

西部太平洋および東部インド洋におけるOithona科かいあし類の鉛直分布

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Vertical Distribution of Cyclopoid Copepods of the Family Oithonidae in the Western Pacific and Eastern Indian Oceans^{1), 2)}

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Abstract

Vertical distribution of cyclopoid copepods of the family Oithonidae was investigated at 10 stations in the western Pacific and eastern Indian Oceans. Samples were collected with Motoda horizontal nets, mostly at 14 different depths between 0 and 1000 m. Patterns of vertical distribution were described for 18 species of the genus *Oithona* and for *Paroithona* spp. Although the family Oithonidae is distributed widely from the surface to 1000 m, most oithonids are found in the upper 200 m. Each species occupied a stratum peculiar to the species or a species group. Three vertical zones inhabited by different species groups have been recognized: upper epipelagic, lower epipelagic and mesopelagic zones. Hydrographically, the epipelagic and mesopelagic zones are separated by the base of permanent thermocline, although, in some cases, lower epipelagic species were distributed slightly deeper than this boundary. The upper epipelagic zone contains species more or less associated with the surface mixed layer, while the lower epipelagic zone lies mostly between the mixed layer and permanent thermocline. Morphologically similar species tend to show different vertical distributions, while the species with similar distribution are morphologically distinct.

Cyclopoid copepods of the family Oithonidae are among the most common and numerous marine zooplankters (FISH 1936, DEEVEY 1948, MARSHALL 1949, etc.). They are distributed throughout the world oceans from the tropics to the Arctic and Antarctic, in epipelagic and mesopelagic zones of the open ocean, and in coastal waters and estuaries (NISHIDA 1981). Species of this family are mostly minute and are major constituents of small-sized pelagic copepods. Despite their small size several species are known as the major food for carnivores such as larvae of pelagic fish and chaetognaths (SYSOEVA & DEGTEREVA 1965, SULLIVAN 1980) and may be important in the biological production of the ocean.

Studies on the vertical distribution of Oithonidae, however, are scarce and scattered. The most comprehensive data have been reported by ZALKINA (1970a, b, 1972, 1977) from the tropical Pacific and northeastern Indian Oceans and by BOXSHALL (1977) from the northeastern Atlantic. Even in these studies, data available are restricted to a few large-sized, abundant species, probably due to the small size of this group and difficulties in the identification of species.

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²⁾ 西部太平洋および東部インド洋における *Oithona* 科かいあし類の鉛直分布

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This study examines the vertical distribution of cyclopoid copepods of the family Oithonidae in the western Pacific and eastern Indian Oceans. Fine-mesh nets (0.10 mm mesh openings) were used to catch all sizes, and the pattern of vertical distribution is described for all the species collected and discussed in relation to the hydrographic conditions. Biological zonation within Oithonidae is also discussed.

Materials and Methods

Samples were collected with Motoda horizontal nets (MTD nets, MOTODA 1971) during the cruises of the R/V 'Hakuho Maru' (KH-76-3 and KH-76-5 Cruises) and R/V 'Tansei Maru' (KT-74-8 Cruise) of the Ocean Research Institute, University of Tokyo, in 1976-77 and 1974, respectively. Collections were made at five stations in the eastern Indian Ocean, two stations

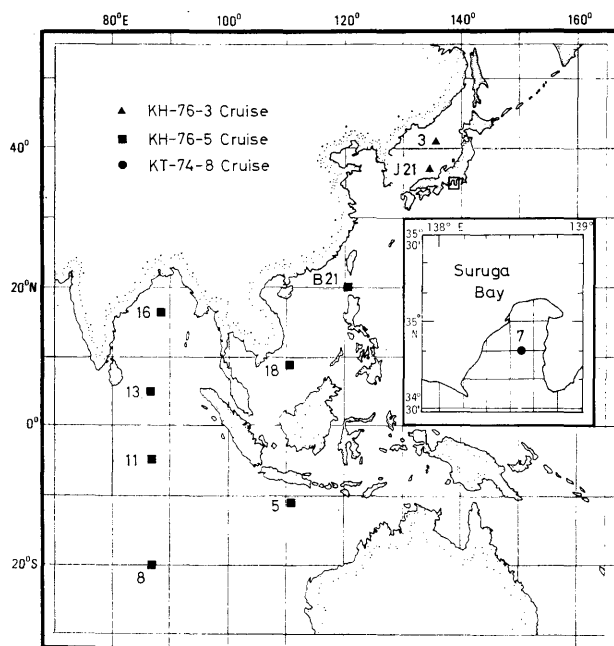


Fig. 1 Sampling stations. KH and KT indicate the cruises by the R/V 'Hakuho Maru' and R/V 'Tansei Maru', respectively.

in the South China Sea, two stations in the Sea of Japan and one station in Suruga Bay (Fig. 1, Table 1). In the eastern Indian Ocean, the South China Sea and the Sea of Japan samples were collected only at night except at Sts. 11 and 13 in the eastern Indian Ocean, where daytime samples were also collected. In Suruga Bay, on the other hand, collections were made only in the daytime.

Nets with 0.10 mm mesh openings were used except in Suruga Bay, where those with 0.33 mm mesh openings were used. Simultaneous sampling with the fine-(0.10 mm) and coarse-mesh (0.33 mm) nets (NISHIDA, unpublished) showed that the numbers of the adult oithonids collected with the fine-mesh nets are 6.7 to 17.3 times ($n=6$) higher than in coarse-

mesh nets. Thus, the 0.33 mm mesh is considered too coarse to collect the oithonids effectively. The 0.10 mm mesh, on the other hand, is considered suitable to collect most of the adult oithonids, because their lengths and widths exceed 0.50 mm and 0.10 mm, respectively, although some individuals of the two smallest forms, *Oithona simplex* and *Paroithona* spp., about 0.40 mm long and 0.08 mm wide, may have escaped through the 0.10 mm mesh. At most stations copepods were collected from 14 different strata from the surface to 1000 m by

TABLE 1. DATA ON THE MTD NET COLLECTIONS.

Cruise	Station	Date	Time	Location (middle point)	Day or night - shallow or deep series
KH-76-3	3	1976, July 15	1828-1903	40-55.7N 135-24.0E	Night-deep
"	"	"	1644-1718	40-56.0N 135-23.5E	Night-shallow
"	J 21	1976, July 30	0230-0304	37-01.8N 134-23.9E	Night-shallow
"	"	"	0043-0121	37-02.3N 134-21.5E	Night-deep
KH-76-5	5	1977, Jan. 11 -12	2258-0004	10-56.9S 111-02.4E	Night-deep
"	"	1977, Jan. 12	0056-0130	10-55.6S 111-03.5E	Night-shallow
"	"	"	0210-0230	10-54.9S 111-05.3E	Night-shallow
"	8	1977, Jan. 18	1933-2037	19-54.2S 86-58.7E	Night-deep
"	"	"	2143-2218	19-54.8S 87-01.1E	Night-shallow
"	11	1977, Jan. 23 -24	2330-0030	4-51.3S 87-03.6E	Night-deep
"	"	1977, Jan. 24	0132-0205	4-52.2S 87-04.8E	Night-shallow
"	"	"	1005-1110	4-47.7S 87-14.4E	Day-deep
"	"	"	1213-1245	4-47.9S 87-12.9E	Day-shallow
"	13	1977, Feb. 8	0035-0111	5-02.4N 86-47.4E	Night-shallow
"	"	"	0211-0317	5-03.3N 86-48.7E	Night-deep
"	"	"	1247-1357	5-08.3N 86-43.3E	Day-deep
"	"	"	1450-1523	5-08.0N 86-44.3E	Day-shallow
"	16	1977, Feb. 16	1933-2035	16-33.8N 88-24.9E	Night-deep
"	"	"	2135-2207	16-33.8N 88-24.9E	Night-shallow
KH-76-5	18	1977, Mar. 1	0046-0147	9-01.1N 110-30.1E	Night-deep
"	"	"	0246-0321	9-03.0N 110-30.0E	Night-shallow
"	B 21	1977, Mar. 8	1955-2100	20-04.2N 120-35.4E	Night-deep
"	"	"	2208-2238	20-05.7N 120-35.7E	Night-shallow
KT-74-8	7	1974, June 12	0827-0947	34-49.8N 138-35.2E	Day-deep
"	"	"	1026-1056	34-51.0N 138-34.0E	Day-shallow

