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# New Patterns of Diurnal Vertical Migration of Some Deep-Water Copepods in the Tyrrhenian and Adriatic Seas

J. Hure[1] and B. Scotto di Carlo[2]

[1]Biološki Institut; Dubrovnik, Yugoslavia and
[2]Stazione Zoologica di Napoli; Naples, Italy

## *Abstract*

The diel vertical migration of copepods from intermediate water layers of the Tyrrhenian and Adriatic Seas has been studied on the basis of plankton samples made from depths down to 1000 m, with a Nansen net, mesh size 250 μ, diameter 113 cm. The species considered display two different patterns of migration: (1) nocturnal ascent, e.g. *Pleuromamma abdominalis* and *Euchaeta acuta*; (2) nocturnal descent, e.g. species of the genera *Spinocalanus*, *Scaphocalanus*, *Temoropia*, *Mormonilla* and *Oncaea*. These two patterns are compared on the basis of the dimensions of the species and of their different capacities for active movement. Illumination is considered to be the most important factor influencing vertical movements. The behaviour of *Pleuromamma gracilis* is also described, the adult population of which is divided in two discrete sections, each one showing a different pattern of migration.

## *Introduction*

During the course of previous research in the southern Adriatic Sea, it was observed that the copepods of the intermediate layers display two different patterns of diurnal vertical migration. Large species, such as *Pleuromamma abdominalis* and *Euchaeta acuta*, make a strong migration towards the surface during the night, while smaller copepods of the genera *Spinocalanus*, *Temoropia* and *Oncaea* are found during the night in deeper levels than during the daytime (Hure and Scotto di Carlo, 1969b).

The phenomenon of nocturnal sinking of the small copepods of the intermediate layers has not been noted previously in the Mediterranean, nor in other seas. Moreover, since sampling was by a vertical haul with a net without a closing device, it was first of all necessary to confirm our earlier results, using a method more adequate for the sampling of this material. It was also our intention to check whether this phenomenon of nocturnal sinking could be verified in other areas of the Mediterranean, and if the same species were involved.

## *Material and Methods*

During 1972, plankton studies were made in the Tyrrhenian Sea, 4 miles south of the island of Capri, and in the southern Adriatic, 20 miles SSW of Dubrovnik. The sampling stations were situated in open sea with a depth of a little over 1000 m. For the collection of plankton at both localities, a nylon net of the type Indian Ocean Standard Net was used, diameter 1.13 m, length 4 m, mesh size 250 μ.

Material was collected in the Tyrrhenian Sea on the 27-28 June with a closing net at 9 levels, beginning always at the deepest level: 1000-800, 800-600, 600-500, 500-400, 400-300, 300-200, 200-100, 100-50 and 50-0 m. In total, during 24 h, 4 series of hauls were made. Each series of 9 hauls lasted a little over 4 h. The meteorological conditions were ideal during the whole period of sampling. The lunar phase was 2 days after full moon.

Table 1. Temperature (T) and salinity (S) in Tyrrhenian and Adriatic Seas in June and November, 1972

| Depth (m) | Tyrrhenian Sea 28 June | | Adriatic Sea 7 November | |
|---|---|---|---|---|
| | T(°C) | S(‰) | T(°C) | S(‰) |
| 0 | 24.80 | 37.46 | 18.06 | 38.68 |
| 10 | 23.72 | 37.46 | 18.82 | 38.72 |
| 20 | 19.60 | 37.54 | 18.84 | 38.72 |
| 30 | 16.46 | 37.75 | 18.80 | 38.72 |
| 50 | 14.58 | 37.77 | 16.70 | 38.74 |
| 100 | 14.26 | 37.98 | 14.82 | 38.75 |
| 200 | 14.30 | 38.40 | 13.90 | 38.77 |
| 300 | 14.42 | 38.57 | 13.85 | 38.77 |
| 500 | 14.44 | 38.60 | 13.54 | 38.74 |
| 1000 | 13.62 | 38.56 | - | - |

In the Adriatic, plankton was sampled on the 6-7 November with a net without a closing device in the sequence from depth to surface: 600, 500, 400, 350, 250, 200, and 150 m. During 24 h, 8 series of hauls were made. The duration of each series was a little under 3 h. The sea was a little choppy during the day, but at night was calm, with a clear sky and a new moon.

