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Seasonal Variability in Abundance and Composition of Zooplankton in the Vicinity of the Tsushima Straits, Southwestern Japan Sea*

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Abstract

This paper describes the seasonal pattern of the zooplankton community structure in the southwestern Japan Sea. Samples were taken during a series of monthly vertical hauls (0-126 m) with NORPAC nets at an offshore station close to the Tsushima Straits from January to December 1992. Both the total wet weight and individual number of zooplankton peaked in March, June and November. A typical herbivore, Copepoda was the most dominant group and accounted for 50-60% of the total abundance. This group was an important determinant of the seasonal variation pattern of zooplankton abundance. Biomass of the carnivorous group (mainly Cheatognatha and Hydrozoa) was higher from June to November, accounting for 28-36% of the total. The group diversified the trophic structure of the zooplankton community. Prey-predator interactions between Copepoda and Chaetognatha became more clear during the summer-autumn inflow of high temperature and low salinity water masses which indicated the seasonal fluctuations of the Tsushima Current.

Key words : Chaetognatha, Copepoda, prey-predator interaction, seasonal variation, Tsushima Current, zooplankton abundance

Introduction

Theoretical modeling studies on the seasonal cycle of secondary production in planktonic ecosystems require detailed information about the trophic structure of the zooplankton community (DAVIS 1984, 1987). In the Japan Sea, however, there have been few studies on seasonal patterns in the abundance and composition of warm-water zooplankton, since the cooperative observations on the Tsushima Current only were carried out by some agencies for five years from 1953 to 1957 (FISHERIES AGENCY 1958). With regards to zooplankton, most research had concentrated on species composition and seasonal distribution of the major individual groups (FISHERIES AGENCY 1958), and little attention has been

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given to the community structure of zooplankton including all the taxa.

OGAWA and NAKAHARA (1979) reported that Thaliacea was responsible for the spring (April-May) peak of total zooplankton biomass (as settled volume) and Copepoda for the autumn (October-November) peak in coastal waters of the southwestern Japan Sea. They also showed a significant positive correlation between the number of Copepoda and Chaetognatha (*Sagitta* spp.), implying a prey-predator relationship. Copepoda is the principal component of the diet of the primary carnivore, Chaetognatha (e.g. FEIGENBAUM and MARIS 1984). Although the most dominant constituent in the Tsushima Straits and adjacent waters was Copepoda (MORIOKA 1985), its seasonal abundance and species composition may vary with both biotic and abiotic environmental factors.

This paper describes seasonal variations in the numerical abundance, biomass, composition and trophic interrelations of zooplankton throughout the year in the southwestern Japan Sea. This paper also discusses the interrelationship between biological interactions (Copepoda vs. Chaetognatha) and the seasonally changing hydrographic structure of the water column.

Materials and Methods

Samples were taken within the first 10 days of each month from January through to December (for practical reasons December's sampling was carried out on the 30th November) 1992, using the R/V "Kuroshio-Maru" of the Yamaguchi Prefectural Open Sea Fisheries Experimental Station at an offshore station close to the Tsushima Straits (34°38′ N, 130°41′E, Fig. 1). The sampling station is located in the Tsushima Current flowing into the Japan Sea and shows little year-to-year variation in temperature and salinity (OGAWA 1983). The samples were collected by a vertical tow of twin-type NORPAC nets (45 cm mouth diameter, 0.33 mm and 0.10 mm mesh apertures) from near bottom depth (ca. 126 m) to the surface. Each net was equipped with a Rigosha flow-meter on the mouth ring to register the water volume passing through the net. After collection, the samples were preserved in a 10% buffered formalin-seawater solution. At each sampling time, temperature and salinity profiles from the near bottom depth to the surface were recorded with a CTD system (AST 1000, Alec Electronics Co., Ltd.).

In the land laboratory, the 0.33 mm mesh net-samples were sorted under a dissecting microscope into each taxonomic group of animals. Large siphonophores were often broken and thus its data were omitted from the results because of difficulties in quantitatively assessing their abundance. The samples were then split into 1/2 or 1/4 aliquots for sorting smaller zooplankton using a Folsom plankton splitter. After sorting, each taxonomic group was weighed (wet weight) on a top-pan balance, accurate to 0.01 mg. Species analyses were made for Copepoda (copepodids and adults) and Chaetognatha. The 0.10 mm mesh net-samples were split into 1/2 aliquots using a Folsom plankton splitter; one sample for investigating copepod naupliar abundance, and the other for the phytoplankton biomass (as total cell counts).