two series of horizontal hauls: a shallow series (0, 10, 30, 50, 75, 100, 150 and 200 m) and a deep series (300, 400, 500, 600, 800 and 1000 m). Positions of the attachment of the MTD nets on the wire were preset on the basis of the desired sampling depth and the wire angle, which was maintained at 45° during a haul, assuming a straight wire. The fluctuation of the depth of haul of an MTD net was not observed in the present study, but available data taken by Y. HIROTA of the Ocean Research Institute (unpublished) in the Bering Sea (KH-78-3 Cruise) with a Depthtime meter (Yanagi Keiki, Type BS-04) indicated that the mean depth of the nets which intended to sample at 400 m ranged from 351 to 413 m (n=10, \bar{x} =379.5 m, SD=21.5 m). Therefore, the deviation of the actual mean depth of tow from the desired depth is presumed

to be around these values, about $95 \pm 5\%$ (SD) of the desired depth. Nets were towed horizontally for about 30 and 60 minutes in a shallow and a deep series, respectively. A net was equipped with a flowmeter in the mouth to estimate the volume of water filtered. Volumes were generally 50 to 200 m³ and 200 to 600 m³ in the shallow and the deep series, respectively. Estimates of copepod abundance were standardized for 1 m³ of water filtered. No special attempt was made to judge the occurrence of contamination in an MTD net. However, in order to check this possibility, the individual numbers of the shallow-living species in the deeper nets were examined. In the Bay of Bengal (St. 16), *Oithona attenuata*, *O. plumifera* and *O. fallax* were abundant, each with its maximum number of adult females of more than 60 indiv·m⁻³, and distributed mostly in the upper 50 m. No *O. attenuata* and *O. fallax* were found in the nets which worked below 75 m. Only one specimen of *O. plumifera* was found in the 800 m net, but none in the other nets below 300 m. Thus, contamination of deeper hauls by shallow-living species during the lowering of nets was considered to be negligible at this station. Similar examination made on the other hauls equally showed that contamination was insignificant in these vertical series of collections. But the data obtained in the present study are not suitable to examine the species composition in each layer, because the contaminant individuals, when introduced into a sample with low copepod density even in small numbers, have a serious effect on the species composition of the original sample.

Samples were fixed in 5 to 10% formalin/seawater solution buffered with sodium tetraborate. In laboratory subsampling was generally carried out before counting and identification. In the case of the samples from Suruga Bay, the Folsom plankton sample splitter was used to obtain a 1/2, 1/4, 1/8 or 1/16 aliquot. In all the other cases, 5% formalin/seawater solution was added to the sample and the total volume was adjusted to 100, 200 or 400 ml. From this ten 1-ml subsamples were obtained with a Stempel pipette. Identification and counting were made for 2 to 10 subsamples according to copepod density. Some of the samples from the layers below 500 m contained only a small quantity of oithonids, usually less than 100 indiv. per a haul. These samples were identified and counted in their entirety. Each subsample was transferred into a covered Sedgwick-Rafter cell (capacity about 4 ml, 4 mm deep) and the oithonids from the entire subsample were identified and counted under a compound microscope. Specimens which required further observation were sorted out from the original- or subsample and examined by HUMUS & GOODING's method (HUMUS & GOODING 1964). The taxonomy of the larval stages and males of Oithonidae lags far behind that of the females, and it was impossible to identify all the species of Oithonidae except for adult females. The density of the oithonids, therefore, was estimated only for adult females. In the analysis of the vertical distribution, 95% confidence intervals were indicated in the figures to eliminate the spurious peak of density introduced by subsampling errors (see VERNICK 1978).

Hydrographical observations were made for temperature, salinity, dissolved oxygen and chlorophyll *a* content at the stations in the eastern Indian Ocean and the South China Sea (TAGA, unpublished), while measurements were made only for temperature and salinity in

the Sea of Japan (TANAKA 1979). Hydrographical data in Suruga Bay, where observation of temperature and salinity was not made in conjunction with the sampling of copepods, are based on the observation by the Shizuoka Prefectural Fisheries Experimental Station (JAPAN FISHERIES AGENCY 1979, p. 268).

Results and Discussion

Hydrographic Characteristics of the Area Investigated (Fig. 2)

The eastern Indian Ocean was investigated in winter, when the northwestern monsoon predominated. St. 5 is situated in the oceanographic front at about 10° S characterized by the low-salinity waters between Australia and Indonesia (WYRTKI 1973). At this station, three distinct layers were recognized: the mixed layer from 0 to 30 m; the low-temperature, high-salinity and low-oxygen water underlying the steep thermocline from 75 to 100 m; the intermediate layer from 30 to 75 m characterized by low salinity and high oxygen content. The

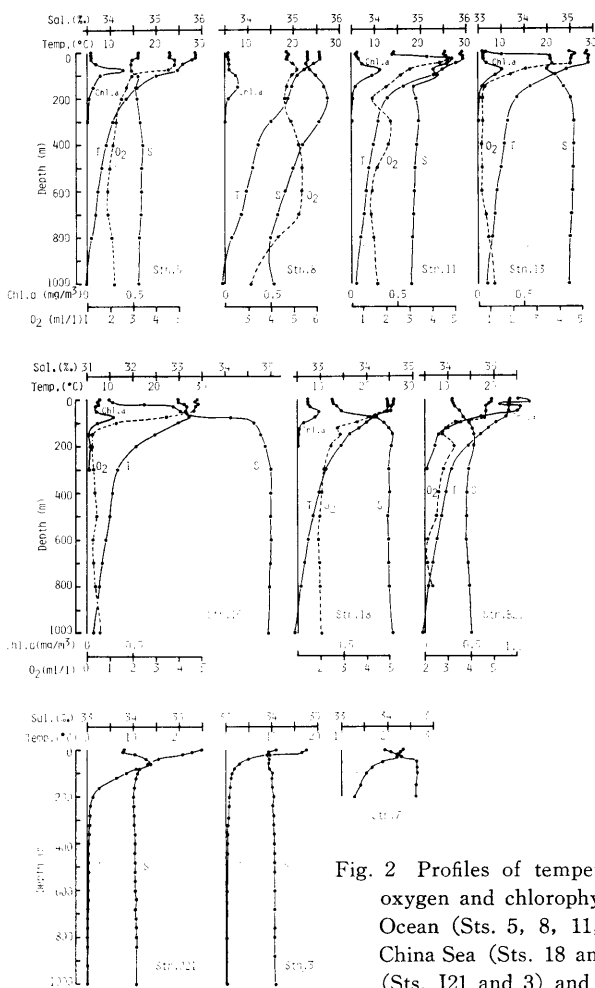


Fig. 2 Profiles of temperature, salinity, dissolved oxygen and chlorophyll *a* in the eastern Indian Ocean (Sts. 5, 8, 11, 13 and 16), the South China Sea (Sts. 18 and B21), the Sea of Japan (Sts. J21 and 3) and Suruga Bay (St. 7).

thermocline corresponded with the steep oxycline and marked decrease of chlorophyll *a*. St. 8 belongs to the Indian Central Water characterized by the high salinity and high oxygen content in the upper 400 m. The permanent thermocline was recognized between 200 and 300 m, while the seasonal thermocline was between 30 and 75 m. At St. 11, which is situated between the Indian Equatorial and Central Waters, the surface mixed layer and thermocline were observed from 0 to 30 m and 100 to 150 m, respectively. Sts. 13 and 16 belong to the Indian Equatorial Water. The low-salinity surface water and the layers below 150 m with low oxygen content less than $1.0 \text{ ml} \cdot \text{l}^{-1}$ were peculiar to these stations. The mixed layer occupied the upper 50 m at St. 13 and the upper 75 m at St. 16, while the thermocline was found between 50 and 150 m at St. 13 and between 75 and 200 m at St. 16.

At St. 18 in the South China Sea, the surface mixed layer in the upper 50 m was characterized by the water with high temperature, low salinity and high oxygen content. The thermocline was recognized between 50 and 150 m. At St. B21 in the Bashi Channel, the mixed layer and the thermocline were recognized in the upper 75 m and between 75 and 200 m, respectively. The high value of chlorophyll *a* at this station may be due to the influence of coastal water, because *Gephylocapsa oceanica*, a typical coastal coccolithophorid, occurred abundantly in the upper layers (ISHIMARU 1978).

