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Community structure and spatial distribution of chaetognaths in Tosa Bay on the temperate Kuroshio coast of Japan

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Abstract: Studies on seasonal and spatial variations in the community structure of chaetognaths are limited despite their importance in marine plankton ecosystems. We examined community structures of chaetognaths in one-year monthly samples collected at three stations from inshore (Stn 1) to the shelf edge (Stn 3) in Tosa Bay on the Kuroshio coast of Japan. The yearly mean density of chaetognaths was 22.2 ind. m^{-3}, consisting of *Zonosagitta nagae* (50.0%), *Flaccisagitta enflata* (17.4%), *Serratosagitta pacifica* (9.4%), and *Aidanosagitta regularis* (9.3%). The monthly dominant species were *Z. nagae* from March to July, *F. enflata* and *A. reguralis* from August to October, and *F. enflata* and *S. pacifica* from November to February. The densities of *Z. nagae* and *F. enflata* in the top 50 m were generally higher at Stn 1. In the 200-m water column at Stn 3, the densities of the dominant species were generally highest in the 0–25 or 25–50 m layer, and *A. regularis* was generally distributed in the shallowest layer, followed by *F. enflata*, *Z. nagae* and *S. pacifica* according to their population mean depths. The present results on the community structure and vertical distribution agree well with those in bays located further downstream the Kuroshio Current, indicating that the results are general features in temperate Kuroshio coastal waters. Comparison of chaetognath community structures with those in adjacent regions indicates that the dominance of *Z. nagae* in regard to the yearly mean abundance is characteristic to temperate Kuroshio Current coasts.

Key words: Chaetognatha, community structure, Kuroshio coastal water, vertical distribution, *Zonosagitta nagae*

Introduction

The phylum Chaetognatha is a ubiquitous marine zooplankton taxon inhabiting polar to tropical waters and from epi- to bathypelagic in all oceans (Bone et al. 1991). In pelagic waters they are generally the second most dominant net-caught zooplankton group, following copepods in terms of both numerical abundance and biomass (Coston-Clements et al. 2009). They are known to be predators, feeding on various micro- and mesozooplankters and even fish larvae (Feigenbaum 1991). Accordingly they have been assumed to play a substantial role in the marine zooplankton community. However, the biology and ecology of chaetognaths are much less studied than copepods. In warm temperate waters around Japan, there have been only three studies on the seasonal variation in the community structure of chaetognaths (Marumo & Nagasawa 1973, Itoh et al. 2006, Miyamoto et al. 2012). These studies were made in the two neighboring bays, Sagami and Suruga Bays (Fig. 1), which are located on the coast within the final precincts of the Kuroshio Current. Thus, detailed seasonal variations in the chaetognath community have never been studied in temperate coastal waters closer to the main part of the Kuroshio Current.

Chaetognaths are well known as indicator organisms of water masses (e.g. Hardy 1956, Villenas et al. 2009), because each species has its own distribution range associated with water masses. Their abundances vary depending on water mass structure within their distribution ranges. This implies that each water mass has its own chaetognath community structure, and therefore that the community structure of chaetognaths is also a sensitive indicator of water structure. The most important indicator of the community is generally the dominant species. Kuroda & Nagai

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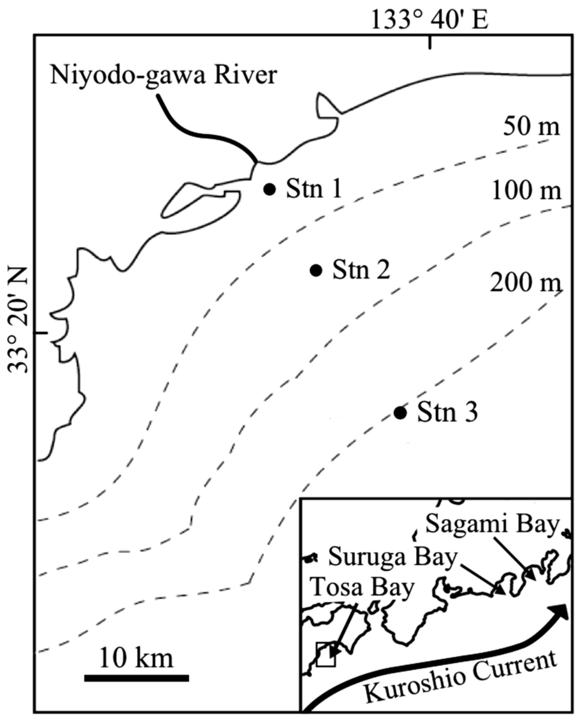

Fig. 1. Sampling stations in Tosa Bay, with map showing locations of Tosa, Suruga, and Sagami Bays and a typical flow path of the Kuroshio Current.

(2012) reviewed the chaetognath communities in the warm temperate seas of central and western Japan, as well as in the Kuroshio Current. They summarized that the dominant species were *Aidanosagitta crassa* (Tokioka) in nearshore waters, *Zonosagitta nagae* (Alvariño) in coastal waters, *Flaccisagitta enflata* (Grassi) in the Kuroshio water, and *Pterosagitta draco* (Krohn) in offshore-oceanic waters. To know the characteristics of the chaetognath community in these waters, however, studies covering the entire range of the waters are necessary. As for the warm temperate Kuroshio coastal waters along the Pacific coasts of western Japan, *Z. nagae* is known to be the most important species from the viewpoints of numerical abundance and seasonal period of the dominance. This knowledge was provided by studies in Suruga and Sagami Bays (Marumo & Nagasawa 1973, Nagasawa & Marumo 1977, Itoh et al. 2006, Miyamoto et al. 2012), which are located near the last coastal region in which the Kuroshio Current dominates. Therefore, information on seasonal community structures in coastal waters more upstream is necessary for understanding their general features in temperate Kuroshio coastal waters. Quantitative comparisons of these community structures with those of surrounding regions are also necessary, because these dominant species have wide distribution ranges in the Northwest Pacific (Kuroda et al. 2012).

The vertical distributions of chaetognaths have so far been studied mainly at oceanic sites, and species are generally classified into epipelagic, mesopelagic, and bathypelagic forms. Compared to information on their vertical distribution in oceanic waters, the knowledge of their species-specific vertical distribution in the coastal or epipelagic waters is limited, despite the importance of these waters for biological production in the sea. The vertical distribution of chaetognaths in epipelagic waters should be studied more to gain a better understanding of marine food webs, because their prey and predators are generally unevenly distributed in the 0–200 m deep layer.

We investigated species-specific abundances and spatial distributions of chaetognaths in Tosa Bay on the south coast of Shikoku Island, western Japan (Fig. 1). The bay is located in the Kuroshio Current-affected waters and >500 km upstream of Suruga and Sagami Bays. Three large-scale tidal currents per 24 hour period are known in the bay, i.e. counter clockwise in the central part and clockwise along the west and east sides (Miyamoto et al. 1980). Seasonal variations in primary production in the bay were studied by Hirota et al. (2002), Ichikawa & Hirota (2004) and Hirota & Ichikawa (2012). There have been no published studies on zooplankton ecology or fauna in the bay except for that of Nishibe et al. (2009) on the vertical distribution of oncaeid copepods and Ohnishi et al. (2013) on the occurrence of a rare chaetognath. The aim of this paper is to illustrate (1) chaetognath community structure in Tosa Bay with a comparison to previous studies in Sagami and Suruga Bays on the temperate Kuroshio coast, (2) characteristics of the chaetognath community structure along the temperate Kuroshio coast (i.e. the common features of the community in Sagami, Suruga and Tosa Bays) compared to neighboring regions, i.e. the Japan Sea, the East China Sea, the northern NW Pacific, and the Inland Sea of Japan, and (3) horizontal and vertical distribution patterns of epipelagic chaetognath species in the bay.

