

## Seasonal Variability of the Copepod Assemblage and Its Relationship with Oceanographic Structures at Yamato Tai, Central Japan Sea

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### Abstract

Abundance and species composition of the copepod assemblage at Yamato Tai (Rise), central Japan Sea, were investigated using samples obtained by vertical hauls (mainly 0-500 m depth) of a NORPAC net in February, April, June, August and October, 1995. Numerical abundance was influenced by seasonal variations of both cold- and warm-water species. A high abundance yet low diversity in spring was due to the dominance of cold-water species such as *Metridia pacifica*, *Pseudocalanus newmani* and *Oithona atlantica*. In contrast, lower summer and autumn abundances were due to a decrease of the cold-water species. However, the autumn copepod assemblage structure was more diverse because of the seasonal increase of warm-water species. The seasonal distribution of the dominant copepods was closely associated with both their ecological significance and movements of the cold- and warm-water masses (i.e., the "Subarctic Water", "Deep Water" and "warm Tsushima Current"). We consider these features to play an important role in determining biological processes in the frontal zone of the Japan Sea.

**Key words** : cold-water species, copepod assemblage, frontal zone, Japan Sea, seasonal variability, species diversity, warm-water species

### Introduction

Copepods are the most dominant mesozooplanktonic group at Yamato Tai (HIRAKAWA *et al.* 1999), a rise located at the center of the Japan Sea where the warm Tsushima Current meets the subarctic waters throughout the year. This area is well known as a good demersal fishing ground (mainly pink shrimp) with pelagic fisheries for squid, salmon and mackerel also exploited. From the results of stomach content analyses of these nektonic animals (KUN 1951; FUKATAKI 1967, 1969; OKIYAMA 1965, 1971 etc.) and their major food organisms, the amphipod *Themisto japonica* (IKEDA *et al.* 1992) and the mesopelagic fish *Maurolicus muelleri* (IKEDA *et al.* 1994), the copepod assemblage has been shown to be an inevitable component of the food web

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structure in the frontal zone of the Japan Sea. According to HIRAKAWA *et al.* (1999), the spatio-temporal distribution of copepod biomass at Yamato Tai may vary with the ecological characteristics of the cold- and warm-water species, due to seasonal change of the two different water masses. However, few studies have provided detailed information about the relationships between seasonal changes in the abundance and structure of the copepod assemblage and hydrographic conditions.

In order to evaluate the effect of the copepod assemblage on biological processes in the frontal zone, we examined in detail any changes in the abundance and species composition of the copepod assemblage, and discuss their relationships with both the biotic and abiotic environments. The results of the present paper indicate that seasonal variability of the copepod assemblage is a possible key factor in secondary production mechanisms, which are in turn related to food availability for the schools of migrating fish which form at Yamato Tai, central Japan Sea.

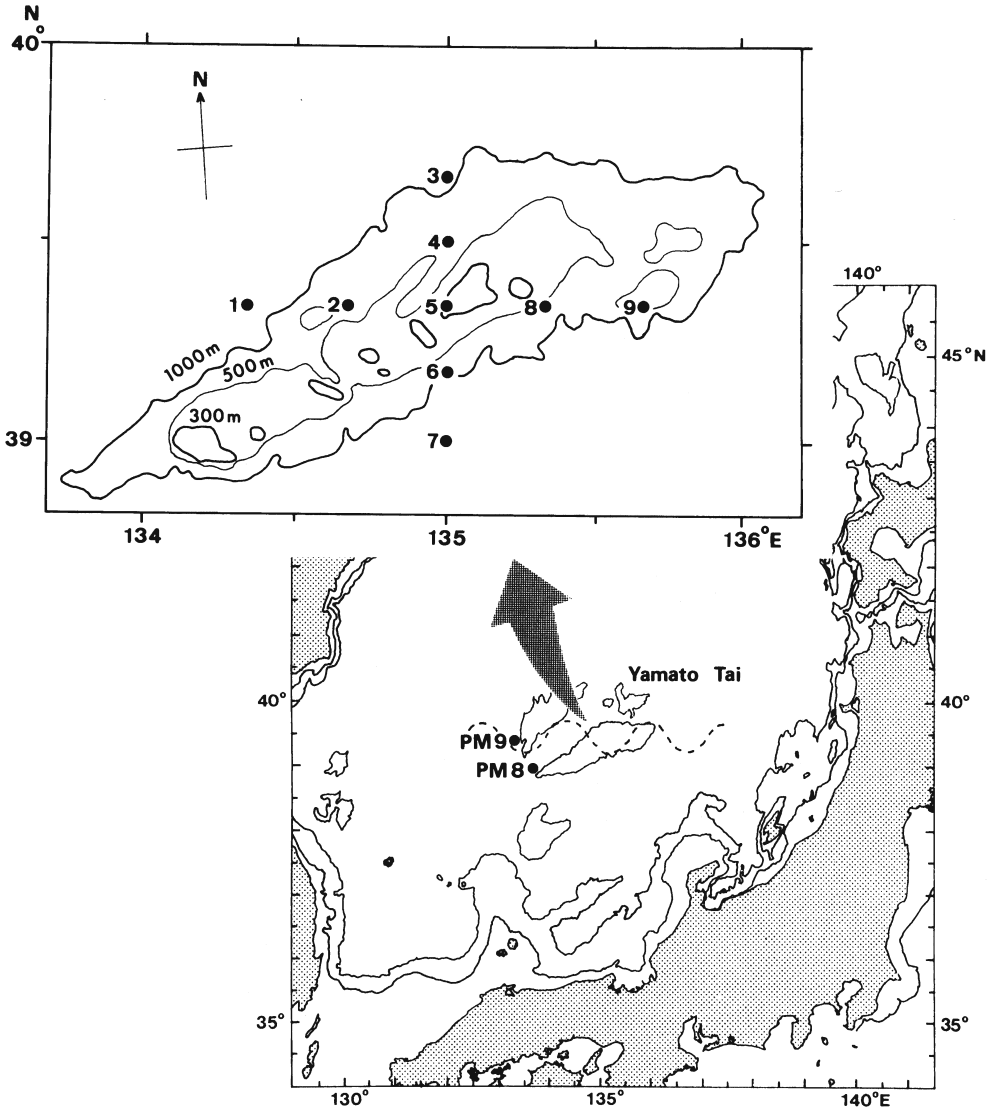
### Materials and Methods

Sampling was conducted aboard the R/V “Mizuho-Maru” of the Japan Sea National Fisheries Institute at and around Yamato Tai in the central Japan Sea (Fig. 1) in April, June, August and October, 1995. The nine sampling stations were positioned in five different parts of the Yamato Tai: the eastern (Stns. 8 and 9, 530-610 m depth), the western (Stns. 1 and 2, 530-2000 m depth), the southern (Stns. 6 and 7, 1000-2800 m depth), the northern (Stns. 3 and 4, 740-1020 m depth) and the central part (Stn. 5, 310 m depth). In addition, winter sampling was conducted aboard the R/V “Seifu-Maru” of the Maizuru Marine Observatory at the two reference stations near Yamato Tai (Fig. 1) in February, 1995. Zooplankton were collected using a NORPAC net (45 cm mouth diameter, 0.33 mm mesh aperture, 180 cm length of filtering portion) equipped with a Rigosha flow-meter on the mouth ring to register the water volume passing through the net. Vertical net tows were conducted from 500 m depth or near the bottom depth (Stn. 5) to the surface at a speed of 1 m/s. After collection, samples were preserved in a 10% buffered formalin-seawater solution.

CTD casts were made at each sampling location to assess the vertical profiles of temperature and salinity at the sampling site. In April, August and October, 260 ml seawater samples, taken from 1.7 l Niskin sampling bottles from the standard upper 200 m depths (0, 10, 20, 30, 40, 50, 60, 75, 100, 150 and 200 m) at each station, were filtered onto 25 mm Whatman GF/F filters. These filters and non-filtered seawater were stored at ca.  $-20^{\circ}\text{C}$  for a maximum of one month. Chlorophyll *a* concentrations were determined with a fluorometer (Japan Spectroscopic Inc., FP-777) for samples extracted with *N,N*-dimethylformamide (SUZUKI and ISHIMARU 1990). Inorganic nitrogen (nitrate) and inorganic phosphorus (phosphate) concentrations were determined using a Bran-Luebbe Autoanalyzer II.

Copepod assemblage species diversity was calculated using the SHANNON and WEAVER's (1963) formula:

$$H' = - \sum_{i=1}^S (n_i/N) \log_2 (n_i/N)$$



**Fig. 1.** Maps showing the location of Yamato Tai (lower panel), and the position of the present study (Stns. 1 - 9) and reference (Stns. PM 8 and PM 9) sampling stations at Yamato Tai (upper and lower panels, respectively). Bathymetric contours (300, 500 and 1000 m) for Yamato Tai are also given. The broken line denotes schematically the position of the subarctic front.

where  $N$  is the total number of copepods,  $n_i$  is the number of copepods of the  $i$ -th species, and  $S$  is the number of species.

Dominant species of copepods were 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 the individual number of the  $i$ -th species and  $S$  is the total number of species.