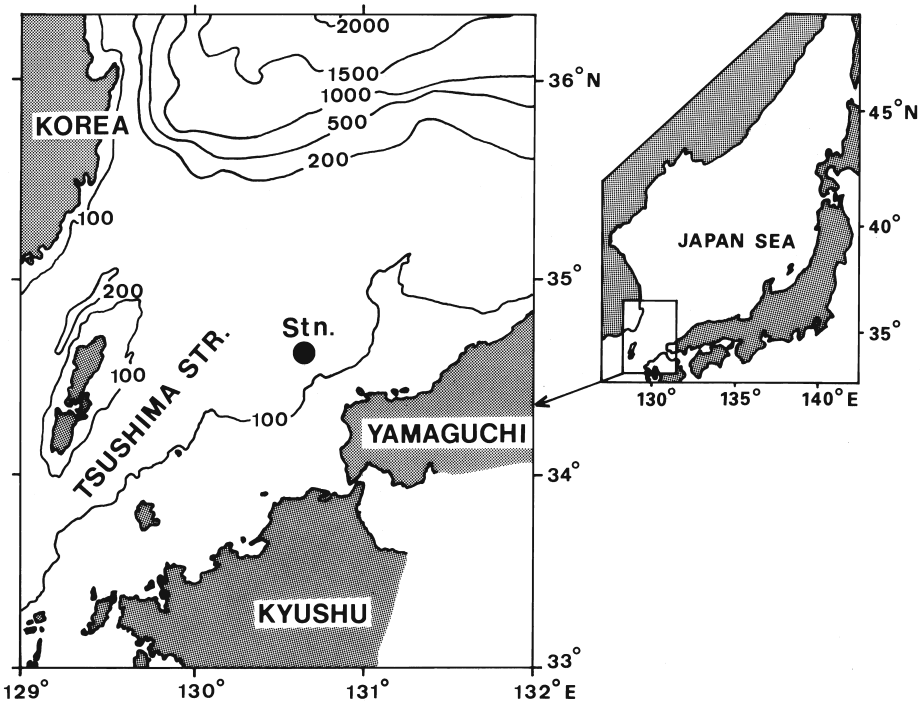

Fig. 1. Maps showing the location of the Tsushima Straits and its environs (right), and position of the present sampling station off Yamaguchi Prefecture (left). Bathymetric contours (100, 200, 500, 1000, 1500 and 2000 m) are also shown.

Results

1 Temperature and salinity structures

Figure 2 shows the vertical profiles of the temperature and salinity of the whole water column from January to December 1992. The water temperature varied from a minimum of 14.4°C at 125 m depth in March to a maximum of 26.6°C in the upper 20 m depth in September. The water column was thermally homogeneous during the cooling season from December to April. Surface warming occurred from May to September. During the warming season, a weak seasonal thermocline began to form in May and became more distinct from July through to September when the temperature of the upper mixed layer (< 25 m depth) reached 26°C. Surface cooling and subsequent vertical mixing began to break up the seasonal thermocline in October.

Salinity of the water column was nearly homogeneous from January to May, showing a high value above 34.5. High salinity water above 34.1 appeared at deeper depths (>100 m depth) until December. The maximum salinity of over 34.6 occurred from February to April. In contrast, low salinity water (<34.0), termed the "Upper Water of the Tsushima Current" (MIYAZAKI 1953; YASUI *et al.* 1967), prevailed within the surface layers during the