Materials and Methods

Plankton samples used in the present study were collected as part of the monthly oceanographic monitoring survey conducted by the zooplankton laboratory of the Usa Marine Biological Institute, Kochi University, at three stations in Tosa Bay. The three stations were from inshore to offshore (Fig. 1), i.e., Stn 1 (22 m deep, about 2 km off the mouth of the Niyodo-gawa River), Stn 2 (72 m deep, about 10 km offshore), and Stn 3 (210 m deep, at the shelf edge about 30 km offshore). Samples were collected during the daytime once a month at 15–43 day intervals by vertical hauls of an opening-closing bongo-type plankton net (100 μm mesh, 45 cm mouth diameter×2) (Ueda 2013) from four discrete layers (0–25, 25–50, 50–100 and 100–200 m) at Stn 3, two layers (0–25 and 25–50 m) at Stn 2, and a single layer (0–20 m) at Stn 1. The two samples from the double-ring net in each haul were fixed separately in 1–2% buffered formalin-seawater solution immediately after sampling. The water volume filtered through the net was calculated from the count of a flow-meter (Rigosha & Co., Ltd., Japan) equipped to each mouth ring. Vertical profiles of water temperature, salinity and chlorophyll concentration from the surface to the maximum sampling depths were measured at 0.5 m depth intervals using a CTD logger equipped with a chlorophyll concentration sensor (AST1000, Alec Electronics Co., Ltd., Japan), simultaneously with sampling.

Chaetognaths were analyzed in the samples from a one-year period from May 2009 to April 2010; of the two samples from each haul, the one with the larger filtered water volume was generally used in the present study. All chaetognath specimens, including early juveniles in the samples, were sorted under a stereomicroscope. Identification was made at the species level under a stereomicroscope or a regular light microscope for all specimens except for a few samples that contained a large number of chaetognaths. In the latter cases, specimens were identified to species level for a 1/2 or 1/4 ariquot (corresponding to 100–200 individuals) which was divided using a box-type plankton splitter (Motoda 1959). The species identification followed Kitou (1967) and Terazaki (1997). Eye pigments were also used for identification of early juveniles, following Nagasawa & Marumo (1976). Genus names follow Bieri (1991). The classification of species into epipelagic (0–200 m depth), mesopelagic (200–1000 m depth), and bathypelagic species (>1000 m depth) follows Kuroda & Nagai (2012).

The term "monthly mean density" of chaetognaths represents the weighted mean density based on the data from all sampling layers in each month, calculated by the following equation:

$$\text{monthly mean density} = \sum(d \times L)/\sum(L)$$

where d is chaetognath density in each sampling layer and L is vertical length of the layer. The "yearly mean density" is an arithmetical average of the monthly mean densities during the 12-month study period. To compare vertical distribution among the species, the population mean depth of each species at Stn 3 was calculated by the following equation:

$$\text{population mean depth} = \sum(Dm \times d \times L)/\sum(d \times L)$$

where Dm and L are median depth and vertical length of each sampling layer, respectively, and d is chaetognath density in the layer.

Outlier values of temperature and salinity at 0–1 m depths and chlorophyll concentration at all depths were excluded using Smirnov–Grubbs' rejection test, in which each value was tested with the values at the 20 nearest neighboring depths at the 0.01 probability level, because these exceptional values probably resulted from unexpected conditions, such as cooling or heating of the CTD on board for temperature, rainfall during sampling for salinity, and passing of large phytoplankton colonies in front of the sensor for chlorophyll concentration. The mean values of the environmental variables at 0.5 m intervals within each sampling layer were used for correlation analyses with chaetognath density.

Results

Oceanographic conditions

The surface water temperature was highest in September on average and lowest in March; the temperature at 5 m depth at Stn 1 ranged from 16.4 to 28.1°C (Fig. 2A). Vertical profiles of temperature revealed a strong thermal stratification in the 40–80 m depth layer from August to October (Fig. 3A). The seasonal variation in the bottom layer at Stn 3 was independent from that in the surface layer, with lower temperatures at 200 m depth (<12°C) in July, September, January, and March—probably resulting from upwelling of deep ocean waters (Ichikawa & Hirota 2004).

Salinity in the surface water greatly decreased in July and August, especially at Stn 1 in the rainy month July (Fig. 2B), indicating the effect of discharge from the Niyodo-gawa River. Another weak decrease was observed at Stn 1 in March. Salinities of the bottom water at Stn 3 were generally lower than in middepth waters (Fig. 3B), probably due to upwelling (Hirota & Ichikawa 2012).

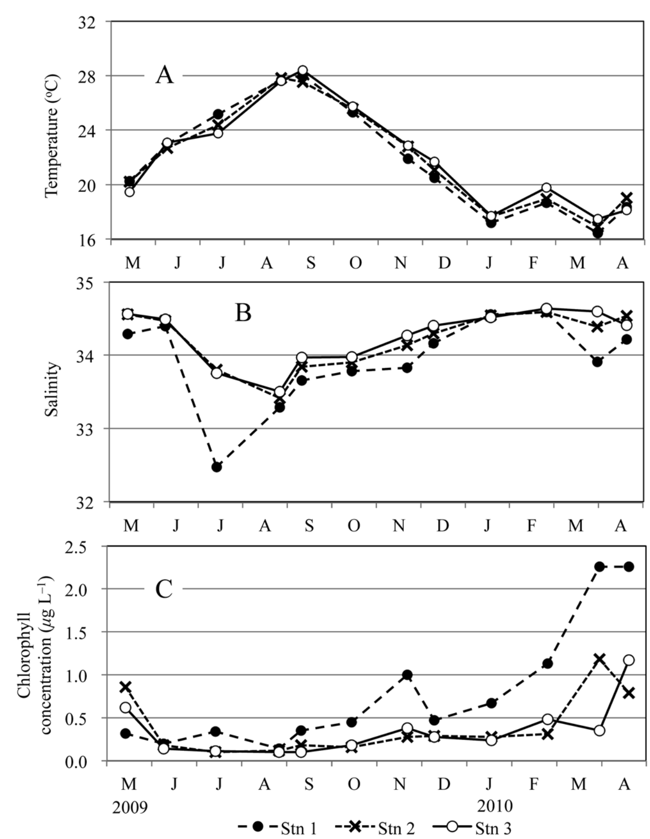

Fig. 2. Seasonal variations in (A) temperature, (B) salinity, and (C) chlorophyll concentration at 5 m depth at the three sampling stations in Tosa Bay.

