The Journal of the Korean Society of Oceanography
Vol. 32, No. 1, pp. 38-45, March 1997

Patterns of Vertical Distribution and Diel Vertical Migration of Zooplankton in the East Sea of Korea (Sea of Japan)

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To find out the changes in vertical distribution patterns over the 24-h period, a key and the first step to tackle the problem of adaptive significance of diel vertical migration (DVM), vertically stratified time series samplings with multiple opening/closing plankton samplers were done in the East Sea of Korea (Sea of Japan). Sampling was done almost every 4 h for one day period following the same water parcel in Nov. 1995 and May 1996, respectively. Resultant patterns of vertical distribution showed that some species such as most abundant taxa *Metridia pacifica* and *Scolecithricella minor*, both Copepoda, performed DVM even in the study area of strong thermal stratification. Their patterns of DVM such as distance scales and timing of movements were not the same each other, and they were separated from other taxa in the dendrogram obtained by the cluster analyses. Most minor taxa grouped in one, however, seemed not to do DVM in the study area of strong thermal stratification. They usually preferred the warmer surface layer where the foods were probably more abundant.

INTRODUCTION

Diel vertical migration (DVM) is one of the prominent behavioral repertoire of marine zooplankton (Paffenhöfer and Price, 1988; Ohman, 1990). It occurred in diverse animal phyla and various geological locales. In spite of this widespread nature of DVM, conflicting views persist regarding its adaptive significance (Kerfoot, 1985; Haney, 1988).

In broad terms the hypotheses to explain the adaptive significance of DVM fall into two categories. First, it has been suggested that DVM can reduce the risk of predation from visual predators. It is because the normal pattern of DVM shows that the center of distribution lies in deeper layer during the daytime and in shallower layer at night time (Zaret and Suffern, 1976). Although there is considerable field and experimental evidence in support of this hypothesis (Gliwicz, 1986), the presence of reverse DVM (Ohman *et al.*, 1983; Park *et al.*, 1989) as well as changing pattern with respect to seasons and developmental stages of a species (Park *et al.*, 1991; Osgood and Frost, 1994) compels to think of other hypothesis.

Second, it has been explained that DVM across a thermocline may provide the zooplankter's metabolic advantage in that they feed at night in warmer surface waters and rest during the day time in cooler deeper waters (McLaren, 1963). However, this hypothesis can also not argue down the report of Petipa (1967) that showed the energy requirement needed for the upward movement far exceeded the metabolic advantage gained by passive sinking. The presence of reverse DVM as well as changing pattern of DVM with respect to seasons and developmental stages of a species can also be mentioned against this second explanation as in case of the first.

In these circumstances, it may be said that DVM is not a fixed trait but shows great plasticity varying both spatially and temporally, and that finding changes in vertical distribution pattern over a 24 h period is a key and the first step to find out plausible explanation for the adaptive significance of DVM.

Contrary to many reports on vertical distribution in foreign literatures, there are very limited reports on this in the neighboring seas of Korea. In the East Sea of Korea (the Sea of Japan), Morioka and Komaki (1978) and Vinogradov and Sazhin (1978) reported vertical distribution of zooplankton biomass. In the west coast of Korean Peninsula, Park (1990) and Park *et al.* (1991) reported that there were significant differences in zooplankton catches with respect to the time of the day of sampling and depths in the relatively strong tidal mixing zone.

Present study was aimed to find the changes in vertical distribution pattern over a 24 h period in the

East Sea of Korea (Sea of Japan) using multiple open/closing plankton samplers. That is, 5 or 9 strata were sampled in the present study almost every 4 h for one day period to find out the time-dependent vertical distribution of zooplankton in the relatively weak tidal mixing zone. Above mentioned adaptive significance of DVM, one of the prominent behavioral repertoires of zooplankton still remains for the further study.

MATERIALS AND METHODS

Zooplankton samples were collected twice in the East Sea of Korea (Sea of Japan, Fig. 1), the first in November 1995, and the second in May 1996. Each of the sampling consisted of seven consecutive vertically stratified net tows of 4 h intervals. An MPS (Multiple Plankton Sampler, Hydro Bios) and an 1 m^2 MOCNESS (Multiple Opening/Closing Nets with Environmental Sensing System; Wiebe *et al.*, 1976) were used in the first and second series of sampling, respectively.