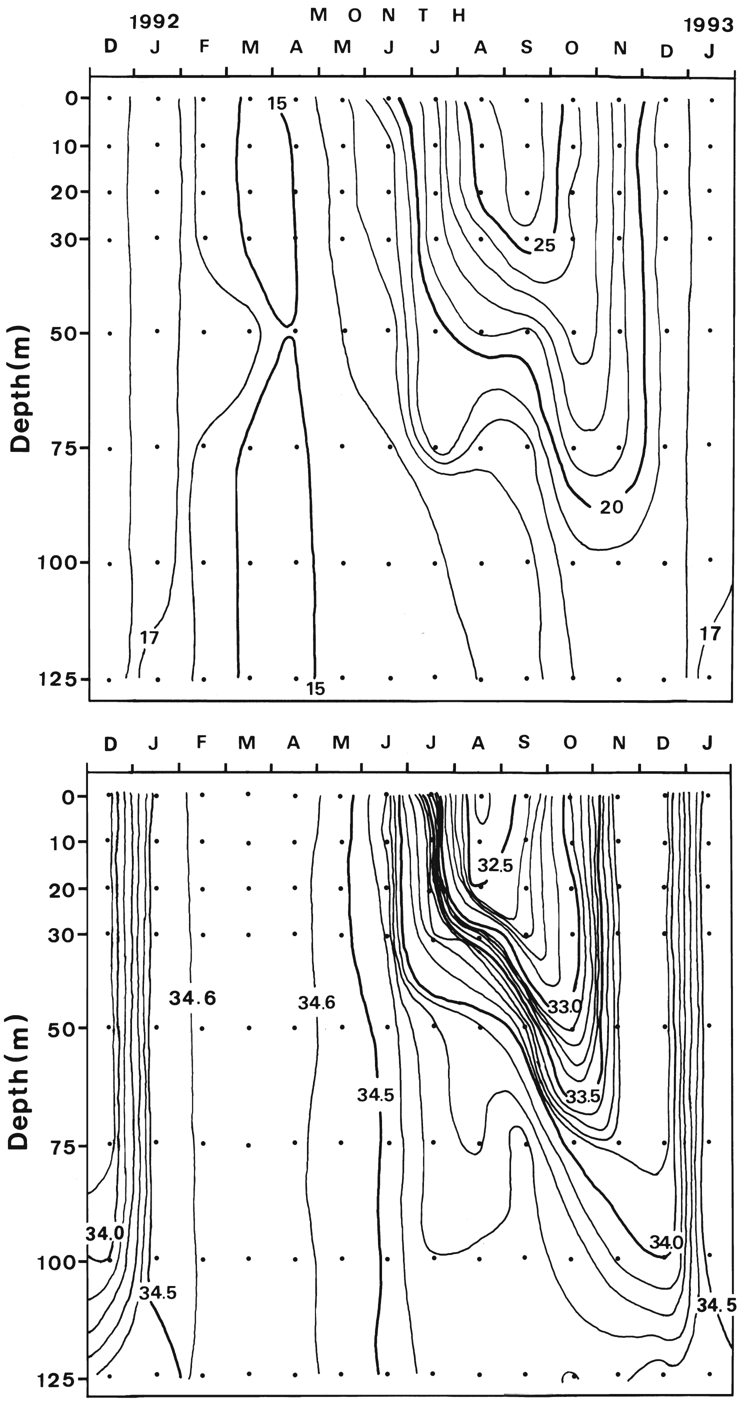

Fig. 2. Seasonal changes in temperature (upper, ℃) and salinity (lower) in the upper 125 m depth range at the station off Yamaguchi Prefecture from January to December 1992.

summer and autumn. The minimum salinity, below 32.4, was observed at the surface in August.

Thus, there occurs seasonally distinct alternations of water masses: high temperature/low salinity water masses appear during the summer and autumn, while low temperature/high salinity water masses occur during the winter and spring, as reported by OGAWA (1983). These are hydrographic characteristics of seasonal changes of the Tsushima Current water in the Tsushima Straits as shown by KOSHIMIZU (1958), NAN-NITI and FUJIKI (1967) and OGAWA (1983).

2 Individual numbers and composition of zooplankton

The zooplankton consisted of various taxa including Copepoda, Cladocera, Chaetognatha, Hydrozoa, Thaliacea, Ostracoda, Euphausiacea, Appendicularia, Decapoda (larvae), benthic invertebrate larvae such as barnacles and echinoderms, fish eggs and larvae, and others. According to the annual mean percentage contributions by the nine common zooplankton taxa (Table 1), Copepoda was the most significant component in terms of numbers of individuals, constituting 18.6-77.5% (annual mean; 58.2%) of the total zooplankton number throughout the year.

Figure 3 shows the seasonal variations in the total number of individuals/m^3 and composition of zooplankton. The total number showed three annual peaks: the 1st in March, the 2nd in June and the 3rd in November, with troughs in February, April and August. The early summer peak (June) showed the annual maximum (924 ind/m^3), and a winter trough (February) the annual minimum (77 ind/m^3). Copepoda showed numerically two spring peaks (March and May) and one autumn peak (November). Copepoda was most abundant (annual maximum; 456 ind/m^3) in March after its annual minimum (54 ind/m^3) in February. The number of Copepoda decreased toward the August trough and then increased gradually in autumn, forming a 3rd peak (260 ind/m^3) in November. Although the 2nd peak (May) of Copepoda was not synchronized with the total annual peak (June), of which the dominant group was Cladocera (mostly *Penilia avirostlis*; 559 ind/m^3, 60.4% of the total number), Copepoda appears to be the most important group determining the major features of variation of the total zooplankton number.

