Latitudinal distribution of chaetognaths in winter along the 137°E meridian in the Philippine Sea

NAOKI NAGAI1,*, KAZUAKI TADOKORO2, KAZUNORI KURODA3 & TAKASHIGE SUGIMOTO4

1 Okinawa Meteorological Observatory, Hikawa, 1–15–15, Naha, Okinawa 900–8517, Japan
2 Tohoku National Fisheries Research Institute, Oceanography Division, Niihamacho, 3–27–5, Shiogama, Miyagi 985–0001, Japan
3 3–6–1–1009, Akitsu Narashino, Chiba 275–0025, Japan
4 Institute of Oceanic Research and Development, Tokai University, Orido 3–20–1, Shimizu-ku, Shizuoka 424–8610, Japan

Received 20 March 2015; Accepted 28 May 2015

Abstract: Latitudinal distributions of pelagic chaetognaths from 3–34°N along the 137°E meridian in the Philippine Sea in winter from 1967 to 1995 were studied using the data of oceanographic observations by the Japan Meteorological Agency. Zooplankton was collected at almost every latitudinal degree in every winter (mid-January to early-February) by vertical hauls of a 0.33-mm mesh NORPAC net from 150-m depth. Twenty-six chaetognath species, including four mesopelagic species, were recorded. Flaccisagitta enflata was most abundant, comprising 25%, on average, of the chaetognath community, followed by Serratosagitta pacifica and Pterosagitta draco. The community structure was analyzed according to the following five areas along the survey line: Japan coast area (JC), Kuroshio Current area (KC), subtropical area (ST), North Pacific Equatorial Current area (NEC), and North Pacific Equatorial Counter Current area (NECC). The dominant species were S. pacifica and Mesosagitta minima in JC, Pseudosagitta lyra and Pt. draco in KC and ST, and F. enflata in NEC and NECC. The cluster analysis revealed that the community was generally more similar among the samples from the same area than those from different areas except for KC and ST, which were not separated into different cluster groups. This suggests that the chaetognath communities are location-specific. Multiple comparisons of the mean densities of 17 common species among these areas revealed six distribution types, i.e. JC type, JC-KC type, KC-ST type, NEC-NECC type, NECC types, and bimodal type. Possible mechanisms determining the distribution types, especially the bimodal distribution, are discussed in terms of environmental factors.

Key words: community structure, epipelagic chaetognaths, latitudinal distribution, Philippine Sea, 137°E meridian

Introduction

Since 1967, oceanographic observations for the CSK project (Co-operative Study of Kuroshio) on board the R/V Ryofu Maru of the Japan Meteorological Agency (JMA) have been carried out every winter along the 137°E meridian in the Philippine Sea, from the Cape of Daio of the Kii Peninsula in Japan at 34°N to the southernmost station near the New Guinea Islands at 3°N (Masuzawa 1967a, 1967b). This survey line is situated near the longitudinal center of the Philippine Sea. We call this line “the Masuzawa Line” after Dr. Jotaro Masuzawa, the late Japanese physical oceanographer of the JMA, who supervised this project. The JMA has reported the chaetognath data of this routine survey in its annual observation reports (Japan Meteorological Agency 1970–1994, and unpublished reports).

The phylum Chaetognatha comprises 115 species (Bieri 1991) and plays an important role in marine ecosystems, especially as carnivores of secondary producers. Thomson (1947) summarized previous studies on chaetognaths in the Pacific Ocean until the 1940s. Bieri (1959) carried out an extensive study on chaetognaths in the Pacific and subarctic waters for the first time, and made a major contribution to synoptic knowledge about the distribution and ecology of chaetognaths in the Pacific, including the Philippine Sea. Tokioka (1959) showed several examples of distribution patterns of chaetognaths in the Pacific Ocean. Distributions of chaetognaths in the Philippine Sea were also studied by Kawarada et al. (1968), Kitou (1974), and Kawashima & Nagai (1990).

The surface water of the subtropical gyre in the Philippine Sea, excluding the coastal water near the Japanese
Islands, is covered wholly by western North Pacific Central Water (Sverdrup et al. 1942). The Philippine Sea along the Masuzawa Line is divided into the following five areas (Nagai 2004) according to the directions of the water flow estimated from geopotential dynamic height: the Japan Coast area (JC), the Kuroshio Current area (KC), the subtropical area (ST), the North Pacific Equatorial Current area (NEC) and the North Pacific Equatorial Counter Current area (NECC) (Fig. 1, left). The oceanographic structures along the Masuzawa Line according to Masuzawa & Hasunuma (1977) are as follows: KC is characterized by the Kuroshio Current, which originates from NEC and runs eastwards as a western intensification boundary current with the strong Kuroshio Front between the western North Pacific Central Water and the coastal waters in the East China Sea and south of Japan. The eastward Subtropical Counter Current develops in winter around the Tropic of Cancer (22–25°N) in ST. The Subtropical Front is formed at the surface in winter along the northern boundary of the NEC (Uda 1966). The boundaries of these areas showed considerable interannual fluctuations during the study period (Fig. 1, right). The water of the gigantic NEC flows westwards between 10 and 20°N with a velocity of about 0.5–2.0 knots, driven by the semi-permanent Northeast Trade Wind (Uda 1966) and the water in the NECC flows eastwards from 8 to 3°N as its countercurrent (JMA, unpublished data).

Distributional patterns of the zooplankton generally exhibit close relationships to those of water masses (Fager & McGowan 1963). It is well known that the subtropical and tropical plankton communities display high diversity and low biomass (Hattori & Motoda 1983). Kitou (1974), who summarized the distribution of pelagic chaetognaths in the Philippine Sea, classified 18 epipelagic species into four groups. Kawashima & Nagai (1990) also described latitudinal distribution of chaetognaths along the Masuzawa Line from 1976 to 1988, and grouped the species into four types. However, statistical analyses has never been done on the species-specific distribution pattern of chaetognaths in the Philippine Sea. The present study analyzes the latitudinal distribution of chaetognaths among the five areas along the Masuzawa Line using the long-term data from 1967 to 1995, to show more precise general distribution patterns of the species and classify them statistically, and discusses the factors causing the distribution patterns.