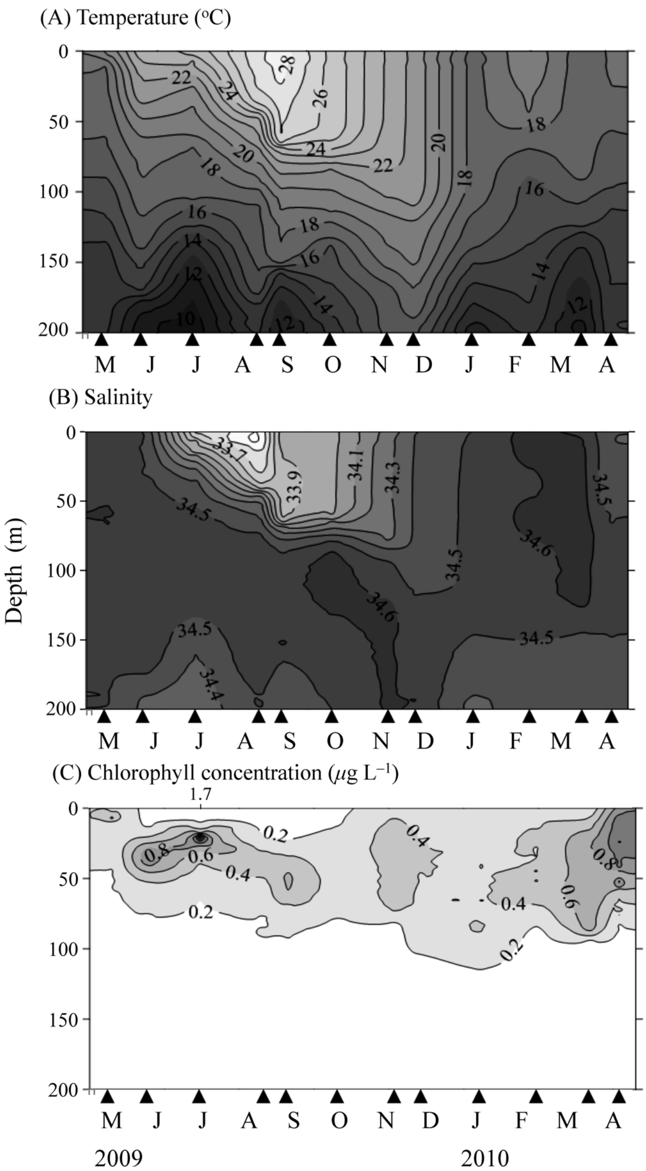

Fig. 3. Seasonal variations in vertical profiles of (A) temperature, (B) salinity, and (C) chlorophyll concentration at Stn 3 in Tosa Bay. The sampling dates are denoted by arrow heads.

Chlorophyll concentration at 5 m depth was higher at Stn 1 than at the other two stations with an exception being in May, and during the spring (March and April) with secondary peaks in November at Stn 1 and in May at Stn 2 (Fig. 2C). However, the vertical profiles at Stn 3 revealed subsurface chlorophyll maxima in the 20–60 m layer throughout the year and high chlorophyll concentration values (>1.0 μg L^{-1}) in July and April (Fig. 3C). The values below 100 m depth were generally <0.2 μg L^{-1} throughout the year.

Table 1. Nighteen species of chaetognaths identified from Tosa Bay from May 2009 to April 2010 and yearly mean density, i.e. arithmetical average of monthly mean density, which is weighted mean density at the three stations in each month . The top four dominant species, which had yearly mean densities of >1.0 ind. m^{-3}, are in bold face. Mesopelagic species are marked with an asterisk.

	Yearly mean density (ind. m^{-3})
Aidanosagitta crassa	0.04
Aidanosagitta neglecta	0.68
Aidanosagitta regularis	**1.85**
*Eukrohnia hamata**	0.01
Ferosagitta ferox	0.31
Ferosagitta robusta	0.07
Flaccisagitta enflata	**3.47**
Flassisagitta hexaptera	0.03
Krohnitta pacifica	0.49
*Krohnitta subtilis**	0.04
Mesosagitta decipiens	0.03
Mesosagitta minima	0.83
*Mesosagitta neodecipiens**	0.01
Pseudosagitta lyra	0.02
Pterosagitta draco	0.13
Sagitta bipunctata	0.02
Serratosagitta pacifica	**1.86**
Serratosagitta pseudoserratodentata	0.04
Zonosagitta nagae	**9.96**
Total chaetoganaths (including unidentified specimens)	22.2

Yearly and monthly mean densities of chaetognaths and community structure based on the monthly mean density

A total of 6,199 chaetognath specimens belonging to 19 species of 11 genera were identified among 6,864 individuals examined during the study period (Table 1). Of the 665 unidentified specimens, 391 were of too early stages to be identified even with eye pigment and 274 were broken and had lost their diagnostic morphologies. The monthly species richness varied between 10 in July and 15 in December with no notable seasonal trend. The monthly mean density of chaetognaths varied between 3.7 ind. m^{-3} in February and 49.3 ind. m^{-3} in April, with a yearly mean density of 22.2 ind. m^{-3}. On the basis of the yearly mean density, *Zonosagitta nagae* was the most dominant species comprising 50.0% of chaetognaths (excluding unidentified individuals), followed by *Flaccisagitta enflata* (17.4%), *Serratosagitta pacifica* (Tokioka) (9.4%), *Aidanosagitta regularis* (Aida) (9.3%), *Mesosagitta minima* (Grassi) (4.2%), and *A. neglecta* (Aida) (3.4%); henceforth these species are referred as to as the six dominant species and the former four, of which the yearly mean densities were >1.0 ind. m^{-3} (Table 1), are referred to as the four dominant species.

The monthly mean density of total chaetognaths gradu-

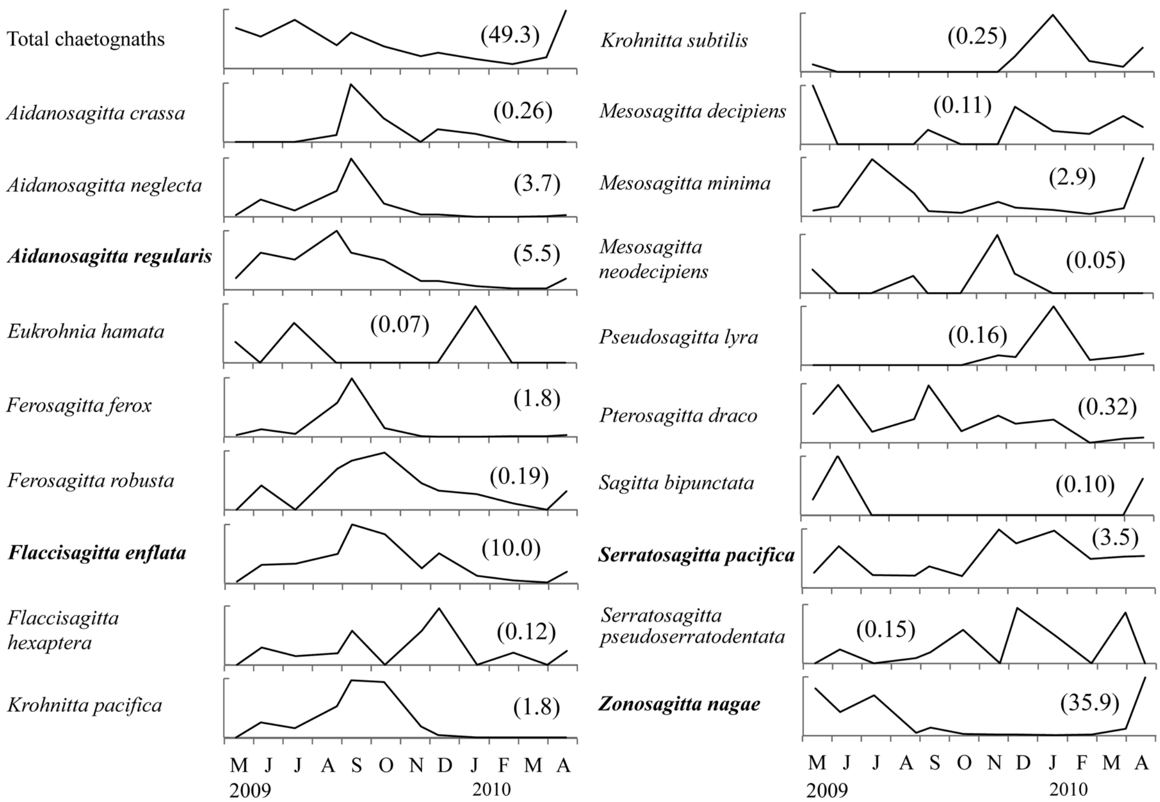

Fig. 4. Seasonal variation in the monthly mean density (ind. m^{-3}) of chaetognaths in Tosa Bay. The full scale of the Y-axis of each species is set to the highest monthly mean density, which is presented in parentheses. The four dominant species are shown in bold face. See Table 1 for explanation of the monthly mean density.