Temperature and salinity were measured at each level from the surface to 1000 m and the surface to 500 m in the Tyrrhenian and Adriatic Seas, respectively (Table 1). The vertical gradients of temperature and salinity at the stations in the months of June and November were insignificant below 100 m, and annual variation was very slight (Gamulin *et al.*, 1968).

## *Results*

Because the samples were not taken at the same time of year, and because in the Tyrrhenian Sea deeper levels were involved than in the southern Adriatic, it is understandable that only a small number of the same species were found abundantly in the two areas (*Spinocalanus neospinosus* Grice[1], *S. parabyssalis* Park, and *Mormonilla minor* Giesbrecht). Of the other copepods of the intermediate layers, in the Tyrrhenian Sea only *Scaphocalanus invalidus* Hure and Scotto di Carlo, *Temporopia mayumbaensis* T. Scott, *Pleuromamma gracilis* Claus, and *Oncaea ornata* Giesbrecht were numerous, and in the southern Adriatic only *Euchaeta acuta* Giesbrecht and *Pleuromamma abdominalis* Lubbock.

Observations on these species confirm that the copepods exhibit two distinct patterns of vertical migration. One corresponds to species of relatively large dimensions, such as *Euchaeta acuta* (length 3.6 to 4.8 mm) and *Pleuromamma abdominalis* (2.6 to 3.5 mm). In the afternoon, the adults of these species migrate rapidly from levels below 300 m, where they live during the day, moving near to the surface at midnight; they then rapidly descend into deep water again, which they reach during the hours of maximum light intensity (Fig. 1).

The other pattern of migration is observed amongst small species (not larger than 1.5 mm). In general, these are found at deeper levels during the night than at midday. We have analysed in detail the behaviour of 3 such species found in large numbers in both investigational areas: *Spinocalanus neospinosus*, *S. parabyssalis* and *Mormonilla minor*.

In the Adriatic Sea, where the intervals between the series of plankton hauls were 3 h, it was possible to distinguish, for these species, two characteristic vertical movements. The first corresponds to the morning and afternoon hours, when the organisms move towards the surface; the second occurs in full darkness and during the period of maximum insolation, when these copepods descend into the deeper layers. The night-time