Materials and Methods

The data used in the present study are archived in the annual observation reports of JMA, of which the data from 1967 to 1992 are published (Japan Meteorological Agency 1970–1994) and those from 1993 to 1995 are in unpublished reports. These data were produced by the following methodologies. Oceanographic observation and plankton sampling were done during winter (mid-January to early-February) on the Masuzawa Line (Fig. 1, Table 1) using the
R/V *Ryofu Maru* of JMA. Zooplankton samples in each year were collected at 24–33 stations, which were set at almost every latitudinal degree (Table 1), by vertical hauls with a NORPAC net (mouth diameter 45 cm, mesh size 0.33 mm) from 150 m depth to the surface. The data in 1971 and 1976 are absent because the routine observation was not made in 1971 due to reconstruction of the research vessel and the samples were lost due to an accident during transport in 1976. Those in 1978 and 1979 were only seven as the other samples are missing.

Zooplankton wet weight (ZWW) was measured after dewatering the samples following the methodology for CSK (Basic Study Group for Kuroshio Oceanography 1965). Seven researchers in total were in charge of chaetognath identification and enumeration (Table 1). Chaetognaths in the whole samples or a 1/2–1/4 subsample, which was divided using a Folsom or Motoda plankton sample splitter, were identified to the species level following Kitou (1967), except for those which could not be identified due to damage or being of a too-early developmental stage, and counted under a microscope. Samples were usually examined within a year after sampling. The archived data of chaetognath densities were rounded to integral numbers in 10-m$^3$ seawater, in which the water volume filtered through the net was calculated by a flowmeter equipped within the mouth of each net. When the density was $<0.5\times10^{-3}$ ind. m$^{-3}$, which was recorded as “+” in the reports, the density 0.5–$10^{-3}$ ind. m$^{-3}$ was used for the present analyses.

From 1967 to 1992, water temperature (WT) and salinity (SAL) were measured at 0, 10, 20, 30, 50, 75, 100, 125, 150, and 200 m depths at each station, using Nansen bottles with a reversing thermometer and a salinometer. Those from 1988 to 1995 were measured by a CTD equipped with a Niskin bottle. Chlorophyll-$a$ (Chl-$a$) measurement was carried out from 1971 to 1995 in a 200-mL aliquot of each water sample using a fluorometer (Japan Meteorological Agency 1970a). Depth-integrated average values of these environmental variables from 0 to 150 m depth were calculated as:

$$\sum((V_i + V_{i+1}) \times D_i / 2) / 150,$$

where $V_i$ is the value at the sampling depth $i$ and $D_i$ is the distance (m) between depths $i$ and $i+1$; henceforth the values of the variables at each station are represented by the integrated averages from 0 to 150 m depth. The mean WT and SAL at which each species occurred were calculated as:

$$\sum(N_i \times V_i) / \sum N_i,$$

where $N_i$ and $V_i$ are the population density and the value of WT or SAL, respectively, of the sample $i$. Mixed layer depth (MLD) was defined as the shallowest depth where the density difference by 10 dbar was $>0.125\sigma_r$ using the data of WT and SAL from 0 to 200 m depths. Stratification degree (STD) was defined as the differences of density between 0 and 150 m depths.

The rank of the species’ contribution to chaetognath community structure, which is called the “contribution rank index” (CRI) in this paper, was calculated by multiplying two different ranks, i.e. the rank of the mean population density and the rank of the percent occurrence (=the percent ratio of the number of samples in which they occurred to the total number of samples examined). This index is analogous to Pitcher’s (1981) “combination rank index”. A multiple comparison to test significant differences in the mean densities of chaetognath species among the five areas was made by Tukey’s post-hoc test using the computer software SPSS® ver. 11. To analyze similarities in the chaetognath communities among the stations and of the distribution pattern among the species, cluster analyses

The Latitudinal distribution of chaetognaths

### Table 1. Sampling date, the number of samples and names of the scientists giving species identities for chaetognath samples collected on board the Ryofu Maru along the 137°E meridian (Masuzawa Line) from 1967 to 1995.

| Year | Date   | Scientist(s)                  | No. of Samples |
|------|--------|-------------------------------|----------------|
| 1967 | Jan.12–22 | K. Furuhashi                  | 32             |
| 1968 | Jan.13–24 | M. Kitou                      | 27             |
| 1969 | Jan.15–25 | M. Kitou                      | 33             |
| 1970 | Jan.17–27 | M. Kitou                      | 24             |
| 1971 | no observation |                          | 0              |
| 1972 | Jan.14–25 | M. Kitou                      | 32             |
| 1973 | Jan.14–24 | M. Kitou                      | 33             |
| 1974 | Jan.16–26 | K. Kuroda                     | 31             |
| 1975 | Jan.16–27 | K. Kuroda                     | 27             |
| 1976 | no data |                              | 0              |
| 1977 | Jan.15–26 | K. Furuhashi & K. Kuroda     | 33             |
| 1978 | Jan.15–24 | K. Furuhashi                  | 7              |
| 1979 | Jan.19–29 | K. Furuhashi                  | 7              |
| 1980 | Jan.17–27 | M. Matsuzaki & K. Kuroda     | 26             |
| 1981 | Jan.21–31 | M. Matsuzaki                  | 33             |
| 1982 | Jan.20–30 | M. Imai & K. Kuroda          | 33             |
| 1983 | Jan.19–29 | M. Imai                       | 31             |
| 1984 | Jan.20–31 | K. Furuhashi                  | 33             |
| 1985 | Jan.19–29 | K. Furuhashi                  | 33             |
| 1986 | Jan.19–30 | K. Kawashima                  | 33             |
| 1987 | Jan.15–26 | N. Nagai                     | 33             |
| 1988 | Jan.17–29 | N. Nagai                     | 33             |
| 1989 | Jan.20–29 | K. Kawashima                  | 33             |
| 1990 | Jan.21–Feb.1 | N. Nagai                   | 33             |
| 1991 | Jan.19–30 | N. Nagai                     | 33             |
| 1992 | Jan.20–Feb.2 | H. Kamiya & K. Kuroda     | 31             |
| 1993 | Jan.20–Feb.2 | H. Kamiya & K. Kuroda     | 33             |
| 1994 | Jan.20–31 | H. Kamiya & K. Kuroda        | 31             |
| 1995 | Jan.21–Feb.11 | N. Nagai                 | 33             |

| total | 801 |
were made on a Bray-Curtis similarity index calculated from the log-transformed \[ \log (X+1) \] data of chaetognath density using the Primer® ver. 5 package.

