

Seasonal variation in copepod abundance in relation to other zooplanktonic groups in the northwestern Mediterranean

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Abstract

Abundance of adult copepods and late copepodid stages from the upper 50 m in the Golfe du Lion (N.W. Mediterranean) was studied by the author in 1986, 1987, and 1988 for each season. Altogether 87 stations at 22 fixed locations were sampled in the frame of the multidisciplinary French/Spanish programme Pélagolion/Leopel in the near-coastal region (≤ 25 m bottom depth), the Rhone dilution zone, the neritic region (≤ 200 m bottom depth), and the oceanic region (200–2000 m bottom depth). Abundance of other zooplanktonic groups was estimated and total zooplankton biomass was determined for the upper 50 m. Copepod abundance was highest during September 1986 (all regions) and July 1987 (neritic). Total biomass was highest during July 1987 and May/June 1988, caused by high abundance of many other zooplankters.

Most abundant copepod species were: *Clausocalanus* spp., *Paracalanus parvus* (Claus, 1863), *Oithona* spp., *Oncaea* spp., *Corycaeus* spp., *Centropages typicus* Krøyer, 1849, *Calanus helgolandicus* (Claus, 1863), and *Temora stylifera* (Dana, 1849). Generally, copepodids slightly outnumbered the adult copepods in the coastal and neritic region, but they were twice to three times more numerous than adults in the oceanic region. Beside copepods, Cladocera formed the most important group at the near-coastal stations near the Rhone mouth; Siphonophora and Salpidae were most abundant at the neritic and oceanic stations.

Résumé

L'abondance des Copépodes adultes et des copépodites des 50 m supérieurs dans le Golfe du Lion (Méditerranée du N.O.) a été étudiée par l'auteur en 1986, 1987, et 1988 pendant chaque saison. On a réalisé des prélèvements à totalement 87 stations sur 22 locations fixes dans la région côtière (profondeur du fond ≤ 25 m), la zone de dilution du Rhône, la région néritique (profondeur du fond ≤ 200 m), et la région océanique (profondeur du fond 200–2000 m) dans le cadre du programme multidisciplinaire Franco/Espagnol Pélagolion/Leopel. L'abondance d'autre groupes zooplanctoniques a été estimée et la biomasse

zooplanctonique totale a été déterminée pour les 50 m supérieurs. L'abondance des Copépodes était la plus élevée pendant septembre 1986 (pour toutes les régions) et pendant juillet 1987 (dans la région néritique). La biomasse totale était la plus élevée pendant juillet 1987 et mai/juin 1988, à cause de l'abondance considérable d'autres groupes zooplanctoniques.

Les espèces de Copépodes les plus abondantes étaient: *Clausocalanus* spp., *Paracalanus parvus* (Claus, 1863), *Oithona* spp., *Oncaea* spp., *Corycaeus* spp., *Centropages typicus* Krøyer, 1849, *Calanus helgolandicus* (Claus, 1863) et *Temora stylifera* (Dana, 1849). En général, les copépodites étaient légèrement plus nombreux que les adultes dans la région côtière et dans celle néritique, tandis qu'ils étaient deux à trois fois plus nombreux dans la région océanique. Après les Copépodes, les Cladocères formaient le groupe zooplanctonique le plus important dans les stations côtières près de l'embouchure du Rhône; les Siphonophores et les Salpides étaient abondants dans les stations néritiques et océaniques.

Introduction

Copepods are the most abundant of the secondary producers in the oligotrophic northwestern Mediterranean. Depending on the season, epipelagic copepods form the greater part of mesozooplankton biomass (Razouls, 1972), being a main component in diets of predatory zooplankton, crustacean and fish larvae, and adult fish. The (sub)surface layer (the upper 50 m) contains highest concentrations of zooplankton.

Climate influences, such as hot summers, dominating wind regimes "Tramontane" and "Mistral", and river inflow from Pyrenees and Alps are responsible for strong and rapid fluctuations in salinity, temperature, and nutrient input in the (sub)surface layer (Fig. 1).