Table 2 shows the species composition of dominant copepods and their relative abundances in each peak. For the 1st peak, the combination of only three species (*Calanus sinicus, Paracalanus parvus* and *Ctenocalanus vanus*) accounted for approximately 80% of the total. The first two of these are typical temperate species. Contrastingly, 12 copepod species contributed to form the 3rd peak and each of these dominant species had a low relative abundance rarely exceeding 10% of the total. They were mainly composed of small-sized (BL$<$1.5 mm) temperate-subtropical species ($>$50% of the total copepods). In the 2nd peak, however, components of both of the 1st and 3rd peaks were found: seven dominant species which were a combination of three temperate species with four temperate-subtropical species. These data revealed that the diversity of the copepod assemblage was higher in the 3rd peak (November) than in the other two peaks (March and May).

Table 1. Annual mean percentages (ranges) in individual number of the nine zooplankton groups at the station off Yamaguchi Prefecture from January to December 1992.

Zooplankton group	Percentage (Individuals/m³)
Copepoda	58.2 (18.6-77.5)
Cladocera	14.3 (1.4-60.4)
Cheatognatha	3.4 (0.1- 7.8)
Hydrozoa	2.1 (0.4- 7.7)
Thaliacea	1.3 (0.1- 8.1)
Euphausiacea	2.4 (0.0-18.3)
Appendicularia	5.2 (0.3-13.1)
Decapoda (larvae)	1.3 (0.1- 4.4)
Others	11.8 (4.2-39.0)

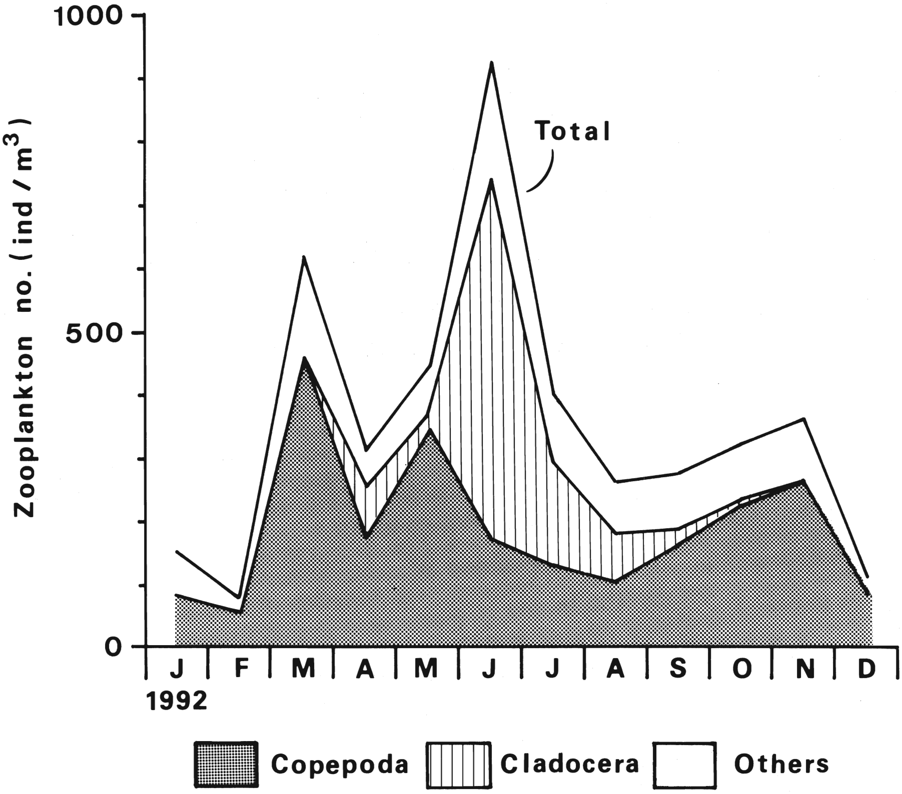

Fig. 3. Seasonal variations in the total number of individuals/m³ and composition of zooplankton community at the station off Yamaguchi Prefecture from January to December 1992.

Table 2. Species composition of dominant copepods[a] at the station off Yamaguchi Prefecture in each peak of copepod abundance; March, May and November 1992. Numbers denote their relative abundance in percentages to the total. Dominant species were listed in rank order of numerical importance.