Both MPS and MOCNESS, equipped with underwater sampling unit and deck command unit, are plankton collector with closing device which can be used for horizontal as well as vertical collections. The differences are that the MPS has five nets and net frame dimension of 50×50 cm, while the 1 m^2 MOCNESS has nine nets and 1.0×1.4 m net frame (all the nets had mesh aperture of 330 μm), and that the former is designed to be towed in right angle while the latter is to be tilt during the tow. The 5 or 9 net bags enable the user to carry out collections in different depths.

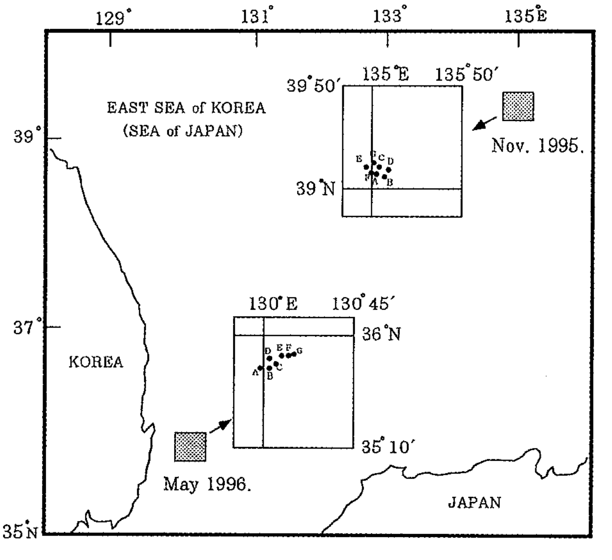

Fig. 1. Sampling sites. Local sampling times are: A, 21:00; B, 02:00; C, 06:00; D, 10:30, E, 14:00; F, 18:30; G, 22:00 in case of sampling event of November 1995, and A, 18:00; B, 22:00; C, 02:00; D, 06:00, E, 10:00; F, 14:00; G, 18:30 in case of May 1996.

The MPS we used has no environmental sensors so that we assumed the depth of opening/closing of the net by the cable layout and the angle of the cable. Seawater volume filtered by each net was calculated from the digital flowmeters attached to each net bag. And, temperatures and salinities were measured with CTD casts prior to each tow. However, in case of the MOCNESS, we obtained real time depth of net system, temperature, salinity, volume filtered by each net from the reading of net angle and flow counts at the same time with the tow of the net system. Those data were processed by the computer connected to the deck command unit.

Water column from surface to 250 m depth with 50 m intervals were sampled in the first sampling series (with an MPS), and water column down to 270m depth with 30 m intervals were sampled in the second series of sampling (with a MOCNESS). Therefore, a total of 35 and 63 samples were collected in the first and second series of sampling, respectively.

To tow the net in the same water parcel, a buoy with two drogues at 50 and 150 m depths was deployed at the beginning of each tow series. Every 4 h the net was towed at random point around this buoy, and the starting points of each tow were shown in Fig. 1 (seven starting points were alphabetically denoted in the figure from A to G, and local sampling times for the given alphabets were shown in the figure legend). As shown in Fig. 1, the seven starting points of each tow series lay within a circle of 5 km radius for both sampling events of November 1995 and May 1996.

Collected samples were fixed with 5% neutralized formalin on board. All the larger animals were picked out prior to subsampling. A Folsom plankton splitter was used to split the samples into subsamples of countable sizes. Usually each subsample contained about 1,000 individuals. The two components of a subsample (one of larger animals picked out prior to splitting and the other splitted) were counted under a dissecting microscope with identification to the lowest practical taxon.