## Results

### 1 Hydrographic conditions

Figure 2 shows the vertical distributions of temperature and salinity. Temperature and salinity below 200-300 m depth were nearly homogeneous over all stations and remained unchanged during the study period. This “Deep-Water (Dw)” is characterized by temperature lower than 1.0°C and salinity of 34.05 - 34.10 PSU and spreads widely over the entire Japan Sea (NISHIMURA 1969).

In April, temperature and salinity were higher (10 - 12°C, 34.3 - 34.5 PSU) in the upper 100 m in the eastern part and in the upper 40m in the southernmost part (Stn. 7), but were lower at every depth in the western and near the southernmost part (Stn. 6). In particular, the cold-water (5 - 8 °C) upwelled remarkably at Stn. 2. These warm- and cold-water masses are defined as “Intermediate Depth Water (Tw-1) of the warm Tsushima Current” with higher temperature (10 - 20°C) and salinity (34.2 - 34.6 PSU), and the “Subarctic Water (Sa)” with lower temperature (5 - 18°C) and salinity (<34.1 PSU), respectively (JAPAN MARINE FISHERY RESOURCES RESEARCH CENTER 1992).

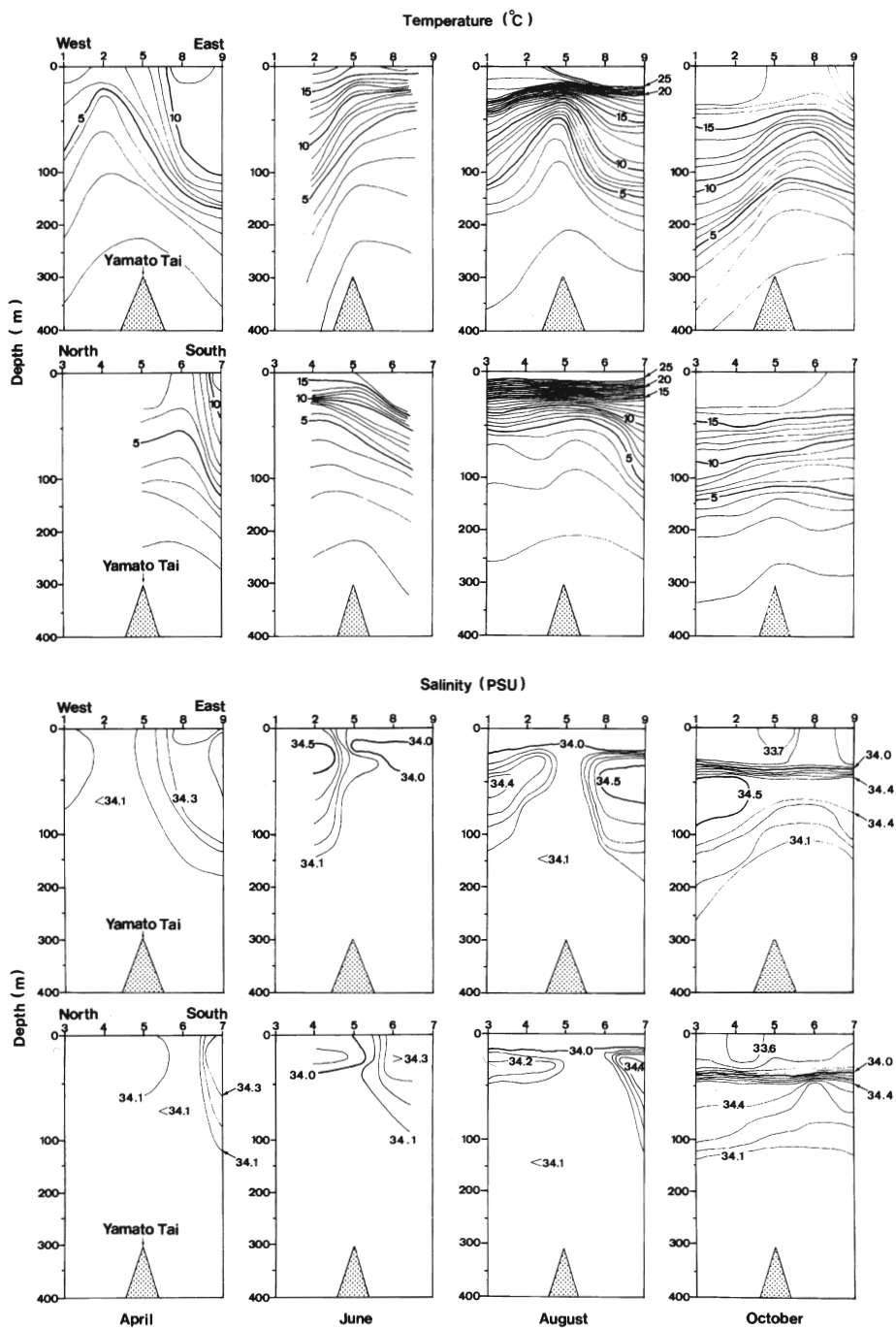
In June, the effect of the warm-water (Tw-1) was stronger in the western and southern parts, but absent in the eastern part. The northern and eastern parts were more or less under the influence of upwelling cold-water (Sa).

The August hydrographic structure was characterized by inflow of surface water of higher temperature (>20°C) and lower salinity (<34.0 PSU), termed the “Upper Water (Tw-2) of the warm Tsushima Current” (See OGAWA 1981), in the upper 30 m at each station. Between 30 and 100 m depth, warm-water (Tw-1) was found at all stations (especially in the eastern, western and southern parts), except for the central part which was affected by the upward movement of cold-water (Sa).

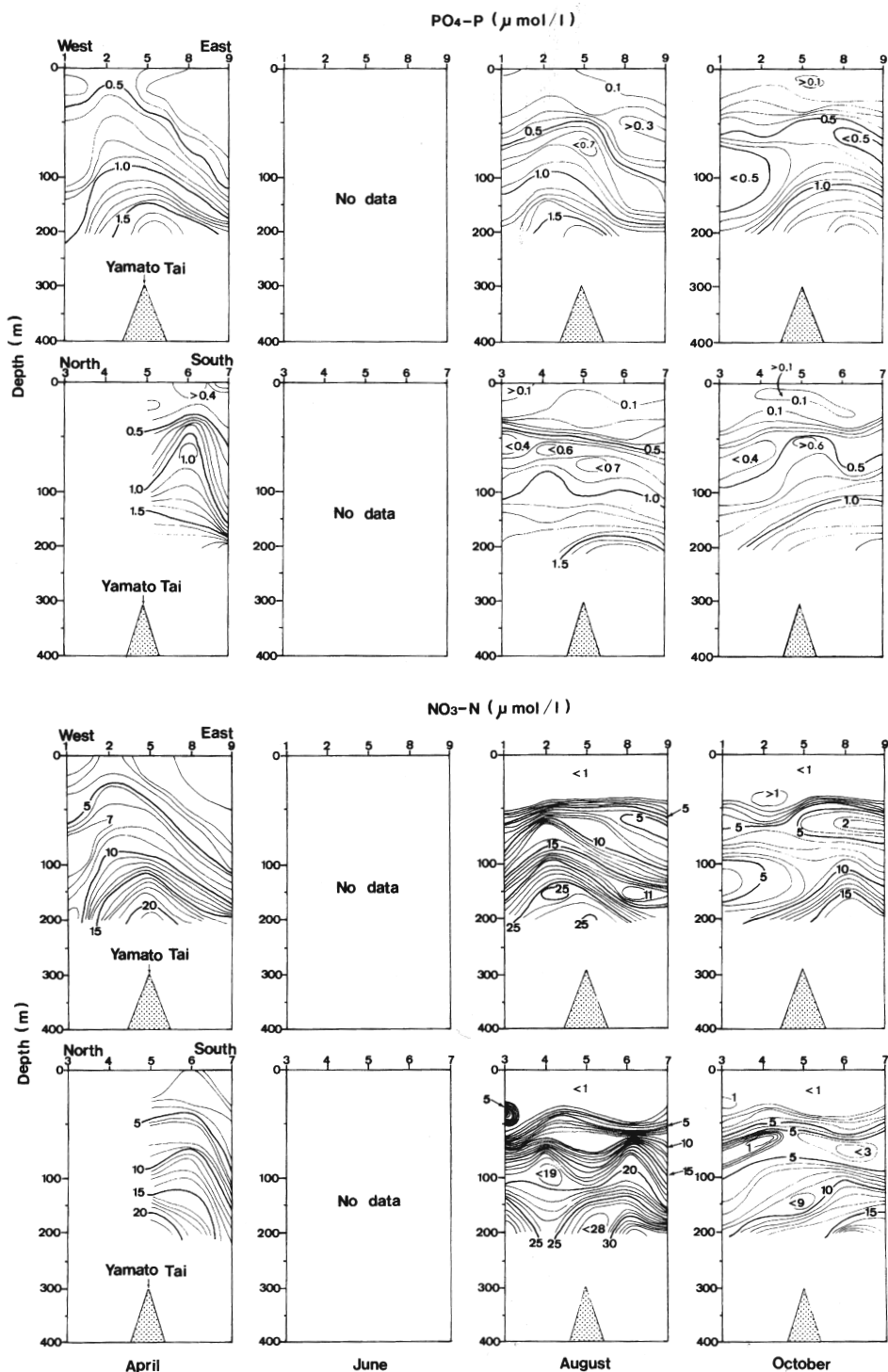
The horizontal and vertical distribution range of warm-waters (Tw-1·2) extended in October. However, surface cooling and the subsequent vertical mixing (maximum depth: near 40 m) lowered the temperature and the seasonal thermocline began to break up. Below these warm-waters, the upward movement of cold-water (Sa) remained unchanged in the eastern part.

