

**Vertical distribution and nutritional behaviour of *Cyclothone braueri*,  
*Nematoscelis megalops*, *Meganctiphanes norvegica* and *Salpa  
fusiformis* in the NW Mediterranean mesopelagic zone**

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**Abstract**

Vertical distribution and migration, stomach content and population structure of four characteristic macrozooplanktonic species were determined during 4 cruises in the Ligurian Sea, NW Mediterranean. Two instruments were used: the BIONESS multiple net system for the sampling, and the Underwater Video Profiler for the “in situ” estimations. The non migrating gonosthomatiid *Cyclothone braueri* forms the main macrozooplanktonic biomass from 300 to 600 m deep in the studied stations. Its stomach content shows that it is a carnivore, feeding efficiently on migrating mesozooplanktonic populations. Although the euphausiid *Nematoscelis megalops* can be observed from the surface to the depth of 800 m the major part of its population lives in the 300 - 600m layer. Only one part of the population is migrating. In the aphotic layer its nutritional behaviour is mainly carnivorous, while in the subsuperficial layer *N. megalops* is omnivorous. *Meganctiphanes norvegica* displays a strong migrating behaviour and feeds intensely during the night in the superficial layer both on animal prey and on phytoplanktonic/detritic material. During the daytime *M. norvegica* seems to be dispersed in the mesopelagic layer. *Salpa fusiformis* is a filter feeding tunicate. The oozoids and the large blatozoids seem to migrate, while the small blastozoids remain in the superficial layer during the day. The role of these organisms in the mesopelagic food web and in the carbon cycling will be discussed.

**Keywords**

*Cyclothone braueri*, *Nematoscelis megalops*, *Meganyctiphanes norvegica*, *Salpa fusiformis*, Ligurian Sea, vertical distribution, nutrition

**Introduction**

A species is a component of a food web and its contribution or role is made according not only to the spatial and temporal abundance in the water column but also to the nutritional level. Then the characterization of the role of that species should include, among others, the population characteristics, vertical distribution and nutrition. The vertical distribution may have specific pattern of residing at a specific depth or vertically migrating in the water column. The nutrition in turn could be carnivorous, herbivorous or omnivorous. In the mesopelagic realm, non-migratory animals remain deep water layers and use the energy transported from the epipelagic zone via physical or biological conveyor system (Gorsky et al., 1991; Gorsky et al., 2002; Stemmann et al., 2007). Migratory animals actively search energy in the superficial layer and eventually transport energy of the epipelagic layer to the deep water via vertical migration.

In the Ligurian Sea, northwestern Mediterranean, such mesopelagic animals of importance are Gonostomatiidae *Cyclothone braueri*, Euphausiacea *Nematoscelis megalops* and *Meganyctiphanes norvegica*, and Salpidae *Salpa fusiformis*. *C. braueri* is the most dominant mesopelagic fish in the Mediterranean Sea (Jespersen and Taning, 1926; Aboussouan, 1971; Goodyear et al., 1972; Palma, 1982; Andersen and Sardou, 1992; Baussant et al., 1993; Cuttitta et al., 2004). This species is recognized as non-migrating fish for which the vertical distribution depends on the development stage, season and latitude (Badcock, 1982). Its main depth is between 300 and 600m (Palma, 1982; Roe and Badcock, 1984; Andersen and Sardou, 1992; Sardou and Andersen, 1993). Vertical migration is, however, suggested by several previous studies (Gibbs and Roper, 1970; Roe and Badcock, 1984). Their nutritional status is carnivore, feeding on copepods and ostracods (Palma, 1982, 1990; Roe and Badcock, 1984). *N. megalops* is one of the main euphausiids species in the Mediterranean Sea (Soulier, 1963; Franqueville, 1971; Casanova, 1974; Andersen and Sardou, 1992; Sardou and Andersen, 1993). They are vertically migrating with spatial and temporal variation (Roe, 1983; Roe et al., 1984; Andersen and Sardou, 1992). The larva and juveniles are in the epipelagic zone, whereas the adults in the 200-600m water depth (Mauchline and Fisher, 1969; Sardou and Andersen, 1993). Only a subpopulation of *N. megalops* effectuates vertical migration (Casanova, 1974; Roe, 1983; Andersen and Sardou, 1992; Sardou and Andersen, 1993). Their nutritional status is omnivore-carnivore (Mauchline and Fisher,

1969; Mauchline, 1980) with high intensity of feeding during the nighttime (Barange et al., 1991). Their nutrition is based on detritus and small crustacean (Casanova, 1974). *M. norvegica* is one of the most studied species among euphausiids. They are present only in the northern Atlantic including Mediterranean Sea (Einarsson, 1945; Mauchline and Fisher, 1969) representing the most abundant euphausiid species (Franqueville, 1971; Casanova, 1974). This species is well known for compact vertical migratory behavior from 400-500m to 0-100m (Mauchline, 1969; Franqueville, 1971; Casanova, 1974; Berkes, 1976; Sameoto, 1984; Simard et al., 1986a; Balino and Aksnes, 1993; Sardou and Andersen, 1993) with high swimming capability (Tarling et al., 1998; Tarling et al., 2001;). This species is recognized as predator-omnivore (Mauchline, 1980) feeding on copepods and detritus (Einarsson, 1945; Fisher and Goldie, 1959; Casanova, 1974; Berkes, 1976; Mauchline, 1980; Sameoto, 1980, 1984; Simard et al., 1986b). *M. norvegica* is intensely feeding during the nighttime (Casanova, 1974; Simard et al., 1986b, Balino and Aksnes, 1993). The most abundant salp, after *Thalia democratica*, with great temporal variation in the Ligurian Sea is *S. fusiformis* (Braconnot, 1970). This gelatinous filter feeder is known for their extremely high reproduction rate (Braconnot et al., 1988). Vertical migration was suggested by several authors (Franqueville, 1971).

In the present study, the population structure, vertical distribution, and nutrition of the four macrozooplanktons, the most abundant in the Ligurian Sea were undertaken with aim to understand their contribution in the energy flux from the epi- to the mesopelagic layer.

### **Materials and Methods**

One station in the Ligurian Sea, Northwestern Mediterranean, was visited 4 times, seasonally, from Nov. 1992 to Aug. 1993. The station was located 8 miles (43° 35.60 N-7° 29.40E) off Nice, France. Description of the station as well as its physical features was made by Stemmann et al. (2007). The most abundant macrozooplankton of that station throughout the year was chosen, which are *C. braueri*, *N. megalops*, *M. norvegica*, and *S. fusiformis*. Sampling was done with BIONESS (mouth: 1×1m; pore size: 500µm, Sameoto, 1980, 1983a) opening closing multi-net system. Table 1 summarizes the layer and frequency of the tows, and figure 1 is the graphic representation.

In brief, tow consisted of oblique and horizontal tows. Oblique tows were made to follow the spatial and temporal variation in vertical distribution. It was done at every 4 hours during 32 hours, when possible. Depths sampled were 800-700, 700-600, 600-500,

500-400, 400-300, 300-200, 200-100, 100-50, and 50-0m, designated as F1, F2, F3, F4, F5, F6, F7, F8 and F9, respectively. Horizontal tows were made to follow the variation of population structure and nutrition at predetermined depth which was inferred from literature. For *C. braueri*, the sampling depth was 500 m regardless of the day or night. For euphausiids, it was 400 m during the daytime and 50m during the nighttime. For salp, it was 20m throughout the day. The samples once on board were rinsed and preserved in formaldehyde solution at final concentration of 10% v/v. Later in laboratory, *C. braueri*, *M. norvegica*, *N. megalops* and *S. fusiformis* were isolated, counted, and their length measured. They were dissected, stomach repletion by coding estimated, and the gut content examined under a microscope in order to estimate the diurnal feeding rhythm, nutritional status and the prey.

The length measurement was done as follows: standard length for *C. braueri*, length from the base of eye to the end of the abdomen for euphausiids, and the oral to aboral distance for *S. fusiformis*.

Abundance, standardized in individuals per 1000 m<sup>3</sup>, was plotted in time vs. depth graph (Fig 1), and WMD (weighted mean depth) estimated with the following equation. These two were used in estimating the vertical distribution and migration.

The WMD (Barange, 1990; Andersen and Sardou, 1992) was calculated with data from oblique tows exclusively;

$$\text{WMD} = \frac{\sum(n_i \times d_i)}{N}$$

$n_i$ : number of individuals at that depth

$d_i$ : mean depth of a sample

$N$ : sum of the number of individuals over all sampling depth

In the time vs. depth plot, vertical tows from 800 to 0m formed the frame of depth-time in which data from horizontal tows were incorporated. A preliminary examination of the plots with and without data from horizontal tows was performed graphically and revealed that they can be incorporated without biasing the figures.

