

Biology of Cladocerans and Copepods in Ise Bay — 2
Vertical Distribution of Neritic Copepods in Relation
to their Life Histories

By

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Ontogenetic change of vertical distribution of copepods was investigated in detail with Van-Dorn water sampler during the daytime in three occasions in Ise Bay along the Pacific coast of central Japan. We placed great importance on the dominant copepods such as *Acartia clausi*, *Calanus sinicus*, *Paracalanus parvus* and *Oithona brevicornis*. The copepods, *Acartia*, *Calanus* and *Paracalanus*, which shed eggs free in water, showed remarkable ontogenetic change. The eggs and nauplii were found largely in 2-8 m layers; the adults in the water much close to the bottom of the bay; the copepodites in the intermediate layers. Three results indicate that to sample copepods quantitatively during the daytime is difficult. Furthermore, our investigation showed that any life stage, especially the eggs, were always found in aggregations. This suggests that the adult females tend to swarm for releasing their eggs, presumably at night. On the other hand, *Oithona* which carries eggs until nauplii emerge did not show such ontogenetic change. This copepod was found mainly in 0-8 m layers through the life cycle.

Key words: ontogenetic, vertical distribution, copepods

Zooplankton communities generally show marked spatial and temporal changes in the neritic waters where the water is rich in nutrients and highly turbid due to freshwater discharge, sewage effluent and active production of phytoplankton. In the waters zooplanktons are often represented by a small number of the dominant species. This is the case with the free-living neritic copepods which by far outnumber the other components of the zooplankton communities (JEFFRIES, 1967; SEKIGUCHI, 1978). These copepods must have developed various responses or adaptations in evolutionary process for succeeding to reproduce and to maintain their populations in the particular environments. Thus, potential competitors have come to be segregated through mutually exclusive combination of spatial, temporal and biological

attributes (MARSHALL, 1979), so that various behavior including vertical distribution patterns tend to reduce interspecific competition among the copepods with similar nutritional habits (ZALKINA, 1970).

Specific features of vertical distribution and migration of the neritic copepods would play an important role in reducing potential competition among them in the environments. Up to date, various aspects of the vertical distribution of the copepods have been studied to considerable extent (e.g., VINOGRADOV, 1968; MILLER, 1970). These previous works, however, were only concerned with the late copepodites including the adult stage. In contrast to cold water oceanic copepods of which their ontogenetic vertical migration plays an important role in functioning communities along with a superior adaptation for continuing to maintain their populations (HEINRICH, 1962; VINOGRADOV, 1968; SEKIGUCHI, 1975), it has generally been emphasized that diel vertical migration is more important than ontogenetic migration in the neritic zooplankton (MCLAREN, 1963; ZARET and SUFFERN, 1976). Only little is known about the ecological roles of the ontogenetic vertical migration in the neritic copepods. The present study examines various types of the ontogenetic vertical distribution of the neritic copepods in Ise Bay for better understanding interspecific relation among the copepods.

Materials and Methods

General description on topographic and oceanographic conditions of Ise Bay, which is located along the Pacific coast of central Japan, have been given in my previous paper (SEKIGUCHI, 1978).

Studying area is shown in Fig. 1. Eight sampling stations were established on a transect from "Tsu" to "Noma": each station is separated at the distance of 3.7 kilometers. Sampling zooplankton and routine oceanographic observation were made during the daytime at these stations on Aug. 11 1980, Nov. 28 1980 and May 21 1981. In each time, the work in the sea was accomplished within 4 hours.

A 20 liters of seawater was sampled with the Van-Dorn sampler from each depth of the water column at each station: the depth intervals were 2 meter from