Thus, the hydrographic features at Yamato Tai were determined mainly by the spatio-temporal distribution of both the cold-(Sa·Dw) and warm-(Tw-1·2) waters: permanent upwelling of the cold-water (“Subarctic Water”) and a seasonal increase of the inflow of warm-water (Tw-1·2: “Tsushima Current”). In addition, the spring hydrographic structure was unstable because of weak thermal stratification of the water column by winter convection. In contrast, summer waters are highly stable with a well-developed two-layer system due to the formation of a distinct thermocline (10-50 m depth) and the inflow of less saline (<34.0 PSU) surface water (Tw-2).

Figure 3 shows the vertical distributions of nutrients. Isopleths of the higher concentrations of  $\text{PO}_4\text{-P}$  (>ca. 0.5  $\mu\text{mol/l}$ ) and  $\text{NO}_3\text{-N}$  (>ca. 5  $\mu\text{mol/l}$ ) were distributed in a dome-like

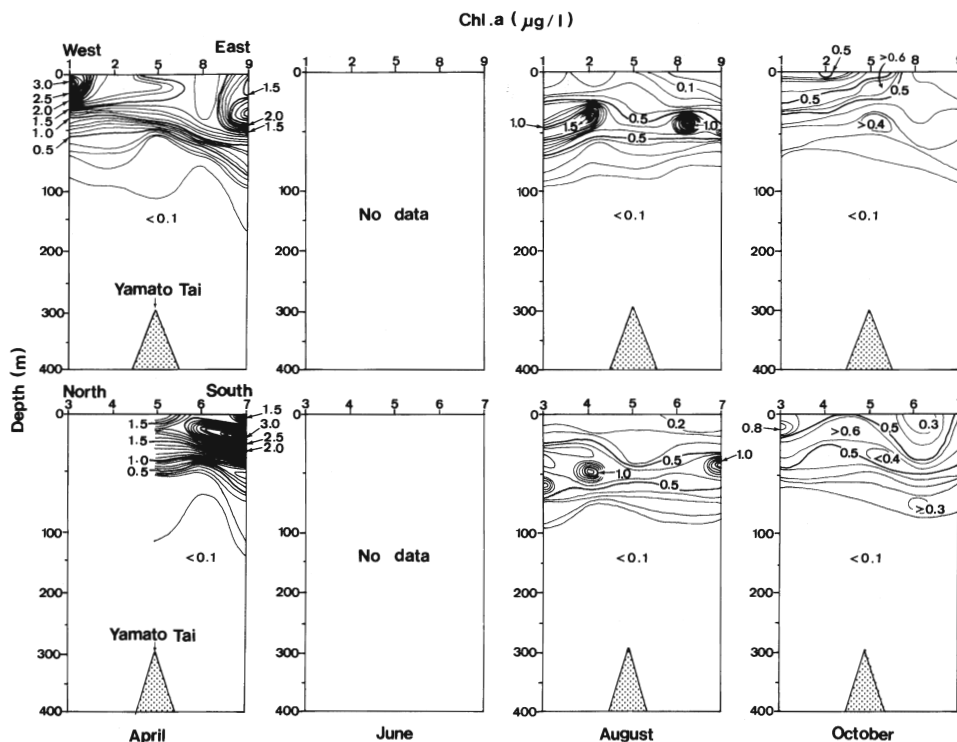


**Fig. 2.** Vertical distributions of temperature (upper two panels) and salinity (lower two panels) in the upper 400 m of the east-west and south-north sections of Yamato Tai in April, June, August and October, 1995.



**Fig. 3.** Vertical distributions of PO<sub>4</sub>-P (upper two panels) and NO<sub>3</sub>-N (lower two panels) in the upper 200 m of the east-west and south-north sections of Yamato Tai in April, June, August and October, 1995.

manner, similar to the distribution patterns of temperature and salinity in each month, except for June when no nutrient data was recorded. This implies that nutrient supply is closely associated with the vertical distribution of the water masses, especially the cold-water (Sa). Doming of the isopleths was most conspicuous in April. This indicates that the deep-lying stores of nutrients were being supplied into the euphotic zone most intensively in spring.



**Fig. 4** Vertical distribution of chlorophyll *a* in the upper 200 m of the east-west and south-north sections of Yamato Tai in April, June, August and October, 1995.

Figure 4 shows the vertical distributions of chlorophyll *a*. Higher concentrations of chlorophyll *a* were found between 10 and 50 m depth in the eastern, western and southern parts in April, in almost all parts in August, and in the western, northern and southern parts in October. Concentrations decreased from April (ca. 2.0 - 3.0  $\mu\text{g/l}$ ) to October (ca. 0.5 - 0.8  $\mu\text{g/l}$ ). The chlorophyll *a* distribution pattern in August was different from those in April and October, exhibiting higher concentration sections (Chl. *a* maximum depth: ca. 50 m) confined to the subsurface layers around the central part.

From the relationships between vertical distributions of chlorophyll *a*, nutrients and water mass structures, it must be noted that higher phytoplankton biomass (chlorophyll *a*) occurred in the warm-waters (mainly Tw-1) affected by nutrient rich cold-water (Sa) upwelled from the depths.

## 2 Copepod abundance and species composition

A total of 62 copepod species were identified (Table 1), including 45 warm-water species, 16 cold-water species and one eurythermic species, categorized by geographical distribution criteria (See HIRAKAWA *et al.* 1990; HIRAKAWA and OGAWA 1996).

**Table 1.** List of copepod species identified at Yamato Tai in April, June, August and October, 1995. ○: Warm-water species, ●: Cold-water species, △: Eurythermic species.

CALANOIDA	
○ <i>Calanus pacificus</i> BRODSKY	○ <i>Chiridius gracilis</i> FARRAN
○ <i>Calanus sinicus</i> BRODSKY	○ <i>Centropages furcatus</i> (DANA)
○ <i>Calanus minor</i> (CLAUS)	○ <i>Centropages bradyi</i> WHEELER
○ <i>Calanus pauper</i> GIESBRECHT	○ <i>Temora discaudata</i> GIESBRECHT
○ <i>Undinula vulgaris</i> (DANA)	● <i>Metridia pacifica</i> BRODSKY
● <i>Neocalanus cristatus</i> (KRÖYER)	○ <i>Lucicutia flavicornis</i> (CLAUS)
● <i>Neocalanus plumchrus</i> (MARUKAWA)*	● <i>Candacia columbiae</i> CAMPBRECHT
○ <i>Mesocalanus tenuicornis</i> (DANA)	○ <i>Candacia bipinnata</i> (GIESBRECHT)
● <i>Eucalanus bungii</i> GIESBRECHT	○ <i>Candacia truncata</i> (DANA)
○ <i>Eucalanus attenuatus</i> (DANA)	○ <i>Labidocera euchaeta</i> GIESBRECHT
○ <i>Eucalanus hyalinus</i> CLAUS	○ <i>Acartia danae</i> GIESBRECHT
○ <i>Eucalanus subtenuis</i> GIESBRECHT	○ <i>Acartia negligens</i> DANA
○ <i>Eucalanus crassus</i> GIESBRECHT	○ <i>Acartia pacifica</i> STEUER
○ <i>Eucalanus subcrassus</i> GIESBRECHT	○ <i>Acartia erythrae</i> GIESBRECHT
○ <i>Mecynocera clausi</i> THOMPSON	CYCLOPOIDA
○ <i>Paracalanus parvus</i> (CLAUS)	● <i>Oithona atlantica</i> FARRAN
○ <i>Paracalanus aculeatus</i> GIESBRECHT	● <i>Oithona similis</i> CLAUS
○ <i>Acrocalanus gracilis</i> GIESBRECHT	○ <i>Oithona nana</i> GIESBRECHT
○ <i>Clausocalanus arcuicornis</i> (DANA)	POECILOSTOMATOIDA
○ <i>Clausocalanus</i> spp.	● <i>Oncaea borealis</i> SARS
△ <i>Ctenocalanus vanus</i> GIESBRECHT	○ <i>Oncaea mediterranea</i> (CLAUS)
● <i>Pseudocalanus minutus</i> (KRÖYER)	○ <i>Oncaea conifera</i> GIESBRECHT
● <i>Pseudocalanus newmani</i> FROST	○ <i>Oncaea venusta</i> PHILIPPI
● <i>Pseudocalanus</i> sp.	○ <i>Sapphirina intestinata</i> GIESBRECHT
● <i>Microcalanus pygmaeus</i> (SARAS)	○ <i>Copilia mirabilis</i> DANA
○ <i>Calocalanus pavo</i> (DANA)	○ <i>Corycaeus speciosus</i> DANA
● <i>Gaidius variabilis</i> BRODSKY	○ <i>Corycaeus affinis</i> McMURRICH
● <i>Gaetanus</i> sp.	○ <i>Corycaeus clausi</i> F.DAHL
● <i>Paraeuchaeta elongata</i> (ESTERLY)	○ <i>Corycaeus catus</i> F.DAHL
● <i>Scolecithricella minor</i> BRADY	○ <i>Corycaeus crassiusculus</i> DANA
○ <i>Scolecithricella dentata</i> (GIESBRECHT)	HARPACTICOIDA
○ <i>Scolecithrix danae</i> (LUBBOCK)	○ <i>Micosetella rosea</i> (DANA)
	○ <i>Clytemnestra scutellata</i> DANA