The length of animals collected in a sample was compared with others using ANOVA test according the procedure described in Sokal and Rohlf (1982).

## Results

Hydrological characteristics at the station were derived from temperature (Fig. 2) and salinity data (Fig. 3). It showed a well developed thermal stratification in autumn, spring and summer. In winter the water column was mixed without eminent difference among the depths. The salinity, on the other hand, did not vary along the season.

WMD of *Cyclothone braueri* varied along the season: the shallowest in winter and the deepest in summer (Tab. 2). Diurnal variation was insignificant. *C. braueri* was concentrated always in the depth of 300-600m (Fig. 4). Weak variation in vertical distribution, however, was noted (Fig 4c). During the night they were present in the water column between 150-800m, but absent in the midnight below 700m. During the daytime, very high abundance was observed in the depth of 300-450m. We noted also a slight increase of abundance between 200m and 700m at sunset.

The length of *C. braueri* collected in vertical tows was significantly different (Tab. 3) for autumn and spring samples due to the length difference of animals from 300-400m and 400-500m, the length of the latter population was slightly higher than the length of the former (2.19cm vs. 1.93cm). These values correspond approximately to the females and the males, respectively.

*C. braueri* fed mostly on copepods (67.5%), ostracods (18.2%), and on the eggs and larvae of euphausiids, and amphipods. On 24h basis, copepods occurrence in stomachs varied little with 67.4 and 66.1% for day- and nighttime samples, respectively. Ostracod was more numerous in nighttime than in daytime (15.9 vs. 23.8%). Eggs and larvae of euphausiids were more numerous in daytime than in nighttime (2.6 vs. 0.5%). This observation indicates that the migratory copepods (*Euachaeta* sp.) were used as food during the daytime and that non-migratory copepods (*Corycaeus* sp.) and ostracods during the nighttime.

WMD of *Nematoscelis megalops* was not statistically different between day and night, indicating no diurnal vertical migration (Tab. 2). In fact, throughout the study period, the vertical distribution was between 300 and 600m with slight seasonal difference (Tab. 2, Fig. 5); the WMD was shallowest in winter and deepest in the autumn. In summer, individuals remained in the superficial layer both during the day and during night. The diurnal variation was quite complex but seemed to be repeated diurnally. A small part of the population began to ascent at the end of the afternoon, about 2 h before the sunset. We found individuals in the superficial layer only before the sunset and during the sunrise but not in between. During the night in the layers below 100m, the migration patterns were extremely complicated indicating probably successive up and downward migration of individuals. The vertical migration pattern of this euphausiid is not clear. Most of the individuals were descending to the 300-600m layer before the sunrise. However a small part of the population remains above 200m in autumn, spring and summer.

The length of the euphausiids from samples of oblique tows was statistically different

(Tab. 4). For example, a tow carried out at 14h, for which the vertical migration seemed start, resulted in small individuals (1.35cm) in the layer of 200-300m and large ones in 300-400m (1.44cm). This and other differences in size from samples of different water depths seemed indicate that the euphausiid population was divided during the daytime and migrated differently according to their length, and thus age.

The individuals collected in the superficial layer during the nighttime had a conspicuous trophical rhythm with elevated stomach repletion and the content was in the major part represented by detritic material. During the daytime in the depth, animal content was prevalent. Individuals collected in the 100-300m layer during the nighttime had a not well defined trophical rhythm. The stomach content varied with time but detritic material prevailed during the nighttime. In the 300-600m depth during the day- or nighttime, the trophical rhythm varied extremely, and animal content was dominating during the nighttime.

Abundance of *Meganyctiphanes norvegica* varied a lot along the season (Fig. 6). Number of individuals collected was 361 in autumn, 16898 in winter, 679 in spring and 6 in summer. Due to this large variation, vertical migration could be only suggested for autumn, winter, and spring. In winter, the most abundant season, *M. norvegica* appeared in the superficial and subsuperficial layers by sunset, remained in these layers during the whole night and descended by sunrise to the daytime layer of 200-500m. This vertical migration was compact and performed at population level (Fig. 6b). This vertical migration pattern is similar to the patterns of autumnal and spring populations (Fig. 6a, c). ANOVA test for the length of individuals collected in winter revealed significant differences between individuals collected in 0-100m and 100-200m, the former smaller than the latter (Tab. 5).

*M. norvegica* had well defined trophical rhythm with high nutritional intensity during the nighttime in the super- and subsuperficial layer. The food at these layers was composed of animal and detritus.

*Salpa fusiformis* varied a lot in abundance along the season; total number of individual was zero in autumn and spring, 3 blastozooids in summer, and 121 oozoids and 9349 blastozooids in winter. In winter during the daytime, the oozoids were in the depth of 350-500m, whereas during the nighttime they were in the superficial layer, indicating a quite clear pattern of vertical migration (Fig. 7a). By the sunrise, they returned to the daytime depth. The length of oozoids were in average 2.2cm and statistical test showed no diurnal difference ( $\alpha < 0.05$ ). The blastozooids divided into 3 size classes according to

their length performed different vertical migrations (Fig. 8a, b, c). The small size individuals were all day in the superficial layer, and the medium size individuals were not only in the superficial layer during day and night but also in the deep layer during the daytime. The large sized individuals were absent in the superficial layer only during the day and in the deep during the night, indicating quite clear vertical migration.

### Discussion

In the Mediterranean Sea *C. braueri* is the most frequent and abundant mesopelagic fish (Jespersen and Taning, 1926; Aboussouan, 1971; Goodyear et al., 1972; Palma, 1982; Andersen and Sardou, 1992; Baussant et al., 1993). *C. braueri* is recognized as non-migrating fish for which the vertical distribution depends on the development stage, season and latitude (Badcock, 1982). Its main depth is between 300 and 600m (Palma, 1982; Roe and Badcock, 1984; Andersen and Sardou, 1992; Sardou and Andersen, 1993). Vertical migration is, however, suggested by several previous studies (Gibbs and Roper, 1970; Roe and Badcock, 1984). In the present study, our main findings with respect to the vertical distribution of *C. braueri* are seasonal variation of the WMD and diurnal variation in the distribution pattern.

Seasonal variation of WMD might be related with factors such as hydrological and trophical ones.

Hydrological factors taken into account here are temperature and salinity. They could affect the seasonal vertical distribution with their absolute values or by forming stratification or destratification in the water column. The population of *C. braueri* was in the same water depth ( $450\pm 100\text{m}$ ), in which the seasonal variation of temperature and salinity, in absolute values, were insignificant. On the other hand, the stratification of the water column seemed plausible. Indeed the stratification in temperature and salinity was high in summer and a little less in autumn and spring and was totally absent in winter. This order is the same with that of WMD: WMD was deepest in summer, followed by spring and autumn and the shallowest in winter. This coincidence might imply that the vertical distribution of this non-migrating mesopelagic fish might be affected by the stratification of the water column.

The second factor, trophical interaction is in fact closely related to the hydrological factor, because the latter could determine the vertical distribution of prey and predator at the same time.

Our data on the nutrition of *C. braueri* showed that the fish had no diurnal nutritional rhythm and that the main prey were copepods and ostracods. Among the copepods, the vertical migrator (*Pleuromamma* sp., *Euchaeta* sp.) and non-migrator (*Monascilla* sp.,

*Gaetanus* sp.) were consumed differently: the migratory copepods during the day, and the non-migratory during the day and night. This indicates that *C. braueri* fed on the preys present nearby at any time, then, without distinct diurnal nutritional rhythm. Merret and Roe (1974) reported similar feeding pattern for *Valenciennellus tripunctulatus*, a non-migratory mesopelagic fish, and Hu (1978) for *Nematobrachion sexspinosus*, a non-migratory euphausiid. In the Mediterranean Sea, Boucher et al. (1987) reported that copepods, including the preys of *C. braueri*, showed seasonal variation in their vertical distribution, reinforcing our interpretation that the pattern of vertical distribution of *C. braueri* might move seasonally with that of their prey.

This last hypothesis might explain also to the diurnal variation of vertical distribution. Even though the distribution of this mesopelagic fish population was vertically confined in 300-600m, a quite small part of it, maybe negligible, ascended and descended from that depth all over the season, behavior resembling to a diurnal vertical migration. This pattern could be stimulated by the migrating copepods, and could occur at individual level.