**Results**

The “mean” value of each environmental variable at each station used here represents an arithmetic mean of the data from 1967 to 1995. The names of the five areas noted above are abbreviated as shown in Fig. 1.

**Environmental and biological variables**

*Water temperature (WT)*

The mean WT increased southwards from 34 to 15°N and then decreased once in the NECC (between 5 and 10°N) with the minimum at 7°N (Fig. 2A). The highest mean WT (26.4°C) was recorded at 14°N in the NEC and the lowest (16.2°C) in the JC. The order of the mean WT in the five areas was NEC > NECC > ST > KC > JC. Interannual variations were larger between 5 and 7°N, in the northern part of the NECC (Fig. 1), than at higher and lower latitudes.

*Salinity (SAL)*

The highest SAL in each year was found at 21–23°N in the ST or 3–4°N in the NECC, but the mean SAL was higher in the NECC than in the ST on average (Fig. 2B). The mean SALs between 5 and 14°N in the southern NEC and NECC were remarkably lower than in the neighboring areas, with the lowest value at 10°N. Those in the JC were generally the second lowest. Interannual variations of SAL were largest at 3–5°N in the NECC, followed by those at 11–13°N in the NEC.

*Mixed layer depth (MLD)*

The mean MLD exhibited its maximum value (170 m depth) at 30°N in the KC and the minimum (27 m depth) at 3°N in the NECC, with the former being 6.3 times deeper than the latter (Fig. 2C). The mean MLDs in the five areas became shallower southwards from KC to NECC.

*Stratification degree (STD)*

The latitudinal distribution of the mean STD showed the opposite pattern to that of the mean MLD, i.e., stratification became stronger northwards, being weakest (0.11 kg m\(^{-3}\)) at 30°N in the KC and strongest (4.03 kg m\(^{-3}\)) at 7°N in the NECC (Fig. 2D).

*Chlorophyll-a (Chl-a)*

The mean Chl-a was highest (0.37 μg L\(^{-1}\)) at 34°N in the JC, decreasing gradually southwards with its lowest value (0.11 μg L\(^{-1}\)) at 12°N in the NEC, then increasing into the NECC, where the values were almost at the same level as those at around 25°N in the ST (Fig. 2E). Highest to lowest mean Chl-a in the five areas was in the order of JC > KC > ST > NECC > NEC.

*Zooplankton wet weight (ZWW)*

The latitudinal distribution of the mean ZWW exhibited a similar pattern to that of Chl-a (Fig. 2F). The greatest

---

Fig. 2. Latitudinal variations of the mean values of water temperature (WT), salinity (SAL), surface mixed layer depth (MLD), stratification degree (STD), chlorophyll-a (Chl-a), zooplankton wet weight (ZWW), chaetognath abundance (CH-A), and chaetognath species number (CH-S) in the 0–150 m layer along the Masuzawa Line (137°E meridian) from 1967 to 1995. Vertical line indicates standard deviation.
ZWW in each year was found in the NECC or JC, and the lowest occurred between 10° and 15°N in the southern NEC and always at or near the station with the lowest Chl-a. Interannual variations of the mean ZWW were larger in the JC and NECC, especially at 3°N where the maximum weight in a single sample (238 mg m\(^{-3}\)) was recorded.

**Chaetognath abundance and species number**

**Chaetognath abundance (CH-A)**
The highest CH-A in each year was found in the JC or NECC, but the mean CH-As were obviously higher in the latter area, with the highest value of 8.12 \(\times 10^{-1}\) ind. m\(^{-3}\) at 5°N (Fig. 2G). The lowest mean CH-A of 1.18 \(\times 10^{-1}\) ind. m\(^{-3}\) was observed at 12°N in the southern NEC. The order of the mean CH-As was NECC > KC > JC > ST > NEC.

**Chaetognath species number (CH-S)**
The mean CH-S at each station was similar around 10 species, in the JC, KC, and ST (Fig. 2H). As with Chl-a and ZWW, it decreased in the NEC, where the minimum value of 5.7 species was at 14°N, and then increased into the NECC, with the maximum value of 11.3 species at 5°N. The interannual variation of the mean CH-S was almost the same throughout the Masuzawa Line regardless of the maximum mean CH-S value being twice that of the minimum.