1st peak (March)		2nd peak (May)		3rd (November)	
○ *Calanus sinicus*	49.7	○ *Calanus sinicus*	41.1	● *Paracalanus aculeatus*[b]	13.5
○ *Paracalanus parvus*[b]	19.1	○ *Ctenocalanus vanus*[b]	10.7	● *Euchaeta plana*	12.2
○ *Ctenocalanus vanus*[b]	10.0	● *Oithona plumifera*[b]	5.8	● *Oithona plumifera*[b]	9.1
		● *Eucalanus spp.*	5.5	● *Euchaeta flava*	8.6
		○ *Mesocalanus tenuicornis*	4.9	○ *Paracalanus parvus*[b]	7.0
		● *Clausocalanus arcuicornis*[b]	4.5	● *Clausocalanus arcuicornis*[b]	5.2
		● *Rhincalanus nasutus*	4.2	● *Clausocalanus furcatus*[b]	4.9
				● *Oncaea venusta*[b]	4.9
				○ *Ctenocalanus vanus*[b]	4.4
				● *Calanus minor*	3.4
				● *Eucalanus subtenuis*	2.6
				● *Undinula vulgaris*	2.1
Total	78.8		76.7		77.9

[a] determined for each sample using the definition and formula of HOSOKAWA *et al.* (1968) as follows,

$$\text{Dominant species: } N_i > (1/S) \sum_{i=1}^{S} N_i$$

where N_i is number of the i-th species and S is the total number of species.

[b] Body length of adult females <1.5 mm (MORI 1937; YAMAJI 1984)

○ ; Temperate species, ● ; Temperate-subtropical species

Figure 4 shows the seasonal variations in the number of copepod nauplii/m^3 (all species combined) and phytoplankton biomass. The naupliar abundance showed three annual peaks: the 1st in March, the 2nd in June and the 3rd in October, with three annual troughs (January, May and July). A spring peak in March showed the annual maximum (2101 ind/m^3) and a summer trough in July the annual minimum (149 ind/m^3). For phytoplankton biomass, there also occurred three annual peaks (February, May and September) and troughs (January, April and July). The February peak showed the annual maximum (288×10^6 cells/m^3) and the July trough, which was as low as the January one, the annual minimum (4×10^6 cells/m^3). Copepod nauplii showed peaks in abundance, following the phytoplankton biomass peaks. There is a definite relationship between the occurrence of copepod naupliar and phytoplankton biomass peaks. This relationship suggests that the annual peaks of copepod nauplii depend on the improved food conditions provided by the phytoplankton blooms.

3 Biomass and composition of zooplankton

Copepoda was also the most important zooplankton group by wet weight composition, comprising of 23.6-81.5% (annual mean; 50.7 %) of the total biomass throughout the year

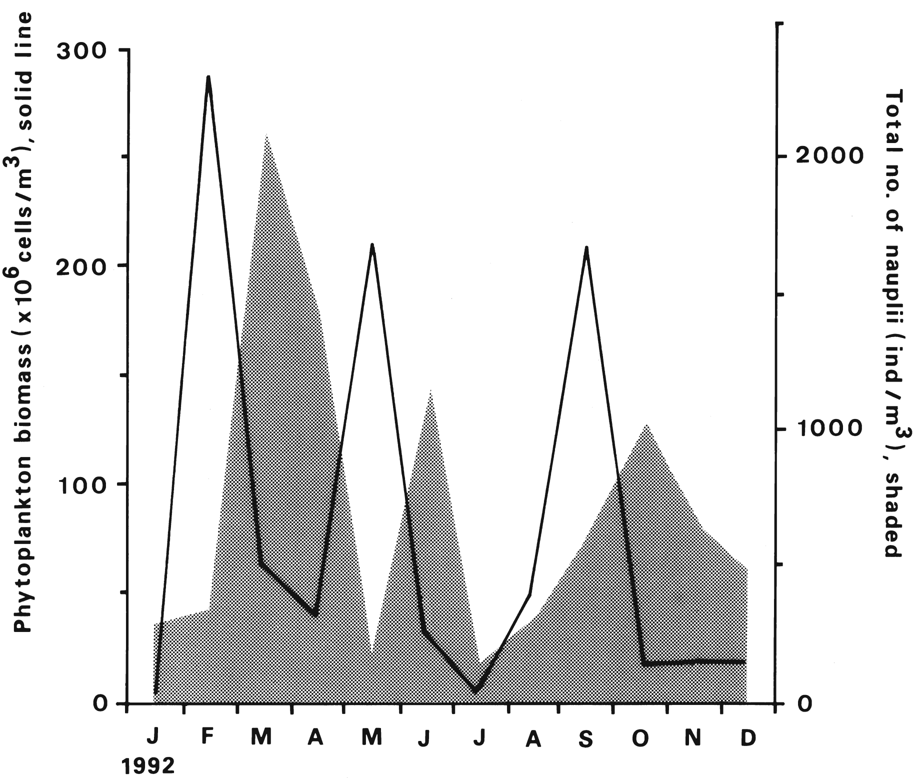

Fig. 4. Seasonal variations in the number of copepod nauplii (shaded, individuals/m^3) and in the phytoplankton biomass (solid line, $\times10^6$ cells/m^3) at the station off Yamaguchi Prefecture from January to December 1992.