ally decreased from summer to the winter and abruptly increased during the spring (Fig. 4). The most dominant species, *Z. nagae*, was abundant from May to July 2009 and in April 2010, with monthly mean densities of 14.6–35.9 ind. m^{-3}, while during the winter from November 2009 to February 2010 the abundance was contrastingly low (0.4–0.8 ind. m^{-3}). The second most dominant species, *F. enflata*, exhibited "typical" seasonal variation for a summer species in accordance with the temperature variation. The monthly mean density gradually increased to its highest value (10.0 ind. m^{-3}) in the warmest month, September 2009, and then decreased to the lowest value (0.2 ind. m^{-3}) in the coldest month, March 2010. A similar seasonal pattern was observed for *Aidanosagitta regularis*, *A. neglecta*, *Krohnitta pacifica* (Aida), *Ferosagitta ferox* (Doncaster), and *A. crassa*, for which the highest densities were observed in September, except for *A. regularis*, which was most abundant in August.

The third most dominant species, *Serratosagitta pacifica*, exhibited the "typical" pattern of an autumn–winter form, i.e., relatively abundant (2.7–3.5 ind. m^{-3}) from November 2009 to January 2010 and less abundant (0.7–1.3 ind. m^{-3}) from July to October 2009. A similar pattern was seen in the rare species *K. subtilis* (Grassi), *Fl. hexaptera* (d'Orbigny), and *Pseudosagitta lyra* (Krohn), which were more abundant in December 2009 or January 2010 than in the other months, although the number of individuals collected in the present study were limited (11–22 individuals for each species).

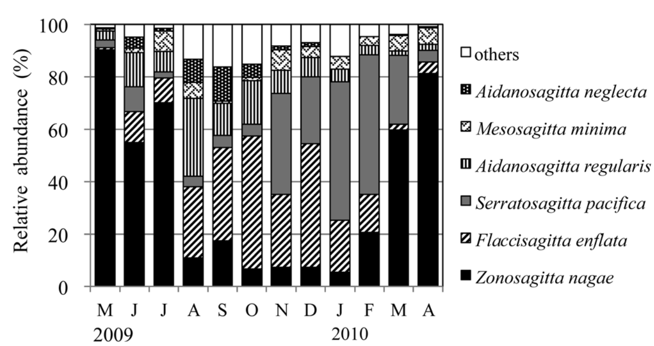

Fig. 5. Seasonal variations in the community structure of chaetognaths (excluding unidentified individuals) in Tosa Bay, based on the monthly mean density. See Table 1 for explanation of the monthly mean density.

The seasonal variation in the community structure, based on the monthly mean densities, is shown in Fig. 5, in which the ratios of the six dominant species are presented. *Zonosagitta nagae* was dominant for four months from March to July 2009. During these months, its relative abundance with respect to total chaetognaths (excluding unidentified individuals) was 74%, with the highest ratio of

90% in May 2009. The community during the other months was dominated by *A. regularis* in August 2009, by *F. enflata* in September, October, and December 2009, and by *S. pacifica* in November 2009 and January and February 2010.

Horizontal variations in chaetognath density

Horizontal distributions of chaetognaths along the inshore-offshore axis were analyzed by comparing the mean population densities at the three stations in each month. The data from the 50–100 m and 100–200 m layers at Stn 3 were excluded from this analysis, because the densities below 50 m depth were generally much lower than above 50 m depth, as described below, and therefore these data, if used, would mask the horizontal variation in the 0–50 m water columns.

The density of total chaetognaths was almost the same between the three stations, e.g. in July, October, November 2009, February, and March 2010, or decreased towards the offshore, e.g. in May, August, September, December 2009 (Fig. 6). *Zonosagitta nagae* generally exhibited the highest density at Stn 1 during the high-density season from May to September 2009 and in April 2010. The highest density of *Flaccisagitta enflata* among the three stations was generally recorded at Stn 1, especially in most of the colder months (May, November and December 2009 and from February to April 2010), when the densities at Stn 1 were remarkably higher than at the two offshore stations.

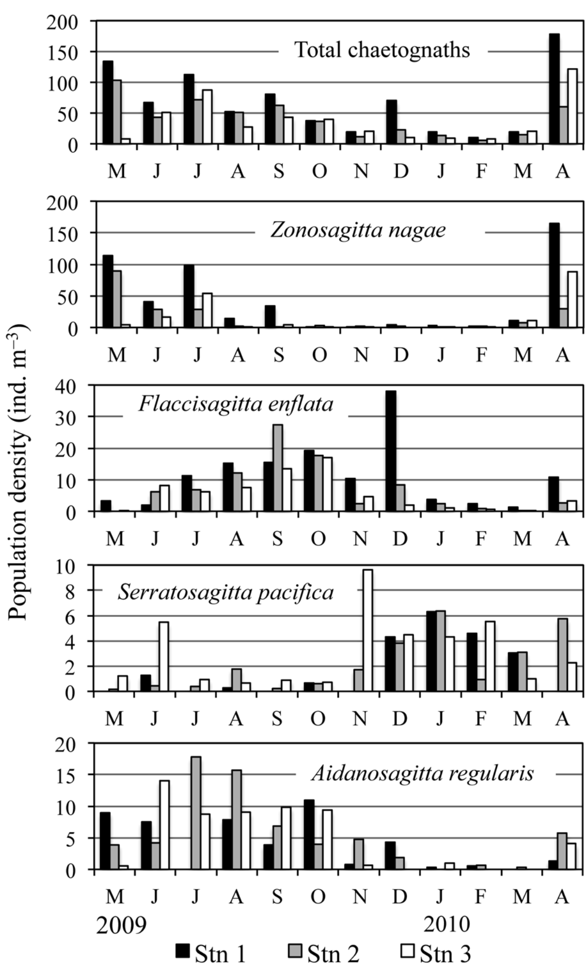

Fig. 6. Seasonal variations in horizontal distributions of total chaetognaths and the four dominant chaetognath species in Tosa Bay based on data from the layers above 50 m depth; for the densities at Stns 2 and 3, the mean values of the 0–25 and 25–50 m layers are used.

The horizontal distributions of *Serratosagitta pacifica* and *Aidanosagitta regularis* varied among the months with no consistent seasonal patterns. For example, the densities of *S. pacifica* were extremely high at Stn 3 in June and November 2009, almost even in October, December 2009 and January 2010, and much lower at Stn 3 than at Stn 1 in March 2010.