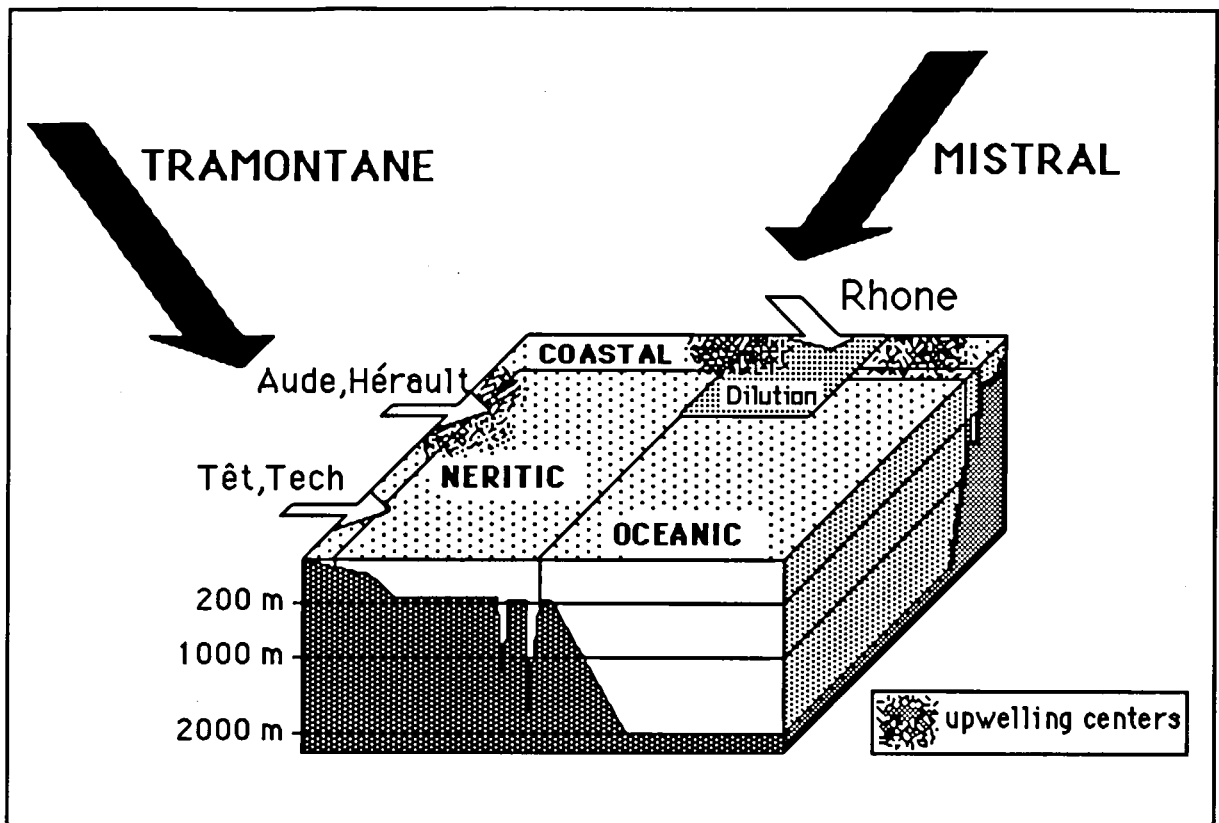


Fig. 1. A three-dimensional schematic presentation of the Golfe du Lion with the Rhone dilution zone and outflow of other rivers, dominating wind regimes, and upwelling centers (after Millot, 1979).

Low salinities in the Rhone dilution zone ($\leq 34.5\text{‰ S}$) contrast with the more saline adjacent surface and subsurface waters ($38.0\text{--}38.3\text{‰ S}$) in winter and spring. During summer, strong evaporation generates a highly saline (38.4‰ S) surface layer (Margalef, 1984).