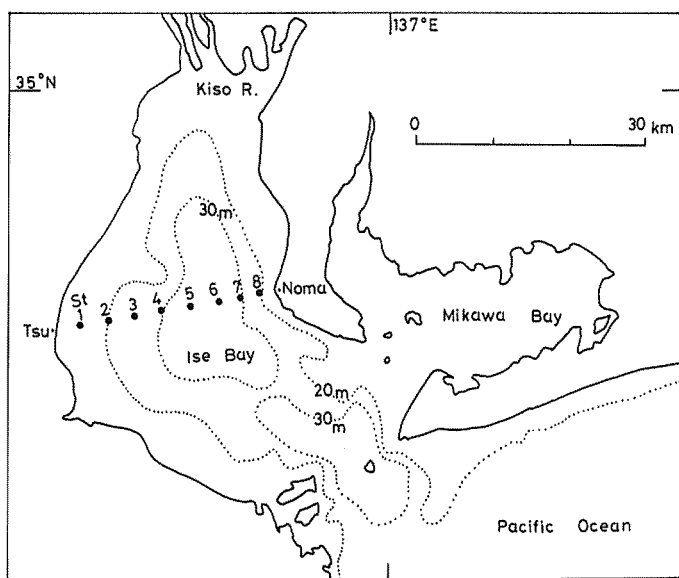


Fig. 1. Study area and sampling positions.

the surface to 10 m depth, and 5 meter from 10 m depth down to the bottom. Sometimes the water from 1 m above the sea floor was also sampled. These water was then strained through a net with $45\ \mu\text{m}$ mesh—openings on board and the samples were immediately fixed with 10% neutralized formalin.

The net with $45\ \mu\text{m}$ mesh—openings was sufficient for catching all developmental stages of major dominant copepods belonging to the genera *Acartia*, *Calanus*, and *Paracalanus* in Ise Bay. Close inspection of *Oithona brevicornis*, however, indicated that the first naupliar stage was not contained in the samples probably due to their passing through the net; the second nauplius was not so many sampled.

The copepod egg and nauplius were generally identified by comparison with those obtaining from mature females of the wild copepods kept in my laboratory. As occasion calls, identification of the nauplii of the copepods was made following the published papers (OBERG, 1906; CONOVER, 1956; FABER, 1966; UCHIMA, 1979).

The water temperature, salinity, dissolved oxygen contents, and chlorophyll *a* were measured at every sampling stations. Chlorophyll *a* was measured by a fluorescent method with sample water of 50–300 ml.

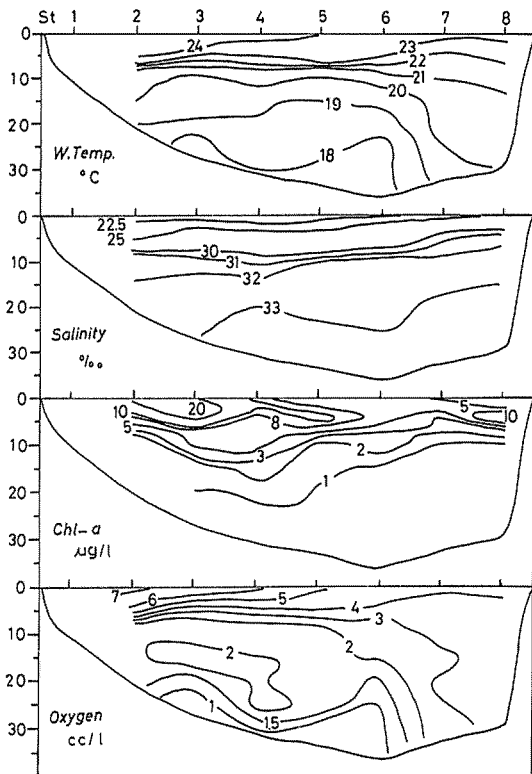


Fig. 2a. Profile of water temperature, salinity, dissolved oxygen and chlorophyll *a* contents in August 1980.

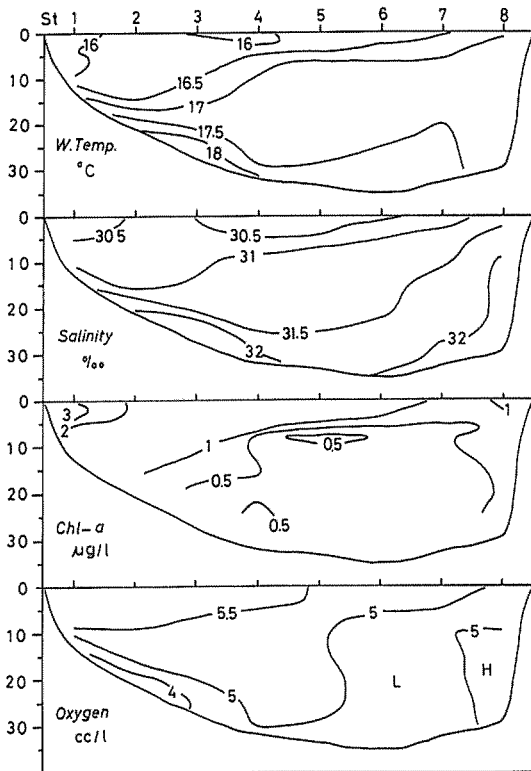


Fig. 2b. In November 1980.