Aidanosagitta crassa, which has been considered an embayment species (Marumo & Nagasawa 1973), was recorded only in the 0–25 m layer of Stn 2 from August 2009 to January 2010, except for a single specimen collected at Stn 1 in October 2009. The species that did not occur at Stn 1 throughout the year but did occur in the 0–50 m layer of Stn 3 in some months were *Ferosagitta robusta* (Doncaster), *Flaccisagitta hexaptera*, *Krohnitta subtilis*, *Pseudosagitta lyra*, *Sagitta bipunctata* Quoy, and *Serratosagitta pseudoserratodentata* (Tokioka), which are regarded as oceanic species.

Vertical variations in chaetognath density at Stn 3

Vertical distributions of chaetognaths were analyzed based on the data from the four sampling layers at Stn 3. The density of total chaetognaths was always highest in the 0–25 or 25–50 m layer, and very much lower below 100 m depth than above 50 m depth with the exception of May 2009, when chaetognaths had two peaks: in the 0–25 and 100–200 m layers (Fig. 7). The vertical distributions of the four dominant species were analyzed in the months when the mean population density in the 0–200 m water column was >1.0 ind. m^{-3}. The density of *Zonosagitta nagae* was highest in the 0–25 m or 25–50 m layer in all of the six months analyzed. This species was very rare in the 100–200 m layer in four of the six months, and was concentrated in the top 50 m in three months. However, the distribution pattern was not consistent between the six months. For example, the pattern in May and September 2009 was very different from the other four months, with exceptionally low densities in the 25–50 m layer and relatively high densities in the 100–200 m layer.

Flaccisagitta enflata generally exhibited much higher densities in the 0–50 m layer than in the 50–200 m layer and was almost absent in water below 100 m depth. *Serratosagitta pacifica* showed a somewhat different pattern. The highest density was observed at middepths (25–50 or 50–100 m) in all the months analyzed, and no specimens of the species were collected from the 0–25 m layer in June, July 2009 or April 2010. *Aidanosagitta regularis* was al-

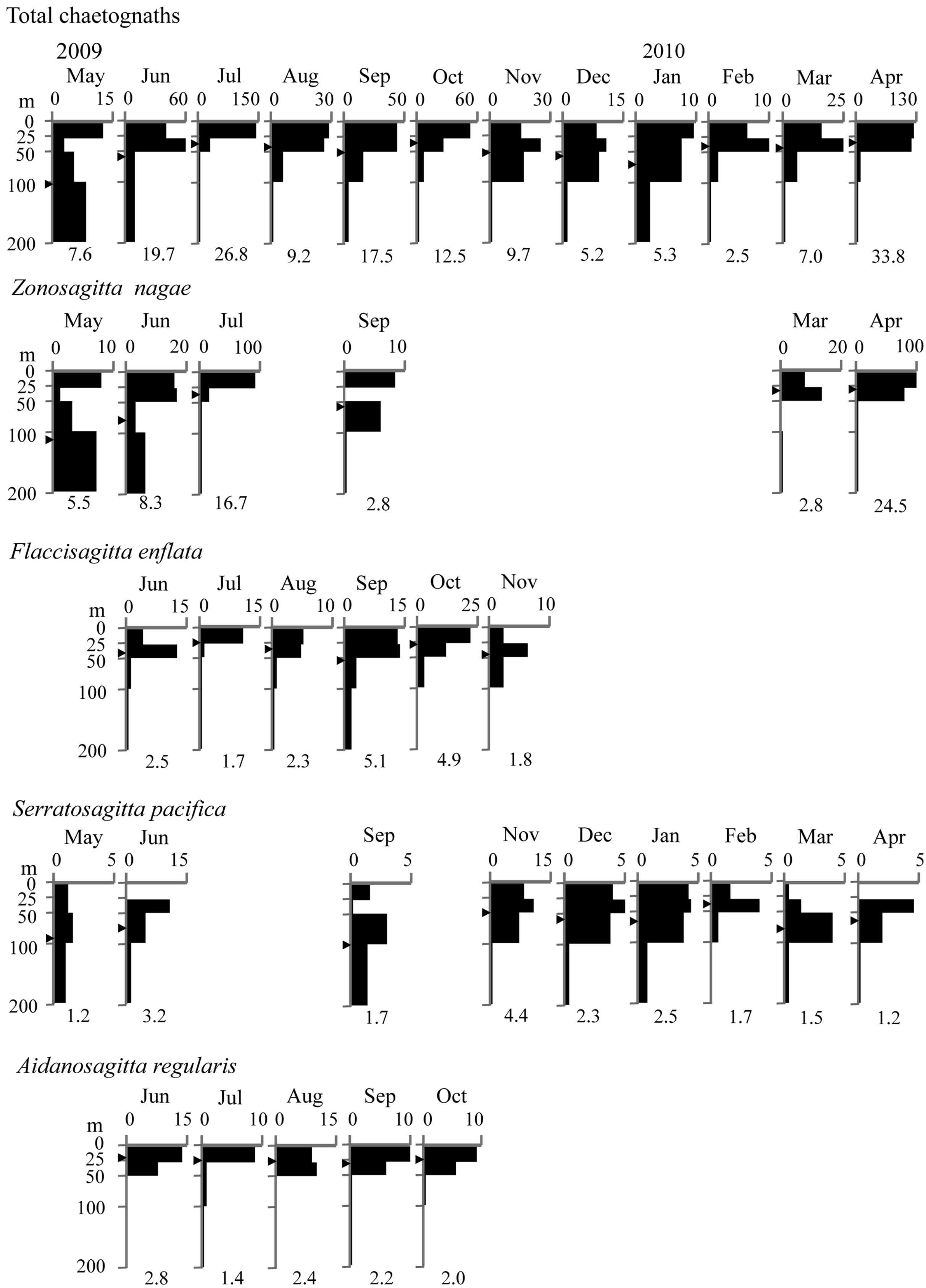

Fig. 7. Vertical distributions of total chaetognaths and the four dominant species at Stn 3 in Tosa Bay. The results are shown for the months when the population density in the 0–200 m water column, of which the value (ind. m^{-3}) is presented below each panel, was >1.0 ind. m^{-3}. The population mean depths are indicated by arrow heads.

most always restricted to the top 50 m in all the months analyzed.

Different vertical distribution patterns of *Z. nagae* and *S. pacifica* among the months resulted in large variations of their population mean depths, ranging between 32 and 111 m in *Z. nagae* and between 38 and 100 m in *S. pacifica* among the months shown in Fig. 7. In contrast, the population mean depths of *F. enflata* and *A. regularis* were more consistently within the range of 28–55 m and 22–31 m, respectively. As a result the mean values of the population mean depths shown in Fig. 7 were shallowest in *A. regularis* (26 m), followed by *F. enflata* (39 m), *Z. nagae* (59 m), and *S. pacifica* (72 m).

Among the other species, the species for which the population density at Stn 3 was >1.0 ind. m^{-3} were *Aidanosagitta neglecta* in August (1.1 ind. m^{-3}) and September 2009 (1.7 ind. m^{-3}), *Mesosagitta minima* in July 2009 (2.8 ind. m^{-3}) and April 2010 (3.1 ind. m^{-3}), and *Krohnitta pacifica* in October 2009 (1.5 ind. m^{-3}). Their distribution patterns were similar to *A. regularis*, i.e. almost restricted to the top 50 m. A total of 6, 14, and 5 individuals of the mesopelagic species *Eukrohnia hamata*, *Mesosagitta decipiens,* and *M. neodecipiens*, respectively, were identified during the study period. These were collect from the 100–200 m layer with the exception of two individuals of *M. neodecipiens* collected in from the 50–100 m layer.