The water of the Sea of Japan can be divided into cold and warm current areas. St. 3 is situated in the cold current area; the layer below 100 m was characterized by the water with low temperature and salinity, and the seasonal thermocline was well developed in the upper 75 m (TANAKA 1979). St. J21 was covered with the Tsushima Warm Current and the column of water with high temperature and salinity was very thick. The thermocline was recognized in the upper 175 m.

In Suruga Bay (St. 7), a steep seasonal thermocline was recognized between 30 and 50 m, underlying the low-salinity surface water.

Vertical Distribution of the Family Oithonidae

Fig. 3 shows the vertical distribution of the family Oithonidae in the different regions investigated in this study. Most oithonids were concentrated in the epipelagic zone above 200 m, although the patterns of vertical distribution differed markedly among different stations.

In the eastern Indian Ocean (Sts. 5 to 16), the vertical range of oithonids increased from north to south, corresponding with the increase of the depth of thermocline, while the density of oithonids decreased from north to south. Another characteristic phenomenon in this region is the existence of the two conspicuous maxima of the oithonid densities at Sts. 13 and 16. The shallow maxima consist of species almost completely different from those forming the deep maxima. Some of the constituent species of the shallow maxima were restricted to the Equatorial Water and were absent from Sts. 5, 8 and 11, whereas the others occurred in low densities beneath the surface mixed layers at these stations. The patterns of day and night distribution were similar at St. 13. At St. 11, maximal density occurred slightly shallower by day than night.

At Sts. 18 and B21 in the South China Sea, most oithonids were restricted to the depths above the base of the thermocline, and the highest densities were observed just beneath the surface mixed layers.

In the Sea of Japan, oithonid density was highest within the thermocline, but significant densities were observed beneath the thermocline as well. At St. J21 the deeper water was inhabited mostly by subarctic species indicating the existence of cold water in the layers beneath the thermocline. At St. 3, north of the polar front, the whole water column above 1000 m was occupied by the subarctic species, *Oithona similis* and *O. atlantica*.

In Suruga Bay (St. 7) oithonids occurred in low densities but through a wide vertical range from 0 to 400 m. The low density observed in the shallow layers and the inconspicuous maxima at 30 and 75 m are attributable to the coarse mesh of MTD nets used at this station.

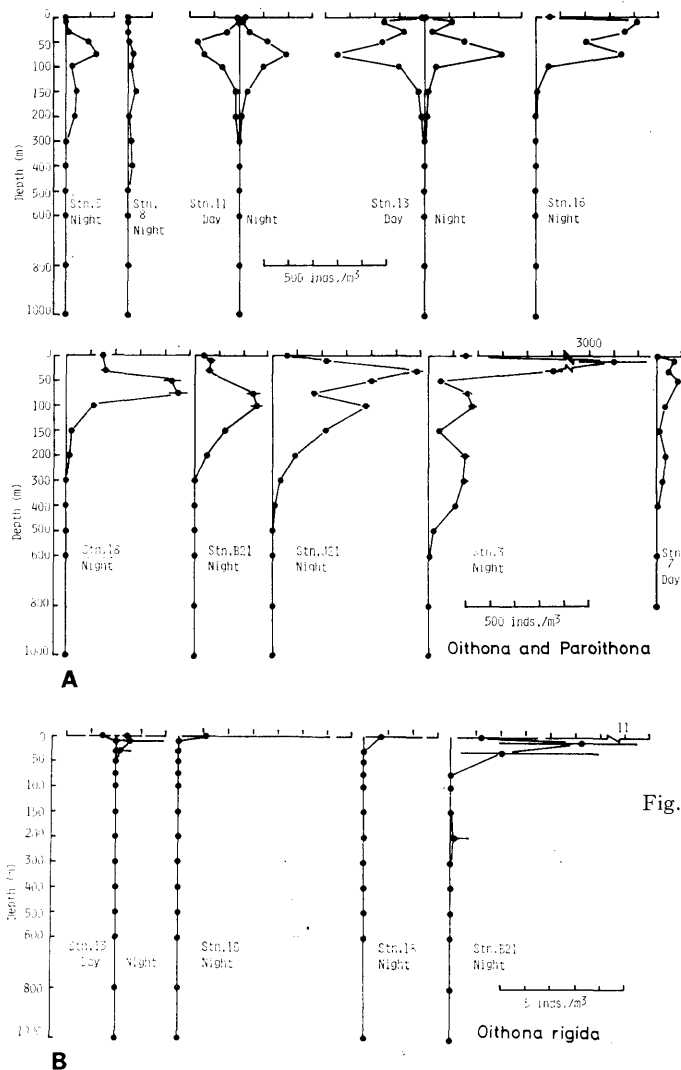


Fig. 3 Vertical distribution of (A) the family Oithonidae and (B) *Oithona rigida*. Horizontal bars indicate 95% confidence intervals of the copepod density estimated by subsampling. Note that the depth scales are doubled in the upper 200 m.

Smaller species such as *O. decipiens*, *O. fallax*, *O. nana* and *O. similis*, which are considered major components at 30 and 75 m, were not collected effectively due to mesh escapement, whereas the large-sized *O. atlantica*, a major inhabitant of the deeper layers, was well retained.

Oithona rigida GIESBRECHT

Out of the five inlet species distributed in the Indo-West Pacific region (NISHIDA 1981), only *O. rigida* was collected in this study. This species occurred in low densities at Sts. 13, 16, 18 and B21 where the surface layers were under strong influence of coastal waters; the maximum density estimated was $5 \text{ indiv} \cdot \text{m}^{-3}$. Vertically it was restricted to the surface layers above 30 m, corresponding to the waters of coastal origin (Fig. 3).

Oithona attenuata FARRAN and *O. fallax* FARRAN

Geographically these two species are restricted to the tropical waters (NISHIDA 1981). They showed similar vertical distribution and occupied the shallowest layers of all the oceanic oithonids (Fig. 4). At St. 5 in the eastern Indian Ocean, where *O. attenuata* was almost absent, *O. fallax* was distributed mostly in the thermocline between the seasonal and permanent thermoclines, with a conspicuous peak at 50 m. *Oithona fallax* was absent from the surface mixed layer which had salinity higher than the water of thermocline. At Sts. 13 and 16 in the Indian Equatorial Water, they were distributed mostly in the upper 30 m, showing high densities at 10 m. At Sts. 18 and B21 in the South China Sea, on the other hand, they showed rather wide vertical ranges and were distributed mostly within and above the upper part of the thermocline. This regional difference of vertical distribution of these species coincides with the regional difference of hydrographical conditions. At Sts. 13 and 16 steep salinity gradients were found between 10 and 30 m, which separate the low-salinity surface water from the high-salinity subsurface water, whereas at Sts. 18 and B21 such a steep salinity gradient was not observed.

The occurrence of *O. fallax*, though in low density, at 10 and 30 m at St. J21 in the Sea of Japan is interpreted as indicating the influence of the Tsushima Warm Current covering the surface layer at this station.

There was no marked difference between day and night vertical distribution of these species at St. 13.

Oithona plumifera BAIRD

This species, in contrast to *O. attenuata* and *O. fallax*, is distributed widely in the tropical and subtropical waters, and was collected at all the stations except St. 3. The vertical distribution of *O. plumifera* at Sts. 13, 16, 18 and B21 closely resembles those of *O. attenuata* and *O. fallax*, and at St. 5 that of *O. fallax*. At Sts. 8 and 11, *O. plumifera* was scarce in the surface mixed layer and distributed principally in the upper part of the thermocline. In the warm current area of the Sea of Japan (St. J21) and in Suruga Bay, it occurred in low densities in the upper 50 m with maximal densities at 10 m (Fig. 4).