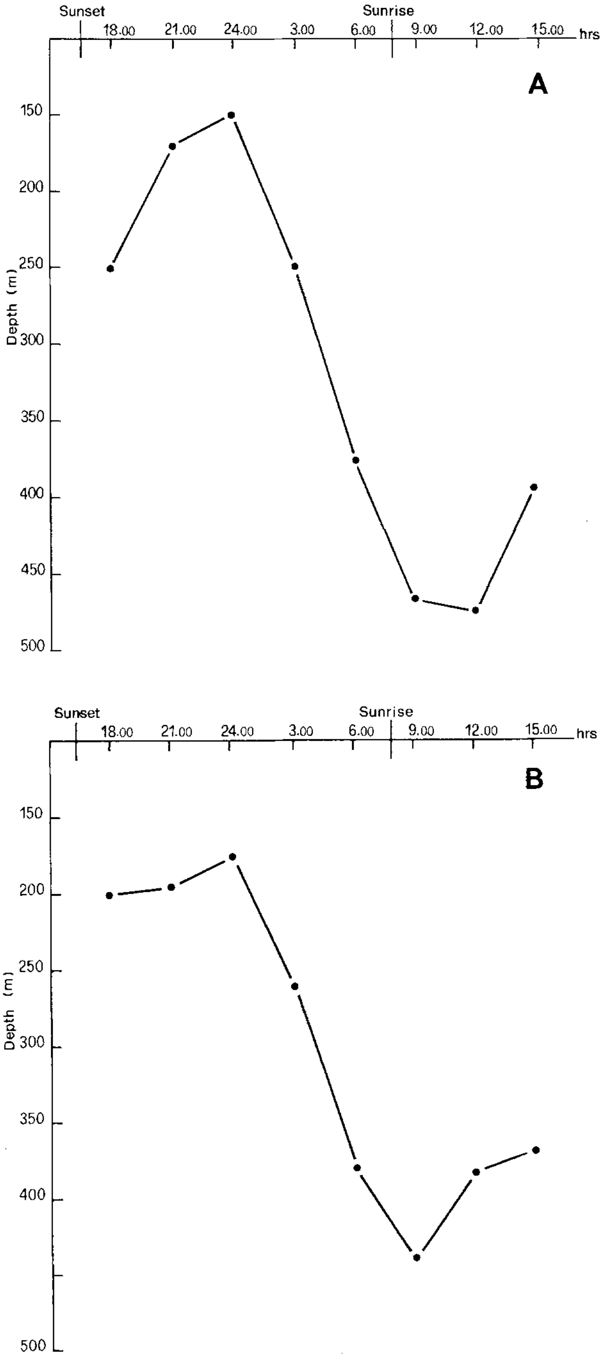

Fig. 1. (A) *Euchaeta acuta*; (B) *Pleuromamma abdominalis*. Diurnal variations of the mean depth of occurrence in Adriatic Sea, 6-7 November, 1972

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[1] In a previous paper we quoted *Spinocalanus paraoligospinosus* Grice, *in litteris* (Hure and Scotto di Carlo, 1969b). This was a manuscript name which was changed to *Spinocalanus neospinosus* prior to publication (Grice, 1971). *S. paraoligospinosus*, therefore, has no valid taxonomic status.

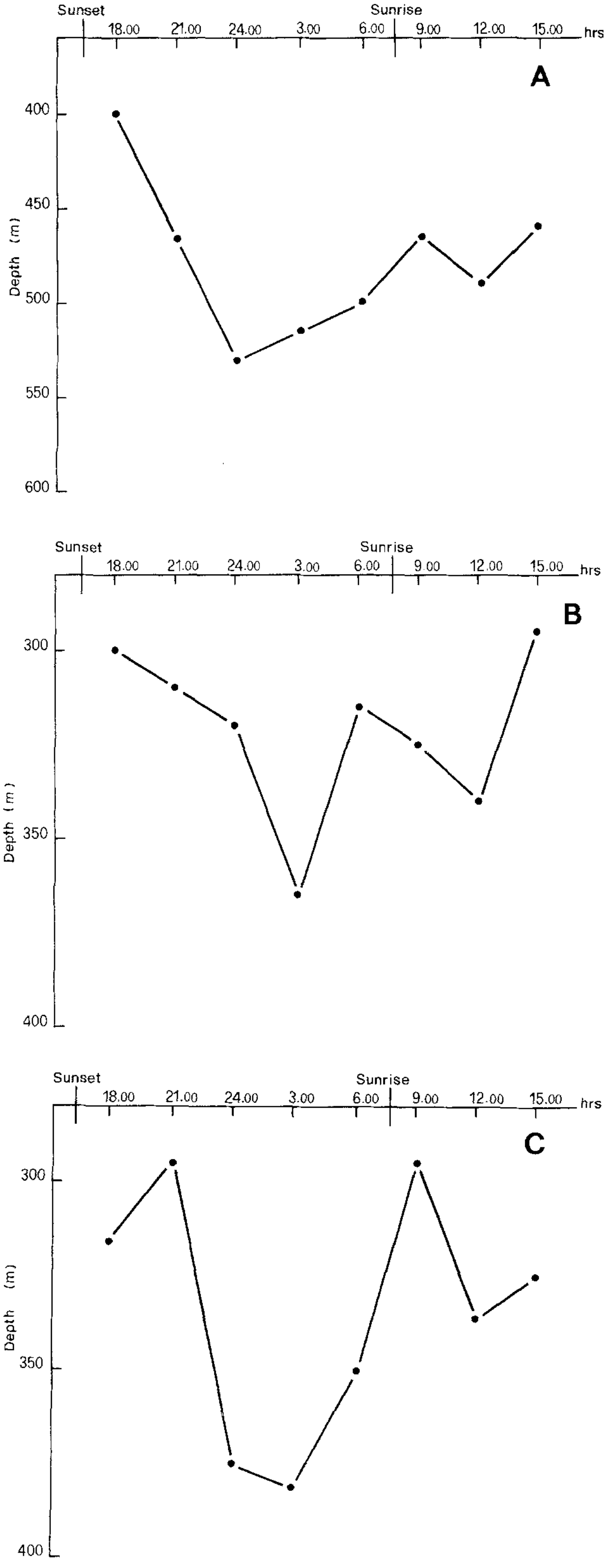

Fig. 2. (A) *Spinocalanus neospinosus*; (B) *S. parabyssalis*; (C) *Mormonilla minor*. Diurnal variations of the mean depth of occurrence in Adriatic Sea, 6-7 November 1972