*Nematoscelis megalops* is one of the main euphausiids species in the Mediterranean Sea (Soulie, 1963; Franqueville, 1971; Casanova, 1974; Andersen and Sardou, 1992; Sardou and Andersen, 1993). They are vertical migrators with various patterns (Roe, 1983; Roe et al., 1984; Andersen and Sardou, 1992). The larva and juveniles are in the epipelagic zone, whereas the adults in the 200-600m water depth (Mauchline and Fisher, 1969; Sardou and Andersen, 1993) of which a small part of the population effectuates vertical migration (Casanova, 1974; Roe, 1983; Andersen and Sardou, 1992; Sardou and Andersen, 1993). Our results agree well with the previous studies with respect to the range of vertical distribution, partial migration of the population, and distribution in patch. Moreover, our results showed in detail the temporal variation of *N. megalops* in the superficial layer and evolution of vertical distribution along the season. The latter might be related to the hydrological and biological factors, as for *C. braueri*. Seasonal evolution of the hydrological characteristics in terms of water column stratification, was determined by temperature rather than by the salinity. Seasonal temperature evolution was clear in the superficial and sub-superficial layers, resulting in stratification of the water column, and this seemed affect the WMD as well as the vertical distribution of the euphausiid population. This influence of thermal stratification on the vertical distribution was suggested previously by Brinton (1967), Youngbluth (1976), Wiebe and Boyd (1978), Sameoto (1986), Barange (1990), and Barange et al. (1991). However, the

stratification of the water column should affect also the vertical distribution of other zooplankton, especially the prey of *N. megalops*, and this point should be considered. *N. megalops* feed in principle on crustacean zooplankton and detritus (Mauchline, 1980). Gorsky et al. (unpublished data) followed the vertical distribution of particles of larger than 100µm and found seasonal vertical variation of the highest concentration: less than 100m in winter and deeper than 480m in summer. Concerning crustacean zooplankton, Boucher et al. (1987) reported seasonal variation in vertical distribution of some copepods that were in the superficial or sub-superficial layer in the winter and descended deeper in the summer. Others reported similar results in the Mediterranean Sea (Vucetic, 1966; Gaudy, 1972, Scotto di Carlo et al., 1984) and in the Pacific and Atlantic (Marshall and Orr, 1972; Binet and de Saint Claire, 1975). Scotto di Carlo et al. (1984) specified that the vertical distribution of copepods (*Oncaea mediterranea*, *Pleuromamma abdominalis*) was shallower in winter than in summer. We speculate then, that seasonal thermal variation generates stratification of the water column which in turn strongly affects the vertical distribution of prey and predator. Related to this feature, variation in transparency due to wintertime mixing should be considered. Less light and more suspended particles in deep water due to vertical mixing attract marine animals to a depth of appropriate light intensity and of high food concentration, which in turn affects the vertical distribution of *N. megalops*.

It is noteworthy to follow the temporal variation of abundance in the superficial layer except summer season: appearance in this layer before sunset, absence during midnight, and reappearance before sunrise. Hypothesis was proposed to explain this pattern. The first is “hunger-satiation” (Rudjakov, 1970; Simard et al., 1985). This hypothesis delineates that hungry individuals mount to the superficial layer to feed and descend to the sub-superficial layer once satiated, and remount once more to feed before descending down to the deeper daytime depth. We tested this hypothesis by comparing depth with the stomach repletion. The relationship was not significant therefore we rejected this hypothesis. The second hypothesis is the “vertical segregation” (Angel and Fasham, 1974; Hirota et al., 1984; Hargreaves, 1985; Simard et al., 1986b; Barange, 1990; Barange et al., 1991). This hypothesis delineates efficient sharing of food among congeneric species in avoiding competition (Berkes, 1976; Ambler and Miller, 1987). We observed that the appearance of the population of *N. megalops* was closely related with that of *M. norvegica*; high abundance of *N. megalops* in the superficial layer before sunset - absence of *M. norvegica*, high abundance of *N. megalops* in the sub-superficial layer – high abundance of *M. norvegica* in the superficial layer, and reappearance of *N. megalops* in the superficial layer before sunrise - the absence of *M. norvegica*. We

suggest then a negative relationship between *N. megalops* and *M. norvegica*, the latter compelling the former.

*M. norvegica* is a well known vertical migrator with daytime depth of 100-400m and nighttime depth of 0-100m (Mauchline and Fisher, 1969; Casanova, 1970, 1974; Berkes, 1976; Tarling et al., 2001). Our results agree with theirs. Sardou and Andersen (1993) reported that the population of *M. norvegica* in April at a station located 28 miles off Nice, was divided into two parts according to the individual length; the small individuals were in the superficial layer during the whole day without diurnal difference and performed vertical migration of a small distance (45m), whereas the large individuals were in the depth of 350-550m during the day and performed vertical migration to the surface. Our results showed that the population was not segregated according to the length and performed vertical migration in compact mass at population level.

In *Salpa fusiformis* diurnal vertical migration was previously suggested (Franqueville, 1971; Harbison and Campenot, 1979; Bruland and Silver, 1981; Laval et al., 1992; Madin et al., 1996). Franqueville (1971) reported that, in the Mediterranean Sea, *S. fusiformis* performed vertical migration from 300-800m to the surface with identical migration pattern for the 2 life stages, oozoids and blastozooids. Laval et al. (1992) had also suggested that, in the Ligurian Sea, a part of the population of *S. fusiformis* could migrate to 400-600m. Our results clearly showed vertical migration of oozoids and large sized blastozooids. The length of oozoids and blastozooids for which vertical migration occurred deserves further consideration. The average length of oozoids we presented here was 2.2cm which corresponds to the size of oozoids just liberated from blastozooids (Braconnot et al., 1988). Then it seems certain that the oozoids perform vertical migration since the first day of birth. The smallest blastozooids which were 0.3cm were collected only in the superficial layer regardless day or night. This size corresponds in fact to the first stage liberated by oozoids. This signifies that the vertically migrating oozoids liberate blastozooids in the superficial layer during the nighttime. Blastozooids reach adult size of 1cm by the 6<sup>th</sup> day (Braconnot et al., 1988) of their life cycle. With the oozoids inside, blastozooids perform vertical migration and liberate oozoids in the superficial layer during the nighttime. This hypothesis is supported by the fact that the blastozooids were present during the whole 24 hours in the superficial layer and that the oozoids were absent in the deep layer during the nighttime. For a neighboring species, *Cyclosalpa bakeri*, the reproduction was closely

related with the vertical migration and happened in the superficial layer (Purcell and Madin, 1991) during the nighttime.

In summary, *C. braueri* did not migrate and remained in the depth of 300-600m regardless of the season. The WMD varied slightly with season and seems to be related with the water stratification and distribution of their preys. *M. megalops* were mainly in the depth of 300-600m regardless of the season. Vertical migration was performed for a part of the population with quite complicated variation in the subsuperficial layer during the nighttime. *M. norvegica* showed large seasonal variation in abundance and performed quite clear vertical migration of population level. *S. fusiformis* oozoids performed clear vertical migration. Small blastozooids that were just liberated from oozoids stayed in the superficial layer during the day and night, and performed vertical migration as they reached adult size.

## References

- Aboussouan, A., 1971. Contribution à l'étude des Téléostéens récoltés à chalut pélagique en relation avec la D.S.L. durant la période du 1er Novembre 1967 au 31 Décembre 1968. *Cah. Océanogr.*, 23, 85-89
- Ambler, J. W. and C. B. Miller, 1987. Vertical habitat-partitioning by copepodites and adults of subtropical oceanic copepods. *Mar. Biol.*, 94, 561-577
- Andersen, V. and J. Sardou, 1992. The diel vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 1. Euphausiids, mysids, decapods and fishes. *J. Plank. Res.*, 14, 1129-1154
- Angel, M. V. and M. J. R. Fasham, 1974. Sond Cruise 1965: Further factor analyses of the plankton data. *J. mar. biol. Ass. U.K.*, 54, 879-984
- Badcock, J., 1982. Gonostomatidae. In: Poissons de l'Atlantique du Nord-Est et de la Méditerranée. Eds: P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielson and E. Tortonese, Vol. 1, 284-300
- Balino, B. M. and G. L. Aksnes, 1993. Winter distribution and migration of the scattering layers, zooplankton and micronekton in Masfjorden, western Norway. *Mar. Ecol. Prog. Ser.*, 102, 35-50
- Barange, M., 1990. Vertical migration and habitat partitioning of six euphausiid species in the northern Benguela upwelling system. *J. Plank. Res.*, 12, 1223-1237
- Barange, M., K. J. Gibbons and M. Carola, 1991. Diet and feeding of *Euphausia hanseni* and *Nematoscelis megalops* (Euphausiacea) in the northern Benguela Current: ecological significance of vertical space partitioning. *Mar. Ecol. Prog.*