Horizontal and vertical variations in community structure of chaetognaths

The spatio-temporal variations in the community structure are presented in Fig. 8, in which the communities in the 0–25 m and 25–50 m layers were compiled at both Stns 2 and 3 to get data for the 0–50 m layer as in Fig. 6. The horizontal variations in the community structure in the top 50 m of the three stations (Fig. 8A–C) are outlines below. The relative abundances of *Zonosagitta nagae* to total chaetognaths from May to September and of *Flaccisagitta enflata* from November 2009 to February 2010 were higher at Stn 1 than at Stn 3. The station-specific yearly mean density of *Z. nagae* at Stn 3 was much lower (15.1 ind. m^{-3}) than that at Stn 1 (40.8 ind. m^{-3}), which was mainly due to horizontal variations in these months, but was still about three times higher than that of the second most dominant species, *F. enflata* (5.4 ind. m^{-3}). Apart from the two most dominant species, the ratio of *Serratosagitta pacifica* was lower at Stn 1 than at Stn 3 in May 2009 and from November 2009 to February 2010. This

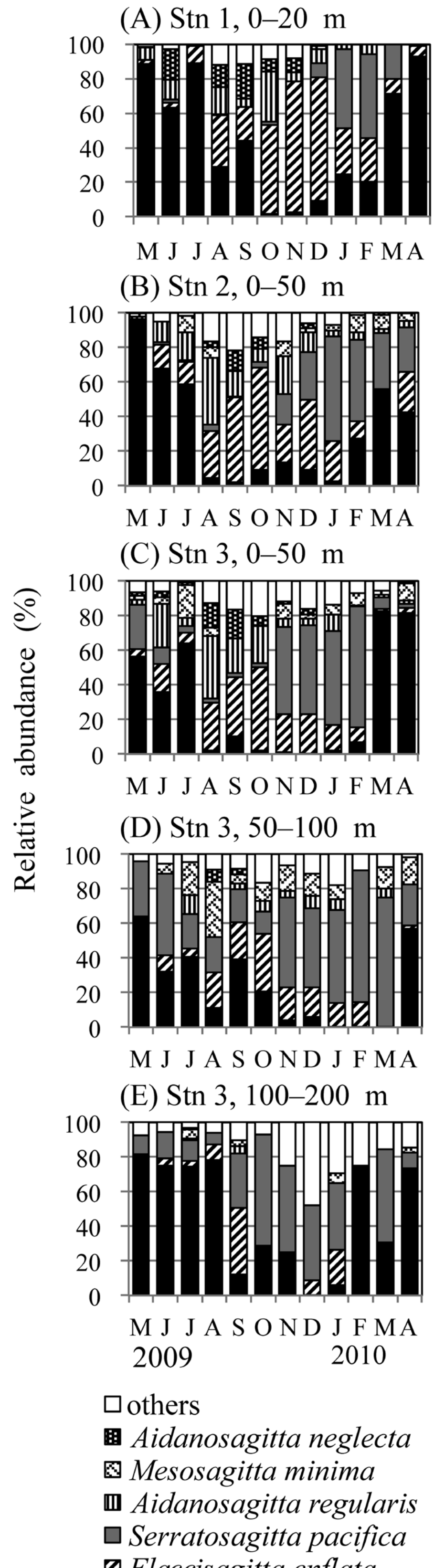

Fig. 8. Seasonal variations in the community structure of chaetognaths (excluding unidentified individuals) in (A) the 0–20 m layer at Stn 1, (B) the 0–50 m layer at Stn 2, (C) the 0–50 m layer at Stn 3, (D) the 50–100 m layer at Stn 3, and (E) the 100–200 m layer at Stn 3 in Tosa Bay. For the community structures in the 0–50 m layers at Stn2 and 3, the mean densities in the 0–25 and 25–50 m layers are used.

Table 2. Pearson's correlation coefficients between environmental variables and densities of the four dominant chaetognath species based on the data excluding those from the layers deeper than 50 m. Coefficients with * and ** are significant at the 0.05 and 0.01 probability levels (2-tailed), respectively.

	Zonosagitta nagae	*Flaccisagitta enflata*	*Serratosagitta pacifca*	*Aidanosagitta regularis*
temperature	−0.180	0.636**	−0.337**	0.637**
salinity	0.007	−0.625**	0.397**	−0.507**
chlorophyll	0.493**	−0.213	0.087	−0.313*

species became the second dominant chaetognath in the top 50 m layer at Stn 3, comprising 23.4% of the community, based on the yearly mean density in the layer.

The vertical variation in the community structure at Stn 3 (Fig. 8C–F), especially between the layers above and below 100 m depth, was more obvious than the horizontal variation in the surface layers. In the 100–200 m layer, the ratios of *F. enflata*, *Aidanosagitta regularis*, *Mesosagitta minima*, and *A. neglecta*, which were concentrated in the top 50 m layer (Fig. 7), were generally very low when compared to densities in the 0–50 m layer. Because of the low abundances of these species, the community in the 100–200 m layer was dominated by *Z. nagae* and *S. pacifica* in most months.

Relationships between chaetognath density and environmental variables

Pearson's correlation coefficients were analyzed between environmental variables and chaetognath density. Data from the 50–100 m and 100–200 m layers at Stn 3 were exclude, because these data would mask the relationship in the surface layer due to the much lower chaetognath abundances and the different seasonal changes in environmental variables in water of >50 m depth.

The density of *Zonosagitta nagae* showed significant positive correlation with chlorophyll concentration ($p<0.01$), while no significant correlation was seen with temperature or salinity. *Flaccisagitta enflata* and *Aidanosagitta regularis* were correlated significantly positively with temperature and negatively with salinity ($p<0.01$). The correlations with chlorophyll were negative in these two species but the significant correlation was seen only in *A. regularis* ($p<0.05$). The correlations of *Serratosagitta pacifca* with environmental variables were significantly negative with temperature and positive with salinity ($p<0.01$).

Discussion

Comparison with two bays further downstream the Kuroshio Current

The community structures of chaetognaths along the warm temperate Kuroshio Current coast were studied in Sagami Bay (Marumo & Nagasawa 1973, Nagasawa & Marumo 1977, Miyamoto et al. 2012) and Suruga Bay (Marumo & Nagasawa 1973, Itoh et al. 2006). In Sagami Bay, *Zonosagitta nagae* comprised an average of 48% of the numerical standing stock of all chaetognaths throughout the 0–1,400 m water column in the slope water and reached 84% when it was most abundant (Miyamoto et al. 2012). Nagasawa & Marumo (1977) also revealed that *Z. nagae* was the dominant species in Sagami Bay, comprising 31% of the chaetognath community on average. In the slope water of Suruga Bay, the species was the dominant chaetognath throughout the year with the exception of October (Marumo & Nagasawa 1973). According to Itoh et al. (2006), *Z. nagae* was the dominant species in the inner part of Suruga Bay during the six months from March to August (see their fig. 3). Since the population densities of chaetognaths as a whole in most of these months was much higher than in the months from September to February, it is obvious that *Z. nagae* was the dominant species, even when considered a yearly basis. The present study also revealed the dominance of *Z. nagae* in Tosa Bay on a yearly basis. Thus the dominance of *Z. nagae*, not only during the period of its highest abundance (from spring to summer) but also on a yearly basis, is a common feature for the chaetognath community along the temperate Kuroshio coast of Japan.