1. Oceanographic conditions Aug. 1 1980 (Fig. 2 a)

Profiles of water temperature and salinity indicated strong summer stratification: steep thermocline and halocline developed around 8 m depth. Brackish water, characterized with more than 20 ‰ and less than 30 ‰, was probably originated from the freshwater discharge of the Kiso River in the innermost part of the bay, it prevailed in the water shallower than 10 m depth. The brackish water was deeper in the western part than in the eastern part of the bay. Dense phytoplankton population (over 5 $\mu\text{g chl./l}$) which were composed mainly of the dinoflagellates was found above the thermocline and was remarkable in the surface water in the western part of the bay; below the thermocline phytoplankton was less than 1 $\mu\text{g chl./l}$. The oxygen contents were high above the thermocline, while it was less than 2 ml/l below that excluding the eastern part of the bay. It was extremely low (less than 1 ml/l) in the water close to the bottom in the central part of the bay.

Nov. 28 1980 (Fig. 2 b)

Profiles of water temperature and salinity indicated that steep thermocline and halocline in summer disappeared and vertical mixing was advanced to some extent. The temperature ranged 16 – 18 °C, the salinity 30.5 – 32.5 ‰, and the oxygen contents were relatively high to be 3.5 ml/l or above. The water close to the bottom in the western part of the bay showed lower oxygen contents than that in the central to eastern parts. Apart from the water close to the bottom, population density of phytoplankton was generally low (less than 2 $\mu\text{g chl./l}$): it was less than 1 $\mu\text{g chl./l}$ in the water deeper than 10 m depth.

Results

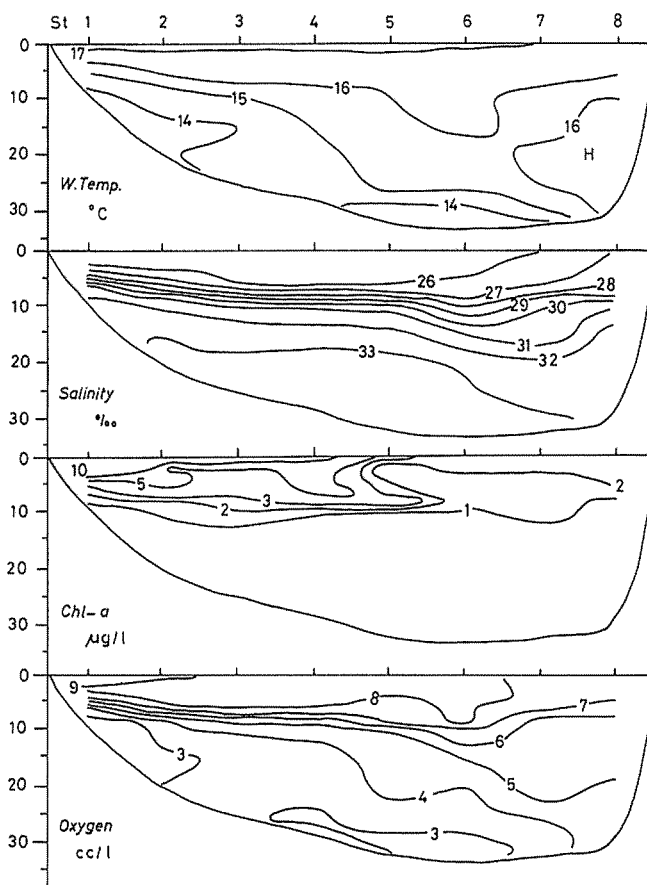


Fig. 2 c. In May 1981.