*Ser.*, 73, 173-181

- Baussant, T., B. Gasser, G. Gorsky and A. Kantidakis, 1993. Mesoscale micronekton and macrozooplankton observed by echosounding, multiple-net sampling and video profiling across the Almeria-Oran Front (W Mediterranean Sea). *Ann. Inst. Oceanogr.*, 69, 87-93
- Berkes, F., 1976. Ecology of euphausiids in the Gulf of St. Lawrence. *J. Fish.Res. Board Can.*, 33, 1894-1905
- Binet, D. and S. de Saint Claire, 1975. Le copépode planctonique *Calanoides carinatus*: répartition et cycle biologique au large de la côte d'Ivoire. *Cah. ORSTOM, sér. Océanogr.*, 13, 15-30
- Boucher, J., F. Ibanez and L. Prieur, 1987. Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. *J. Mar. Res.*, 45, 133-173
- Braconnot, J. C., 1970. Contribution à l'étude biologique and écologique des Tuniciers pélagiques. Salpides et Doliolides. Thèse de Doctorat d'Etat de l'Université Paris VI, 112 pp
- Braconnot, J. C., S. M. Choe and P. Nival, 1988. La croissance et le développement de *Salpa fusiformis* Cuvier (Tunicata, Thaliacea). *Ann. Inst. Oceaogr., Paris*, 64, 101-114
- Brinton, E., 1967. Vertical migration and avoidance capability of euphausiids in the California Current. *Limnol. Oceanogr.*, 12, 451-483
- Bruland, K. W. and M. W. Silver, 1981. Sinking rates of fecal pellets from gelatinous zooplankton (Salps, Pteropods, Doliolids). *Mar. Biol.*, 63, 295-300
- Casanova, B., 1974. Les Euphausiacés de Méditerranée. Thèse de l'Université de provence (Aix-Marseille I), 380 pp
- Cuttitta A., A. Arigo, G. Basilone, A. Bonanno, G. Buscaino, L. Rollandi, J. G. Lafuente, A. Garcia, S. Mazzola and B. Patti, 2004. Mesopelagic fish larvae species in the Strait of Sicily and their relationships to main oceanographic events. *Hydrobiologia*, 527, 177-182
- Einarsson, H., 1945. Eupahusiacea I. North Atlantic species. Dana Report, No. 27, 185 pp
- Fisher, L. R. and E. H. Goldie, 1959. The food of *Meganyctiphanes norvegica* (M. Sars), with an assessment of the contributions of its components to the vitamin A reserves of the animal. *J. mar. biol. Ass. U.K.*, 38, 291-312
- Franqueville, C., 1971. Macroplancton profond (Invertébrés) de la Méditerranée Nord-Occidentale. *Téthys*, 3, 11-56

- Gaudy, R., 1972. Contribution à la connaissance du cycle biologique de copepods du Golfe de Marseille. 2. Etude du cycle biologique de quelques espèces caractéristiques. *Téthys*, 4, 175-292
- Gibbs, Jr. R. H. and C. Roper, 1970. Ocean acre preliminary report on vertical distribution of fishes and cephalopods. *In: Proceedings of an International Symposium on biological sound scattering in the ocean. Eds: G. B. Farquhar, Washington D.C., Maury Center for Ocean Science, 119-133*
- Gjosaeter, J. and K. Kawaguchi, 1980. A review of the world resources of mesopelagic fish. *FAO Fish. Tech. Pap.*, 193, 151 pp
- Goodyear, R. H., B. J. Zahuranec, W. L. Pugh and R. H. Gibbs, 1972. Ecology and vertical distribution of Mediterranean midwater fishes. *Mediterranean biological studies final report. Report to U.S. Navy Office of naval Research contract no. N00014-67-A-399-000-7, 91-229*
- Gorsky G., N. Lins da Silva. S. Dallot. Ph. Laval. J. C. Braconnot and L. Prieur, 1991. Midwater tunicates: are they related to the permanent front of the Ligurian Sea (NW Mediterranean). *Mar. Ecol. Prog. Ser.*, 74, 195-204.
- Gorsky G., L. Prieur, I. Taupier-Letage, L. Stemmann and M. Picheral, 2002. Large particulate matter in the western mediterranean I. LPM distribution related to mesoscale hydrodynamics. *J. Marine Systems*, 33-34, 289-311
- Harbison, G. R. and R. B. Campenot, 1979. Effects of temperature on the swimming of salps (Tunicata, Thaliacea): Implications for vertical migration. *Limnol. Oceanogr.*, 24, 1081-1091
- Hargreaves, P. M., 1985. The vertical distribution of Decapoda, Euphausiacea, and Mysidacea at 42° N, 17° W., *Biol. Oceanogr.*, 3, 431-464
- Hirota, Y., T. Nemoto and R. Marumo, 1984. Vertical distribution of larvae of *Euphausia nana* and *E. similis* (Crustacea: Euphausiacea) in Sagami Bay and Suruga Bay, Central Japan. *Mar. Biol.*, 81, 131-137
- Hu, V. J. H., 1978. Relationships between vertical migration and diet of four species of euphausiids. *Limnol. Oceanogr.*, 23, 296-306
- Jespersen, P. and A. V. Taning, 1926. Mediterranean Sternoptychidae. Report on the Danish Oceanographical Expeditions 1908-1910 to the Mediterranean and Adjacent Seas. 2 (Biology). 12A, 1-59
- Laval, P., J. C. Braconnot and N. Lins da Silva, 1992. Deep planktonic filterfeeders found in the aphotic zone with the Cyana submersible in the Ligurian Sea (NW Mediterranean). *Mar. Ecol. Prog. Ser.*, 79, 235-241
- Madin L. P., P. Kremer and S. Hacker, 1996. Distribution and vertical migration of salps

- (Tunicata. Thaliacea) near Bermuda. *J. Plank. Res.* 18 (5). 747-755.
- Marshall, S. M. and A. R. Orr, 1972. The biology of marine copepod. Springer Verlag, Berlin, 195 pp
- Mauchline, J., 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.*, 18, 681 pp
- Mauchline, J. and L. R. Fisher, 1969. The biology of euphausiids. *Adv. Mar. Biol.*, 7, 454 pp
- Merret, N. R. and H. S. J. Roe, 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. *Mar. Biol.*, 28, 115-126
- Palma, S., 1982. Contribution à l'étude biologique et écologique de *Cyclothone braueri* Jespersen et Taning, 1926 (Gonostomatidae), en Mer Ligure. Thèse de Doctorat 3e cycle, Université Pierre et Marie Curie, Paris, 186 pp
- Palma, S., 1990. Ecologie alimentaire de *Cyclothone braueri* Jespersen et Taning, 1926 (Gonostomatidae), en Mer Ligure, Méditerranée Occidentale. *J. Plank. Res.*, 12, 519-534
- Purcell, J. E. and L. P. Madin, 1991. Diel patterns of migration, feeding, and spawning by salps in the subarctic Pacific. *Mar. Ecol. Prog. Ser.*, 73, 211-217
- Roe, H. S. J., 1983. Vertical distribution of euphausiids and fish in relation to light intensity in the Northeastern Atlantic. *Mar. Biol.*, 77, 287-296
- Roe, H. S. J. and J. Badcock, 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 5. Vertical migrations and feeding of fish. *Prog. Oceanogr.*, 13, 389-424
- Roe, H. S. J., P. T. James and M. H. Thurston, 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 6. Medusae, ctenophores, amphipods and euphausiids. *Prog. Oceanogr.*, 13, 425-460
- Rudjakov, J. A., 1970. The possible causes of diel vertical migrations of planktonic animals. *Mar. Biol.*, 6, 98-105
- Sameoto, D. D., 1980. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis* (Crustacea Euphausiacea). *J. Plank. Res.*, 2, 129-143
- Sameoto, D. D., 1984. Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. *J. Plank. Res.*, 6, 767-792
- Sameoto, D. D., 1986. Influence of the biological and physical environment on the vertical distribution of mesozooplankton and micronekton in eastern tropical Pacific. *Mar. Biol.*, 93, 263-279
- Sardou, J. and V. Andersen, 1993. Micronekton et macroplancton en Mer Ligure (Méditerranée): migrations nyctémérales et distributions verticales. *Oceanologica*