RESULTS AND DISCUSSION

T, S, and sampled water mass

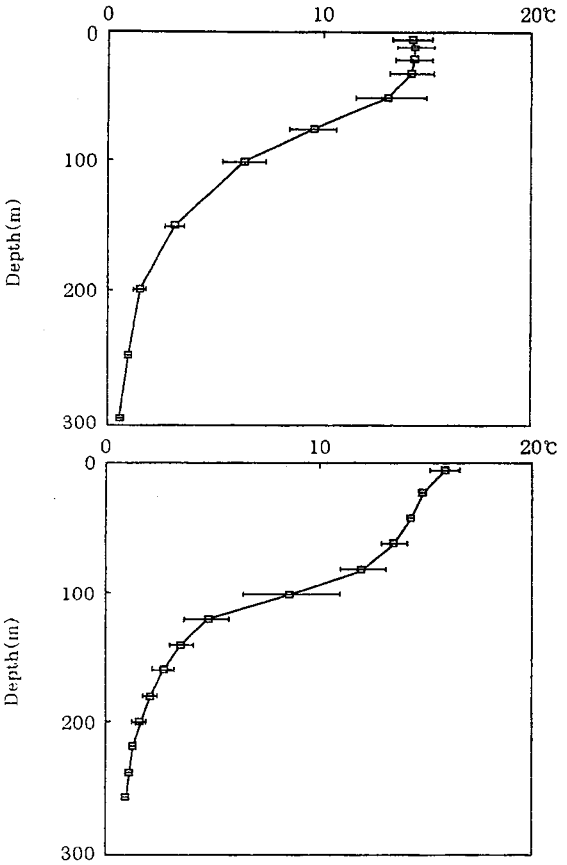

Fig. 2. Vertical profiles of mean temperatures at the sampling sites (A, November 1995; B, May 1996). Horizontal bars indicate the ranges of seven measurements.

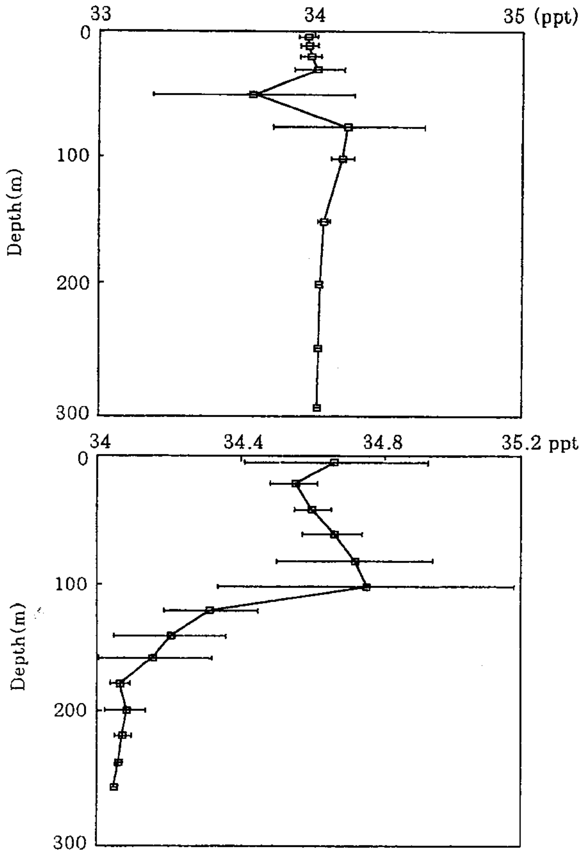

Fig. 3. Vertical profiles of mean salinities at the sampling sites (A, November 1995; B, May 1996). Horizontal bars indicate the ranges of seven measurements.

Obviously the water parcel sampled has moved during the 24 h of sampling period. As mentioned above, however, the positions of seven starting points of each tow lay within a circle of 5 km radius for both sampling events of November 1995 and May 1996. Sea water temperatures in uppermost layer varied a little (Fig. 2), but the ranges at surface, 12.5~15.0°C in November 1995 and 15~16.5°C in May 1996, were much narrower than the temperature ranges in vertical profiles within the sampled layers. Temporal salinity variations within the sampling interval of one day were also very small except the layers of 50 m to 100 m depth (Fig. 3). Salinity variations at these depths were relatively larger, but they were still less than 1 ppt. In these respects, we assumed that the zooplankton collected came from the same water mass. That is, geographic differences of sampling points within a series of seven tows were neglected as a source of variation in zooplankton abundances.

Composition and total abundance

Out of 35 samples in Nov. 1995, a total of 76 taxa in 9 animal phyla was identified. In May 1996, 58 taxa in 8 phyla were observed from 63 samples. These numbers of taxa appeared were far greater than those observed in the western coast of Korean Peninsula (Shim and Park, 1982; Choi and Park, 1993), but similar to the results obtained in the nearby areas (Park and Choi, 1997). In both sampling times, the Copepoda was the most prominent group not only in the diversity but also in quantity as in most results on zooplankton researches done around the Korean Peninsula (Park *et al.*, 1990; Hwang and Choi, 1993).

Metridia pacifica was the most abundant taxon among the sampled zooplankton both in November 1995 and May 1996 (Table 1). Ostracoda, *Calanus sinicus*, post larval stages (copepodid) of calanoid copepods and some eggs were next abundant groups in the sampled areas when all samples collected were pooled. Other major groups are listed in Table 1.

Total abundances obtained in the present study were in the order of tens to hundreds individuals m^{-3}.