**Community structure of chaetognaths**

Twenty six species of pelagic chaetognaths were identified in this study (Table 2). According to the global geographic distributions of chaetognaths reported by Pierrot-Bults & Nair (1991), 11 species are referred to as cosmopolitan, nine as Indo-Pacific, and six as Pacific. According to Kuroda et al. (2012), 22 are epipelagic and 4 are mesopelagic. The most important species according to the CRI calculated from all samples was *Flaccisagitta enflata* (Grassi, 1881), which comprised 25.3% of all specimens (excluding unidentified specimens) and occurred in almost all (98.1%) samples. The second was *Serratosagitta*

| Species type | m±SD | % comp. | max | % occ. | CRI |
|--------------|------|---------|-----|--------|-----|
| Aidanosagitta bedfordii | P | 0.0±0.1 | 0.0 | 2 | 0.6 | 22 |
| A. crassa f. naikaiensis | P | 0.0±0.0 | 0.0 | 1 | 0.2 | 23 |
| A. neglecta | IP | 0.8±1.6 | 2.4 | 16 | 43.7 | 11 |
| A. oceania | IP | 0.0±0.3 | 0.1 | 6 | 1.4 | 21 |
| A. regularis | IP | 2.1±3.1 | 6.7 | 36 | 77.3 | 5 |
| A. tropica | IP | 0.0±0.0 | 0.0 | 1 | 0.1 | 24 |
| Eukrohnia hamata* | C | 0.0±0.0 | 0.0 | 1 | 0.1 | 24 |
| Ferosagitta ferox | IP | 0.3±0.6 | 0.9 | 4 | 27.1 | 16 |
| Fe. robusta | IP | 0.7±1.2 | 2.0 | 11 | 48.2 | 10 |
| Fe. tokioi | P | 0.0±0.1 | 0.0 | 2 | 0.1 | 24 |
| Flaccisagitta enflata | C | 8.0±9.4 | 25.3 | 72 | 98.1 | 1 |
| Fl. hexaptera | C | 1.3±1.2 | 4.1 | 10 | 80.5 | 5 |
| Krohnitta pacifica | C | 0.7±2.1 | 2.0 | 35 | 32.5 | 13 |
| K. subtilis | C | 0.9±1.2 | 2.7 | 8 | 61.7 | 8 |
| Mesosagitta decipiens* | C | 0.3±0.7 | 1.0 | 8 | 28.1 | 14 |
| M. minima | C | 2.2±4.7 | 6.9 | 66 | 60.4 | 7 |
| M. neodecipiens* | P | 0.1±0.3 | 0.2 | 3 | 9.1 | 17 |
| Pseudosagitta lyra | C | 2.8±4.4 | 8.9 | 34 | 70.2 | 4 |
| Pterosagitta draco | C | 3.5±4.4 | 11.1 | 43 | 88.1 | 3 |
| Sagitta bipunctata | C | 0.6±1.1 | 2.0 | 10 | 44.2 | 11 |
| Serratosagitta pacifica | IP | 5.4±8.4 | 17.0 | 104 | 88.9 | 2 |
| Se. pseudoserratodontata | P | 1.1±1.8 | 3.5 | 14 | 51.2 | 9 |
| Solidosagitta zetesios* | C | 0.1±0.2 | 0.2 | 2 | 8.0 | 18 |
| Zonosagitta bedoti | IP | 0.5±2.0 | 1.6 | 26 | 16.1 | 15 |
| Z. nagae | P | 0.2±2.1 | 0.7 | 48 | 6.0 | 18 |
| Z. pulchra | IP | 0.1±0.6 | 0.3 | 8 | 7.1 | 18 |
Table 3. Top eight chaetognath species according to the contribution rank index (CRI) in the five areas in winter from 1967 to 1995, with mean density (m±SD), percent composition vs. total chaetognaths (excluding unidentified specimens) (% comp.), maximum density (max, \( \times 10^{-1} \) ind. m\(^{-3} \)), and percent occurrence (% occ.). The number of samples examined appears in parentheses. See Fig. 1 for the locations and abbreviations of the five areas, and Table 2 for further explanations.

| CRI | species                        | m±SD   | % comp. | max   | % occ. |
|-----|--------------------------------|--------|---------|-------|--------|
| JC  | Serratosagitta pacifica        | 11.4±17.1 | 32.5 | 104  | 100    |
|     | Mesosagitta minima             | 8.3±12.7  | 23.7 | 66   | 100    |
|     | Flaccisagitta enflata          | 3.8±3.4   | 10.9 | 16   | 91.8   |
|     | Zonosagitta nagae              | 3.5±7.7   | 9.9  | 48   | 83.7   |
|     | Pterosagitta draco             | 1.5±1.2   | 4.2  | 5    | 85.7   |
|     | Aidanasagitta regularis        | 1.9±2.7   | 5.4  | 18   | 77.6   |
|     | Pseudosagitta lyra             | 0.7±0.8   | 2.0  | 4    | 67.3   |
|     | Se. pseudoserratodentata       | 0.7±0.9   | 1.9  | 5    | 59.2   |
| KC  | Pseudosagitta lyra             | 7.2±5.1   | 17.8 | 30   | 100    |
|     | Pterosagitta draco             | 5.5±3.4   | 13.6 | 20   | 100    |
|     | Serratosagitta pacifica        | 8.6±6.6   | 21.3 | 34   | 97.6   |
|     | Flaccisagitta enflata          | 4.7±4.3   | 11.5 | 25   | 99.2   |
|     | Mesosagitta minima             | 3.7±3.0   | 9.2  | 15   | 96.7   |
|     | Se. pseudoserratodentata       | 2.8±2.4   | 7.0  | 14   | 91.9   |
|     | Krohnitta subilis              | 2.1±1.6   | 5.1  | 8    | 88.6   |
|     | Fl. hexaperta                  | 1.6±1.7   | 3.4  | 10   | 84.6   |
|     | Aidanasagitta regularis        | 1.8±2.0   | 4.5  | 14   | 82.1   |
| ST  | Flaccisagitta enflata          | 4.1±3.6   | 14.8 | 23   | 96.4   |
|     | Pseudosagitta lyra             | 5.0±5.4   | 18.0 | 34   | 89.3   |
|     | Pterosagitta draco             | 4.2±3.6   | 15.0 | 19   | 96.0   |
|     | Serratosagitta pacifica        | 3.5±4.8   | 12.5 | 36   | 90.2   |
|     | Se. pseudoserratodentata       | 2.0±2.1   | 7.2  | 12   | 83.9   |
|     | Fl. hexaperta                  | 1.4±1.2   | 5.2  | 8    | 85.7   |
|     | Mesosagitta minima             | 2.2±3.5   | 8.1  | 21   | 71.9   |
|     | Aidanasagitta regularis        | 1.5±1.6   | 5.5  | 8    | 77.7   |
| NEC | Flaccisagitta enflata          | 8.1±6.5   | 44.5 | 46   | 99.3   |
|     | Serratosagitta pacifica        | 1.6±2.1   | 8.9  | 16   | 78.8   |
|     | Aidanasagitta regularis        | 1.7±2.8   | 9.6  | 19   | 69.2   |
|     | Fl. hexaperta                  | 1.0±0.9   | 5.5  | 5    | 78.0   |
|     | Pterosagitta draco             | 1.2±2.0   | 6.5  | 26   | 73.6   |
|     | Ferosagitta robusta            | 0.9±1.4   | 4.8  | 11   | 59.0   |
|     | A. neglecta                   | 0.7±1.5   | 4.1  | 11   | 48.4   |
|     | Pseudosagitta lyra             | 0.5±0.7   | 2.8  | 5    | 51.6   |
| NECC| Flaccisagitta enflata          | 19.0±15.5 | 34.0 | 72   | 100    |
|     | Serratosagitta pacifica        | 10.9±11.9 | 19.5 | 85   | 95.5   |
|     | Pterosagitta draco             | 6.1±7.1   | 10.9 | 43   | 94.7   |
|     | Aidanasagitta regularis        | 4.3±5.1   | 7.7  | 36   | 88.6   |
|     | Fl. hexaperta                  | 1.6±1.3   | 2.8  | 6    | 83.3   |
|     | Krohnitta pacifica             | 2.6±4.5   | 4.6  | 35   | 68.9   |
|     | A. neglecta                   | 2.3±2.9   | 4.0  | 16   | 75.8   |
|     | Zonosagitta beboti             | 2.5±4.4   | 3.9  | 26   | 55.3   |
Latitudinal distribution of chaetognaths

