr. Atsushi Yamaguchi (Hokkaido University) and two anonymous reviewers provided helpful comments on this manuscript. This study is part of the Census of Marine Zooplankton (CMarZ), an Ocean Realm Field Project of the Census of Marine Life. The data will be made accessible through the CMarZ-Asia database (<http://cmarz-asia.org>).

References

- Alvariño A (1965) Chaetognaths. *Oceanogr Mar Biol Annu Rev* 3: 115–194.
- Alvariño A (1967) The Chaetognatha of the NAGA Expedition (1959–1961) in the South China Sea and the Gulf of Thailand. Part I-Systematics. *NAGA Rep* 4: 1–197.
- Angel MV (1993) Biodiversity of the pelagic ocean. *Conserv Biol* 7: 760–772.
- Angel MV (1997) Pelagic biodiversity. In: *Marine Biodiversity: Patterns and Processes* (eds Ormond RFG, Gage JD, Angel MV). Cambridge University Press, Cambridge, pp. 35–68.
- Aurich HJ (1970) The distribution of the chaetognaths in the region of the North Atlantic current system. *Ber Dtsch Wiss Komm Meeresforsch* 22: 1–30.
- Ball EE, Miller DJ (2006) Phylogeny: the continuing classificatory conundrum of chaetognaths. *Curr Biol* 16: R577–R578.
- Bieri R (1959) The distribution of planktonic Chaetognatha and their relationship to water masses. *Limnol Oceanogr* 4: 1–28.
- Bieri R (1991) Systematics of the Chaetognatha. In: *Biology of Chaetognaths* (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 122–136.
- Bone Q, Goto T (1991) Nervous system. In: *Biology of Chaetognaths* (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 18–31.
- Bone Q, Kapp H, Pierrot-Bults AC (1991) Introduction and relationships of the group. In: *Biology of Chaetognaths* (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 1–4.
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27: 325–349.
- Casanova J-P (1992) Chaetognaths from the Alvin dives in the Santa Catalina Basin (California), with description of the two new *Heterokrohnia* species. *J Nat Hist* 26: 663–674.
- Casanova J-P (1994) Three new rare *Heterokrohnia* species (Chaetognatha) from deep benthic samples in the Northeast Atlantic. *Proc Biol Soc Wash* 107: 743–750.
- Casanova J-P, Chidgey K (1987) A new species of *Heterokrohnia* (Chaetognatha) from “Discovery” cruise in the northeast Atlantic. *Bull Mus Natl Hist Nat Paris* 9: 877–883. (in French with English abstract)
- Casanova J-P, Chidgey K (1990) A new benthopelagic species of *Heterokrohnia* (Chaetognatha) from the North Atlantic water. *Bull Zool Mus Univ Amsterdam* 12: 109–116.
- Cheney J (1985) Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic-II. Vertical distribution and migrations. *Deep-Sea Res* 32: 1061–1075.
- Fagetti E (1972) Bathymetric distribution of chaetognaths in the South Eastern Pacific Ocean. *Mar Biol* 17: 7–29.
- Feigenbaum D (1991) Food and feeding behavior. In: *Biology of Chaetognaths* (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 45–54.
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing mutispecies distribution patterns. *Mar Ecol Prog Ser* 8: 37–52.
- Furuhashi K (1961) On the distribution of some plankton animals in the Kuroshio region south of Honshu, Japan, with notes on

- the nature and origin of the cold water mass Appearing in the region. I. The distribution of copepods and chaetognaths. *Umi to Sora* 37: 45–80. (in Japanese with English abstract)
- Hirota Y, Nemoto T, Marumo R (1982) Seasonal variation and horizontal distribution of Euphausiids in Sagami Bay, central Japan. *Bull Plankton Soc Jpn* 29: 37–47. (in Japanese with English abstract)
- Hunt JC, Lindsay DJ (1999) Methodology for creating an observational database of midwater fauna using submersible: Results from Sagami Bay, Japan. *Plankton Biol Ecol* 49: 75–87.
- Iwata S (1979) Long-term temperature and salinity averages in Sagami Bay. *Bull Regional Fish Lab, Kanagawa Pref* 2: 15–26. (in Japanese)
- Iwata S (1986) Studies on the short-term variations of oceanic conditions in Sagami Bay. *Special Rep Kanagawa Pref Fish Exp Sta* 2: 1–66. (in Japanese)
- 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.
- Johnson TB, Terazaki M (2004) Chaetognath ecology in relation to hydrographic conditions in the Australian sector of the Antarctic Ocean. *Polar Biosci* 17: 1–15.
- Johnson TB, Nishikawa J, Terazaki M (2006) Community structure and vertical distribution of chaetognaths in the Celebes and Sulu Seas. *Coast Mar Sci* 30: 360–372.