Table 1. Averaged abundances of the major taxa appeared in the study area. The numbers are pooled for all sampled strata and times of the day, and percent compositions are based on those pooled numbers.

Rank	Nov. 1995			May 1996		
	Taxon	ind. m^{-3}	%	Taxon	ind. m^{-3}	%
1	*Metridia pacifica*	9.46	14.2	*Metridia pacifica*	29.12	23.3
2	Copepodid of *Calanus*	5.09	7.6	Ostracoda	15.33	12.3
3	Ostracoda	4.98	7.5	*Calanus sinicus*	13.36	10.7
4	Calanoid copepodid	4.45	6.7	Unid. egg (type 3)	12.36	9.9
5	Unid. egg (type 1)	4.31	6.5	*Scolecithricella minor*	8.49	6.8
6	*Scolecithricella minor*	4.08	6.1	Copepodid of *Euchaeta*	5.95	4.8
7	*Sagitta elegans*	3.59	5.4	*Euphausia pacifica*	4.86	3.9
8	*Parathemisto japonica*	3.50	5.3	Copepodid of *Calanus*	4.64	3.7
9	*Nannocalanus minor*	3.06	4.6	Siphonophora	4.39	3.5
10	*Euchaeta plana*	2.86	4.3	Nauplius of Euphausiid	3.47	2.8
11	*Oncaea conifera*	2.30	3.5	Unid. egg (type 2)	3.23	2.6
12	Copepodid *of Eucalanus*	1.89	2.8	Unid. egg (type 1)	2.73	2.2
13	*Centropages bradyi*	1.74	2.6	Immature Amphipoda	2.56	2.1
14	*Oithona similis*	1.66	2.5	*Clausocalanus furcatus*	1.92	1.5
15	*Sagitta bedoti*	1.08	1.6	*Corycaeus affinis*	1.44	1.2

Since zooplankton abundances are dependent on the sampling strategies such as the mesh size of the net used and type and size of the sampling gears used (Wiebe and Holland, 1968; Wiebe, 1972; Park, 1989), direct comparisons with other results may be meaningless. However, total abundances as well as major groups were generally comparable with the previous results obtained nearby seas (Park and Choi, 1997). Regardless of sampling time of the day both in November 1995 and May 1996, vertical patterns in total zooplankton abundances showed high abundance in the surface layer of high temperature and low abundances in the down layers of low temperatures generally but not always (Fig. 4). Deviations from the general patterns as in cases of 18:30 tow series in November 1995 and 06:00 tow series in May 1996 suggested that there might exist vertical migration of certain taxa in the study area in spite of the big vertical difference in water temperatures greater than 10°C.

Species association

Prior to the examination of the graphic presentation of time-dependent vertical distribution of each taxon, cluster analysis was done to group the taxa of similar patterns of abundance distributions. That is, species association based on covariances of time-dependent vertical distributions was evaluated by the cluster analysis (average linkage method; SAS, 1985) for the data of November 1995 and May 1996, respectively.

When eggs and immature forms of copepods were excluded, *Metridia pacifica* (Copepoda), Ostracoda, *Sagitta elegans* (Chaetognatha), *Calanus minor* (Copepoda), and *Parathemisto japonica* (Amphipoda) were separated from other taxa in Novem-