\* : mixed with *Neocalanus flemingeri*



Numerical abundances and species diversity indexes of the copepod assemblage are summarized in Appendixes 1 - 5 and illustrated in Fig. 5. The total number of copepods (Fig. 5, upper panel), based on the mean value for all stations in each month, reached a seasonal maximum (348 inds./m<sup>3</sup>) and widest range of densities (18 - 671 inds./m<sup>3</sup>) in April. The copepod number then decreased towards a summer minimum (53 inds./m<sup>3</sup>, range: 41 - 76 inds./m<sup>3</sup>) in August. There was a very small increase (76 inds./m<sup>3</sup>, range: 46 - 112 inds./m<sup>3</sup>) in the total abundance in autumn (October). The range of copepod abundance was more variable in spring than in summer-autumn.

The species diversity index (*H'*) increased from winter to autumn, with a seasonal maximum (mean: 3.9, range: 3.5 - 4.1) in October (Fig. 5, middle panel). This increase was positively correlated with the seasonal increase in the relative abundance of the warm-water copepod assemblage, in contrast to the decrease in the relative abundance of the cold-water copepod assemblage (Fig. 5, lower panel).

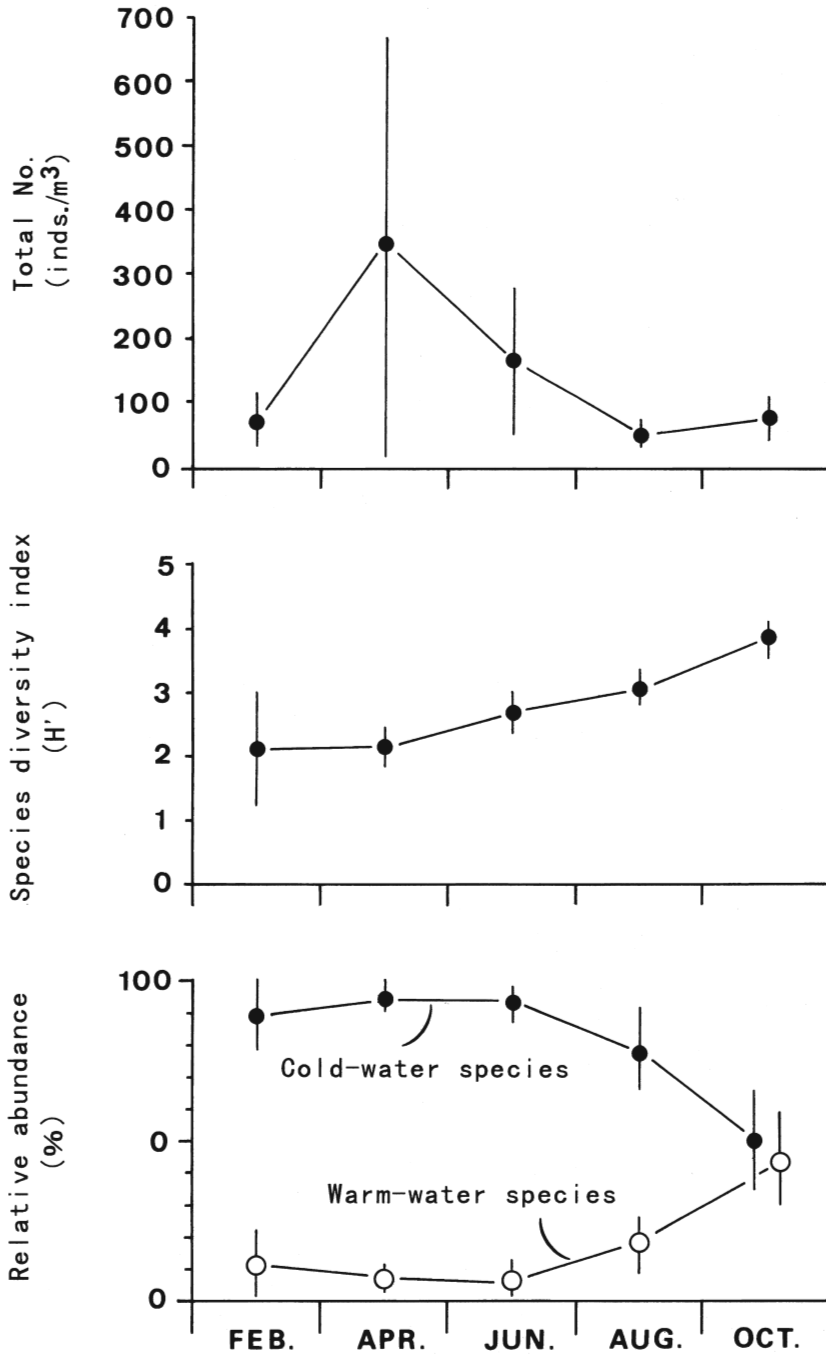
Copepod abundance at Yamato Tai was dominated by the cold-water species, which comprised 89% of the total numbers in February, 94% in April and June, 79% in August and 51% in October. In contrast, the diverse species composition was predominantly due to the presence of the warm-water species.

### 3 Abundance and species composition of the dominant copepods

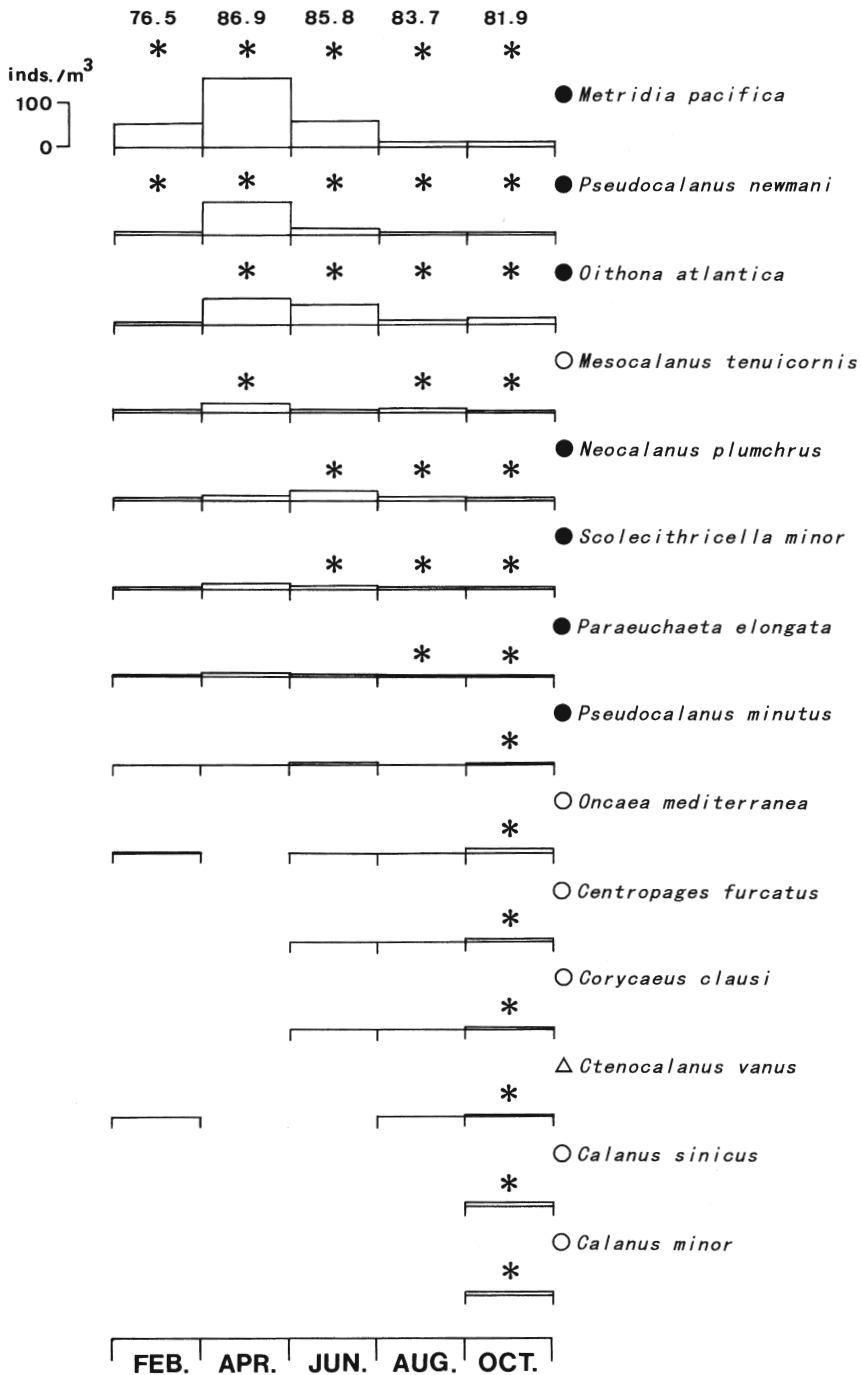
Figure 6 shows the seasonal variability of the 14 dominant species (seven cold-water species, six warm-water species and one eurythermic species), based on their mean numerical abundance over all stations in each month. Total relative abundance of the dominant species ranged from 76.5% in February to 86.9% in April.