Jacinta pacifica (Tokioka, 1940) (percent composition 17.0%, occurrence frequency 88.9%), followed by Pterosagitta draco (Krohn, 1853) (11.1%, 88.1%) and Pseudosagitta lyra (Krohn, 1853) (8.9%, 70.2%). These four species numerically comprised, in total, 62.4% of the chaetognath community.

To show the differences in the chaetognath community among the five areas, the eight most important species, evaluated by CRI based on all the data in each area, are listed in Table 3. The usual community structure in each area is summarized as follows.

JC was characterized by a high abundance of Se. pacifica (percent composition 32.5%) and Mesosagitta minima (Grassi, 1881) (23.7%) compared to ≤21.3% and ≤9.2%, respectively, in the other areas, and by the occurrence of Zonosagitta nagae (Alvariño, 1967) at the fourth rank, in contrast to its absence or its rarity in the other areas.

KC and ST had similar community structures to each other and were characterized by high proportions of Ps. lyra (17.5% in KC and 18.0% in ST) and Pt. draco (13.6% in KC and 15.0% in ST) in contrast to their low relative percentages (≤2.8% and <10.9%, respectively) in other areas. However, the communities differed between the KC and ST by a markedly higher percent composition of Se. pacifica in the KC (21.3%) than in the ST (12.5%).

NEC and NECC were similar to each other and different from the other areas because of a high dominance of Fl. enflata, for which the percent compositions in the two areas were 44.5 and 34.0%, respectively, much higher than in the other three areas (10.9–14.8%). The differences in the eight top-ranked species between the NEC and NECC were seen in the presences of Ferosagitta robusta (Doncaster, 1902) and Ps. lyra in the NEC but not in the NECC, and for Krohnitta pacifica (Aida, 1897) and Z. beboti (Beranek, 1895) in the NECC but not in the NEC.

To evaluate to what degree the chaetognath communities differed among the five areas, a cluster analysis was performed on the station-specific data. For simplification of the illustration, 223 samples representing the five areas were analyzed. Two samples for each area were chosen, being those at one third and two thirds of the North-South extent of each area in each year. When the number of stations in the area was <4, a single sample, that furthest from the northern and southern boundaries, was used. The analysis found that the samples divided into two major groups (G1 and G2) with seven other outlying samples at the 44% similarity level (Fig. 3). Most of the samples in G1 were classified into four groups: G1a, G1b, G1c, and G1d, at the 58% similarity level. Consequently, the major parts of the samples were largely divided into five groups (the four subgroups of G1 and group G2), to which most of the samples belonged. The distribution of the samples among the five areas, presented at the bottom of Fig. 3, revealed that most samples collected from the same area belonged to the same group, i.e. those from the JC, KC, ST, NEC, and NECC belonged to G1c, G1d, G1d, G2, and G1a, respectively. The result that samples from the KC and ST belonged to the same group G1d and were not clearly subdivided within the group indicates that the chaetognath community was very similar between the two areas. G1b also consisted mostly of the two areas NEC and NECC, indicating that the communities in some samples were similar between the two areas. These results suggest that the structure of the chaetognath community along the Matsuzawa Line apparently differed according to the areas defined by the different current systems, except between the KC and ST, which had similar structures according to the “average” communities described in Table 3.

Latitudinal distribution patterns of epipelagic species

Latitudinal distributions of the 17 common epipelagic species using the mean densities at the 33 stations, are shown in Fig. 4. Those of the mean densities in the five areas appear in Fig. 5 to show the statistically significant differences between the areas. Distributions of the five rare species, for which the mean densities were ≤0.1×10⁻¹ ind. m⁻³ and the percent occurrences were ≤6.1% in every area, are presented in Table 4. Based on statistically significant differences in the mean densities between the areas, the following six distribution types were recognized.
Fig. 4. Latitudinal variations of the mean densities of 17 common epipelagic chaetognath species among the sampling stations along the Masuzawa Line (137°E meridian) from 1967 to 1995. Vertical line indicates standard deviation.
JC type:

The JC type is defined by chaetognaths that were largely restricted in occurrence to the JC. *Zonosagitta nagae*, which was predominantly collected from the JC but rarely from other areas, belonged to this type. The rare species *Aidanosagitta crassa f. naikaiensis* (Tokioka, 1939), which is an index species for low-salinity, semi-enclosed waters (Kuroda & Nagai 2012), could belong to this type because only a few specimens were collected, and only once from the northernmost station (34°N) in 1992.