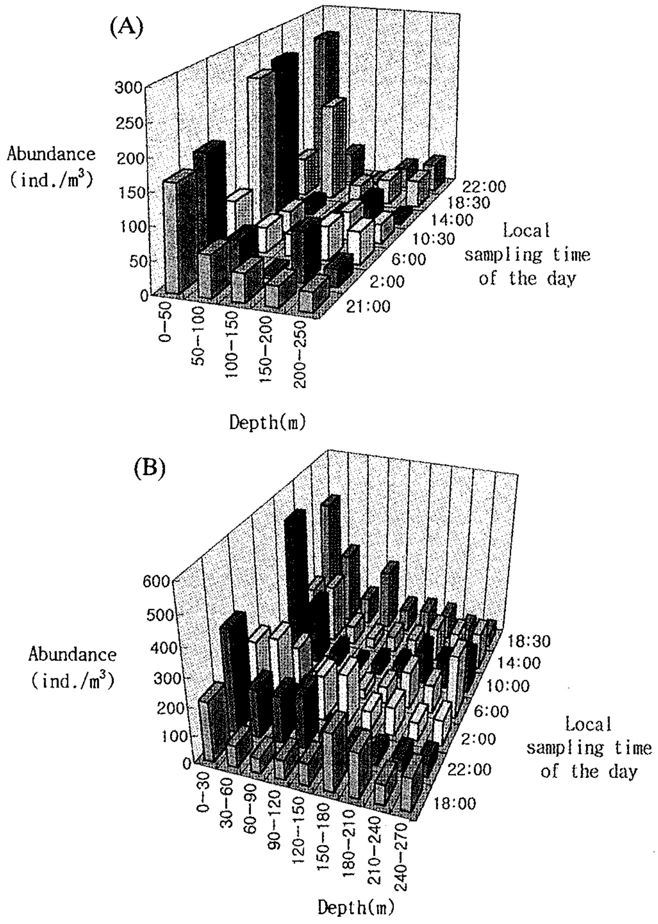

Fig. 4. Time series vertical distribution of total zooplankton abundance (individuals m^{-3}) in the study area in November 1995 (A) and in May 1996 (B).

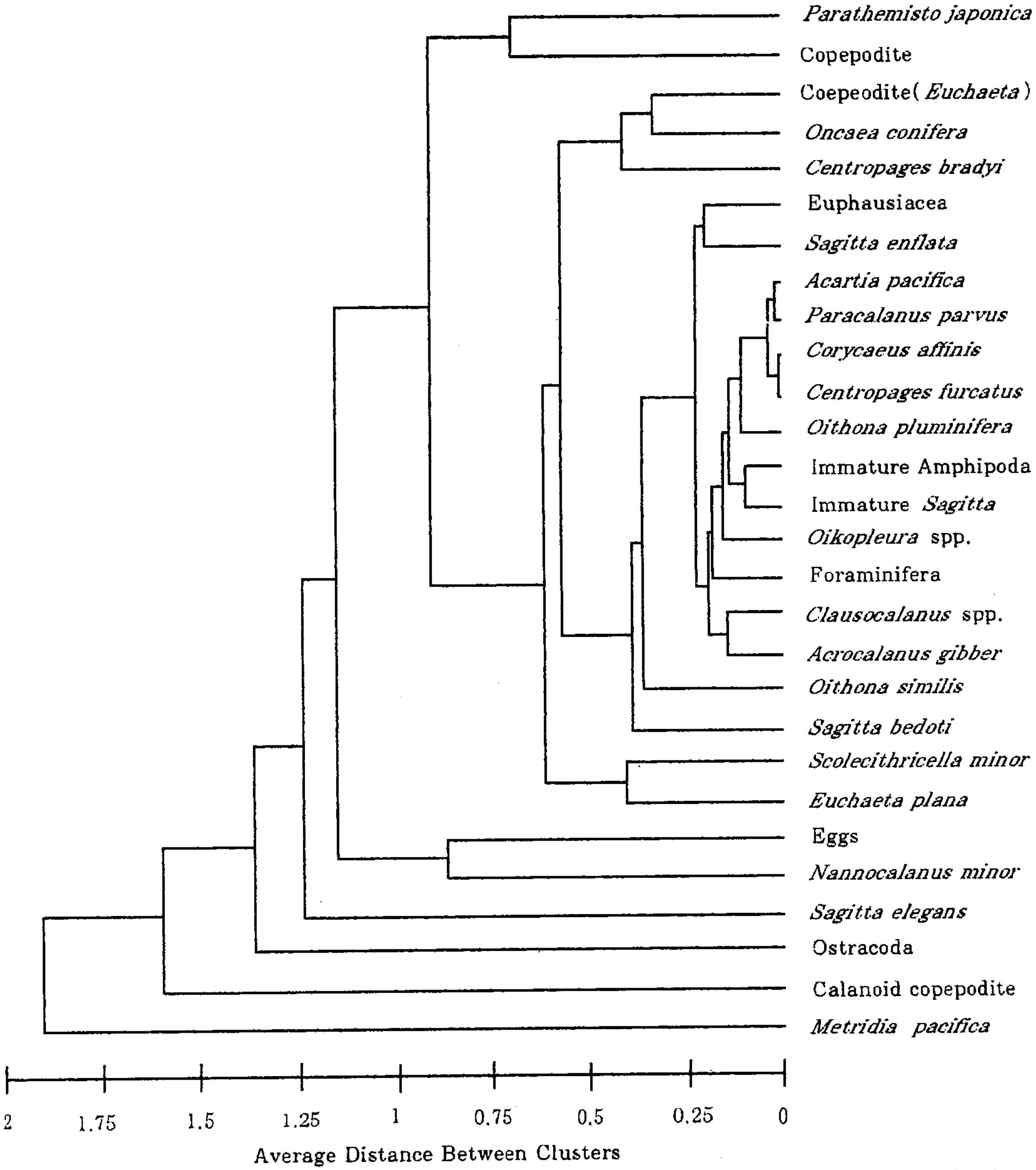

Fig. 5. Zooplankton species association based on covariances of time series vertical distributions in the study area in November 1995.