May 21 1981 (Fig. 2c)

The temperature was 14 – 17 °C, and thermocline was not pronounced as that observed in summer. The brackish water existed widely above 6 m depth and results steep halocline at 4 – 8 m depths. Dense population of phytoplankton (over 5 µg chl./l) was found in the surface water in the western part of the bay as same as in summer. Generally speaking, below the halocline phytoplankton was not abundant. The oxygen content was high being over 6 ml/l in the water shallower than 10 m depth and highest in the surface water in the western part of the bay. It was also high in the deep water in the eastern part of the bay and even in the water close to the bottom.

2. Vertical distribution of the copepods

The four copepods, *Acartia clausi*, *Calanus sinicus*, *Paracalanus parvus* and *Oithona brevicornis* by far outnumbered other copepods including the *Centropages*, *Temora*, *Oncaea* and *Corycaeks*. *Acartia clausi* and *O. brevicornis* were dominant on Aug. 11, whereas *A. clausi*, *O. brevicornis* and *P. parvus*, and *A. clausi* and *C. sinicus* were numerous on Nov. 28 and May 21, respectively.

2 – 1. *Acartia clausi*

Aug. 1 1980 (Fig. 3a)

The eggs and nauplii were mainly found above or in the thermocline, while the copepodites and adults were largely sampled below it. Thus, the *Acartia* populations moved from the surface water down to the bottom sediments through the life history. They made aggregation at each life stage. Phytoplankton was remarkably concentrated in the surface water in the western part of the bay, while the *Acartia* populations were found mainly in the eastern part of the bay.

The distributional pattern of the eggs and nauplii showed resemblance, largely localized in the eastern part of the bay. The highest density of the copepodites was in the eastern part of the bay. The nauplii and copepodites were concentrated in the belt-shaped zone at a different layer in the eastern part of the bay, the nauplii at 4 – 8 m and the copepodites at 10 m depth, respectively. The distributional pattern of the adults was much different from that of the younger stages: they occurred in the water close to the bottom. The adults tended to avoid the water of extremely low oxygen contents (less than 1 ml/l) close to the bottom.

Nov. 28 1980 (Fig. 3b)

The *Acartia* populations did not show considerable change of vertical distribution in relation to their life history. Apart from the eggs, they remained in the shallower water than 10 m depth, though they were largely localized in the western to central parts of the bay. They aggregated at each life stage. However, it was difficult to find certain relation between the vertical distribution of the copepods and the oceanographic conditions.

The eggs and nauplii occurred mainly in the central part of the bay where they were abundantly found from the surface to the bottom, with the highest density in the surface water. The copepodites were abundant in the western part, with the highest density in the surface water. The adults aggregated in the water close to the bottom in the western part, and in the surface water in the central part.

May 21 1981 (Fig. 3 c)

The *Acartia* populations tended to touch off from the water close to the bottom through all the stage, though this tendency was not so remarkable as observed in summer. They were relatively abundant in the central to eastern parts of the bay, while the converse was true in phytoplanktons.

The eggs, sampled mainly in the surface water, were abundant in the eastern part of the bay, and the nauplii showed aggregation in the surface water in the central part. The copepodites aggregated in the western part and also in the eastern part of the bay. The distributional pattern of the adults was similar to that of the copepodites, although they occurred in the deeper water than the copepodites. They aggregated in the eastern part of the bay.

2 - 2. *Calanus sinicus*

May 21 1981 (Fig. 3 c)

The *Calanus* populations moved from surface waters to near sea floor with progress of the development. Thus, remarkable difference was seen in vertical distributions especially between the adults and eggs. They tended to aggregate in all the stage.

The eggs densely occurred in the surface water where the brackish water prevailed. Two centers of aggregation were detected: one was in the western part, and the other in the eastern part of the bay. The nauplii were concentrated in the surface water in the central part of the bay. The distributional pattern of the copepodites was different from that of the eggs and nauplii: they were largely localized in the eastern part of the bay and occurred wholly from the surface to the bottom waters. The adults were found only in the water column within 5 m above the bottom.

2 - 3. *Paracalanus parvus*

Nov. 28 1980 (Fig. 3 b)

The *Paracalanus* populations showed ontogenetic movement from the surface water to the bottom water. Thus, difference of vertical distribution was striking between the adults and the other developmental stages. They aggregated at each life stage.