ZALKINA (1970b, 1972) investigated the eastern Indian Ocean during northeastern monsoon period and reported that *O. plumifera* had its "core of population" between 44 and 96 m in the Equatorial Water (corresponding to Sts. 13 and 16 in the present study) and between 61 and 182 m in the halistatic zone in the Central Water (St. 8 in the present study). She

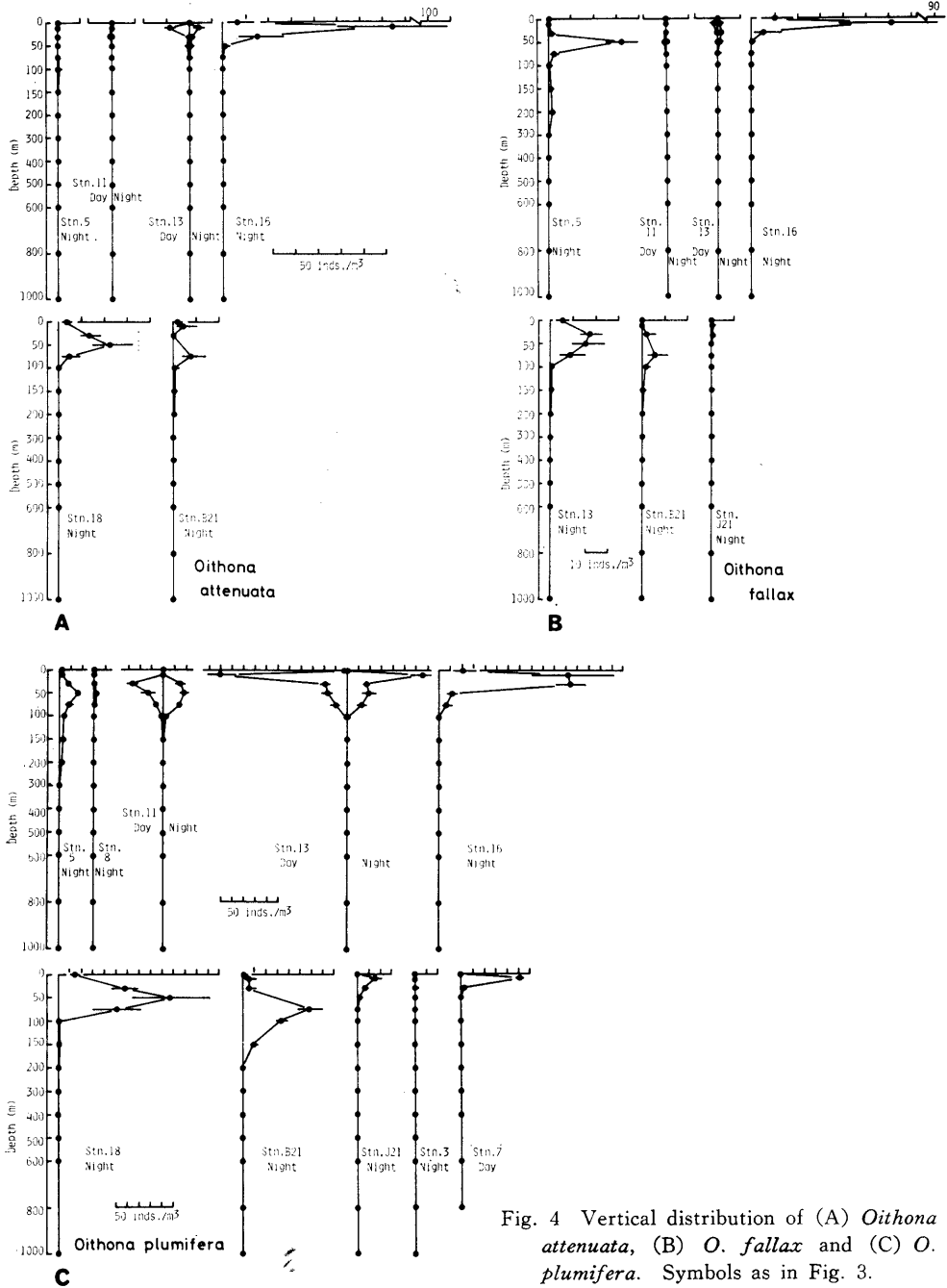


Fig. 4 Vertical distribution of (A) *Oithona attenuata*, (B) *O. fallax* and (C) *O. plumifera*. Symbols as in Fig. 3.

calculated the core of population as the layer between the 25 and 75% population number levels of the species (ZALKINA 1970b). Thus the core of population tends to be deeper than the layer of maximum density when a species is concentrated in shallow, thin layers but is also common in deeper waters. According to ZALKINA (1970a), the upper limit of the core of population of a cyclopid species corresponds to the depth of its maximum density. This may be a part of the reason why the layer with the maximum densities of *O. plumifera* in the present study is much shallower than the depths of the core of population observed by ZALKINA. Another cause of this difference may be the difference of sampling methods. Collections were made at six depths between 0 and 100 m in the present study, whereas they were made in three layers (0-25, 25-50 and 50-100 m) in ZALKINA's study. Apparently, the difference of densities within these layers is not detected by the latter method. Later ZALKINA (1977) examined the small-scale vertical distribution of Cyclopoida up to 10 m interval in the Sulu Sea and the waters of the North Trade Winds Current, and reported a marked oscillation of copepod densities from 0 to 100 m in *O. tenuis*, *O. plumifera* and *O. setigera*, all of which showed unimodal distribution at most stations in the present study. This difference, which is most remarkable in *O. plumifera*, is also attributable to the difference in sampling methods. Vertical hauls by 10 m intervals detect small-scale patches more effectively than long, horizontal hauls, which obtain a more generalized pattern of vertical distribution. BOXSHALL (1977) reported that at 18°N, 25°W in North Atlantic, *O. plumifera* was found mostly between 29 and 60 m and in much lower densities as deep as 1250 m (see p. 114, *O. atlantica*).

Oithona nana GIESBRECHT and *O. tenuis* ROSENDORN

These species showed vertical distributions similar to *O. plumifera* but a little deeper than the latter especially at Sts. 5, 8, 11 and 13 (Fig. 5). The difference between the former two species and the latter, however, is slight and almost undetectable in the Equatorial Water (Sts. 16, 18 and B21). The highest density of *O. nana* (about 140 indiv·m⁻³) was observed at 30 m of St. J21 in the warm current area in the Sea of Japan.

Oithona simplex FARRAN

Oithona simplex showed two conspicuous peaks of densities, one of which corresponds to the maximum layer of the upper epipelagic species and the other to that of the lower epipelagic species (see discussion). This was evident at St. 11 at night, at St. 13 both day and night, and at St. 18 (Fig. 5). The shallow peak was less conspicuous at St. 5 and absent at St. 8 in the Indian Central Water. This pattern of vertical distribution which is peculiar to *O. simplex* is related to the intraspecific variability of this species. In the inlet water, *O. simplex* occurs usually as the typical, short form, while in the oceanic water it occurs as the long form (NISHIDA 1981). If it is assumed that the surface mixed layers in the Equatorial Water were under strong influence of coastal waters, the individuals which constituted the shallow and the deep peaks are considered representatives of the two different populations, one of which was derived from the coastal water and the other from the oceanic subsurface water. A further analysis on the morphological variability in relation to the vertical distri-

bution is necessary.