- Kawabe M, Yoneno M (1987) Water and flow variations in Sagami Bay under the influence of the Kuroshio Path. *J Oceanogr Soc Jpn* 43: 283–294.
- Kinoshita J, Hiromi J (2005) Mass occurrence of jellyfishes and their influence on fisheries in Sagami Bay, Japan. *Bull Plankton Soc Jpn* 52: 20–27. (in Japanese with English abstract)
- 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 (1967a) Chaetognaths collected on the eighth cruise of Japanese expedition of deep seas. *La Mer* 5: 33–36.
- Kitou M (1967b) Chaetognatha. In *Illustration Book of Japanese Marine Plankton*, V (ed Motoda S). Soyo-sha, Tokyo, pp 40–51. (in Japanese)
- Kotori M, Nishiyama T, Tanimura A, Watanabe K (1987) Abundance and vertical distribution of the chaetognath *Parasagitta elegans* (Verrill) under the sea ice in Saroma Ko, lagoon on Hokkaido, Japan. *Proc NIPR Symp Polar Bio* 11: 138–144.
- Kuriyama M, Nishida S (2006) Species diversity and niche-partitioning in the pelagic copepods of the Family Scolecitrichidae (Calanoida). *Crustaceana* 79: 293–317.
- Lindsay DJ, Hunt JC (2005) Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific. *J Mar Biol Ass UK* 85: 503–517.
- Marumo R (1966) *Sagitta elegans* in the Oyashio undercurrent. *J Oceanogr Soc Japan* 22: 129–137.
- Marumo R, Kitou M (1966) A new species of *Heterokrohnia* (Chaetognatha) from the western North Pacific. *La Mer* 4: 178–180.
- Marumo R, Nagasawa S (1973) Pelagic chaetognaths in Sagami Bay and Suruga Bay, central Japan. *J Oceanogr Soc Jpn* 29: 267–275.
- Matsuura H, Nishida S (2000) Fine structure of the “button setae” in the deep-sea pelagic copepods of the genus *Euaugaptilus* (Calanoida: Augaptilidae). *Mar Biol* 137: 339–345.
- Matsuura H, Nishida S, Nishikawa J (2010) Species diversity and vertical distribution of the deep-sea copepods of the genus *Euaugaptilus* in the Sulu and Celebes Seas. *Deep-Sea Res II* 57: 2098–2109.
- Matsuzaki M (1975) On the distribution of chaetognaths in the East China Sea. *The Oceanogr Mag* 26: 57–62.
- Miyamoto H (2010) Molecular and morphological studies on the diversity and biogeography of pelagic chaetognaths. PhD thesis. University of Tokyo, Tokyo, Japan.
- Miyamoto H, Nishida S (2011) A new deep-sea benthopelagic chaetognath of the genus *Bathyspadella* (Chaetognatha) with ecological and molecular phylogenetic remarks. *J Nat Hist* 45: 2785–2794.
- Motoda S (1959) Devices of simple plankton apparatus. *Mem Fac Fish Hokkaido Univ* 7: 74–94.
- Nagai N, Tadokoro K, Kuroda K, Sugimoto T (2006) Occurrence Characteristics of Chaetognath Species along the PM Transect in the Japan Sea during 1972–2002. *J Oceanogr* 62: 597–606.
- Nagai N, Tadokoro K, Kuroda K, Sugimoto T (2008) Chaetognath species-specific responses to climate regime shifts in the Tsushima Warm Current of the Japan Sea. *Plankton Benthos Res* 3: 86–95.
- Nagasawa S, Marumo R (1975) Distribution of chaetognath, *Sagitta nagae* Alvarinho in Suruga Bay, central Japan with notes on the zooplankton biomass. *Bull Plankton Soc Jpn* 21: 87–104.
- Nagasawa S, Marumo R (1977) Seasonal variation in composition and number of epipelagic chaetognaths in Sagami Bay, Japan. *La Mer* 15: 185–195. (in Japanese with English abstract)
- Nagasawa S, Marumo R (1982) Vertical distribution of epipelagic chaetognaths in Suruga Bay, Japan. *Bull Plankton Soc Jpn* 29: 9–23. (in Japanese with English abstract)
- Nair VR, Terazaki M, Jayalakshmy KV (2002) Abundance and community structure of chaetognaths in the northern Indian Ocean. *Plankton Biol Ecol* 49: 27–37.
- Nishida S, Ohtsuka S (1996) Specialized feeding mechanism in the pelagic copepod genus *Heterorhabdus* (Calanoida: Heterorhabdidae), with special reference to the mandibular tooth and labral glands. *Mar Biol* 126: 619–632.
- Nishida S, Ohtsuka S (1997) Ultrastructure of the mouthpart sensory setae in the mesopelagic copepods of the family Scolecitrichidae. *Plankton Biol Ecol* 44: 81–90.