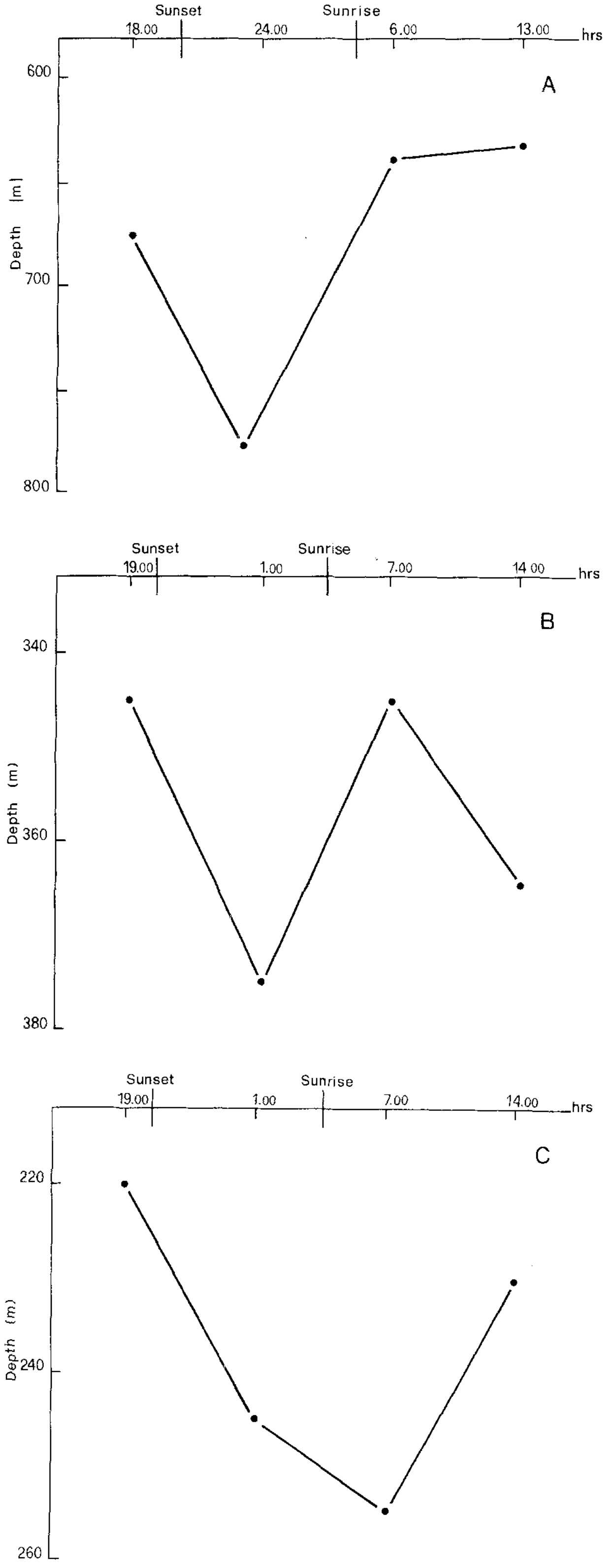

Fig. 3. (A) *Spinocalanus neospinosus*; (B) *S. parabyssalis*; (C) *Mormonilla minor*. Diurnal variations of the mean depth of occurrence in Tyrrhenian Sea, 27-28 June, 1972

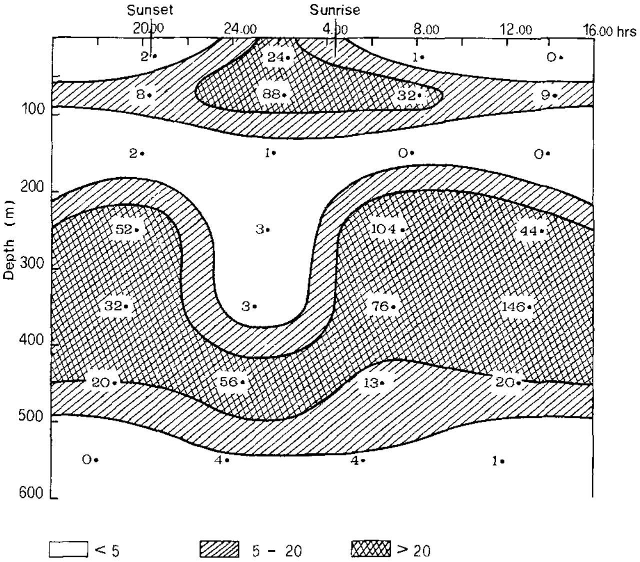

Fig. 4. *Pleuromamma gracilis*. Vertical distribution of two concentrations exhibiting different migration patterns at various times during 24-h period in Tyrrhenian Sea, 27-28 June, 1972. The black dots correspond to the number of specimens