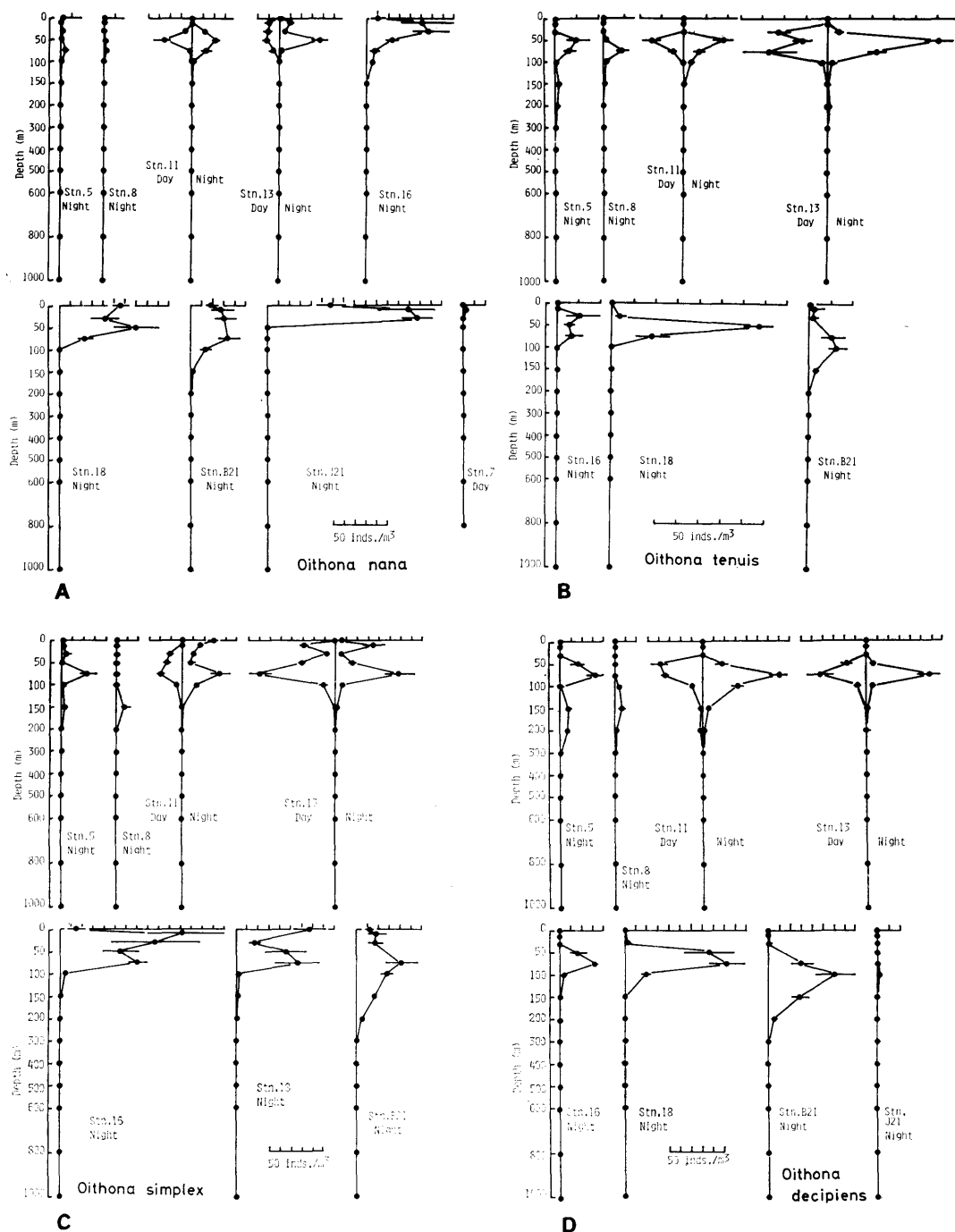


Fig. 5 Vertical distribution of (A) *Oithona nana*, (B) *O. tenuis*, (C) *O. simplex* and (D) *O. decipiens*. Symbols as in Fig. 3.

Oithona decipiens FARRAN, *O. setigera* DANA, *O. vivida* FARRAN and *O. robusta* GIESBRECHT

These four species were abundant and showed extremely similar patterns of vertical distribution throughout the area investigated (Figs. 5 and 6).

In the eastern Indian Ocean and the South China Sea, the major part of the population of these species occurred within the thermocline or the thermostad between the seasonal and permanent thermoclines except at St. 16, where the populations were concentrated in the lower part of the surface mixed layer. The marked decrease of individual densities from 75 to 100 m at this station corresponds to that of oxygen content from 75 ($3.45 \text{ ml}\cdot\text{l}^{-1}$) to 150 m ($0.17 \text{ ml}\cdot\text{l}^{-1}$). The depth of the maximum density of these four species coincides with that of subsurface chlorophyll *a* maximum, too. At St. J21 in the Sea of Japan only *O. decipiens*, *O. setigera* and *O. vivida* occurred in low densities in the lower part of the thermocline; the maximum densities were observed at 100 m. At St. 3 in the cold current area, on the other hand, none of these species occurred through the whole water column above 1000 m. In Suruga Bay only *O. setigera* and *O. robusta*, the large-sized species, were collected within and beneath the seasonal thermocline.

In all these species there was no marked difference between day and night vertical distributions at Sts. 11 and 13.

ZALKINA (1970b, 1972) reported that *O. setigera* had its core of population between 97 and 279 m in the halistatic zone of the Indian Central Water and between 76 and 214 m in the Indian Equatorial Water. Although the depths recorded by ZALKINA for the Central Water roughly coincide with the present results, in the Equatorial Water much shallower distribution was observed in the present study, probably due to the difference in the methods of sampling and data presentation. In the tropical Pacific ZALKINA (1970a) found the core of population of *O. robusta* between 87 and 135 m and that of *O. vivida* between 135 and 255 m, both occupying the lower part of the vertical range of oithonids. OWRE & FOYO (1967) recorded *O. setigera* as similar in vertical distribution to *O. robusta* which was fairly common between 127 and 274 m in the Caribbean. In the northeastern Atlantic BOXSHALL (1977) found *O. setigera* mostly between 55 and 194 m during the day and between 25 and 100 m at night. Although these authors showed only rough estimates of the vertical range, our observations agree with all these records in that they show that *O. setigera*, *O. robusta* and *O. vivida* are distributed in the deep epipelagic zone and avoid the surface mixed layer. There is no previous record quotable on the vertical distribution of *O. decipiens*.

Paroithona spp.

Vertical distribution of *Paroithona* spp. was investigated only to the generic level, principally due to the difficulties in the identification.

In the eastern Indian Ocean and the South China Sea, the major part of *Paroithona* spp. showed vertical distribution similar to that of the lower epipelagic species described above (see discussion). *Paroithona* spp. were scarce or missing in the surface mixed layers except

at St. 16. The abundance of this genus beneath the base of permanent thermocline at Sts. 5 and 8 may suggest the existence of some species adapted to the deeper layers. In the warm