In the central part of the bay, the eggs abundantly occurred from the surface to the water close to the bottom: the center of aggregation was at 10 m depth. The nauplii were concentrated in the surface water in the central part of the bay. The copepodites were mainly in the surface water and showed two centers of the aggregation: one was in the western

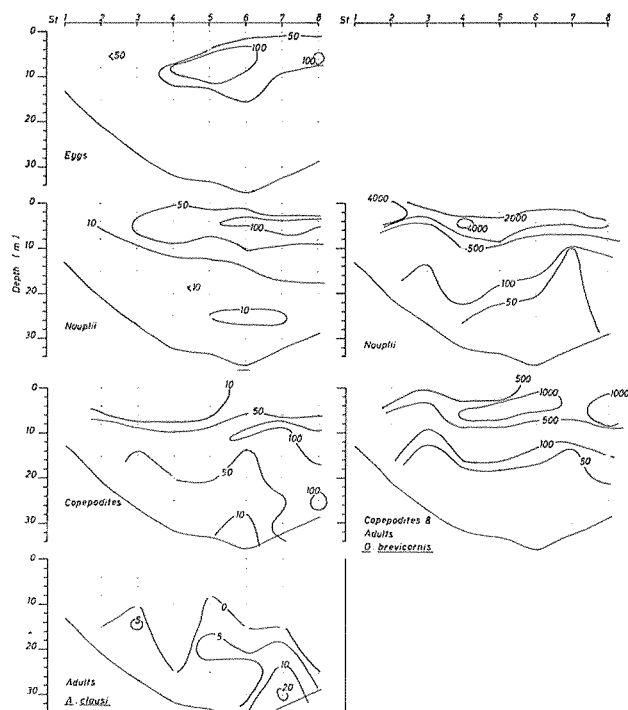


Fig. 3 a. Vertical distribution of the egg, nauplius, copepodite and adult of the copepods in August 1980. Numbers indicate those of each life stage of the copepods contained in 20 liter seawater.

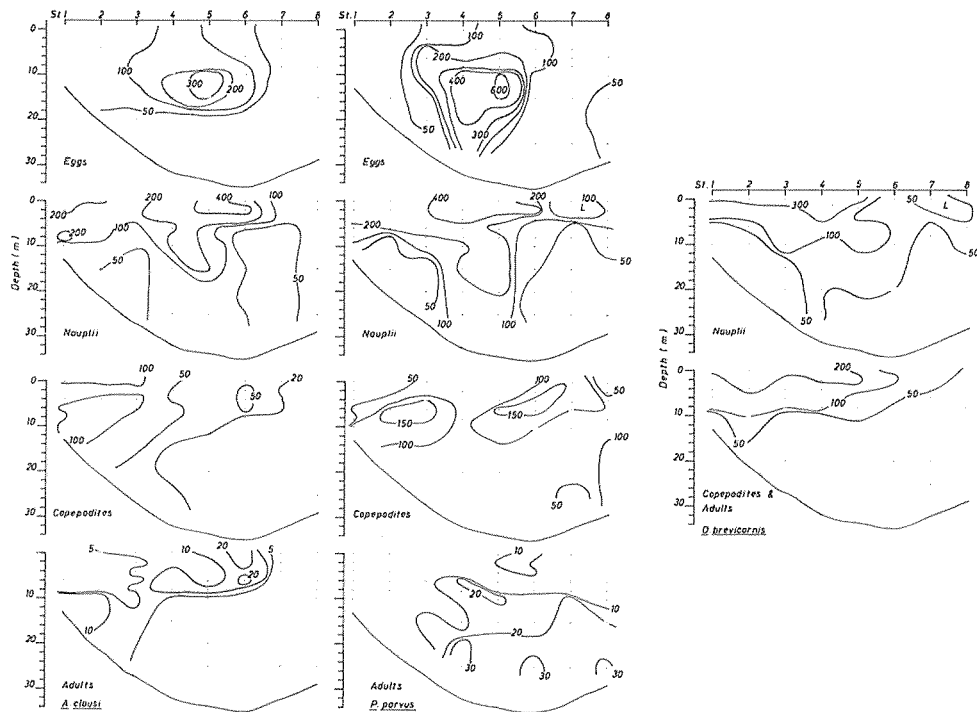


Fig. 3 b. In November 1980.