The difference between Tosa Bay in western Japan and the two bays in central Japan is seen in the other common species. In Suruga Bay, *Mesosagitta minima* or *Serratosagitta pacifica* was the most dominant species from November to February (Itoh et al. 2006), whereas in Tosa Bay the density of *M. minima* was much lower than *F. enflata* in these months. *Mesosagitta minima* is known to be abundant in the mixed water region between the Oyashio and Kuroshio (Kitou 1974) and is mostly distributed in waters of 14–22°C (Nagasawa & Marumo 1982). Accordingly one possible reason for the lower population density of *M. minima* in Tosa Bay is the higher temperature conditions, with a yearly range of 16.4–28.1°C at 5 m depth at Stn 1, compared wih Suruga Bay, where the temperature range was 12.3–26.8°C (Itoh et al. 2006). In Tosa Bay, *Aidanosagitta regularis* was the fourth most dominant species, replacing *M. minima*, while *A. regularis* was a non-dominant species in Suruga Bay. A possible reason for this is again the higher temperature conditions in Tosa Bay than in Suruga Bay. This species has been considered to be a tropical species (Marumo & Nagawasa 1973) and has been found mostly in water of ≥20°C in Suruga Bay (Nagasawa &

Marumo 1982).

Itoh et al. (2006) classified chaetognath species in Suruga Bay into four types according to their seasonal abundances, i.e. the summer–autumn type (*A. crassa* f. *naikaiensis, A. neglecta, Ferosagitta ferox*), the summer–winter type (*A. regularis, Fe. robusta, Flaccisagitta enflata, Z. pulchra*), the autumn–pring type (*S. pacifica, Pterosagitta draco, M. minima*), and the spring–summer type (*Z. nagae*). The seasonal abundances of the common species in Tosa Bay were similar to those in Suruga Bay, but differences were observed in several species, as outlined below. The period of high abundance of *Z. nagae* in Suruga Bay started in May (Itoh et al. 2006: fig. 4), whereas in Tosa Bay the monthly mean density of this species was already very high in April 2010, indicating that the period of high abundance of this species begins earlier in Tosa Bay than in Suruga Bay. This is also the case for *F. enflata*, which began to increase in numbers in July in Suruga Bay and in June in Tosa Bay. These differences in the timing of the population increase between the two bays are again probably caused by the difference in the temperature conditions, because spring temperatures in Suruga Bay were similar to those in Tosa Bay one month earlier. In fact, the monthly temperatures at 5 m depth in Suruga Bay in April and May were about 15 and 16–18°C, respectively (Itoh et al. 2006: fig. 2), while those at 5 m depth at Stn 1 in Tosa Bay were 19 and 21°C, respectively for these months. According to Nagasawa & Marumo (1977), who carried out monthly surveys on chaetognaths in Sagami Bay, the *Z. nagae* population began to increase in April, although the population density in this month was still much lower compared to that in May (see their fig. 5). The surface water temperature in April in their study was 16–17°C (see their fig. 4), which is intermediate between those in the above two studies.

Characteristics of the community structure in the temperate Kuroshio coast region compared to neighboring regions

The above comparison of the chaetognath community structure among three bays revealed that a common feature was the dominance of *Zonosagitta nagae*, not only during the period of highest abundances but also based on the yearly mean population density. Although species-specific quantitative studies on chaetognaths throughout the year are limited in the nearby regions, the dominance of *Z. nagae* in the chaetognath community on a yearly basis is regarded to be characteristic to warm temperate waters along the Kuroshio coast of Japan, except for in the inner parts of enclosed bays. In fact, the chaetognath community in the subtropical coastal waters of Hong Kong was dominated by *F. enflata*, which comprised 40% of the community on average, and the relative abundance of *Z. nagae* was much lower (only 2.5%) (Tse et al. 2007). Kotori (1976) intensively studied chaetognath communities in the northern North Pacific and the Bering Sea (mostly between 40–60°N) during the warm seasons from June to September and did not find *Z. nagae*, except for at two stations with very low abundances. Nagai et al. (2006) investigated the epipelagic chaetognath fauna in the Japan Sea in each season for a 31-year period and revealed that the dominant species was *M. minima*, followed by *F. enflata* and *Z. nagae*. The dominant species in the Inland Sea of Japan and the inner area of Tokyo Bay is *A. crassa* followed by *F. enflata* and *A. neglecta* (Murakami 1958), indicating that *Z. nagae* is not dominant in semi-enclosed, eutrophic waters.

Spatial distribution

The present results on the population mean depths of the four dominant species at Stn 3 in Tosa Bay are 32–111 m (mean 59 m) in *Z. nagae*, 28–55 m (39 m) in *F. enflata*, 22–31 m (26 m) in *A. regularis*, and 38–100 m (72 m) in *S. pacifica*. Nagasawa & Marumo (1982) calculated the daytime population mean depths of epipelagic chaetognaths in Sagami Bay from samples collected five times from six or eight layers between 0 and 100 m depth with horizontally towed nets. The ranges of the daytime population mean depths in their results were 9–28 m in *Z. nagae*, 16–25 m in *F. enflata*, 16–25 m in *A. regularis*, and 22–62 m in *S. pacifica*. The present results for Tosa Bay are similar to those for Sagami Bay with respect to order of the species-specific population mean depth, i.e. *A. regularis* was the shallowest, followed by *F. enflata*, *Z. nagae*, and *S. pacifica*. However, the population mean depth of each species in Tosa Bay is apparently deeper than in Sagami Bay. In *Z. nagae,* for example, the mean of the population mean depths (59 m) in Tosa Bay is much deeper than the deepest mean depth (28 m) in Sagami Bay. This is probably attributable partly to the difference in the sampled depths between the two bays (0–200 m in Tosa Bay vs. 0–100 m in Sagami Bay) and partly to occurrences with substantial densities below 100 m depth in Tosa Bay in some months, e.g. *Z. nagae* in May and June, and *S. pacifica* in September.

Miyamoto et al. (2012) also studied species-specific vertical distributions of chaetognaths seven times in Sagami Bay and calculated the population mean depths, which they referred to as WMD (weighted mean depth). According to their results in Sagami Bay (Miyamoto et al. 2012: table 1), the ranges of the population mean depths were 11–111 m (mean 46 m) in *Z. nagae*, 9–62 m (33 m) in *F. enflata*, 6–32 m (17 m) in *A. regularis*, and 15–135 m (71 m) in *S. pacifica*. This indicates the depth order of the four species was *A. regularis*<*F. enflata*<*Z. nagae*<*S. pacifica*, which is the same as in the present results from Tosa Bay. The good agreement of the results on species-specific vertical distributions between Sagami Bay and Tosa Bay suggests that the relationship in vertical distributions between the four species is consistent and that niche partitioning related to differences in distribution depth within the epipelagic zone is important in chaetognath species.

Compared to vertical distribution, the present study did not indicate any consistent pattern in horizontal distribution, except for in *Z. nagae*, where the density in the surface layer was usually the highest at Stn 1. The possible reason for this inconsistency is mixing of the bay water by clockwise and counter clockwise tidal currents (Miyamoto et al. 1980). The patchy distribution is also possibly attributable to their horizontal distribution. For example, the extremely variable horizontal distribution pattern of *Serratosagitta pacifica*, which was extremely abundant only at Stn 3 in June and November, in contrast to having an almost uniform distribution in most of the other months, would indicate patchy distribution in the former months.