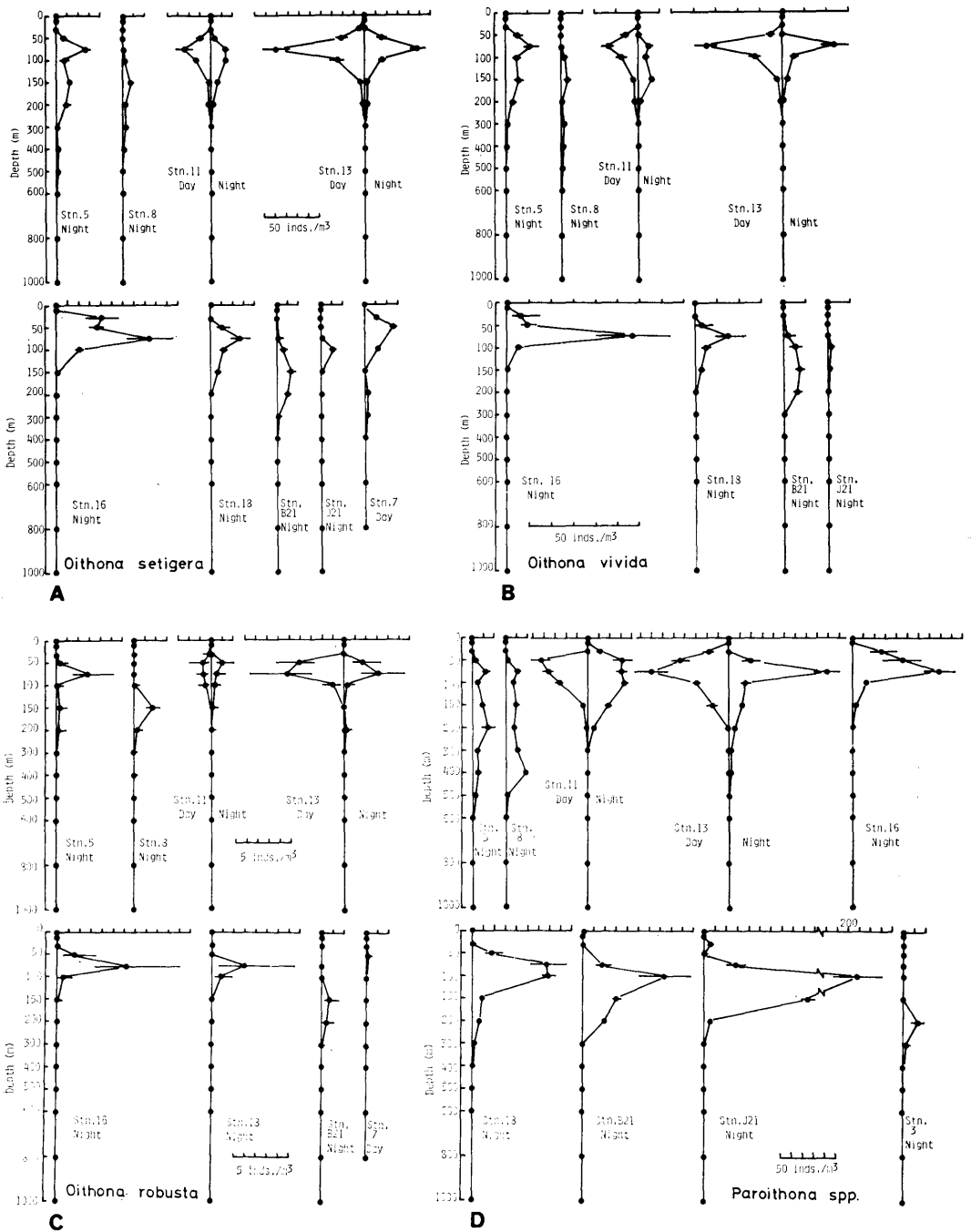


Fig. 6 Vertical distribution of (A) *Oithona setigera*, (B) *O. vivida*, (C) *O. robusta* and (D) *Paroithona* spp. Symbols as in Fig. 3.

current area of the Sea of Japan (St. J21) extremely high density (about $210 \text{ indiv} \cdot \text{m}^{-3}$) was observed at 100 m. In the cold current area (St. 3) *Paroithona* spp. occurred at 200 and 300 m in the deep cold water (Fig. 6).

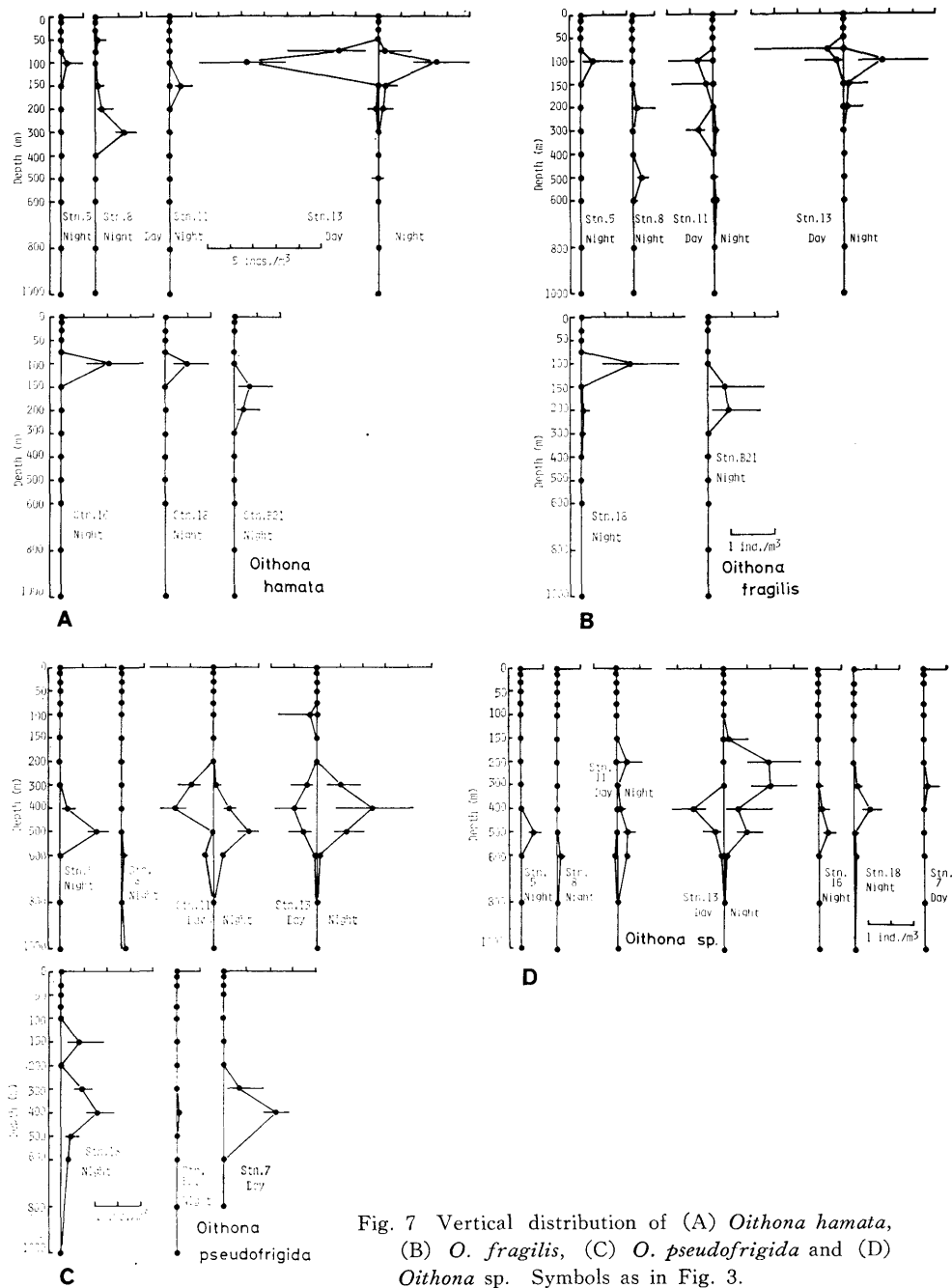


Fig. 7 Vertical distribution of (A) *Oithona hamata*, (B) *O. fragilis*, (C) *O. pseudofrigida* and (D) *Oithona* sp. Symbols as in Fig. 3.

Oithona hamata ROSENDORN and *O. fragilis* NISHIDA

These two species were scarce, the density being less than $6 \text{ indiv} \cdot \text{m}^{-3}$, and occupied the deepest layer of the epipelagic zone. In the eastern Indian Ocean and the South China Sea, they occurred mostly beneath the upper part of the thermocline except at Sts. 13 and 16, where they were collected in the upper part of the thermocline, too. They did not occur in the Sea of Japan. The absence of these species from Suruga Bay may be due to the coarse mesh of the nets used.

Oithona pseudofrigida ROSENDORN and *Oithona* sp.

Oithona sp., an undescribed species, resembles both *O. vivida* FARRAN, 1913, and *O. pseudovivida* SHUVALOV, 1980, but is slightly different from the former in the body length and the shape of genital segment and from the latter in the body length, the shape of rostrum and armature of mandible (NISHIDA 1981). *Oithona pseudofrigida* and *Oithona* sp. occurred in most cases in the layers deeper than the base of permanent thermocline (Fig. 7). They occurred, although in low densities, at all the stations in the eastern Indian Ocean and the South China Sea except at St. 16, where *O. pseudofrigida* was missing. They were not collected in the Sea of Japan, from either the cold or warm current areas. The absence of *Oithona* sp. in Suruga Bay, where *O. pseudofrigida* occurred in densities comparable to other regions, may be due to mesh escapement. There is no previous record on the vertical distribution of these species.

Oithona similis CLAUS

Oithona similis, a bipolar species, was absent from the whole water column above 1000 m at Sts. 5, 11, 13, 16, 18 and B21. The negligible occurrence of *O. similis* at 500 m (about $0.2 \text{ indiv} \cdot \text{m}^{-3}$) in the Indian Central Water (St. 8) indicates expatriation from the subantarctic region (Fig. 8).

In the warm current area of the Sea of Japan (St. J21) the densities of *O. similis* were high at 30 and 50 m ($300\text{--}400 \text{ indiv} \cdot \text{m}^{-3}$) but a little lower above 10 m and between 75 and 150 m, where the upper and lower epipelagic, warm water species predominated, respectively. *Oithona similis* was found in significant densities beneath the thermocline, too, where warm water species were missing. At St. 3 where the influence of the Tsushima Warm Current was minimal, extremely high densities (about $3000 \text{ indiv} \cdot \text{m}^{-3}$) were observed at 10 m, accompanied by marked decrease at other depths. In Suruga Bay *O. similis* was collected in low densities only in the upper 30 m, probably due to mesh escapement.