sinking is longer and more marked than the daytime one, and the ascent in the morning is more intense than that in the afternoon (Fig. 2).

In the Tyrrhenian Sea, the course of the vertical migration of these species shows the same trends but, probably because of the greater intervals between samples (about 6 h), the daytime descent did not appear to be noticeably shorter (Fig. 3).

Recently, Roe (1972) noted that *Spinocalanus abyssalis* var. *pygmaeus* (probably the same as our *S. parabyssalis*) also shows a reversed migration, but states that his evidence is inconclusive.

Particularly interesting, in the Tyrrhenian Sea, is the diel migration of *Pleuromamma gracilis*, a species of intermediate dimensions (length 1.7 to 2.1 mm). The adults of both sexes form two concentrations, almost totally discrete, at different depths: one typically superficial, the other in the intermediate depths between 200 and 500 m. The superficial part of the population displays the normal pattern of vertical migration, coming close to the surface during the night. That part of the population in the deeper waters shows, instead, a migration pattern similar to that of the small species from the intermediate layers, since these copepods are found during the night at deeper levels than during the daytime (Fig. 4). The last copepodite stages (III, IV, V) were most numerous in the layers between the two parts of the population. Their diel migration is of normal pattern, and more intense than that displayed by the adults of the superficial part of the population.

## *Discussion*

When interpreting the differing patterns of vertical migration, one must first consider that the depth at which the organisms can show a photic response is rather great, and that the speed of vertical movements of the different planktonic organisms is very variable.

Observations on the penetration of light into the sea show that there is still some light present even at several hundred metres depth. According to Clarke and Hubbard (1959) and Clarke and Denton (1962), the greatest depth at which planktonic organisms are able to perceive day-night variation in illumination is 700 or even 1000 m. It is not possible to determine exactly the velocity of vertical movements of the various zooplankton organisms under natural conditions. Many experimental data, of which those of Hardy and Bainbridge (1954) seem to be most convincing, show that the swimming velocity of planktonic organisms is often very high and, to a certain extent, seems to be proportional to the size of the organisms.

The planktonic organisms of the deep levels must naturally have a great capacity for movement, since they must be continually active during 24 h to remain at the depth of their optimum intensity of illumination. As the ability to swim fast is, it would appear, an almost exclusive characteristic of the larger organisms, the small copepods of the intermediate waters stay, during the night, far from the depth of their optimum light intensity, as their locomotory activity is clearly reduced. For this reason, night sinking lasts longer and is more marked the deeper the copepods live. The ascent in the morning is interpreted as a resumption of activity as a result of photic stimulation; this enables them to regain the depth of their optimum light intensity. The weak midday sinking and the weak afternoon ascent are interpreted as a tendency of the organisms to maintain themselves at the levels of the most favorable conditions of illumination (Hure and Scotto di Carlo, 1969b).

A series of other external factors can influence to a certain extent the character of the migration patterns described for the small copepods from intermediate waters. Temperature, more often considered as a limiting factor in diurnal migration (Nikitin, 1926; Clarke, 1934; Moore *et al.*, 1953; Vinogradov, 1954; and many others), has a negligible vertical gradient in the two areas, in the water layers below 100 m (Table 1). It is difficult, furthermore, to attribute an important role to pressure which is, according to Moore (1950, 1958) and Moore and Corwin (1956) together with illumination and temperature, a significant factor in diel migration, and yet under the influence of which, only the large copepods (*Euchaeta acuta* and *Pleuromamma abdominalis*) do not appear to suffer.