ber 1995 (Fig. 5). However, it appeared that only *M. pacifica* and Ostracoda showed distinctive patterns of time series vertical distributions (they were similar to the data of May 1996 shown in the following section). On the other hand, most other taxa showed the similar patterns to that of total abundance shown in Fig. 4; high abundances at upper layers of high temperatures and very low abundances at the relatively deep layers of low temperatures regardless of time of the day. They showed no evidence of DVM in the study area.

In May 1996, the number of strata sampled increased from 5 to 9 and the thickness of each stratum reduced from 50 m to 30 m when compared with previous sampling scheme. This modification resulted in quite different form of dendrogram by the same cluster analysis. Most of the taxa included were grouped as one at very low arbitrary unit of between-cluster distance except *Metridia pacifica, Calanus sinicus* (Copepoda), Ostracoda and *Scolecithricella minor* (Copepoda) (Fig. 6). Other taxa showed very similar structure of covariances. The patterns of time series vertical distributions were similar to that of total abundance. Distinctive patterns of the 4 taxa mentioned above were shown in the following section for the data of May 1996

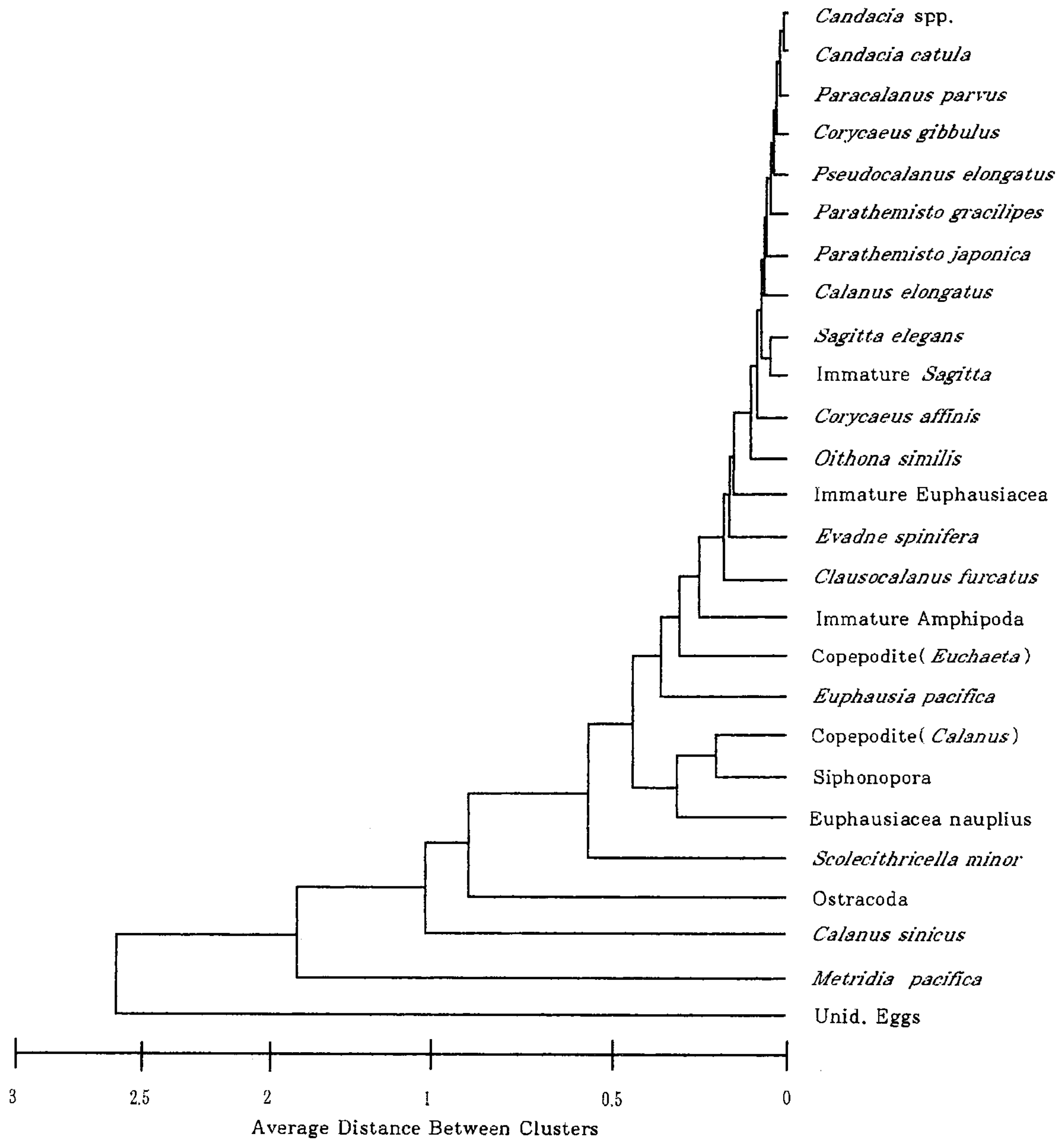

Fig. 6. Zooplankton species association based on covariances of time series vertical distributions in the study area in May 1996.

only. The difference between Figs. 5 and 6 might be the reflections of differences in sampling time of the year and locality. Otherwise, it might be caused by the difference in the thickness of sampled stratum. Regardless of the real reason for the difference, it can be said that thin sampled stratum gives more detailed information than thick stratum does. In this context, only the data of May 1996 are shown in the following section.

Vertical distributions of four major taxa and their relation to water temperatures

Metridia pacifica: This species showed DVM pattern as shown in Fig. 7(A). In the evening at 18:00 local time, the center of distribution lied at about 150 m depth, then it began to rise up to about 90 m depth during the night, 22:00 and 02:00 next day. In the next morning they began to move downward and stayed below 200 m depth during the daytime (10:00 and 14:00). Then again they moved up in the evening (18:30). This pattern of DVM was known as normal type. Considering the thermal stratification of the study area (Fig. 2), the observed vertical shifts of the center of distribution, and the fact that this species was known as cold water species, the relationship between the abundances and habitat temperatures was expected to have no significant or very weak negative correlation. Actually calculated correlation coefficient between these two was -0.42 ($p < 0.05$, $n=63$). This taxon was the only one that showed relatively clear pattern of DVM in the present study.

Ostracoda: This group was classified at the level of Order due to the difficulty in identification. The vertical pattern of distribution was bimodal (Fig. 7(B)). That is, there were two depths with peak abundances at any of sampling time of the day, and those depths, near surface and relatively deep layer, were consistent throughout the sampling period. In this situation the correlation between the abundance and temperature should not be significant. Calculated value of $r=-0.11$ was actually not significant ($p=0.38$). Considering the size and morphology of this taxon, this group seemed to be unable to move actively. In this context, the observed distribution patterns of this taxon suggested that there were at least two different subgroups in this category of taxon, a relatively warm surface dweller and a deep cold water dweller. These two groups seem to be taxonomically different. Ikeda(1990) and Ikeda and Imamura(1992) showed that *Conchoecia pseudodiscophora*, a mesopelagic ostracod, inhabited in the waters of 'subzero' temperature zone in the Sea of Japan. The deep cold water dweller of this study might be this species.

Calanus sinicus: Major portion of this species was distributed in thin surface layer all the time (Fig. 7(C)). The pattern of vertical distribution was very similar to the vertical profiles of seawater temperatures. Actually the correlation between the abundances of this species and seawater temperatures was significant at $\alpha=0.05$ level with $r=0.57$. Therefore, this species could be categorized as a non-migrant in this thermally stratified water column.

Scolecithricella minor: Vertical pattern of this species was quite different from those of the taxa mentioned above in that there were few animals at the uppermost surface layer of high temperature all