JC-KC type:

The JC-KC type is similar to the JC type but differs by significantly higher densities not only in the JC but also in the KC than in the NEC or NECC. Only one species, *Mesosagitta minima*, belonged to the JC-KC type. The mean density of this species was highest in the JC and gradually decreased to its lowest density at 16°N in the NEC.
where the mean densities were very low (ties were not significantly different from the JC to the ST, (Doncaster, 1902), belonged to these types. Their densities were significantly higher in the NECC than in any other area. Eight of the 17 epipelagic species, i.e. Aidanosagitta ne-doserratodentata, and Aidanosagitta lyra, belonged to this type. Among them, Ps. lyra and Se. pseudoserratodentata exhibited very similar distribution patterns to each other, with very low densities in the tropical areas compared to those in the KC or ST (Fig. 5). In contrast, Sa. bipunctata was more evenly distributed from the JC to the NECC, and K. subtilis showed a significant increase from the NEC to the NECC. This pattern in K. subtilis is also similar to the bimodal type described below.

NEC-NECC and NECC types:
These types are those where the population density was significantly higher in the NEC than in any other area. Eight of the 17 epipelagic species, i.e. Aidanosagitta neglecta (Aida, 1897), A. regularis (Aida, 1897), Ferosagitta ferox (Doncaster, 1902), Fe. robusta, Flaccisagitta enflata, Krohnitta pacifica, Zonosagitta bedoti, and Z. pulchra (Doncaster, 1902), belonged to these types. Their densities were not significantly different from the JC to the ST, where the mean densities were very low (<1.0×10^{-1} ind. m^{-3}) except for A. regularis and Fl. enflata. These NECC and NEC-NECC species could be subdivided into two types according to their densities in the NECC. The pattern of one type was that the density increased gradually from the ST to the NECC, with significant differences between the ST and NEC, and where the densities in both the NECC and NEC were significantly higher than in the JC, KC or ST. Aidanosagitta neglecta, Fe. ferox, Fe. robusta, and Fl. enflata were of this type (the NEC-NECC type). However, their distributions within the NECC were different between Fl. enflata and the other three species; Fl. enflata increased but the other species decreased southward. The other type (the NECC type), consisting of the other four species, A. regularis, K. pacifica, Z. bedoti, and Z. pulchra, had the characteristic that the density was not significantly higher in the NEC than in the northern areas, being significantly higher only in the NECC. Aidanosagitta regularis and Fe. robusta, however, also apparently belonging to this type, had their highest mean densities near the boundary between the NEC and NECC (Fig. 4). Accordingly these two types may be called collectively "the tropical type".

The rare species A. bedfordii (Doncaster, 1902), A. ocea-nia (Grey, 1930), A. tropica (Tokioka, 1942), and Fe. tokiokai (Alvariño, 1967), which were collected restrictedly from the NECC or from both the NEC and NECC (Table 4), are regarded to belong to the tropical type. Ferosagitta tokiokai, which was first described from the South China Sea by Alvariño (1967), was only collected once, with just two specimens found at 5°N in 1993. The present paper is the first published record of this species from the Philippine Sea.

Bimodal type:
The bimodal type is characterized by a bimodal distribution with the minimum in the NEC. The three species Flaccisagitta hexaperta (d’Orbigny, 1834), Pterosagitta draco, and Serratosagitta pacifica were of this type. Ptero-sagitta draco and Se. pacifica exhibited typical distribution patterns of this type, because the decrease in the NEC was very conspicuous (Fig. 5). However, the distribution patterns in the JC between the two species were apparently different with respect to their relative abundances, that is, Pt. draco was significantly less dominant in the KC whereas Se. pacifica occurred at almost the same level. The pattern for Flaccisagitta hexaperta was similar to Pt. draco

| Table 4. The mean density (×10^{-1} ind. m^{-3}) of five rare epipelagic species and four mesopelagic species in the five areas, with the percent occurrence in parentheses. See Fig. 1 for the locations and abbreviations of the five areas. |
|---------------------------------|--------|--------|--------|--------|--------|
| Epipelagic species              | JC     | KC     | ST     | NEC    | NECC   |
| Aidanosagitta bedfordii         | —      | —      | —      | —      | 0.0 (3.8) |
| A. crassa f. naikaiensis        | 0.0 (4.1) | —      | —      | —      | —      |
| A. oceania                      | —      | —      | —      | 0.0 (1.1) | 0.1 (6.1) |
| A. tropica                     | —      | —      | —      | —      | 0.0 (0.8) |
| Ferosagitta tokiokai           | —      | —      | —      | —      | 0.0 (0.8) |
| Mesopelagic species            | —      | —      | —      | —      | —      |
| Eukrohnia hamata               | 0.0 (2.0) | —      | —      | —      | —      |
| Mesosagitta decipiens          | 0.6 (49.0) | 0.3 (29.3) | 0.3 (28.6) | 0.1 (13.9) | 0.7 (47.7) |
| M. neodecipiens                | 0.2 (26.5) | 0.1 (9.8) | —      | 0.0 (3.3) | 0.1 (11.4) |
| Solidosagitta zetesios         | 0.1 (10.2) | 0.2 (21.1) | —      | —      | 0.0 (0.8) |
rather than *Se. pacifica* because it became significantly less dominant in the JC. The decrease in *Fl. hexaptera* relative abundance in the NEC was statistically significant, but not as conspicuous as in *Pt. draco*.