FURUHASHI (1966) reported that *O. similis* was common throughout the whole layers above 1646 m in the Oyashio region off Hokkaido. MINODA (1971), who investigated the Bering Sea and the northwestern North Pacific, found *O. similis* through wide vertical range from the surface to more than 1000 m and noted a remarkable abundance of this species in the upper 50 m.

Oithona atlantica FARRAN and *O. longispina* NISHIDA

Oithona atlantica and *O. longispina*, closely allied species (NISHIDA et al. 1977), occupy

different geographical ranges in North Pacific; the former is distributed in the Subarctic Water and the latter in the tropical and subtropical waters (NISHIDA 1981), with some overlap in the transition region. They were not collected in the eastern Indian Ocean north of 20°S except at St. 8, where *O. atlantica* and *O. longispina* occurred at 600 and 150 m, respectively, and at St. 11, where only *O. longispina* occurred at 75 and 100 m.

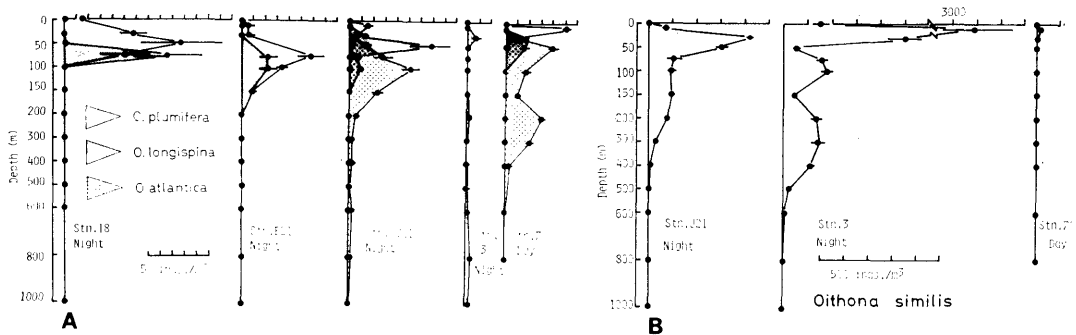


Fig. 8 Vertical distribution of (A) *Oithona plumifera*, *O. longispina* and *O. atlantica* and (B) *O. similis*. Symbols as in Fig. 3.

Fig. 8 shows the vertical distributions of these species and of *O. plumifera* in the western border of North Pacific. Although FARRAN (1908) clearly demonstrated morphological differences between *O. plumifera* and *O. atlantica*, the latter has often been considered a variety of the former by more recent workers (SHUVALOV 1972, NISHIDA et al. 1977). In cold current area of the Sea of Japan (St. 3) where *O. plumifera* and *O. longispina* were missing, *O. atlantica* occurred in low densities intermittently from 0 through 1000 m. In warm current area of the Sea of Japan (St. J21) and in Suruga Bay, *O. atlantica* dominated the lower epipelagic and mesopelagic zones, while *O. plumifera* and *O. longispina* were distributed mostly in the upper 30 m and between 30 and 100 m, respectively. In the South China Sea where *O. atlantica* was missing, *O. longispina* was distributed a little deeper than *O. plumifera*, principally in the upper part of the thermocline.

No previous record is known on the vertical distribution of *O. atlantica* and *O. longispina* except that by BRADFORD (1972), who briefly stated that in the coast of New Zealand *O. atlantica* was often abundant at 100 m. The vertical range of *O. plumifera* has been reported as 70 to 200 m in the Bering Sea (MINODA 1971), 0 to 5200 m in the Caribbean (MICHEL & FOYO 1976) and 0 to 1250 m in North Atlantic (BOXSHALL 1977), although *O. plumifera* was restricted to the epipelagic zone (0 to 200 m) of tropical and subtropical waters in the present study. The specimens identified as *O. plumifera* by previous authors may include *O. atlantica* whose vertical range reaches much deeper than that of *O. plumifera*.

Biological zonation

Fig. 9 shows an idealized vertical zonation of the oithonids in the tropical and subtropical waters. The most distinct difference of species composition exists between the epipelagic and

mesopelagic zones in the sense of VINOGRADOV (1968, p. 245), i. e. zones recognized in various zooplankton taxa. Thirteen species were found in the epipelagic zone and only two species, *O. pseudofrigida* and *Oithona* sp., in the mesopelagic zone. Hydrographically, the epi- and mesopelagic zones are separated by the base of permanent thermocline throughout the area investigated in the present study, although the lower epipelagic species sometimes extended slightly deeper than this boundary. The other species are mostly restricted to the epipelagic zone, each occupying a stratum peculiar to the species or a species group.

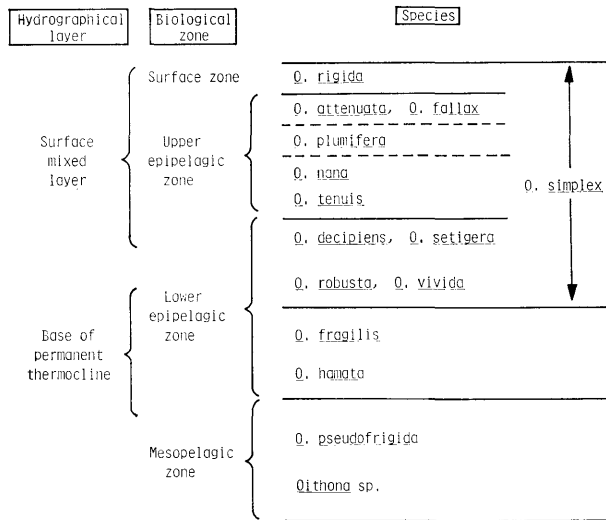


Fig. 9 A schematic diagram showing the vertical zonation within the *Oithona* species in the tropical and subtropical waters.

As the occurrence of *O. rigida* in superficial layers are considered expatriation from coastal waters, it is concluded that no oithonids are neustonic, distributed specifically in superficial layers, or surface films, of oceanic waters (see ZAITSEV 1971). The epipelagic zone can be further divided into two sub-zones: the upper and lower epipelagic zones. The upper epipelagic zone is characterized by species more or less associated with the surface mixed layer, while the lower epipelagic zone lies mostly between the mixed layer and permanent thermocline. Among the upper epipelagic species, *O. attenuata* and *O. fallax* tend to occupy the uppermost layer; *O. plumifera*, *O. nana* and *O. tenuis* are progressively deeper. Differences in the vertical distributions among these species, however, are slight and undetectable in some cases. Two distinct groups are recognized among the lower epipelagic species. *Oithona decipiens*, *O. robusta*, *O. setigera* and *O. vivida* showed extremely similar vertical distributions and are considered sympatric both geographically and vertically, as is the case with *O. fragilis* and *O. hamata*, which constitute the other group inhabiting a somewhat lower layer.

The vertical zonation of the oithonid species described above was consistent at all the stations investigated. In the tropical Pacific ZALKINA (1970a) reported the "step-like distribution" among *O. tenuis*, *O. plumifera*, *O. robusta* and *O. vivida* in this order from the

uppermost to deepest depths. In the eastern Indian Ocean, the waters of the North Trade Winds Current and the Sulu Sea the same author observed the following order of species from the uppermost to lowest steps: *O. tenuis*, *O. plumifera*, *O. setigera* (ZALKINA 1972, 1977). The present observation roughly coincides with these records except for the displacement between *O. tenuis* and *O. plumifera*. The cause of this displacement is unknown.