- Acta*, 16, 381-392
- Scotto di Carlo, B., A. Ianora, E. Fresi & J. Hure, 1984. Vertical zonation patterns for Mediterranean copepods from the surface to 300 m at a fixed station in the Tyrrhenian Sea. *J. Plank. Res.*, 6, 1031-1056
- Simard, Y., G. Lacroix and L. Legendre, 1985. In situ twilight grazing rhythm during diel vertical migrations of a scattering layer of *Calanus finmarchicus*. *Limnol. Oceanogr.*, 30, 598-606
- Simard, Y., R. de Ladurantaye and J.-C. Therriault, 1986a. Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Mar. Ecol. Prog. Ser.*, 32, 203-216
- Simard, Y., G. Lacroix and L. Legendre, 1986b. Diel vertical migrations and nocturnal feeding of a dense coastal krill scattering layer (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in a stratified surface waters. *Mar. Biol.*, 91, 93-105
- Sokal, R. P. and F. J. Rohlf, 1982. Biometry. 2<sup>nd</sup> edition, W. H. Freeman and Company, San Francisco, 859 pp
- Soulier, B., 1963. Pêches planctoniques, superficielles et profondes, en Méditerranée Occidentales (Campagne de la "Thalassa"-Janvier 1961-entre les îles Baléares, la Sardaigne et l'Algérois) IV. Euphausiacés. *Rev. Trv. Inst. Pêches Marit.*, 27, 417-440
- Stemmann L., L. Prieur, L. Legendre, I. Taupier-Letage, M. Picheral, L. Guidi and G. Gorsky, 2007. Effects of frontal processes on marine aggregate dynamics and fluxes: an interannual study in a permanent geostrophic front (NW Mediterranean). *J. Marine Systems*, doi: 10.1016/j.jmarsys.2007.02.014
- Tarling G. A., J. B. L. Matthews, R. Saborowski and F. Buchholz, 1998. Vertical migratory behaviour of the euphausiids, *Meganyctiphanes norvegica*, and its dispersion in the Kattegat Channel. *Hydrobiologia*, 375/376, 331-341
- Tarling G. A., J. B. L. Matthews, P. David, O. Guerin and F. Buchholz, 2001. The swarm dynamics of northern krill (*Meganyctiphanes norvegica*) and pteropods (*Cavolinia inflexa*) during vertical migration in the Ligurian Sea observed by an acoustic Doppler current profiler. *Deep-Sea Res. I*, 48, 1671-1686
- Vucetic, T., 1966. On the biology of *Calanus helgolandicus* (Claus) from the Veliko Jezero. I. Mljet, *Acta Adriatica*, 6, 91 pp
- Wiebe, P. H. and S. H. Boyd, 1978. Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold core rings. I. Horizontal and vertical distributions. *J. Mar. Res.*, 36, 119-142
- Youngbluth, M. J., 1976. Vertical distribution and diel migration of euphausiids in the

central region of the California Current. *Fish. Bull. U.S.*, 74, 925-936

**Tables**

Table 1. Sampling module used in the present study.

<b>Season</b>	<b>Date</b>	<b>Station</b>	<b>Tows</b>
Autumn	25 Nov.-4 Dec. 1992	8 miles	6 obliques of 800-0m 7 horizontals at 500m 4 horizontals at 400m 4 horizontals at 50m 1 horizontals at 20m
Winter	15-22 Jan. 1993	8 miles	8 obliques of 800-0m 10 horizontals at 400m 3 horizontals at 50m 7 horizontals at 20m
Spring	12-20 May 1993	8 miles	7 obliques of 800-0m 5 horizontals at 500m 4 horizontals at 400m 3 horizontals at 50m 6 horizontals at 20m
Summer	17-20 Sep, 1993	8 miles	8 obliques of 800-0m

Table 2. Seasonal and diurnal WMD/SD (m) of *C. braueri* and *N. megalops* in the Ligurian Sea

Season	Total	Day	Night	t-test	df
Autumn	469.5/19.7	462.4/20.6	474.2/21.9	0.01/ns	3
Winter	392.0/38.9	424.9/27.1	372.3/31.3	2.41/ns	6
Spring	404.3/21.5	405.9/24.1	400.1/20.4	0.29/ns	5
Summer	485.8/12.2	486.4/14.0	484.7/11.1	0.17/ns	6

<i>Nematoscelis megalops</i>					
Season	Total	Day	Night	t-test	df
Autumn	393.0/55.4	407.4/62.4	383.4/62.1	0.42/ns	3
Winter	269.3/79.4	327.2/42.4	234.6/78.1	1.86/ns	6
Spring	358.0/44.7	376.5/33.6	311.9/38.3	2.23/ns	5
Summer	369.7/109.2	409.5/99.4	303.4/106.7	1.43/ns	6

Table 3. Results of ANOVA test for the length of *C. braueri* from vertical tows

Season	No. of tows	df	F value	Significativity	Sources of difference
Autumn	1	6;153	2.95	s	F4/F5
	2	6;103	1.06	ns	
	3	6;77	1.51	ns	
	4	4;64	0.51	ns	
	5	6;109	1.14	ns	
	6	4;95	0.01	ns	
Winter	1	4;31	1.87	ns	
	2	3;18	0.65	ns	
	3	3;28	2.59	ns	
	4	3;44	2.29	ns	
	5	4;67	0.98	ns	
	6	3;43	0.14	ns	
	7	3;55	0.29	ns	
	8	3;26	0.41	ns	
Spring	1	4;81	3.3	s	F4/F5
	2	5;73	2.65	s	
	3	5;87	2.01	ns	
	4	2;16	13.29	s	
	5	4;70	2.12	ns	
	6	6;69	1.98	ns	
	7	5;82	3.69	s	
Summer	1	4;69	1.32	ns	
	2	4;74	0.35	ns	
	3	3;90	0.76	ns	
	4	6;69	0.12	ns	
	5	3;65	0.51	ns	
	6	5;66	2.06	ns	
	7	4;62	2.58	ns	
	8	3;80	0.63	ns	

Table 4. 4. Results of ANOVA test for the length of *N. megalops* from vertical tows.

Season	No. of tow	df	F value	S	Sources of difference	Length
Autumn	1	3;42	1.35	ns		
	2	6;90	3.13	s	F7/F5; F7/F1	1.2/1.4; 1.2/1.5
	3	4;63	10.86	s	F7/F4; F7/F5; F7/F6	1.1/1.4; 1.1/1.4; 1.1/1.4
	4	4;92	1.06	ns		
	5	8;118	0.93	ns		
	6	3;73	0.05	ns		
Winter	1	2;60	1.37	ns		
	2	6;108	2.22	ns		
	3	3;83	0.65	ns		
	4	3;48	2.67	ns		
	5	4;82	0.94	ns		
	6	3;47	2.29	ns		
	7	3;63	6.12	s	F6/F5	0.35/1.44
	8	5;65	0.7	ns		
Spring	1	2;12	0.61	ns		
	2	5;36	0.43	ns		
	3	6;42	6.04	s	F7/F3; F7/F4; F7/F8; F6/F4; F6/F8	1.4/1.8; 1.4/1.7; 1.4/1.8; 1.2/1.7; 1.2/1.8
	4	-	-	-	-	-
	5	3;34	5.12	s	F5/F3	1.2/1.8
	6	2;35	0.39	ns		
	7	3;36	3.04	ns		
Summer	1	3;63	8.73	s	F5/F4; F5/F3; F4/F3	0.9/1.2; 0.9/1.4; 1.2/1.4
	2	6;76	6.04	s	F8/F7; F7/F6; F7/F5; F7/F4	1.6/1.6; 1.6/1.1; 1.6/1.3; 1.6/1.3
	3	6;114	0.87	ns		
	4	6;85	10.85	s	F8/F7; F8/F6; F8/F5; F8/F3; F4/F6; F7/F6	1.1/1.2; 1.1/1.4; 1.1/1.3; 1.1/1.3; 1.2/1.4; 1.2/1.4
	5	5;61	2.44	ns		
	6	2;60	24.09	s	F4/F3	1.2/1.4
	7	3;40	18.03	s	F4/F3; F4/F6	1.3/1.4; 1.3/1.6
	8	7;77	3.19	s	F5/F9; F5/F6	1.1/1.6; 1.1/1.3

Table 5. Results of ANOVA test for the length of *M. norvegica* from vertical tows.