**Comparisons of water temperature (WT) and salinity (SAL) preferences for the 17 epipelagic species**

Since the present data are limited to those collected during the winter seasons, the WT and SAL data are not so useful for evaluating the optimum environments of the species. However, these data can reveal which species occurred at higher/lower WT and/or SAL than others. For comparison, the mean WT and SAL are plotted in a WT-SAL diagram (Fig. 6). In this diagram, *Zonosagitta nagae* of the JC type was located far distant from the other species because of the much lower WT at which it occurred. *Mesosagitta minima* was also distant from the others due to the lower WT. The mean SALs for the other 15 species showed a highly significant negative correlation with the mean WTs (\( r = -0.83, p < 0.01 \)). The mean WTs and SALs of the 15 species differed between the distribution types, i.e., the mean WTs tended to be higher in the order of the NEC-NECC>NECC>bimodal>KC-ST types, and the mean SALs were in the order of the KC-ST>bimodal NEC>NECC types.

**Latitudinal occurrence pattern of mesopelagic species**

Four mesopelagic chaetognaths were observed in the present samples that were collected from the epipelagic layer of 0–150 m depth (Table 4). Since mesopelagic species in the epipelagic layer are generally introduced from the mesopelagic layer (>200 m depth), their percent occurrences should indicate the frequency of upwelling in each area. The most common mesopelagic species, *Mesosagitta decipiens* (Fowler, 1905), occurred much more frequently in the JC (percent occurrence 49.0%) and in the NECC (47.7%) than in the other areas (13.9–29.3%), suggesting frequent coastal upwelling in the JC and coastal/equatorial upwelling in the NECC. However, the occurrence patterns of the other mesopelagic species were somewhat different. *Mesosagitta neodecipiens* (Tokioka, 1959) was most frequently collected in the JC (26.5%) but its occurrence in the NECC (11.4%) was comparatively low, being similar to the KC and ST. *Solidosagitta zetesios* (Fowler, 1905) was apparently different from the above two species due to its high percentage occurrence in the KC (21.1%) and ST (14.3%) but being rare (0.8%) in the NECC, suggesting that some factors other than upwelling caused the high occurrence frequencies in the KC and ST. *Eukrohnia hamata* (Möbius, 1875) was the rarest species in this study and was collected only once at 34°N in 1974.

**Discussion**

**Classification of latitudinal distribution patterns**

Kitou (1974) described the species-specific distribution of epipelagic chaetognaths in the Philippine Sea, mainly south of 20°N during the winter (January to March) of 1968. The sampling stations along the Masuzawa Line in his study covered from 2°S to 28°N, including the NECC, NEC, and ST. He identified 18 epipelagic species and divided them into four groups according to their latitudinal distributions, i.e., widespread common group, subtropical group, tropical group, and tropical neritic group. The species of the KC-ST, NEC-NECC, and NECC types in the present study largely agree with those of his subtropical, tropical, and tropical neritic groups, respectively. The major differences in species classification between the two studies, not including the JC and JC-KC types because JC and KC data were absent in his study, were seen in the widespread common group in his study and the bimodal type in the present study. The widespread common group in his classification consisted of the species of the following four types: the bimodal type (*Flaccisagitta hexaptera*, *Pterosagitta draco* and *Serratosagitta pacifica*), the NEC-NECC type (*Fl. enflata*), the NECC type (*A. regularis*), and the KC-ST type (*Krohniella subtilis* and *Pseudosagitta lyra*). This difference is considered to be a result of the different standards in classifying the distribution patterns. The present classification was done strictly, based on statistically significant differences among the areas, and where the absolute abundances were not given much weight. However, in Kitou’s classification the abundances throughout the study areas seems to have been given more weight than the variation among the areas.

A notable difference between the classification of Kitou (1974) and the present study is also seen in *Mesosagitta*...
minima, which belonged to the JC-KC type in the present study but to the subtropical group in his classification. This is due to the difference in the range of the stations, which were limited to subtropical and tropical areas in his study but stretch from temperate to tropical in the present study. This species has been recorded as a common species, occasionally the dominant species, from temperate waters in the Northwest Pacific, e.g. the Kuroshio Current and mixing zone with the Oyashio Current (Kitou 1974), the Japan Sea (Nagai et al. 2006), and temperate coastal areas of Japan (Nagasawa & Marumo 1982, Itoh et al. 2006, Miyamoto et al. 2012, Ohnishi et al. 2014). Nagasawa & Marumo (1982) reported that M. minima was mostly distributed in water of 14–22°C. These studies indicated that M. minima is a temperate species, and therefore the true distribution pattern of the species should be of the JC-KC type. In spite of this, however, M. minima displayed a somewhat bimodal distribution in the present study, with higher densities in both temperate and tropical areas. Further studies are necessary to clarify the distributional characteristics of this species.

Kawashima & Nagai (1990) also divided chaetognath species along the Masuzawa Line from 0–34°N into the following four groups, according to the latitudinal ranges in which the species were abundant: group 1 from 0–5°N (Aindanosagitta neglecta, A. regularis, Fl. enflata, Zonosagitta pulchra, and Z. bedoti); group 2 north of 20°N (Pseudosagitta lyra, Sagitta bipunctata, Serratosagitta pseudoserratodontata, K. subtilis, and M. minima); group 3 at 34°N (Z. nagae); and group 4 between both 0–5°N and north of 25°N (Se. pacifica and Pt. draco). The six types in the present study agree well with these four groups, but the present study also distinguished the NEC and NECC types, which are contained within group 1, and the JC-ST and KC-ST types, which are contained within group 2, because of the detailed division of the areas along the Masuzawa Line in the present study; the study by Kawashima & Nagai (1990) was based on only eight stations set at five degrees of latitude intervals from 1976 to 1988, and was unable to distinguish the five areas.