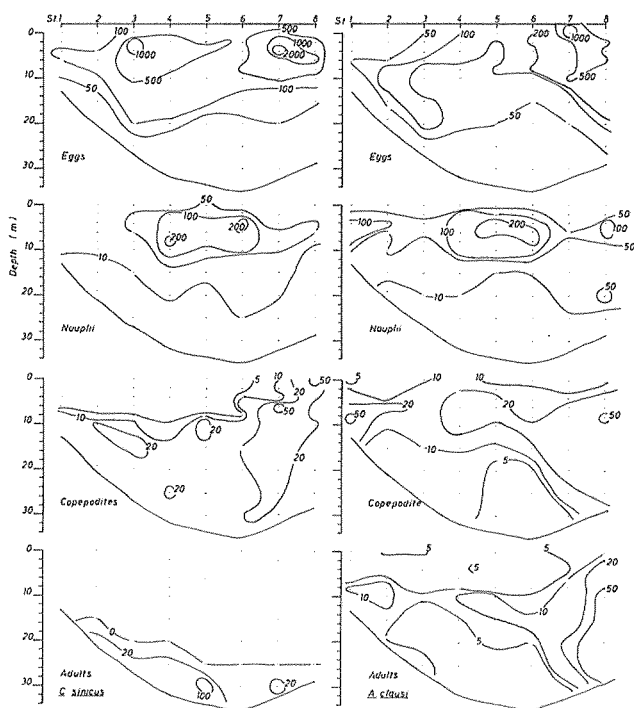


Fig. 3c. In May 1980.

part, and the other in the eastern part of the bay. The vertical distribution of the adults was different from those of the younger stages: they occurred below 10 m depth, especially abundant in the water close to the bottom in the central to eastern parts of the bay.

2 - 4. *Oithona brevicornis*

The *Oithona* populations did not change their inhabiting layers through the life history. The vertical distribution of the early stages (the eggs and nauplii) of *Oithona* was similar to that of *Acartia*, *Calanus* and *Paracalanus* of the same stages, but it was remarkably different in the later stages. They also made aggregation at each life stage.

Aug. 1 1980 (Fig. 3a)

The nauplii occurred mainly in the surface water, where the brackish water prevailed (the highest density of 241 inds./l in the western part of the bay). They were remarkably concentrated into a thin belt zone expanding through all the sampling stations. The copepodites and adults were found mainly in the surface water. The two centers of the aggregation were found: one was in the central part, and the other in the eastern part of the bay.

The *Oithona* were more numerous distributed above the thermocline than below it through the life history. The nauplii abundantly occurred in the surface water in the western part of the bay where phytoplankton was remarkably concentrated up to over 10 $\mu\text{g chl./l.}$

Nov. 28 1980 (Fig. 3b)

The nauplii were concentrated into a thin belt zone in the surface water in the western to central parts of the bay with the highest density of 20 inds./l. The vertical distribution of the copepodites and adults was similar to that of the nauplii, with the highest density of 14 inds./l.

Discussion

Based on the present study, the features of vertical distribution of the four copepod species can be divided into two types: (1) remarkable ontogenetic change of vertical distributions from the surface to the water close to the bay bottom through their life histories (*Acartia*, *Calanus* and *Paracalanus*), and (2) vertical distribution showing resemblance through the life history (*Oithona*). The *Oithona* was always found in the surface water. The copepods are also divided into two groups concerning the spawning types: the *Acartia*, *Calanus* and *Paracalanus* lay their eggs in water, while the *Oithona* carries egg sac until nauplii emerge. Accordingly, we suppose that the neritic copepods laying their eggs in water would show remarkable ontogenetic change of their inhabiting layer from the surface to the water close to the bottom.

In the previous studies of boreal oceanic copepods (*Calanus cristatus*, *C. plumchrus* and *Eucalanus bungii bungii*) (SEKIGUCHI, 1974, 1975), the large-scale ontogenetic * vertical migration was found only in the copepods which lay their eggs in water and the nauplii of which should feed on phytoplankton abundant in the surface water. On the other hand, the deep-sea copepods such as the *Pareuchaeta* which carries egg sac and the nauplii of which lack functional masticatory organ to stop active feeding during naupliar stages did not change their inhabiting layer through the life history. Not all the copepods laying their eggs in water, however, show a large scale ontogenetic vertical migration. In the present study, the extent of the ontogenetic vertical migration of the neritic copepods was a small-scale (i.e. less than the range of diel vertical migration) and this would probably be related to the shallow bottom of the bay (ANRAKU, 1975; LANDRY, 1978).