The dominating, cold wind regimes "Tramontane" and "Mistral" decrease surface temperatures in winter, while subsurface temperatures stay higher. In late winter, temperatures are influenced by vertical mixing, creating so-called "chimneys" with a vertical homothermy ($13.2\text{--}13.4^\circ\text{C}$) over a depth, sometimes more than 1000 m (Margalef, 1984). In summer high surface temperatures (up to 24°C) contrast with low temperatures below the thermocline at 20–25 m (ca. 13°C).

Nutrient input in the (sub)surface layer is determined by various factors. (1) The Rhone River creates a wide, fertilizing dilution zone in winter and

spring (Coste et al., 1977). (2) During vertical mixing in late winter, nutrients are transported from deeper layers to the euphotic upper layer (Jacques & Tréguer, 1986). (3) During summer, local and short-lived upwellings of nutrient-rich intermediate Mediterranean water occur. This water, however, does not pass beyond the thermocline, which then separates an oligotrophic surface layer and an eutrophic subsurface layer (Cahet et al., 1972).

Late copepodid stages often differ in vertical distribution from the adults (Ambler & Miller, 1987); this is possibly related to differences in phototaxis and feeding habits. Little is published about differences in geographical distribution between adult and juvenile copepods.

In this paper only the zooplankton from the upper 50 m layer and over shallower depths near the coast is considered, to facilitate comparison of