(Table 3).

Figure 5 shows the seasonal variations in the total wet weight (mg/m^3) and composition of zooplankton. Three annual peaks (March, June and November) and troughs (February, April and August) occurred and seasonal variation in the total zooplankton biomass showed similar patterns to that of the zooplankton abundance (total number of individuals/m^3). The autumn peak in November showed the annual maximum (120.4 mg/m^3) and a winter trough in February the annual minimum (6.4 mg/m^3). The seasonal pattern of variation in copepod biomass was synchronized with that of numerical abundance, showing three annual peaks (March, May and November) and troughs (February, April and August): the annual maximum (79.2 mg/m^3) occurred in March and the annual minimum (4.2 mg/m^3) in February. During the period from June to December when Copepoda accounted for less than 50% of the total biomass, a large-sized (BL>ca. 10 mm) zooplankton group, which was composed of Chaetognatha, Hydrozoa and Thaliacea, increased and thus diversified the zooplankton composition (Fig. 5).

Chaetognatha (mainly *Sagitta bedoti, S. enflata* and *S. minima*) was the second most dominant taxon by biomass, comprising 1.3-33.7% (annual mean; 15.6%) throughout the year (Table 3). The chaetognath biomass peaked in June (19.9 mg/m^3) and November (annual maximum; 38.5 mg/m^3), and showed a remarkable decrease from winter to spring (Fig. 5). *S. bedoti* and *S. enflata* were the most dominant species in June and November. Both Hydrozoa (Siphonophora) and Thaliacea (mainly Doliolidae) also increased in summer and autumn with their annual maxima in July (Hydrozoa; 16.3 mg/m^3, Thaliacea; 17.5 mg/m^3) and disappeared during the winter and spring (Fig 5).

The data for both biomass and numerical abundance revealed that Copepoda was the most important zooplankton group and determinative of the seasonal changes in the total zooplankton abundance, accounting for more than 50% of the total biomass and number. Moreover, the data showed that a carnivorous biomass consisting of Chaetognatha and Hydrozoa also contributed a significant part of the zooplankton biomass from June to

Table 3. Annual mean percentages (ranges) in the biomass in wet weight of the nine zooplankton groups at the station off Yamaguchi Prefecture from January to December 1992.

Zooplankton group	Percentage (mg wet weight/m^3)
Copepoda	50.7(23.6-81.5)
Cladocera	5.9(1.1-24.8)
Cheatognatha	15.6(1.3-33.7)
Hydrozoa	6.4(0.3-21.3)
Thaliacea	3.4(0.4-22.8)
Euphausiacea	2.5(0.4-10.3)
Appendicularia	2.5(0.5- 5.1)
Decapoda(larvae)	2.4(0.2- 6.1)
Others	10.6(5.7-28.0)