Season	No. of tows	df	F value	S	Sources of difference	Length
Winter	2	2;68	0.42	ns		
	3	2;33	0.77	ns		
	4	3;22	6.21	s	F8/F7; F9/F7	2.23/2.5; 2.25/2.5
	5	2;9	0.39	ns		
	6	2;11	0.08	ns		
	7	2;13	1.55	ns		

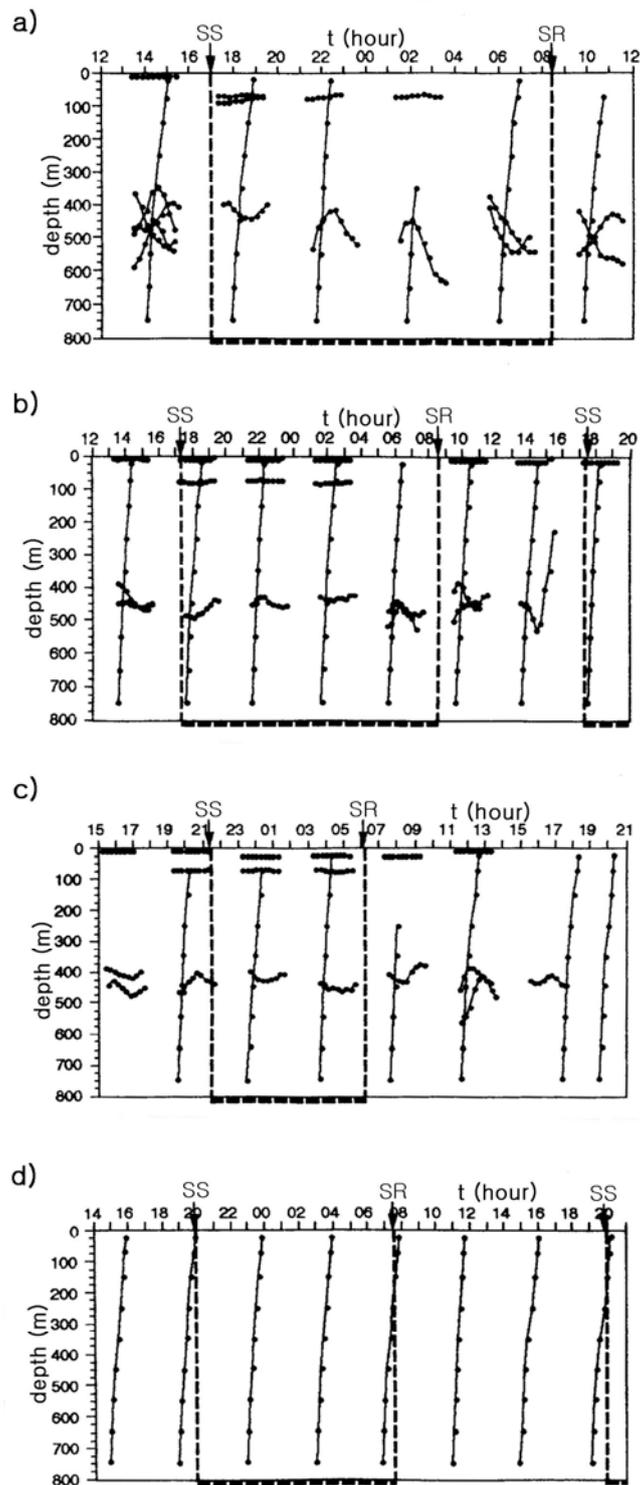


Figure 1. Vertical and horizontal tows integrated into one time vs. depth plot. a: autumn; b: winter; c: spring; d: summer.

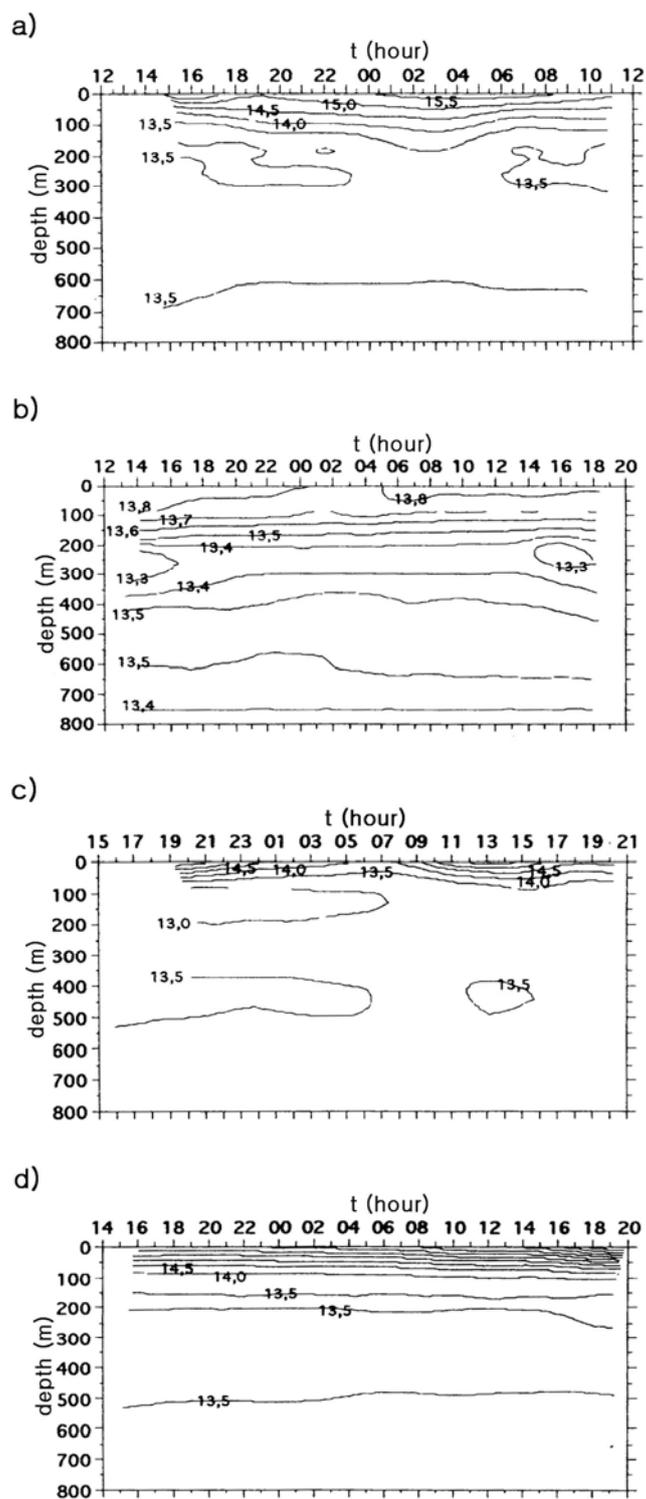


Figure 2. Vertical distribution of temperature in autumn (a), winter (b), spring (c) and summer (d).