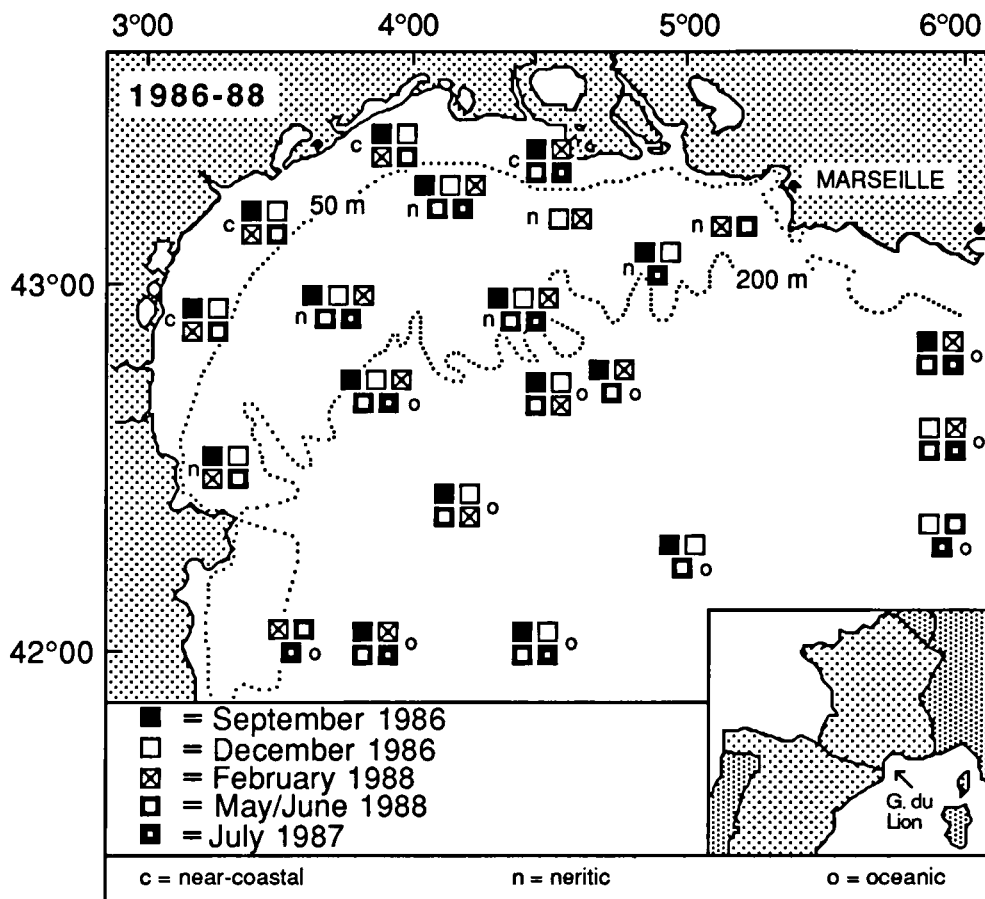


Fig. 2. Location of stations sampled in the Golfe du Lion over the period 1986–1988 in the upper 50 m, with 50 m and 200 m isobaths.

near-coastal, neritic, and oceanic stations. In most seasons this layer represents the euphotic upper layer. Emphasis is given to the distribution and abundance of adult and juvenile copepods from this layer, in relation to climate effects, hydrology, and total zooplankton biomass.

Material and methods

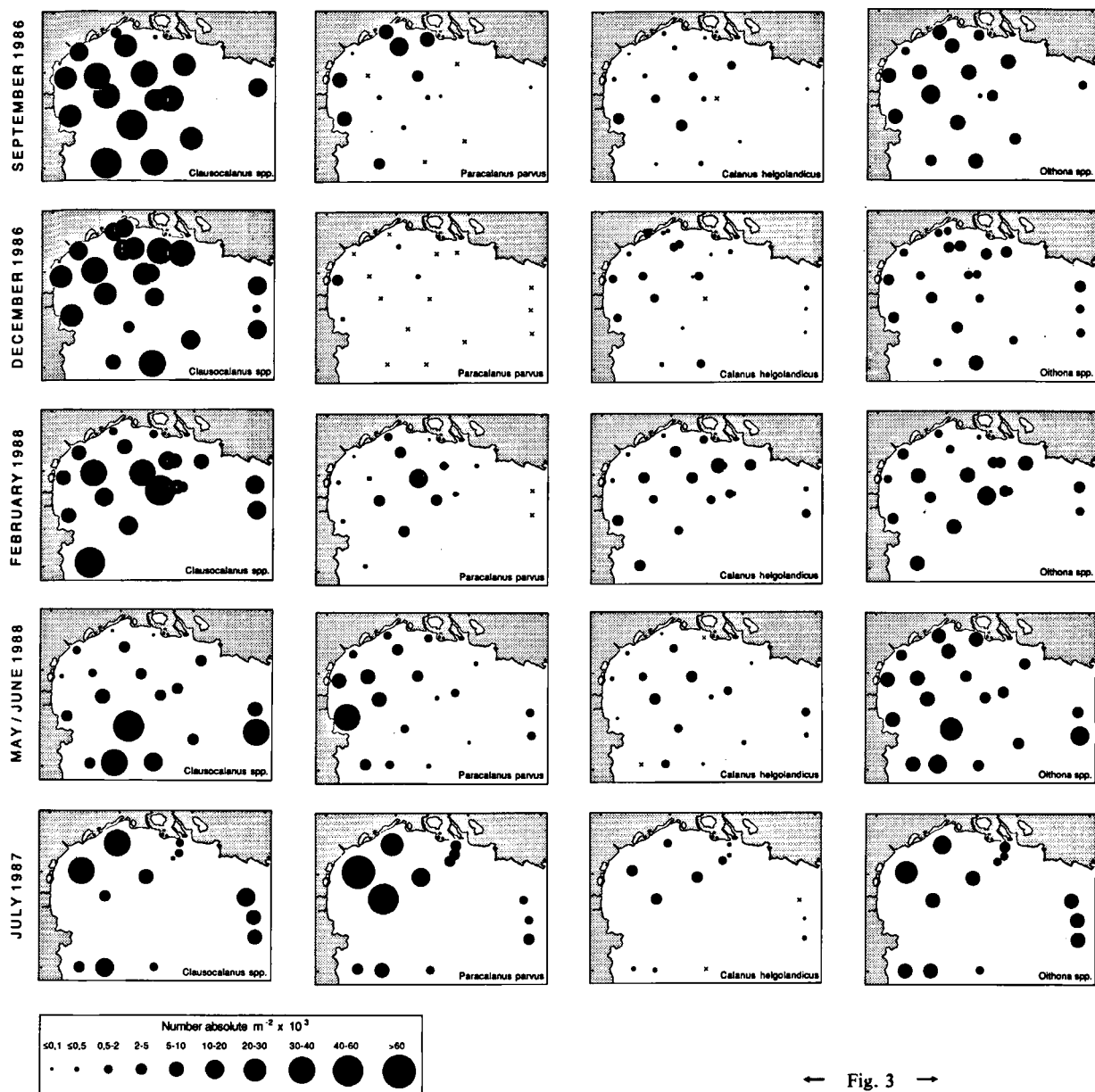
Zooplankton was sampled with a triple-WP2 vertical sampling net (Unesco, 1968), mesh size 200 μ m, mouth diameter of each net 50 cm, in the Golfe du Lion during a series of cruises within the multidisciplinary French/Spanish programme Pelagolion/Leopel. A total of 87 stations at 22 locations were alternately sampled during day- and night-time by vertical hauls from 50 m, 100 m, 200 m, and 600 m to the surface, provided that bottom depth was not limiting. In case of limiting bottom depth, sampling was done from bottom to surface. The area investi-