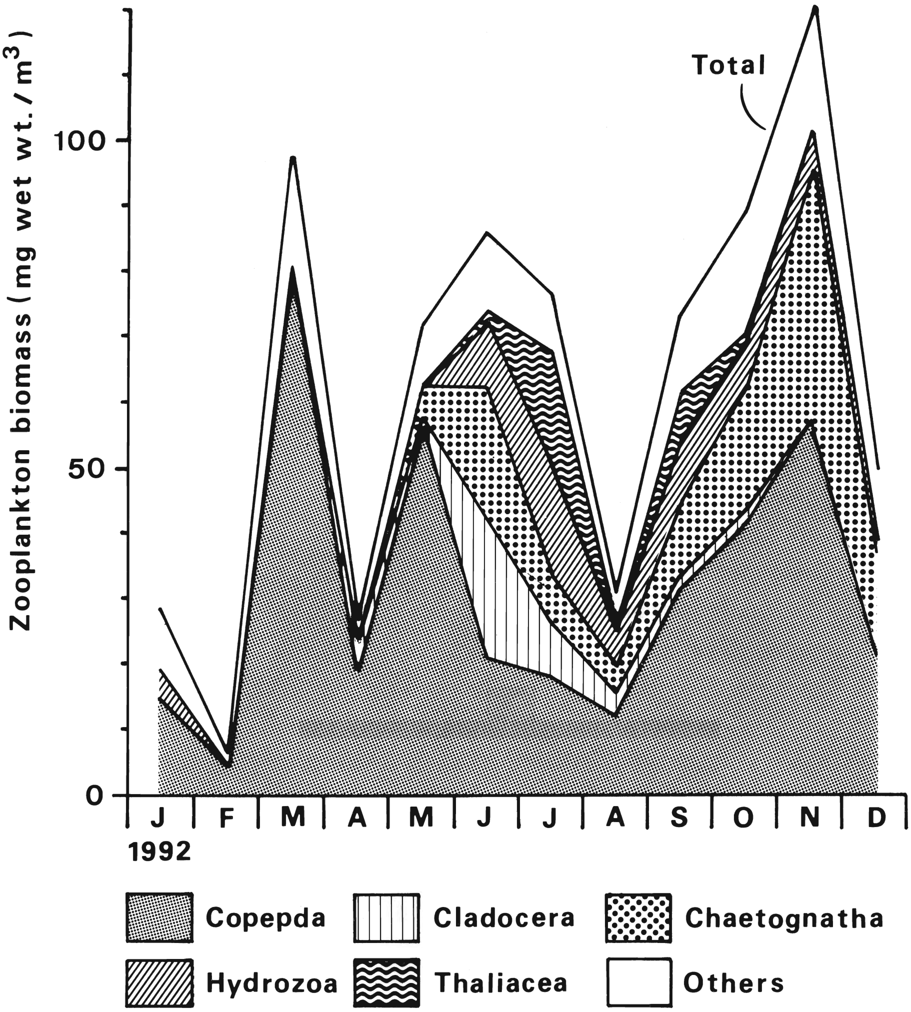

Fig. 5. Seasonal variations in the total biomass (mg wet weight/m^3) and composition of zooplankton community at the station off Yamaguchi Prefecture from January to December 1992.

November, accounting for 27.5–35.8% of the zooplankton biomass.

4 Prey-predator interrelation

Among the carnivorous groups including Decapoda (larvae), Chaetognatha constituted the most significant carnivorous component of the biomass and was the dominant summer/autumn predator. There was a significant positive relationship ($r=0.88$, $P<0.01$) between copepod biomass (mg/m^3, Y) and chaetognath biomass (mg/m^3, X) during the sampling period except for March and May when Copepoda was most predominant (Fig. 6). The regression line yields $Y=1.2X+9.5$. The relationship indicates that the seasonal change of chaetognath biomass almost parallels that of copepod biomass from summer to winter.

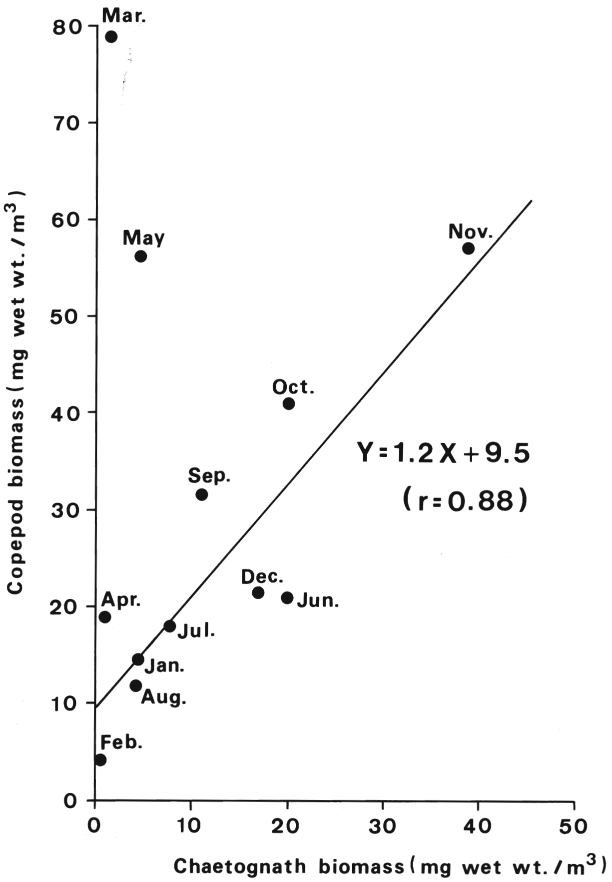

Fig. 6. Relationships between the copepod and chaetognath biomass (mg wet weight/m³) in each month at the station off Yamaguchi Prefecture from January to December 1992. Regression line was drawn excluding the data for March and May.

However, there was no linear relationship between the biomass of Copepoda and Hydrozoa. The correlation coefficient between the two variables was close to zero ($r=-0.04$).