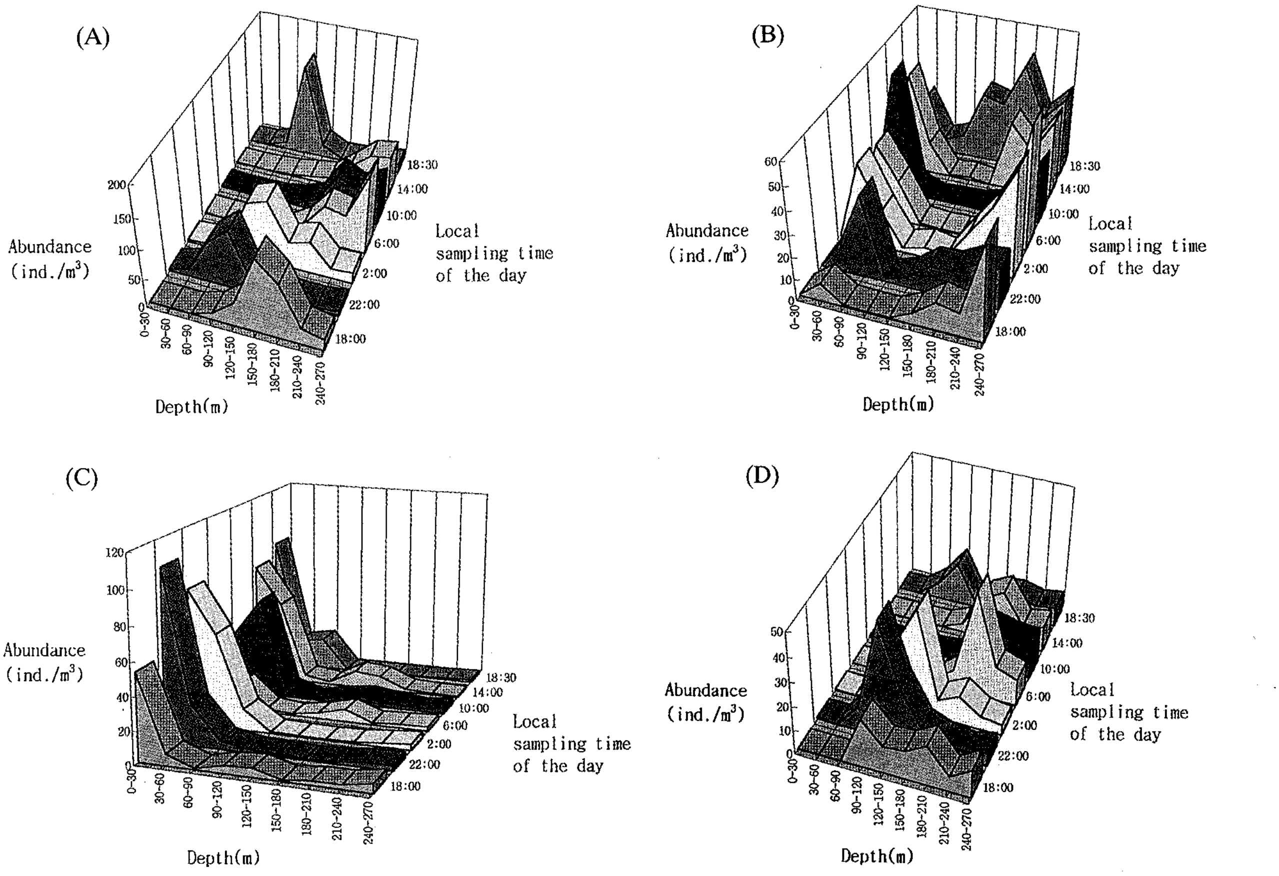

Fig. 7. Time series vertical distribution of major taxa (individuals m^{-3}) in the study area in May 1996. A, *Metridia pacifica*; B, Ostracoda; C, *Calanus sinicus*; D, *Scolecithricella minor*.

the time and the depths of peak abundance oscillated with the progress of time at below 30～60 m depth (Fig. 7(D)). However, the oscillation was not clearly matched with the day-night cycle. The correlation coefficient between the abundance and habitat temperature, $r=-0.45$ ($p<0.05$), was about the same with the case of *Metridia pacifica*. It might be either the case of 'phase elapsed DVM' of Park *et al.* (1989) or the sampled stratum of 30 m interval might not be appropriate to reveal the latent and/or real DVM of this species. In this circumstance, it could be said that this species might do DVM although the pattern, of which phase and scale were not the same with that of the most abundant and comparatively larger-sized *Metridia pacifica*, was not clearly revealed with the given sampling scheme in this study.

In summary, the most abundant zooplankton *Metridia pacifica* showed normal DVM in the thermally stratified waters of East Sea of Korea, and some next abundant zooplankters such as *Scolecithricella minor* showed DVM of which scale and phase were different from those of *M. pacifica*. However, most other less abundant taxa of zooplankton did not show any significant patterns of DVM by the chosen sampling scheme in the study area of relatively strong thermal stratification. They usually preferred the warmer surface layers where the foods were probably more abundant.

ACKNOWLEDGEMENTS

This work was supported by the Oceanographic Research Fund, Ministry of Education, 1995. The authors thank the crew of the R/V Tamyang (Captain Professor J.C. Kim) for their excellent support on board.

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