Cold-water species: Of the dominant cold-water species, *Metridia pacifica*, represented by all adult stages and the 5th copepodite stage (CV), was the most abundant species during the study period. This species reached maximum abundance (155 inds./m<sup>3</sup>) in April and decreased gradually towards October. The seasonal abundance patterns of *Pseudocalanus newmani* and *Oithona atlantica* were similar to that of *M. pacifica*, with maximum abundances (74 and 56 inds./m<sup>3</sup>, respectively) in April. Among some of the oceanic interzonal species, *Neocalanus plumchrus* (mainly CV and possibly mixed with a closely related species, *Neocalanus flemingeri*) occurred abundantly only in June (20 inds./m<sup>3</sup>), with not more than 8 inds./m<sup>3</sup> occurring in other months. *Neocalanus cristatus* (CV) and *Eucalanus bungii* (mainly female) were not dominant. The former was found in all samples, but the latter was sometimes absent. The seasonal occurrence of *Scolecithricella minor*, *Paraeuchaeta elongata* and *Pseudocalanus minutus* was indistinct, due to their low numerical abundance as compared with the other four species.

Warm-water species: All five warm-water species (except *Mesocalanus tenuicornis*) were absent in April when the cold-water copepod assemblage was most predominant. It is interesting to note that a temperate-subtropical species *M. tenuicornis* reached a maximum abundance (18 inds./m<sup>3</sup>) in April, together with the dominant cold-water species (*M. pacifica*, *P. newmani* and *O. atlantica*). *Calanus sinicus* and *Calanus minor* only occurred in October and were dominant along with *Oncaea mediterranea*, *Centropages furcatus* and *Corycaeus clausi*,



**Fig. 5.** Seasonal variations in the total number (upper panel) and species diversity index (middle panel) of copepods, and relative abundance of the cold- and warm-water species to the total (lower panel) at Yamato Tai. The values are means for all stations and vertical bars denote ranges in April, June, August and October, 1995.



**Fig. 6.** Seasonal variations in the abundance of 14 dominant copepod species at Yamato Tai. The values are means for all stations in February, April, June, August and October, 1995. Total relative abundance (%) of the dominant species (\*) was determined by the formula of HOSOKAWA et al. (1968) for each month and appeared on the top of the figure. ○: Warm-water species, ●: Cold-water species, △: Eurythermic species.

which began to appear in June.

Eurythermic species: *Ctenocalanus vanus* was a dominant species in October, along with the warm-water species (except *M. tenuicornis*) mentioned above. This species disappeared in April and June.

Thus, the spring copepod assemblage mainly consisted of a few major cold-water species, with a high abundance and low species diversity, while the autumn copepod assemblage consisted of both cold- and warm-water (temperate and temperate-subtropical) species, and was characterized by low abundance and high species diversity. This difference is attributable to a seasonal increase of warm-water species, accompanied by a decline of the cold-water species under unfavorable high temperature conditions.

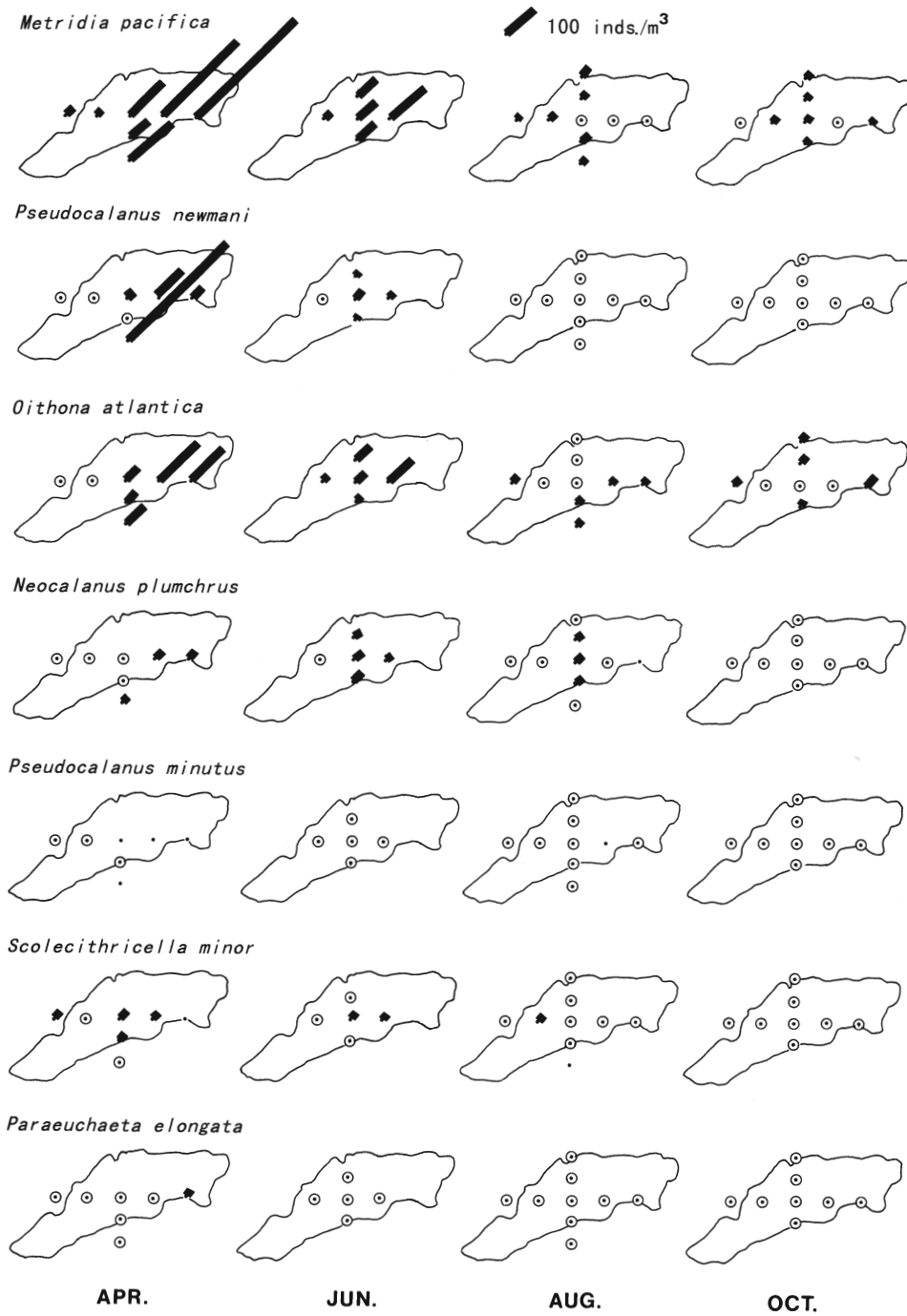
#### 4 Horizontal distributions of cold- and warm-water species and their relationships to temperature

Figures 7 and 8 show the horizontal distributions of the seven cold-water and six warm-water dominant species in each month, respectively.