Recently, Rudjakov (1970) sought to explain many peculiarities of vertical migration of planktonic organisms exclusively in terms of endogenous rhythms. All organisms, during a 24-h period, pass through phases of alternating high and low activity, of which the latter is of importance in determining the direction and velocity of the organisms during the active phase. The phenomenon of midnight sinking can be explained by the fact that certain species can have two peaks of activity: one in the morning, the other in the evening, with a decline at midday for the diurnal species and again towards midnight for the nocturnal ones. This phenomenon, according to Rudjakov, is not brought about by the specific effect of illumination on the behaviour of the animals, since both activity peaks persist under conditions of constant light or when there are sharp changes in illumination.

Esterly (1917, 1919) was the first to suggest the possibility of the existence of endogenous rhythms of activity in marine animals; later this was confirmed by several experiments (Harris, 1963). In nature, however, there are many examples of animals which incontestably demonstrate that light is a much stronger factor than endogenous rhythms of activity. Bogorov (1938, 1946), for example, has stated that at high latitudes plankton, during the summer, exhibits no migration. Wiborg (1954) has observed that in the coastal waters of northern Norway there is no clear variation, during the summer, in the biomass of the plankton in the superficial layers to a depth of 50 m, and has concluded that the only explanation for this is the almost uniform illumination. Also, from the data of Foxton (1956) there appears to be no daily variation in the vertical distribution of plankton in Antartic and Subantartic regions, in which the three species comprising the greater part of the biomass did not migrate during the day. During solar eclipses, planktonic animals have made rapid migrations towards the surface, following the large and unexpected reduction in sunlight (Petipa, 1955; Backus *et al.*, 1965).

By analogy with the examples and considerations outlined above, the nocturnal sinking of the small copepods from intermediate water levels in the Tyrrhenian and Adriatic Seas is, in our opinion, attributable rather to factors of illumination than to endogenous rhythms of activity, which do not allow for any logical connection between the dimensions of the organisms and the different numbers of phases of activity. Following the hypothesis of Rudjakov (1970), the large copepods would have a single peak and the small copepods two peaks of activity.

Many authors have observed that the superficial part of a population which migrates behaves in a different manner from the deeper parts, such that one can have a separation within the population (Moore and O'Berry, 1957). The division into two parts of a population of *Pleuromamma gracilis* was already recorded in the Adriatic Sea in June, 1956, but this phenomenon was not given any special attention (Hure, 1961). It is interesting that this phenomenon in the Tyrrhenian and Adriatic Seas was encountered in completely calm sea conditions and in the same period of the year. In this period, in both seas, all the adult population lives during the daytime in levels below 150 m, with the nucleus of concentration at a depth of 330 to 350 m (Hure and Scotto di Carlo 1969a).

The two different patterns of diurnal migration in the lower and upper sections of the population of adult *Pleuromamma gracilis* are also difficult to explain exclusively in terms of a differing number of peaks of an endogenous activity rhythm over a 24-h period. We are more convinced that illumination, with its regular rhythms, is the most important factor governing the diverse behaviour in the two sections of the population. The individuals comprising the lower part of the population behave similar to the small copepods of the intermediate water layers, and thereby would remain during the night beyond the limits of any zone of illumination that might stimulate migration towards the surface.

The diel sinking of the lower section of the *Pleuromamma gracilis* population must be considered a very rare and perhaps fortuitous phenomenon that, in a certain sense, reminds one of the surface "swarming" of planktonic organisms. In both cases, the animals find themselves far from away from the range of illumination which stimulates them to migrate and which keeps them continually at optimum light conditions.

There are many diverse opinions as to the biological advantages to be gained by vertical migration, but no single one can explain all the known examples of this phenomenon (Vinogradov, 1968). The marked nocturnal upward migration would enable the large copepods to feed upon the richer nutriments of the surface waters and to broaden their habitat range towards more productive coastal regions. In the Adriatic Sea, deep-living species occur regularly near the coast during winter and the greater part of spring (Hure, 1955).

Night sinking of the small copepods, on the other hand, keeps the population of these species always in deep water, where they form a somewhat stable community in trophic equilibrium with their surroundings, and encourages a greater geographic isolation of these organisms (Shmeleva, 1964; Hure, 1965; Hure and Scotto di Carlo, 1968, 1969b).

Presumably the feeding requirements of these two groups of species differ. The two patterns of daily migration based upon differing capacities for active movement, and therefore upon size, would thus be the result of adaptation to the differing trophic needs of the species.

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Dr. J. Hure
Biološki Institut
P.O. Box 39
Dubrovnik
Yugoslavia

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