Some considerations on the bimodal distribution type

The three species Flaccisagitta hexaperta, Pterosagitta draco and Serratosagitta pacifica, of the bimodal type, exhibited two peaks along the Masuzawa Line with a minimum in the NEC, ranging from 8–17°N usually. Kawashima & Nagai (1990) also found bimodal distributions of Pt. draco and Se. pacifica, with high abundances from 0 to 5°N and north of 20°N. The present results revealed that the mean values of Chl-a and ZWW among the five area were lowest in the NEC, which means the lowest primary and secondary productions occurred in the NEC. Low productivity in tropical areas is generally explained by their oceanographic properties. There is strong stratification, even in winter, in tropical areas due to higher surface water temperatures than in temperate and subtropical areas, and this was also seen in the present results of WT, MLD, and STD. Strong stratification results in a low nutrient concentration and thereby low productivity in the surface water due to limitation of nutrient supply from deeper layers. As a result, population densities of chaetognaths are lower due to a shortage of prey, expressed as ZWW in the present study. This is the most likely reason for the lower population densities of the bimodal type in the NEC compared to in the KC and ST.

The reason that the species of the bimodal type were more abundant in the NECC than in the NEC is probably attributable to upwelling, which supplies nutrients to the epipelagic layer in the NECC. Kawashima & Nagai (1990) also suggested upwelling as the reason for high abundances in the area of 0–5°N, not only for species with a bimodal distribution but also for tropical species. The present results apparently support this hypothesis, with mean WT being markedly lower at around 7°N, the northern boundary zone of the NECC. The mean Chl-a was higher in the NECC than in the NEC, and the most common mesopelagic species (Mesosagitta decipiens) occurred mostly in the NECC. This suggests frequent upwelling events occur there. In conclusion, the latitudinal distribution pattern of chaetognaths in the Philippine Sea is determined predominantly by prey abundance and water temperature.

Acknowledgements

We are grateful to Dr. H. Ueda of Kochi University for guidance and advice on analytical methods for long time observations and planning of this study. We also thank Dr. David Casenove of Tokyo University for critical reading and commenting on the English manuscript. In addition, we would like to thank the scientists of the Oceanography Division, and captains and crews of the Ryofu Maru in JMA for their co-operation.

References

Alvariño A (1967) The Chaetognatha of the NAGA Expedition (1959–1961) in the South China Sea and the Gulf of Thailand. Part.1-Systematics. NAGA REPORT 4(2): 1–197.

Basic Study Group for Kuroshio Oceanography (1965) CSK manual for plankton, chlorophyll, and primary production. pp. 1–4. (in Japanese)

Bieri R (1959) The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol Oceanogr 4: 1–28.

Bieri R (1991) Systematics of Chaetognatha. In: The Biology of Chaetognaths (eds Bone Q, Kapp H, Pierrot-Bults AC). Oxford University Press, Oxford, pp. 122–136.

Fager EW, McGowan JA (1963) Zooplankton species groups in the North Pacific. Science 140: 453–460.

Hattori H, Motoda S (1983) Regional difference in zooplankton communities in the western North Pacific Ocean (CSK Data). Bull Plankton Soc Japan 30: 53–63.
Latitudinal distribution of chaetognaths

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 assemblages in inner part of Suruga Bay. J School Mar Sci Technol Tokai Univ 4: 9–19. (in Japanese with English abstract)

Japan Meteorological Agency (1970–1994) The Results of Marine Meteorological and Oceanographical Observations. 41–84. (in Japanese)

Japan Meteorological Agency (1970a) Kaiyou Kansoku Shishin [Manual of Oceanographic Observation]. pp. 250–254. (in Japanese)

Kawarada Y, Kitou M., Furuhashi K, Sano A (1968) Plankton in the western North Pacific in the winter of 1967 (CSK). Oceanogr Mag 20: 9–29.

Kawashima K, Nagai N (1990) Distribution of planktonic chaetognaths in the western North Pacific. Oceanogr Mag 40: 53–64.

Kitou M (1967) Phylum Chaetognatha. In: The Encyclopedia of Marine Plankton in Japan, Vol. 5: Phyla Mollusca, Chaetognatha, Order Thaliacea etc. (ed Motoda S). Soyosha, Tokyo, pp. 40–51. (in Japanese)

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

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 Japan 59: 102–105. (in Japanese with English abstract)

Kuroda K, Kotori M, Nagai N, Yamaguchi A, Miyamoto H, Noblezada MMP (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 Japan 59: 88–93. (in Japanese with English abstract)

Masuzawa J (1967a) Ryofu Maru’s survey for CSK in January to March. Oceanogr Mag 19: 1–5.

Masuzawa J (1967b) An oceanographic section from Japan to New Guinea at 137°E in January 1967. Oceanogr Mag 19: 95–118.

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.

Nagai N (2004) Middle and long-term variations of marine plankton along JMA’s 137°E hydrographic section. Sokko Jiho 71 (special edition): 17–26. Japan Meteorological Agency. (in Japanese)

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 (1982) Vertical distribution of epipelagic chaetognaths in Suruga Bay, Japan. Bull Plankton Soc Japan 29: 9–23. (in Japanese with English abstract)

Ohnishi T, Ueda H, Kuroda K (2014) Community structure and spatial distribution of chaetognaths in Tosa Bay on the temperate Kuroshio coast of Japan. Plankton Benthos Res 9: 176–187.

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

Pitcher KW (1981) Prey of the steller sea lion, Eumetopias jubatus, in the Gulf of Alaska. Fish Bull 79: 467–472.

Sverdrup HU, Johnson MW, Fleming RH (1942) The oceans, their physics, chemistry and general biology. Prentice-Hall, Eaglewood Cliffs, pp. 1087.

Thomson JM (1947) The chaetognaths of southeastern Australia. Council Sci Ind Res Bull 222 (Division Fish. Report, No.14): 1–43.

Tokioka T (1959) Observations on the taxonomy and distributions of Chaetognatha of the North Pacific. Publ Seto Mar Biol Lab 7: 349–456.

Uda M (1966) Philippine Sea and the waters south of Japan. In: Encyclopedia of Oceanography (ed Fairbridge RW). Reinhold, New York, pp. 705–712.