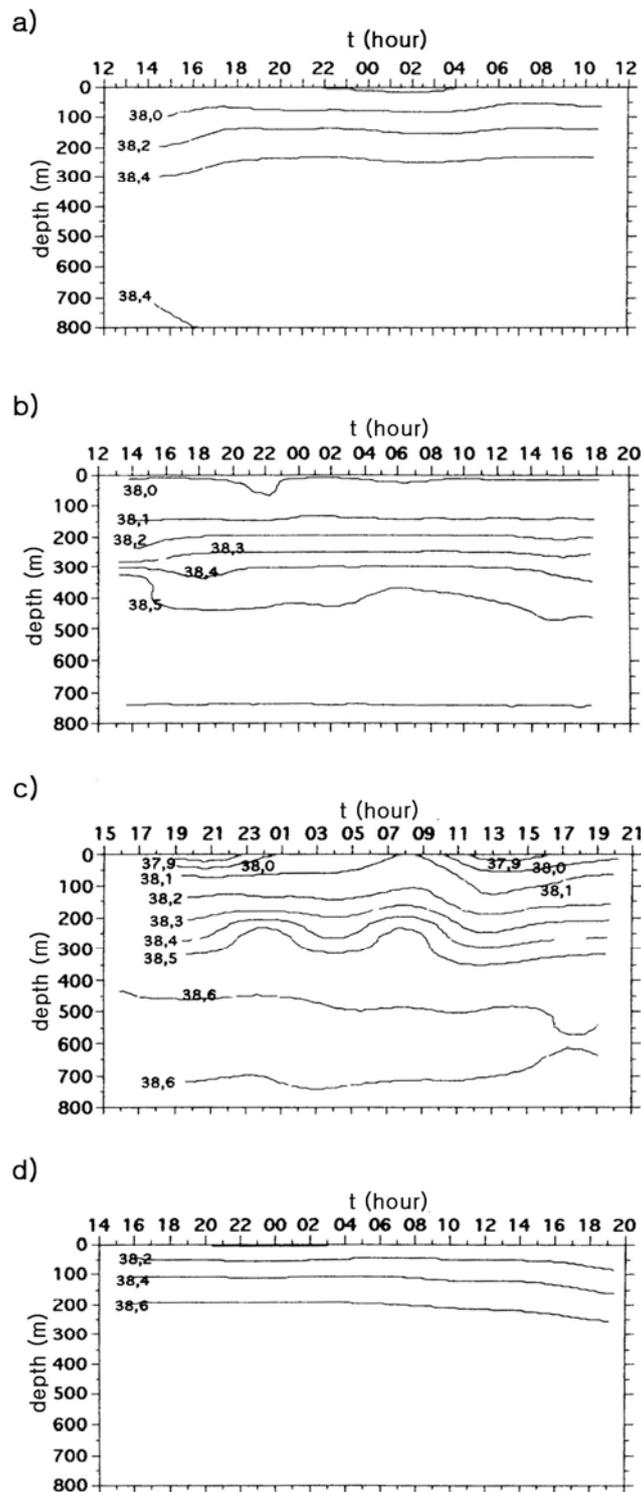


Figure 3. Vertical distribution of salinity (psu) in autumn (a), winter (b), spring (c) and summer (d).

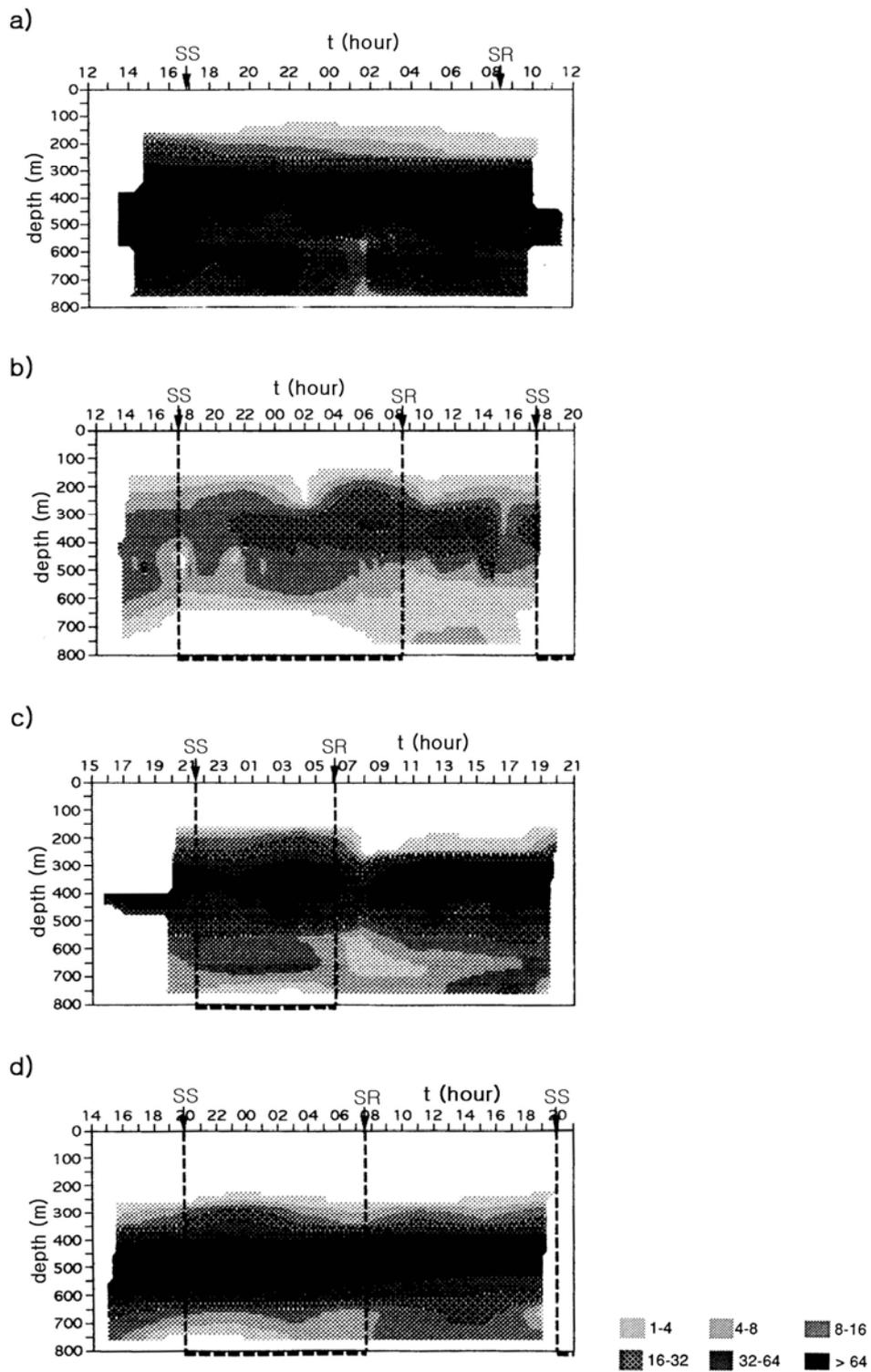


Figure 4. Vertical distribution of *C. braueri* (inds 1000m<sup>-3</sup>) in autumn (a), winter (b), spring (c) and summer (d)

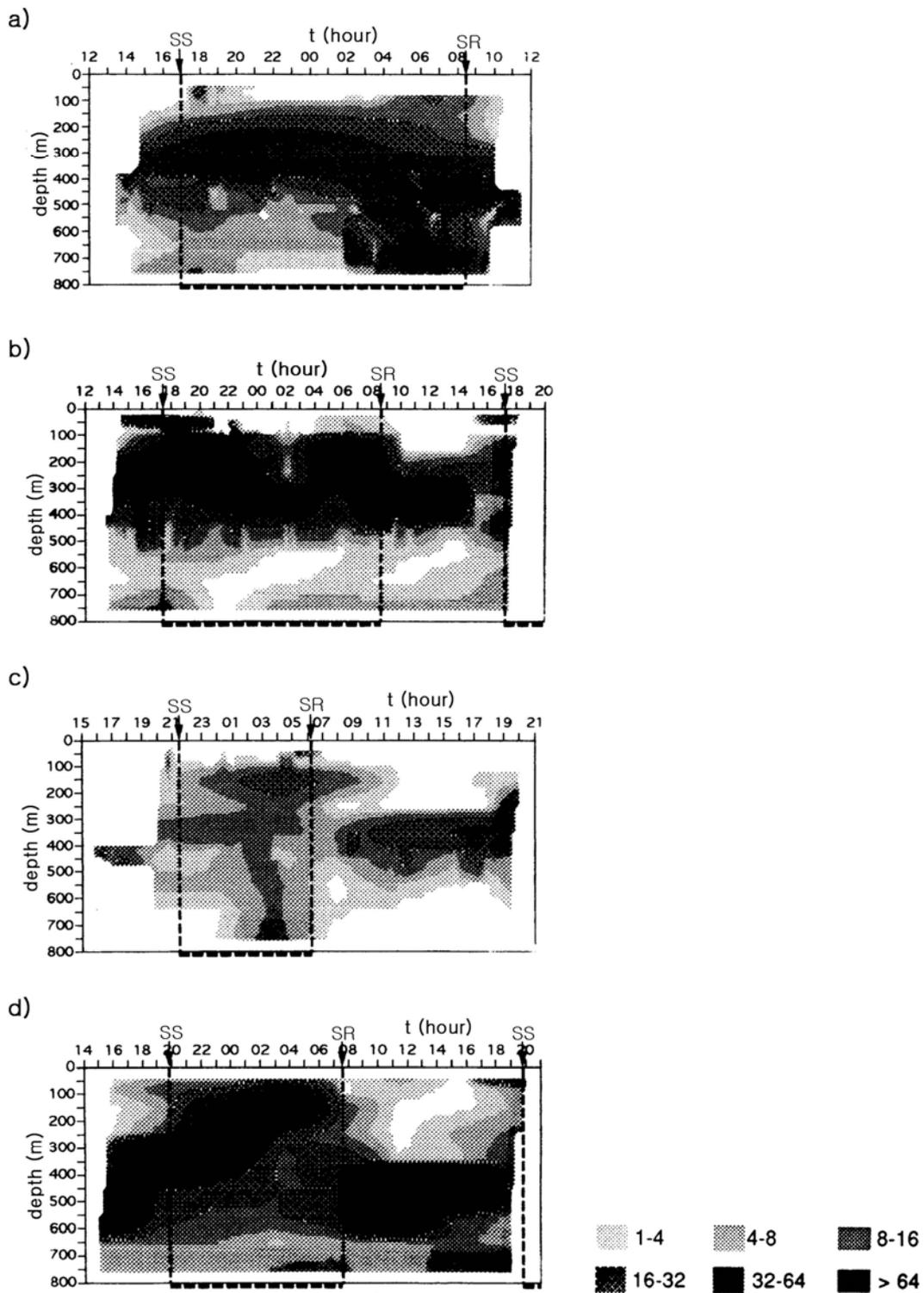


Figure 5. Vertical distribution of *N. megalops* (inds 1000m<sup>-3</sup>) in autumn (a), winter (b), spring (c) and summer (d)