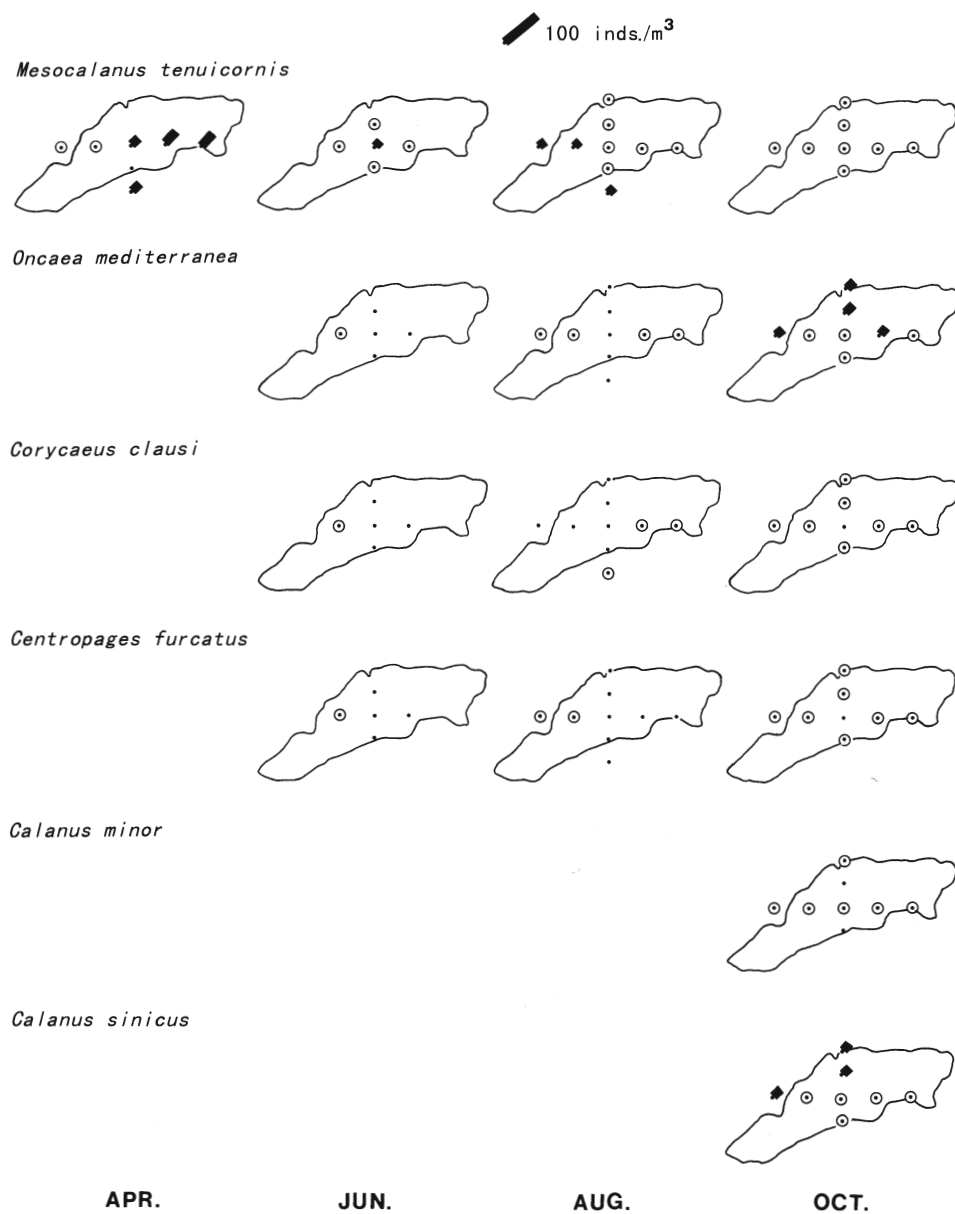
Cold-water species: *Metridia pacifica*, *Pseudocalanus newmani* and *Oithona atlantica* were distributed more abundantly in the eastern and southern parts in April. Maximum abundance occurred at Stn. 9 (389 inds./m<sup>3</sup>) for *M. pacifica*, Stn. 7 (383 inds./m<sup>3</sup>) for *P. newmani* and Stn. 8 (141 inds./m<sup>3</sup>) for *O. atlantica*. Although the abundances of these three species decreased in June, their distribution patterns were similar to those observed in April. In contrast, *Neocalanus plumchrus* was more abundant (22 - 35 inds./m<sup>3</sup>) in June in and near the central part (Stns. 4, 5 and 6), and this species was able to maintain a relatively high abundance (11 - 16 inds./m<sup>3</sup>) for the cold-water copepods even in August. While the four species mentioned above generally decreased in abundance by August or October, they did not disappear from all the study stations. *Pseudocalanus minutus*, *Scolecithricella minor* and *Paraeuchaeta elongata* were less abundant and almost uniformly distributed in each month.

Warm-water species: *Mesocalanus tenuicornis* was distributed more abundantly in the eastern part (Stns. 8 and 9) in April. Although this species maintained a relatively high abundance (>10 inds./m<sup>3</sup>) in some parts until August, abundances decreased (<10 inds./m<sup>3</sup>) at all stations in October. *Oncaea mediterranea*, *Centropages furcatus* and *Corycaeus clausi* appeared at only one station (Stn. 2) in June. However, they occurred at several stations in August and an even greater number of stations in October. In particular, the number of *O. mediterranea* increased (>10 inds./m<sup>3</sup>) in the northern and other parts in October. *Calanus minor* and *Calanus sinicus* appeared only in October. The former was less abundant (<10 inds./m<sup>3</sup>) at almost all stations, while the latter was distributed more abundantly in the northern and western parts, as found for *O. mediterranea*.

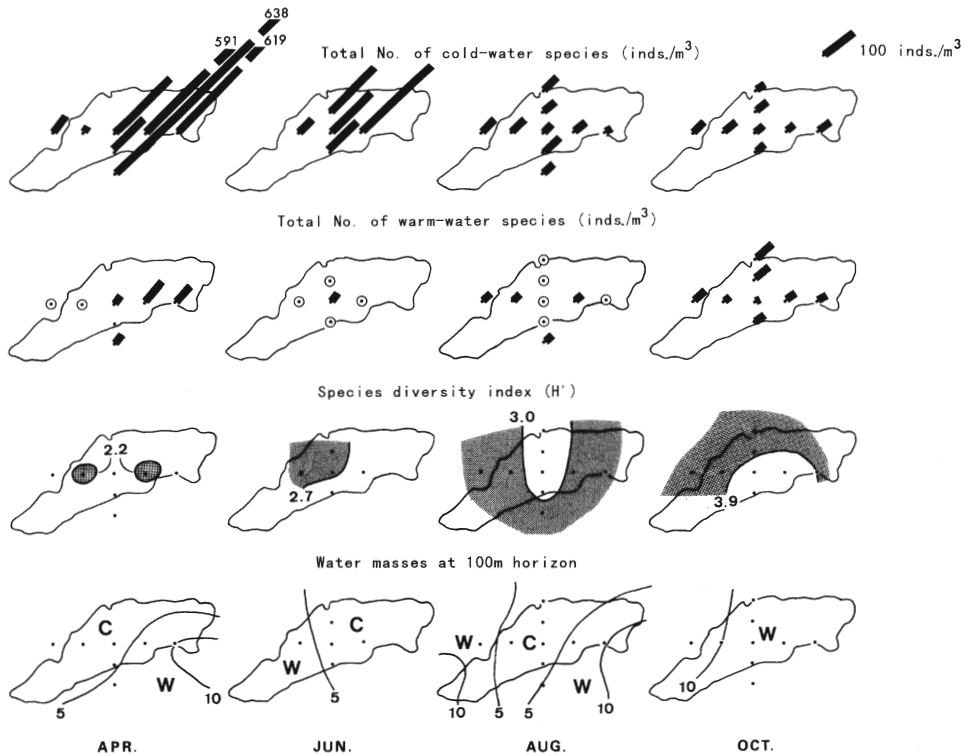
Figure 9 shows the horizontal distributions in total numbers of the cold- and warm-water copepods, and the species diversity index of copepods, in relation to the water masses at the 100 m depth horizon. At Yamato Tai the boundary between the cold- (Sa·Dw) and warm- (Tw-1·2) water masses occurs at approximately the 100 m depth horizon. The April cold-water copepod assemblage was localized with higher abundance (591 - 638 inds./m<sup>3</sup>) in the southeastern part (5 - 10°C), under the influence of the warm-water (Tw-1·2). In June, however, their major



**Fig. 7.** Horizontal abundance distributions of the seven dominant cold-water species in the upper 500 m in April, June, August and October, 1995.  $\odot$ : less than 10 inds./m<sup>3</sup>.



**Fig. 8** Horizontal abundance distributions of the six dominant warm-water species in the upper 500 m in April, June, August and October, 1995.  $\odot$ : less than 10 inds./m<sup>3</sup>.



**Fig. 9** Horizontal distributions of the total abundance of the cold-(top panel) and warm-(second panel from the top) water copepods and their species diversity index (second panel from the bottom) in the upper 500 m, and of the water masses at the 100 m depth horizon (bottom panel) in April, June, August and October, 1995. The species diversity index values (second panel from the bottom) are the mean for all stations in each month. The values in the bottom panel denote temperature ( $^{\circ}\text{C}$ ) at the 100 m depth horizon.  $\odot$ : less than 10 inds./ $\text{m}^3$ , C: Cold-water mass, W: Warm-water mass.

distributional area shifted to the cold-water (Sa·Dw), with a higher species diversity ( $H': > 2.7$ ) recorded for both the cold- and warm-waters. The distributions of total numbers of cold-water copepods in August and October was relatively uniform ( $< 50$  inds./ $\text{m}^3$ ), in contrast to distributions in April and June. Their abundance in these months was sustained by the cold-water (Sa·Dw) below 100 m depth.