Discussion

No Thaliacea were sampled during spring when Copepoda was most predominant. This result is different from the previous one derived from waters near the station studied (OGAWA and NAKAHARA 1979). However, the difference is probably attributed to the opportunistic behaviour of Thaliacea (e.g. ALLDREDGE and MADIN 1982). In either case, a single herbivorous group (Copepoda or Thaliacea) can exclusively regulate the spring trophic structure of the zooplankton community; carnivorous biomass is very scarce with no predominant predators. Compared with the spring community structure, the zooplankton community from early summer to autumn was trophically more complex because of the seasonal increase of carnivorous groups, primarily Chaetognatha and Hydrozoa.

A substantial regulation of copepod production by predation of Chaetognatha has been reported in inshore areas (COLLINS and WILLIAMS 1982; DAVIS 1984; KIMMERER 1984; WILLIAMS 1984; ROFF *et al*. 1988; VILLATE 1991): for the 1st life stages of *Sagitta*, copepod nauplii constitute the most suitable prey (DAVIS 1984). The positive relationship between Chaetognatha and Copepoda (Fig. 6) implies that the warm-water chaetognaths (ALVARIÑO 1965; TERAZAKI 1993) prey on the summer-autumn copepods from June to November. Furthermore, gut content analysis of *Sagitta enflata* collected from this station (Table 4) revealed that all of their diet were Copepoda represented by the small-sized forms (86.7% of the total in number). Of these copepods, *Paracalanus, Clausocalanus* and *Oncaea* have been reported to be numerously eaten by the same species living in the western Mediterranean (PEARRE 1974). These findings suggest that the life history pattern of warm-water chaetognaths in this study area is associated with the seasonal production of the small-sized copepod assemblage with a higher species diversity (Table 2).

Although the autumn (November) peak of chaetognath biomass (Fig. 5) lagged by one month the autumn (October) peak of copepod nauplii in numerical abundance (Fig. 4), the warm-water chaetognaths seem to respond to the autumn reproduction (September to October) of the temperate-subtropical copepods enhanced by the phytoplankton bloom (Fig. 4). According to the hypothesis proposed by DAVIS (1987), the smaller autumn copepods have a higher P/B ratio (the rate of production per unit biomass) which indicates losses to predation rather than the increases in herbivore stock that occurs during spring. Thus, there is a high possibility that the summer-autumn chaetognaths exert a predation impact on the small-sized temperate-subtropical copepods under high temperature and low salinity water conditions (Fig. 2).

In conclusion, the prey-predator interactions between Copepoda and Chaetognatha became more clear in the summer-autumn trophic level system, being closely related to the inflow of the "Upper Water of the Tsushima Current". The alternations of water masses,

Table 4. Gut contents of *Sagitta enflata* (13 individuals) obtained at the station off Yamaguchi Prefecture from August to November 1992. Numbers denote their relative abundance in percentages to the total number ($N=15$) over the period.

	Food organisms	%
Copepoda		
Calanoida	*Paracalanus parvus*[a]	6.7
	Clausocalanus arcuicornis[a]	26.7
	Euchaeta sp. (copepodids)	13.3
	Acartia danae[a]	6.7
	unidentified small calanoids[a]	33.2
Poecilostomatoida	*Oncaea* sp.[a]	6.7
	Coryaeus sp.[a]	6.7

[a] Body length of adult females < 1.5 mm (MORI 1937; YAMAJI 1984)

which reflect the seasonal fluctuations of the Tsushima Current water, play an important role in the physical regulation of the trophic structure and diversity of zooplankton in the southwestern Japan Sea.

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日本海南西部対馬海峡近海における動物プランクトンの出現量及び組成の季節変化

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対馬海峡近海（山口県沖）定点における動物プランクトン群集構造（出現量・組成）の季節変化を明らかにするため，ノルパックネット鉛直曳（0m～近海底；126m 深）採集を1992年１月から12月迄の毎月１回実施した．動物プランクトンは個体数及び現存量（湿重量）共に年間３回(３月，６月，11月)のピークを示した．カイアシ類は年間平均出現割合(全体の50～60%)でみると，最優占群であり，動物プランクトン出現量の季節パターンを決定する主要群の一つとなっていた．他方，ヤムシ類及びクラゲ類から成る肉食性動物群の現存量は６月から11月にかけて高くなり(全体の28～36%)，動物プランクトンの群集構造は多様化していた．被食者(カイアシ類)—捕食者（ヤムシ類）の相互関係は，対馬暖流水の季節的消長を示す高温—低塩分水の流入期（夏～秋季）に一層明らかとなった．