A remarkable difference of vertical distributions was detected between the eggs and adults during the daytime (Fig. 3a,b,c). This would be explained by assuming that the eggs would be released by the adults migrating upward at night (see, MOTODA et al., 1971) and occurring in the bottom water during the daytime. In addition, high density of the eggs in the surface water suggests that these eggs would have been laid in the surface water during the night, because abundant eggs ought to be found also in the water close to the

* "large-scale" means to much exceed the range of diel migration.

bottom if the adults spawn during the daytime. This explanation supports the hypothesis presented by HARDING et al. (1951) that the adults lay their eggs near the surface, thus allowing time for eggs to develop into the nauplii before sinking out of the euphotic zone.

On the other hand, deducing from that the copepod adults (*Acartia*, *Calanus* and *Paracalanus*) occurred in the water close to the bottom during the daytime and that the copepod eggs were very meagre there, most of the released eggs may have deposited on the bottom if the adults could lay their eggs in the water close to the bottom during the daytime. Recent studies have shown that the copepod eggs are common and abundant in the bottom sediments in the neritic and coastal waters (KASAHARA et al., 1974). However, judging from the patterns of the vertical distribution of the copepods in the present study, the eggs deposited on the bottom would not play an important role in sustaining the nauplius populations as compared with those found in the surface water.

The dominant copepods in the bay always occurred in the water close to the bottom during the daytime (Fig. 3a,b,c). This means that it is difficult to quantitatively sample these copepod adults by employing usual vertical hauls of plankton nets during the daytime. Occasionally, some planktonic copepods, e.g. *Calanus*, dig into the bottom sediments to be found in the benthic fauna (KOS, 1969). This would be the case with the adults of the *Acartia*, *Calanus* and *Paracalanus* in Ise Bay as well as in the other neritic waters. This may be in part attributed to the neritic waters having shallow depths in comparison with the distance that the copepods usually move up—or downward daily (MARSHALL and ORR, 1955; ANRAKU, 1975; LANDRY, 1978).

The vertical distribution of *Acartia clausi* showed resemblance at the eggs and nauplii three sampling days, while at the later stages especially the adults remarkably depended on season: the eggs and nauplii always occurred abundantly in the water shallower than 10 m depth, while the adults were mainly sampled in the deep water or in the water close to the bottom in spring and summer, and in the surface water in autumn (Fig. 3a,b,c). The seasonal change of the vertical distribution of the *Acartia* adults would be in part caused by existence of other dominant copepods such as the *Calanus* in May and the *Paracalanus* in November in addition to physical and chemical factors. The profile of the vertical distribution of the adult *Acartia* when extremely low oxygen contents were observed in the water close to the bottom in summer stratification (Fig. 2a) indicated that they were apparently excluded from the water with the oxygen contents less than 1 ml/l. This is also supported by CRANDELL and HORACEK (1973) who made clear that *A. clausi*, inhabiting temperate lagoons where sharp gradients of salinity and deoxygenation developed, was restricted to the layer with the oxygen contents of 1.6 ml/l or above. Vertical distributions of the *Acartia* and *Calanus* did not show any relation to thermocline or halocline even in strong stratification period in Ise Bay.

The four copepods made various types of small-scale aggregations in horizontal and vertical planes through all the stage. Although aggregations have been reported in the later stages of the certain copepods (O'CONNELL, 1971; ANRAKU, 1975; SMITH et al., 1976;

HAMNER and CARLETON, 1979), the present study showed that the small-scale aggregations were common to any life stage.

It is puzzled why the copepods have overlap of their inhabiting layers especially at the early life stages even during the daytime in contrast to the adults. These early stages with weak swimming power would require productive environments such as the euphotic zone. Furthermore, as suggested by LANDRY (1978) for the *Acartia*, separation of their habitats from the adults may prevent the adults from predating their eggs and nauplii as often observed in the laboratory populations of the *Acartia* (SEKIGUCHI et al., 1980).

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