- Nishida S, Ohtsuka S, Parker AR (2002) Functional morphology and food habits of deep-sea copepods of the genus *Cephalophanes* (Calanoida: Phaennidae): perception of bioluminescence as a strategy for food detection. *Mar Ecol Prog Ser* 227: 157–171.
- Noblezada MMP, Campos WL (2008) Spatial distribution of chaetognaths off the northern Bicol Shelf, Philippines (Pacific coast). *ICES J Mar Sci* 65: 484–494.
- Nomura H, Kitabayashi H, Tanaka Y, Ishimaru T (2003) Seasonal occurrence and vertical distribution of the hyperiid amphipods in Sagami Bay, central Japan. *La Mer* 41: 69–76. (in Japanese with English abstract)

- Ozawa M, Yamaguchi A, Ikeda T, Watanabe Y, Ishizaka J (2007) Abundance and community structure of chaetognaths from epipelagic through abyssopelagic zones in the western North Pacific and its adjacent seas. *Plankton Benthos Res* 2: 184–197.
- Pearre SJ (1973) Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* 54: 300–314.
- Pierrot-Bults AC, Nair VR (2010) Horizontal and vertical distribution of Chaetognatha in the upper 1000 m of the western Sargasso Sea and the Central and South-east Atlantic. *Deep-Sea Res II* 57: 2189–2198.
- 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.
- Roe HSJ (1972) The vertical distributions and diurnal migrations of Calanoid copepods collected on the Sond Cruise, 1965. *J Mar Biol Ass UK* 52: 277–314.
- Rottman ML (1978) Ecology of recurrent groups of pteropods, euphausiids, and chaetognaths in the Gulf of Thailand and the South China Sea. *Mar Biol* 48: 63–78.
- Sameoto DD (1987) Vertical distribution and ecological significance of chaetognaths in the Arctic environment of Baffin Bay. *Pol Biol* 7: 317–328.
- Senjyu T, Asano N, Matsuyama M, Ishimaru T (1998) Intrusion events of the intermediate Oyashio water into Sagami Bay, Japan. *J Oceanogr* 54: 29–44.
- Shimode S, Toda T, Kikuchi T (2006) Spatio-temporal changes in diversity and community structure of planktonic copepods in Sagami Bay, Japan. *Mar Biol* 148: 581–597.
- Terazaki M (1973) Ecological study of pelagic chaetognaths. PhD thesis. University of Tokyo, Tokyo, Japan.
- Terazaki M and Marumo R (1982) Feeding habits of meso- and bathypelagic Chaetognatha, *Sagitta zetesios* Fowler. *Oceanol Acta* 5: 461–464.
- Terazaki M, Marumo R (1979) Diurnal vertical migration of *Sagitta elegans* Verill in the western North Pacific Ocean. *Bull. Plankton Soc Jpn* 26: 11–17.
- Terazaki M (1992) Horizontal and vertical distribution of chaetognaths in a Kuroshio warm-core ring. *Deep-Sea Res* 39: S231–245.
- Thuesen EV (1991) The tetrodotoxin venom of chaetognaths. In: *Biology of Chaetognaths* (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 55–60.
- Thuesen EV (2012) Chaetognatha: A list of valid families, genera and species. Available at: <http://academic.evergreen.edu/t/thuesene/chaetognaths/chaetlist.htm> (accessed on 20 February 2012)
- Tokioka T (1939) Chaetognaths collected chiefly from the Bays of Sagami and Suruga with some notes on the shape and structure of the seminal vesicles. *Rec Oceanogr Works Jpn* 10: 122–150.
- Tokioka T (1959) Observations on the taxonomy and distribution of chaetognaths of the North Pacific. *Publ Seto Mar Biol Lab* 7: 349–456.
- Tokioka T (1974) On the specific validity in species pairs or trios of plankton animals, distributed respectively in different but adjoining water masses, as seen in chaetognaths. *Publ Seto Mar Biol Lab* 11: 393–408.
- Ulloa R, Palma S, Silva N (2000) Bathymetric distribution of chaetognaths and their association with water masses off the coast of Valparaíso, Chile. *Deep-Sea Res I* 47: 2009–2027.
- Ulloa R, Palma S, Silva N (2004) Relationship between spatial distribution of chaetognaths and oceanographic conditions off Concepción Bay, Chile. *Deep-Sea Res II* 51: 537–550.
- Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flier GR (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar Biol* 87: 313–323.
- Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MT (2002) Community and trophic structure of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COMIC). *Deep-Sea Res I* 49: 1007–1025.
- Yasuda I (2003) Hydrographic structure and variability in the Kuroshio-Oyashio transition area. *J Oceanogr* 59: 389–402.