On the other hand, the total number of warm-water copepods in April increased markedly in the warmer eastern and southern parts ( $5 - 10^{\circ}\text{C}$ ). The maximum abundance in June, however, was in the colder central part ( $< 5^{\circ}\text{C}$ ), contrary to our expectations. In August, warm-water species occurred more abundantly in the warmer southern, western and eastern parts ( $5 - 10^{\circ}\text{C}$ ), where the species diversity index ( $H': > 3$ ) and abundance was higher than in the cold-waters ( $< 5^{\circ}\text{C}$ ) from the central to northern parts. A rough positive relationship existed between the total abundance of warm-water species and the species diversity index of copepods in October, when warm-water (Tw-1·2) extended over the entire area.

While no information exists about the relationships between copepod assemblage vertical structure and hydrographic conditions in this study, it is evident that horizontal distributions of copepod abundance and species diversity do not necessarily depend on water mass heterogeneity.

### Discussion

The seasonal pattern of copepod abundance at Yamato Tai (Fig. 5, upper panel) is similar to that in Toyama Bay. Both areas have the general oceanographic features of the southern Japan Sea (See NISHIMURA 1969), characterized by a well developed two-layered system produced by the inflow of the warm Tsushima Current from summer to autumn and predominance of the deep cold-water masses. Two copepod abundance peaks occur in the year, a large peak in spring and a smaller peak in autumn (IGUCHI and TSUJIMOTO 1997). In both areas, the autumn abundance peak has possibly been underestimated by the use of averaged densities based on NORPAC net samples from 0-500 m depth, whereas most of the warm-water copepods are distributed in the upper 100 m (HIRAKAWA 1991).

The warm-water copepods, especially the temperate-subtropical species, have been suggested to be more significant for maintaining secondary production during summer and autumn, when the volume transport of the warm Tsushima Current is at a maximum in the Japan Sea (KAWABE 1982; TOBA *et al.* 1982; MINAMI *et al.* 1987). According to MESHCHERYAKOVA (1960), in October and November the waters of the southeastern part of the Japan Sea (38 - 40° N) become saturated by the arrival of both zoo- and phyto-plankton species that are typical of more southerly regions.

The summer-autumn copepod assemblage, which was mainly composed of temperate (*Calanus sinicus*) and temperate-subtropical species (*Calanus minor*, *Centropages furcatus*, *Oncaea mediterranea* and *Corycaeus clausi*), could supplement the seasonal decrease of the cold-water copepod assemblage (Fig. 5, lower panel), depending on small phytoplankton production (Fig. 4). In contrast, the spring copepod assemblage, dominated by only a few cold-water species (*Metridia pacifica*, *Pseudocalanus newmani* and *Oithona atlantica*), would be supported by the large spring phytoplankton bloom (Fig. 4).

Based on the relationships between the vertical distributions of the above-mentioned dominant cold-water species and water temperatures in the Japan Sea (MORIOKA *et al.* 1977; NISHIDA and MARUMO 1982; HIRAKAWA *et al.* 1990; HIRAKAWA and IMAMURA 1993; YAMAGUCHI *et al.* 1998), the cold-water species seem capable of tolerating relatively higher temperatures ( $\geq 10^{\circ}\text{C}$ ) and exploiting food resources even in the upper warm-water mass in spite of adaptation to lower temperatures. It seems reasonable to suppose that these cold-water species are responsible for determining biological productivity in the frontal or mixing zone, along with a dominant warm-water species, *Mesocalanus tenuicornis*, because of their high temperature tolerance.

In conclusion, in light of the copepod assemblage structure at Yamato Tai, we suggest that the biological processes of lower trophic levels are closely linked with the interrelation between the cold- and warm-water masses, and also affected by upwellings and the specific ecological characteristics of dominant copepods to such local hydrographic events.



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## 日本海中央部大和堆水域におけるカイアシ類群集の季節変化およびそれらと海洋構造との関連

ナターリャ ドルガノワ・平川 和正・高橋 卓

大和堆水域の9定点におけるカイアシ類群集構造(個体数・種組成)の季節変化およびそれらと海洋環境,特に水塊構造との関連を明らかにするため,ノルパックネット鉛直曳(0~500 m深,堆頂部では0~300 m深)採集を1995年2月,4月,6月,8月および10月に実施した.カイアシ類の出現量は暖水・冷水性両種の季節変化により影響を受け,春季の高い出現量は種多様性の低い冷水性種によって,他方夏・秋季の低い出現量は多様性に富む暖水性種(主として亜熱帯性種)より各々構成されていた.各暖水・冷水性優占種の時空間的分布は質的に異なる二つの水塊の季節的消長,湧昇および種による生態的特性と密接な関連をもち,日本海のフロント域における生物生産過程を解明していく上で重要な要素となることが指摘された.

**Appendix 1.** Individual numbers (per m<sup>3</sup>) of copepods in February 1995.

Species	Stn.	PM8	PM9
CALANOIDA			
<i>Mesocalanus tenuicornis</i>		5.5	
<i>Neocalanus cristatus</i>		0.2	1.1
<i>Neocalanus plumchrus</i> *		0.4	3.3
<i>Eucalanus bungii</i>		+	0.1
<i>Paraeuchaeta elongata</i>		2.0	3.3
<i>Paracalanus parvus</i>		1.0	0.7
<i>Clausocalanus</i> sp.		0.2	
<i>Scolecithricella minor</i>		3.0	2.6
<i>Pseudocalanus minutus</i>		0.4	1.3
<i>Pseudocalanus newmani</i>		2.8	5.9
<i>Ctenocalanus vanus</i>		0.4	
<i>Gaidius variabilis</i>		0.9	2.0
<i>Metridia pacifica</i>		11.5	92.3
POECILOSTOMATOIDA			
<i>Corycaeus affinis</i>		0.2	
<i>Oncaea mediterranea</i>		0.2	
<i>Oncaea venusta</i>		0.2	
CYCLOPOIDA			
<i>Oithona atlantica</i>		4.8	
Total		33.7	112.6
No. of species		16	10
Diversity		2.95	1.18

\* : mixed with *Neocalanus flemingeri*+ : less than 0.05 inds/m<sup>3</sup>**Appendix 2.** Individual numbers (per m<sup>3</sup>) of copepods in April 1995.

Species	Stn.	1	2	5	6	7	8	9
CALANOIDA								
<i>Calanus pacificus</i>		0.5	0.5		9.0			
<i>Mesocalanus tenuicornis</i>		1.9	0.7	23.4		25.4	35.6	38.9
<i>Neocalanus cristatus</i>		0.6	0.6	5.6	0.6	0.1	15.6	21.7
<i>Neocalanus plumchrus</i> *		2.3	0.4	3.4	1.7	11.3	20.1	21.4
<i>Eucalanus bungii</i>		+	+		+		+	+
<i>Paraeuchaeta elongata</i>		2.3	1.5	7.3	7.8	9.3	7.4	13.4
<i>Paracalanus parvus</i>							17.5	8.7
<i>Microcalanus pygmaeus</i>						8.7	9.1	17.4
<i>Clausocalanus</i> spp.						5.3		
<i>Scolecithricella minor</i>		11.9	1.2	18.3	12.2	8.7	15.5	
<i>Pseudocalanus minutus</i>		0.5	0.4		0.7			
<i>Pseudocalanus newmani</i>		1.4	0.1	13.4	1.7	382.5	80.3	38.9
<i>Gaidius variabilis</i>		0.9	0.7			2.7	1.9	
<i>Gaetanus</i> sp.			0.5					
<i>Metridia pacifica</i>		31.3	10.3	130.3	62.4	158.9	300.4	389.2
POECILOSTOMATOIDA								
<i>Oncaea conifera</i>				1.7				
CYCLOPOIDA								
<i>Oithona atlantica</i>		5.2	0.5	41.7	32.2	55.4	140.5	117.2
HARPACTICOIDA								
<i>Micosetella rosea</i>							4.5	
<i>Clytemnestra scutellata</i>		0.5						
Nauplii								
Total		59.3	17.7	245.1	128.3	668.3	648.4	670.8
No. of species		13	14	9	10	11	13	11
Diversity		2.24	2.39	2.17	2.08	1.87	2.38	2.07

Symbols as in Appendix 1.

**Appendix 3.** Individual numbers (per m<sup>3</sup>) of copepods in June 1995.

Species	Stn.	2	4	5	6	8
<b>CALANOIDA</b>						
<i>Calanus pacificus</i>		0.4	2.7	2.5	1.1	
<i>Neocalanus cristatus</i>		0.2	1	2.8	0.1	4.6
<i>Neocalanus plumchrus*</i>		2.3	22	35	33	12.5
<i>Mesocalanus tenuicornis</i>		2.8	2.7	13.3	1.7	4.5
<i>Paracalanus parvus</i>		0.7				
<i>Pseudocalanus minutus</i>		2.2	8.9	1.7	6.6	4.5
<i>Pseudocalanus newmani</i>		4.6	13	23.3	9.4	21.5
<i>Microcalanus pygmaeus</i>			2.1			2.3
<i>Eucalanus bungii</i>		+	+			+
<i>Paraeuchaeta elongata</i>		3.4	7.5	8	2.3	5.1
<i>Gaetanus</i> sp.			1.4			
<i>Chiridius gracilis</i>			1.4			3.4
<i>Scolecithricella minor</i>		3.3	7.5	10.8	4.4	11.3
<i>Metridia pacifica</i>		16.5	61	57.5	48.4	117.9
<i>Centropages furcatus</i>		0.2				
<b>POECILOSTOMATOIDA</b>						
<i>Corycaeus clausi</i>		2.2				
<i>Oncaea borealis</i>		0.2				
<i>Oncaea mediterranea</i>		0.2				
<b>CYCLOPOIDA</b>						
<i>Oithona atlantica</i>		14.3	50.1	26.6	17.1	87.3
<i>Oithona similis</i>		0.2	2.7	2.5	1.1	5.7
<i>Oithona nana</i>		0.2				
<b>HARPACTICOIDA</b>						
<i>Clytemnestra scutellata</i>		0.2				
Copepodites		0.4				
Total		54.5	184.0	184.0	125.2	280.6
No. of species		20	15	11	11	13
Diversity		3.01	2.76	2.80	2.43	2.36

Symbols as in Appendix 1.