Relationships with environmental variables

The statistical test on the present data, excluding data from layers deeper than 50 m, revealed several significant correlations between chaetognath population density and environmental variables. These correlations are attributable primarily to their seasonal variations. Positive correlations of *F. enflata* and *A. regularis* with temperature are apparently due to their high densities during the warm months, and the negative correlation in *S. pacifica* is due to its higher abundances during the colder months. Correlations of these species with salinity, which were reverse to those with temperature, are explained by the strongly negatively correlation between the temperature and salinity ($r=-7966$, $p<0.001$), i.e. low salinities occurred during the summer months. However, this does not necessarily mean that salinity is a determinant of their seasonal variations because it is unlikely that *F. enflata* and *A. regularis*, which are abundant even in the slope waters in summer or autumn (Marumo & Nagasawa 1973, Miyamoto et al. 2012), prefer low salinities.

The significant positive correlation of *Zonosagitta nagae* with chlorophyll concentration is probably explained by temporal coincidence between the periods of high population density of *Z. nagae* and the spring bloom of phytoplankton. Although this does not mean there is a direct relationship in terms of the food chain between chaetognaths and phytoplankton, population increase during the spring bloom would be advantageous for chaetognaths because their prey, such as copepods, also increase in numbers. The densities of *F. enflata* and *A. regularis*, which had similar patterns of seasonal variations, were negatively correlated with chlorophyll concentration, but the correlation coefficient was significant only in *A. regularis*. The difference between them is probably due to the difference in their spatial distributions. The density of *F. enflata* in the top 50 m was generally highest at Stn 1, while the chlorophyll fluorescence at 5 m depth was also generally highest at Stn 1. The population density of *A. regularis* was generally lower at Stn 1. Furthermore, chlorophyll concentration was generally higher in the 25–50 m layer than in the 0–25 m layer, while higher population densities in the 0–25 m layer than in the 25–50 m layer were more often observed in *A. regularis*. Therefore, the spatial distribution of *A. regularis*, in addition to the seasonal distribution, is considered to have contributed to the significant negative correlation with chlorophyll concentration.

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References

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, Kapp H, Pierrot-Bults AC (1991) Introduction and relationships of the group. In Biology of Chaetognath (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 1–4

Cheney J (1985) Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic—II. Deep-sea Res A 32: 1061–1075.

Coston-Clements L, Waggett RJ, Tester PA (2009) Chaetognaths of the United States South Atlantic Bight: Distribution, abundance and potential interactions with newly spawned larval fish. J Exp Mar Biol Ecol 373: 111–123.

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.

Hardy A (1956) The Open Sea. Its Natural History: Part I, The World of Plankton. Collins Clear-Type Press, London, 335 pp.

Hirota Y, Ichikawa T (2012) Relationship between underwater rising and primary-secondry production of phyto-zooplankton in summer in Tosa Bay, Japan. Fisheries biology and oceanography in the Kuroshio 13: 65–73. (in Japanese with English abstract)

Hirota Y, Ichikawa T, Morimoto H, Sakamoto H (2002) Temporal increase of phytoplankton in summer in Tosa Bay. Fisheries Biology and Oceanography in the Kuroshio 3: 35–46. (in Japanese with English abstract)

Ichikawa T, Hirota Y (2004) Seasonal changes of primary productivity in Tosa Bay, Japan. Oceanogr Jpn 13: 259–269. (in Japanese with English abstract)

Itoh H, Mizushima T, Kubota T (2006) Seasonal occurrence of chaetognaths off Miho Key, Suruga Bay, central Japan in addition to seasonal succession of zooplankton assemblage in inner part of Suruga Bay. J School Mar Sci Technol Tokai Univ 4: 9–19. (in Japanese with English abstract)

Kitou M (1967) *Yamushi kou* [Order Chaetognatha]. In: *Nihon Kaiyou* Plankton *Zukan* [Illustration Book of Marine Plankton in Japan] Vol. 5 (ed Marumo R). Soyo-sha, Tokyo, pp. 40–51. (in Japanese)

Kitou M (1974) *Môgaku rui* [Chaetognatha]. In: *Kaiyô Puranku-*

ton [Marine Plankton] (ed Marumo R). Tokyo University 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.

Kuroda K, Kotori M, Nagai N, Yamaguchi A, Miyamoto H, Noblezada MP (2012) Summary review on the fauna and the distributional ecology of pelagic Chaetognatha in the marginal seas of the North Pacific, especially around Japan. Bull Plankton Soc Jpn 59: 88–94. (in Japanese with English abstract)

Kuroda K, Nagai N (2012) Review on the fauna and the distributional ecology of pelagic chaetognaths in the southern seas of Japan. Bull Plankton Soc Jpn 59: 102–109. (in Japanese with English abstract)

Marumo R, Nagasawa S (1973) Pelagic chaetognaths in Sagami Bay and Suruga Bay, Central Japan. J Oceanogr 29: 267–275.

Miyamoto H, Nishida S, Kuroda K, Tanaka Y (2012) Vertical distribution and seasonal variation of pelagic chaetognaths in Sagami Bay, central Japan. Plankton Benthos Res 7: 51–54.

Miyamoto K, Sakamoto H, Momota M (1980) Oceanographical structure in the Tosa Bay—1. on the tidal current. Bull Nansei Reg Fish Res Lab 12: 115–124. (in Japanese with English abstract)

Motoda S (1959) Devices of simple plankton apparatus. Mem Fac Fish Hokkaido Univ 7: 74–94.

Murakami A (1958) The occurrence of planktonic chaetognaths in the bay and inland sea regions. (1) On the occurring conditions in Tokyo Bay, and the central and western parts of Seto-Inland Sea. Bull Naikai Reg Fish Res Lab 11: 357–384. (in Japanese with English summary)

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.

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

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)

Nishibe Y, Hirota Y, Ueda H (2009) Community structure and vertical distribution of oncaeid copepods in Tosa bay, southern Japan. J Mar Biol Ass UK 89: 491–498.

Ohnishi T, Kuroda K, Ueda H (2013) Second record of *Eukrohnia kitoui* (Chaetognatha) with notes on morphological differences from the closely related *E. calliops*. Plankton Benthos Res 8: 191–194.

Stone JH (1965) The Chaetognatha community of the Agulhas Current: its structure and related properties. Ecol Monogr 39: 433–563.

Terazaki M (1997) Phylum Chaetognatha. In: An Illustrated Guide to Marine Plankton in Japan (eds Chihara M, Murano M). Tokai University Press, Tokyo, pp. 1271–1289. (in Japanese)

Tse P, Hui SY, Wong CK (2007) Species composition and seasonal abundance of Chaetognatha in the subtropical coastal waters of Hong Kong. Est Coast Shelf Sci 73: 290–298.

Ueda H (2013) New messenger-operated opening/closing plankton net and new double release mechanism designed for vertical haul. Bull Plankton Soc Japan 60: 14–17. (in Japanese with English abstract)

Villenas F, Palma S, Soto D (2009) Chaetognath spatial distribution and how egg-carrying affects the vertical distribution of *Sagitta tasmanica* off southern Chile. Sci Mar 73: 29–38.