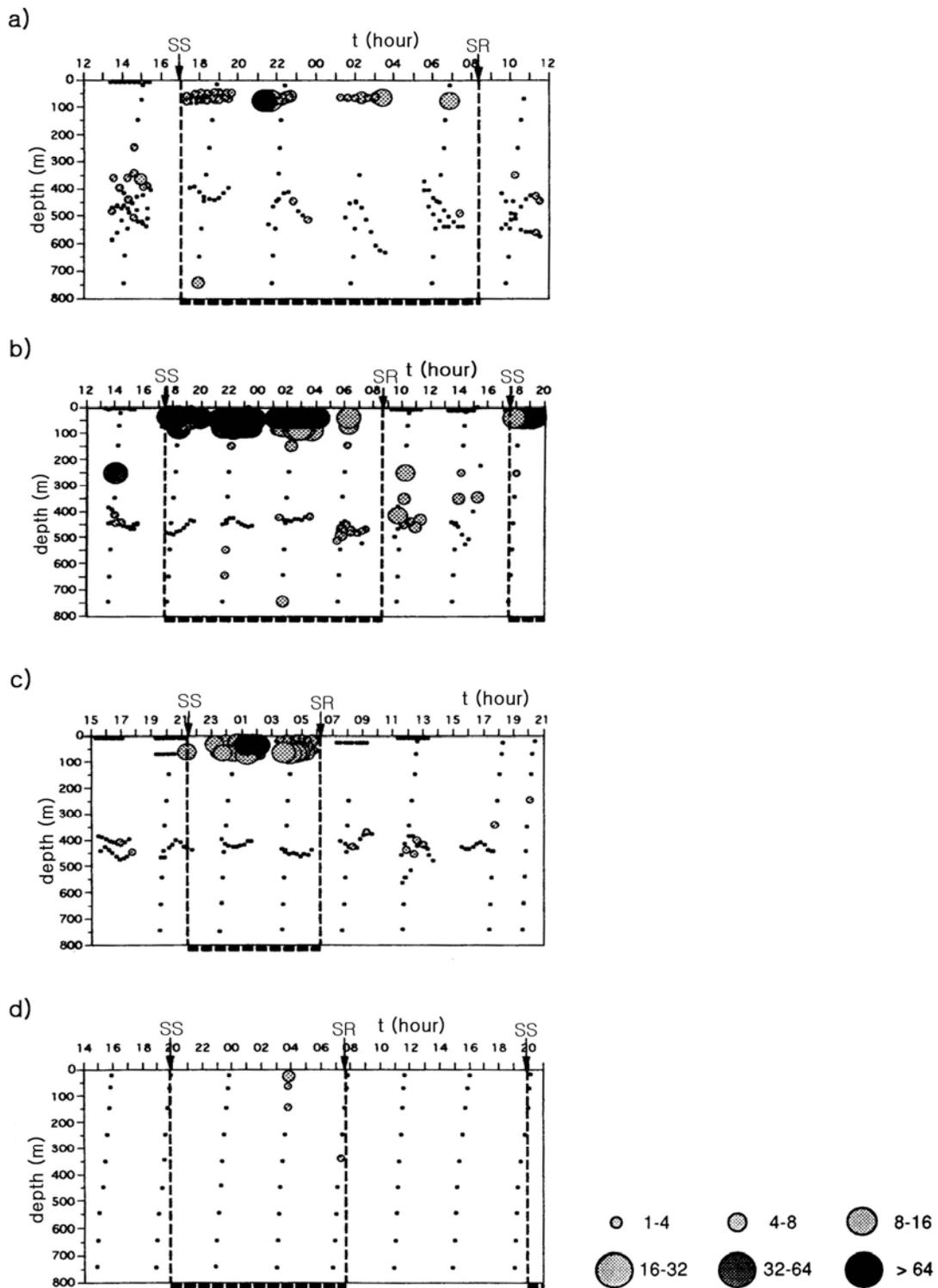


Figure 6. Vertical distribution of *M. norvegica* (inds 1000m<sup>-3</sup>) in autumn (a), winter (b), spring (c) and summer (d)

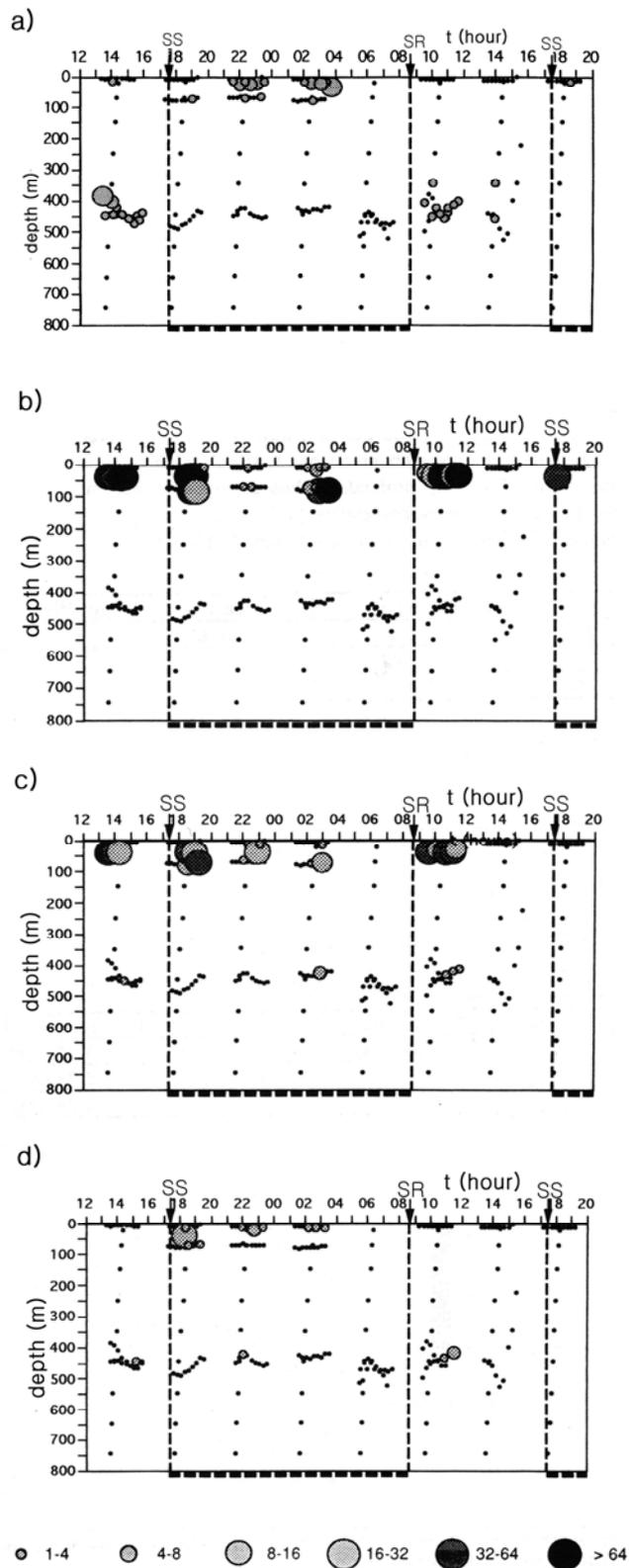


Figure 7. Vertical distribution of *S. fusiformis* oozoids (a), and small (0.3-0.8cm, b), intermediate (0.9-1.1cm, c), and large blastozooids (1.2-2.0cm, d) in inds 1000m<sup>-3</sup> in winter