**Appendix 4.** Individual numbers (per m<sup>3</sup>) of copepods in August 1995.

Species	Stn.	1	2	3	4	5	6	7	8	9
CALANOIDA										
<i>Calanus pacificus</i>		0.3		0.6		0.9	1.2	1	0.4	0.2
<i>Calanus pauper</i>										0.5
<i>Neocalanus cristatus</i>		0.6	0.5	0.9	1.3	0.7	2.2		0.1	0.1
<i>Neocalanus plumchrus*</i>		2.3	8.1	9.1	10.7	16.2	10.7	2.3	1.6	
<i>Mesocalanus tenuicornis</i>		13.3	19.3	5.4	3.9	3.7	5.6	10.1	2.8	3.5
<i>Eucalanus attenuatus</i>		0.3								
<i>Paracalanus parvus</i>		0.3		0.3		0.6		0.3		
<i>Pseudocalanus minutus</i>		1.6	3.5	1.2	2.1	1.5	0.8	1.3		1
<i>Pseudocalanus newmani</i>		1.9	3.9	3.6	3.9	2.1	2.8	1.8		2.6
<i>Pseudocalanus</i> sp.									8.3	
<i>Ctenocalanus vanus</i>		0.6		0.9		0.6		1.8	0.6	2.1
<i>Calocalanus pavo</i>									0.2	
<i>Microcalanus pygmaeus</i>		1.3	2.5				0.8		0.2	
<i>Eucalanus bungii</i>			+							
<i>Eucalanus hyalinus</i>								+	+	
<i>Paraeuchaeta elongata</i>		1.8	1.4	2.3	1.4	0.4	2.1	3.2	4.6	1.4
<i>Gaetanus</i> sp.							0.8	0.3		
<i>Chiridius gracilis</i>								1		0.6
<i>Gaidius variabilis</i>			0.7	0.3	0.4				0.2	
<i>Scolecithricella minor</i>		4.5	10.2	4.8	5	4.6	7.6	3.6	3.6	2.9
<i>Metridia pacifica</i>		12.3	14.1	20.6	14.6	7.6	19.9	10.9	5.8	5.6
<i>Lucicutia flavicornis</i>		0.3		0.3					0.8	0.3
<i>Candacia columbiae</i>										0.2
<i>Centropages bradyi</i>									0.2	0.3
<i>Centropages furcatus</i>		0.3	0.4							
<i>Acartia danae</i>									4.6	
<i>Acartia negligens</i>										0.3
POECILOSTOMATOIDA										
<i>Corycaeus clausi</i>								0.8	0.4	0.5
<i>Oncaea mediterranea</i>		0.3	0.4						1	2.2
<i>Oncaea venusta</i>										0.3
CYCLOPOIDA										
<i>Oithona atlantica</i>		16.9	3.2	5.1	3.2	1.8	10	12.1	13.9	9.7
<i>Oithona similis</i>		1.3	2.5	0.9		0.6				
HARPACTICOIDA										
<i>Clytemnestra scutellata</i>									0.4	
Copepodites		0.6	5.3					0.5	0.6	
Total		60.8	76.0	56.3	46.5	41.3	64.5	51.0	50.3	34.3
No. of species		19	16	15	10	13	12	16	21	19
Diversity		3.02	3.19	2.93	2.78	2.79	2.90	3.10	3.27	3.34

Symbols as in Appendix 1.

**Appendix 5.** Individual numbers (per m<sup>3</sup>) of copepods in October 1995.

Species	Stn.	1	2	3	4	5	6	8	9
CALANOIDA									
<i>Calanus minor</i>		2.3	3.2	6.8	2.9	0.7		0.3	5.2
<i>Calanus pauper</i>				1.5					
<i>Calanus sinicus</i>		13.4	3.2	15.9	10.8	5.4	9.1	4.7	1.2
<i>Mesocalanus tenuicornis</i>		1.9	0.7	7.6	6.8	1	4.3	1.4	4.6
<i>Neocalanus cristatus</i>		0.1	0.5	0.2	3.2	0.3	3.4	1.2	0.6
<i>Neocalanus plumchrus*</i>		3.2	1.4	0.7	1.8	5.5	1	1	1.7
<i>Undinula vulgaris</i>					1.2	0.2			
<i>Eucalanus bungii</i>				+	+			+	
<i>Eucalanus attenuatus</i>		+	0.7	+		0.2			
<i>Eucalanus hyalinus</i>			0.1				+		
<i>Eucalanus subtenuis</i>		1.4		0.7	0.5	0.7			1.7
<i>Eucalanus crassus</i>		0.4					1.9		
<i>Eucalanus subcrassus</i>		0.4		2.2	1.8		0.5		1.2
<i>Eucalanus copepodites</i>		1			1.2	1			1.2
<i>Mecynocera clausi</i>					0.5				1.2
<i>Paracalanus parvus</i>		1.4	1.7	5.3	1.2			0.3	
<i>Paracalanus aculeatus</i>		1.9	1.1						
<i>Microcalanus pygmaeus</i>			0.4						
<i>Acrocalanus gracilis</i>						0.7			1.2
<i>Clausocalanus arcuicornis</i>			0.4				0.5		1.2
<i>Ctenocalanus vanus</i>		1.4	1.4	3.8	2.4		2.4	0.7	3.4
<i>Paraeuchaeta elongata</i>		0.7	0.5	2.6	2.8	0.6	2.1	2.2	1
<i>Scolecithricella minor</i>		5.6	3.7	5.3	9.2	2.8	6.3	3.6	4
<i>Scolecithricella dentata</i>		1.4			0.5	1	0.5		0.6
<i>Scolecithrix danae</i>					1.8	0.2			
<i>Pseudocalanus minutus</i>			5.5	1.5	2.4	0.2	2.9	1.8	0.6
<i>Pseudocalanus newmani</i>		3.2	4.2	1.5	0.5	0.7	1	6.3	2.8
<i>Chiridius gracilis</i>		1.4	0.4				0.5	0.3	0.6
<i>Gaidius variabilis</i>				0.7					
<i>Gaetanus</i> sp.			0.4				0.5		
<i>Centropages furcatus</i>		3.7	1.1	2.2	2.9		1.9	1	1.7
<i>Centropages bradyi</i>		1	1.7	0.7				0.7	
<i>Temora discaudata</i>		0.4	0.7						
<i>Metridia pacifica</i>		8.9	15.7	14.5	14.9	12.8	13.2	8.6	10.3
<i>Lucicutia flavicornis</i>		1			1.2	0.2			
<i>Candacia bipinnata</i>					0.5	0.2			
<i>Candacia truncata</i>					0.5				1.2
<i>Labidocera euchaeta</i>							0.5		
<i>Acartia pacifica</i>		1		3.8	0.5	0.5			1.1
<i>Acartia danae</i>			0.7					0.3	
<i>Acartia erythrae</i>			0.4						
POECILOSTOMATOIDA									
<i>Corycaeus speciosus</i>		0.4		3.8	1.2	1	1	0.3	1.7
<i>Corycaeus clausi</i>		0.4	0.4	1.5	2.4		1.4	3.6	2.2
<i>Corycaeus catus</i>			0.4						
<i>Corycaeus crassiusculus</i>				1.5					
<i>Oncaea venusta</i>		1							
<i>Oncaea mediterranea</i>		9.8	2.1	12.9	13.9	5.5	2.9	11.3	8.5
<i>Sapphirina intestinata</i>							0.5		
<i>Copilia mirabilis</i>						0.2	0.5	0.3	
CYCLOPOIDA									
<i>Oithona atlantica</i>		16.2	8.2	11.6	12.7	1.4	10.5	4.3	22.3
HARPACTICOIDA									
<i>Microsetella rosea</i>			0.4						
Nauplii		0.4	0.7	1.5	0.5	0.5	0.5	0.3	
Copepodites		1.4	1.1	1.5	3.6	1		1.8	0.6
Total		86.7	63.1	111.8	106.3	44.5	69.8	56.3	83.6
No. of species		31	31	28	31	26	26	24	27
Diversity		4.00	3.96	4.02	4.12	3.52	3.83	3.70	3.86

Symbols as in Appendix 1.