Ecological significance of vertical zonation in the oceanic zooplankton has been discussed by VINOGRADOV (1968), who noted the following generalities: (1) in marine pelagic biocenoses occupying rather homogeneous biotopes, ecological differences depend primarily upon feeding characteristics of the species forming these biocenoses; (2) if they live close together, related species should strongly differ in size of their food and in their own size; (3) the principle of competitive elimination should lead to a sharper vertical change in fauna than would be determined only by the effect of the change in the external abiotic conditions. Based on WICKSTEAD (1962), ZALKINA (1970a) considered that all Cyclopoida exhibit a similar type of feeding, and interpreted the "step-like distribution" of Cyclopoida as demonstrating the third

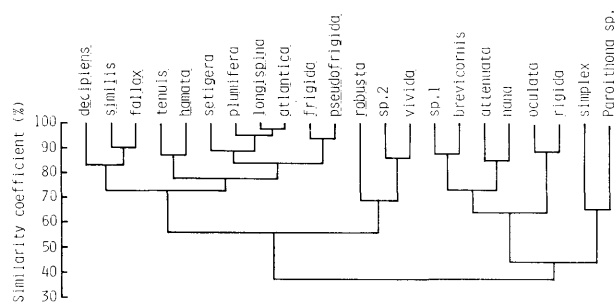


Fig. 10 A dendrogram showing the morphological relationships among 22 species of Oithonidae, analyzed by the complete linkage clustering method (cited from NISHIDA 1981). The analysis is based on the 45 morphological characters observed in each species. The generic name is omitted in the *Oithona* species. The species "sp. 2" indicates *Oithona* sp. in the present study, while does "sp. 1" an inlet species which did not occur in the present study.

principle. The present study, however, showed that several oithonid species can coexist in the same layer, as observed in *O. decipiens*, *O. setigera*, *O. robusta* and *O. vivida*. This suggests that the species in the same layer do not compete for food, and/or they have different feeding habits, although they are congeneric. In this connection, it is interesting to compare the morphological relationships among oithonids with their vertical distributions. Figs. 9 and 10 (cited from NISHIDA 1981) show that the species with similar vertical distributions are morphologically separated from each other, and the allied species, at least the members of a closest species pair, have dissimilar vertical distributions. Thus, *O. plumifera* is vertically separated from closely allied species, *O. setigera*. Other related species that are vertically segregated are: *O. fallax* from *O. decipiens* and *O. vivida* from *Oithona* sp. *Oithona simplex*, morphologically distinct from any other species, is distributed over three different zones and has the broadest vertical distribution. Although these coincide with the

principles quoted above, the possibility of the competition for food among congeneric species with similar vertical distributions should be established directly by measuring the mouthpart morphology, food requirements and gut contents of these species.

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Literature Cited

- BOXSHALL, G. A., 1977. The depth distribution and community organization of the planktonic cyclopoids (Crustacea: Copepoda) of the Cape Verde Islands region. *J. mar. biol. Ass. U. K.*, **57**: 543-568.
- BRADFORD, J. M., 1972. Systematics and ecology of New Zealand central east coast plankton sampled at Kaikoura. *Bull. N. Z. Dep. scient. ind. Res.*, **207**, 87 pp.
- DEEVEY, G. B., 1948. The zooplankton of Tisbury Great Pond. *Bull. Bingham oceanogr. Coll.*, **12**: 1-44.
- FARRAN, G. P., 1908. Note on the copepod genus *Oithona*. *Ann. Mag. nat. Hist.*, pt. 8, **2**: 498-503.
- FARRAN, G. P., 1913. Plankton from Christmas Island, Indian Ocean, II: On Copepoda of the genera *Oithona* and *Paroithona*. *Proc. zool. Soc. Lond.* **1**: 181-193.
- FISH, C. J., 1936. The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Biol. Bull. mar. biol. Lab., Woods Hole*, **71**: 168-187.
- FURUHASHI, K., 1966. Studies on the vertical distribution of copepods in the Oyashio region east of Japan and in the Kuroshio region south of Japan. *Publ. Seto mar. biol. Lab.*, **14**: 295-322.
- HUMES, A. G. and R. V. GOODING, 1964. A method for studying the external anatomy of copepods. *Crustaceana*, **6**: 238-240.
- ISHIMARU, T., 1978. *Taxonomical and Ecological Study on Coccolithophorids*. Ph. D. Thesis, Univ. Tokyo, Tokyo, 219 pp. (In Japanese)
- JAPAN FISHERIES AGENCY, 1979. *The Results of Fisheries Oceanographical Observation, January-December 1974*. Japan Fisheries Agency, Tokyo, 1076 pp.
- MARSHALL, S. M., 1949. On the biology of the small copepods in Loch Striven. *J. mar. biol. Ass. U. K.*, **28**: 45-122.
- MICHEL, H. B. & M. FOYO, 1976. Caribbean zooplankton. Part I- Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae, pp. 1-549. In *Caribbean Zooplankton*. Office of Naval Research, Dept. of the Navy, Washington, D. C.
- MINODA, T., 1971. Pelagic Copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. *Mem. Fac. Fish. Hokkaido Univ.*, **18**: 1-74.
- MOTODA, S., 1971. Devices of simple plankton apparatus V. *Bull. Fac. Fish. Hokkaido Univ.*, **22**: 101-106.
- NISHIDA, S., 1981. *Taxonomic and Ecological Studies on the Copepod Family Oithonidae in the Pacific and Indian Oceans*. Ph. D. Thesis, Univ. Tokyo, Tokyo, 346 pp.
- NISHIDA, S., O. TANAKA & M. OMORI, 1977. Cyclopoid copepods of the family Oithonidae in Suruga Bay and adjacent waters. *Bull. Plankton Soc. Japan*, **24**: 43-82.
- OWRE, H. B. & M. FOYO, 1967. Crustacea. Part I: Copepoda. Copepods of the Florida Current.

- Fauna Caribaea*, **1**: 1-137.
- SHUVALOV, V. S., 1972. Geographical variability of some species of the family Oithonidae (Copepoda, Cyclopoida), pp. 169-185. In *Geographical and Seasonal Variability of Marine Plankton* (ed. ZVEREVA, ZH. A.). Nauka, Leningrad. (English translation, I. P. S. T., Jerusalem, 1975)
- SHUVALOV, V. S., 1980. *Cyclopoid Copepods of the Family Oithonidae in the World Ocean*. Nauka, Leningrad, 198 pp. (In Russian)
- SULLIVAN, B. K., 1980. In situ feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station "P". *Limnol. Oceanogr.*, **25**: 317-326.
- SYSOEVA, T. K. & A. A. DEGTEREVA, 1965. The relation between the feeding of cod larvae and pelagic fry and the distribution and abundance of their principal food organism. *Spec. Pubs int. Commn NW. Atlant. Fish.*, **6**: 411-416.
- TANAKA, S. (ed.), 1979. *Preliminary Report of the Hakuho Maru Cruise KH-76-3*. Ocean Research Institute, Univ. Tokyo, Tokyo, 50 pp.
- VENRICK, E. L., 1978. How many cells to count? pp. 167-180. In *Phytoplankton Manual* (ed. SOURNIA, A.). Unesco, Paris.
- VINOGRADOV, M. E., 1968. *Vertical Distribution of the Oceanic Zooplankton*. Nauka, Moscow. (English translation, I. P. S. T., Jerusalem, 1970), 339 pp.
- WICKSTEAD, J. H., 1962. Food and feeding in pelagic copepods. *Proc. Zool. Soc. Lond.*, **139**: 545-555.
- WYRTKI, K., 1973. Physical oceanography of the Indian Ocean, pp. 18-36. In *The Biology of the Indian Ocean* (ed. ZEITSCHER, B. & S. A. GERLACH). Springer Verlag, Berlin, Heidelberg, New York.
- ZAITSEV, YU. P., 1970. *Marine Neustonology*. Naukova Dumka, Kiev. (English translation, I. P. S. T., Jerusalem, 1971), 207 pp.
- ZALKINA, A. V., 1970a. Vertical distribution and diurnal migration of some Cyclopoida (Copepoda) in the tropical region of the Pacific Ocean. *Mar. Biol.*, **5**: 275-282.
- ZALKINA, A. V., 1970b. The distribution of copepod Cyclopoida in the northeastern part of the Indian Ocean. The Cyclopoida biomass and the horizontal distribution of some species. *Okeanologiya*, **10**: 388-397.
- ZALKINA, A. V., 1972. Vertical distribution and diurnal migration of Cyclopoida (Copepoda) in the northeastern Indian Ocean. *Okeanologiya*, **12**: 566-576.
- ZALKINA, A. V., 1977. Vertical distribution and diurnal migration of Cyclopoida (Copepoda) in the waters of the North Trade Winds Current and the Sulu Sea. *Pol. Archm Hydrobiol.*, **24** (Suppl.): 337-362.