gated was divided into three different regions: the near-coastal region with bottom depth ≤ 25 m; the neritic region, over the continental shelf, and the oceanic region, with bottom depth from 200 to 2000 m and more (see Fig. 1).

The first cruise was made from September 3rd to 12th, 1986, the second from December 5th to 14th, 1986, the third from July 16th to 23rd, 1987, the fourth from February 2nd to 10th, 1988, and the fifth from May 28th to June 4th, 1988, thus all seasons have been covered (Fig. 2). At every station bottom depth was recorded, salinity and temperature were measured by means of a CTD system (Guideline and Seabird), and geographical position, force and direction of wind, cloud cover, time, and date were noted.

Aboard the ship, the sampled zooplankton from two nets of the triple WP2 was preserved in 4% neutralized formalin. The zooplankton from the third net was frozen in order to determine biomass (cf. Lovegrove, 1961). After subsampling with a plankton splitter (Razouls, 1972), generally 1/20 of the initial sample was examined to obtain a number of about one thousand copepods for identification and counting.

Quantitative analysis of copepodid stages (principally stages



← Fig. 3 →

III–V) and adults, and of the most important other zooplankton groups retained by the 200 μm mesh, was made under a stereomicroscope.

Most calanoid copepods were identified to species level (using Rose, 1933), except for the Clausocalanidae, Oithonidae, Oncaeidae, and Corycaidae which were identified to genus level. The abundance of adult and juvenile copepods and other dominating zooplankton groups was calculated as numbers per m^2 for the near-coastal, neritic, and oceanic regions in each season. Most of the counted copepods belonged to the following groups: Cyclopoida Oithonidae, Poecilostomatoida Oncaeidae and Corycaidae, and Calanoida Clausocalanidae, *Calanus hel-*

golandicus (Claus, 1863), *Centropages typicus* Krøyer, 1849, *Temora stylifera* (Dana, 1849), and *Paracalanus parvus* (Claus, 1863). Other common, but not abundant species included in the quantitative analysis form only a fraction of the total numbers.

A difference in copepod abundance between daytime and night was expected, due to the diurnal vertical migration of some copepod species. A one-way analysis of variance was applied, testing the null hypothesis that both samples come from the same population and therefore have the same means and variances ($\mu_1 = \mu_2$; $\sigma_1^2 = \sigma_2^2$). The difference in day and night sample means was not significant at the 5% level, so H_0 was not rejected. Therefore the day and night samples were pooled.

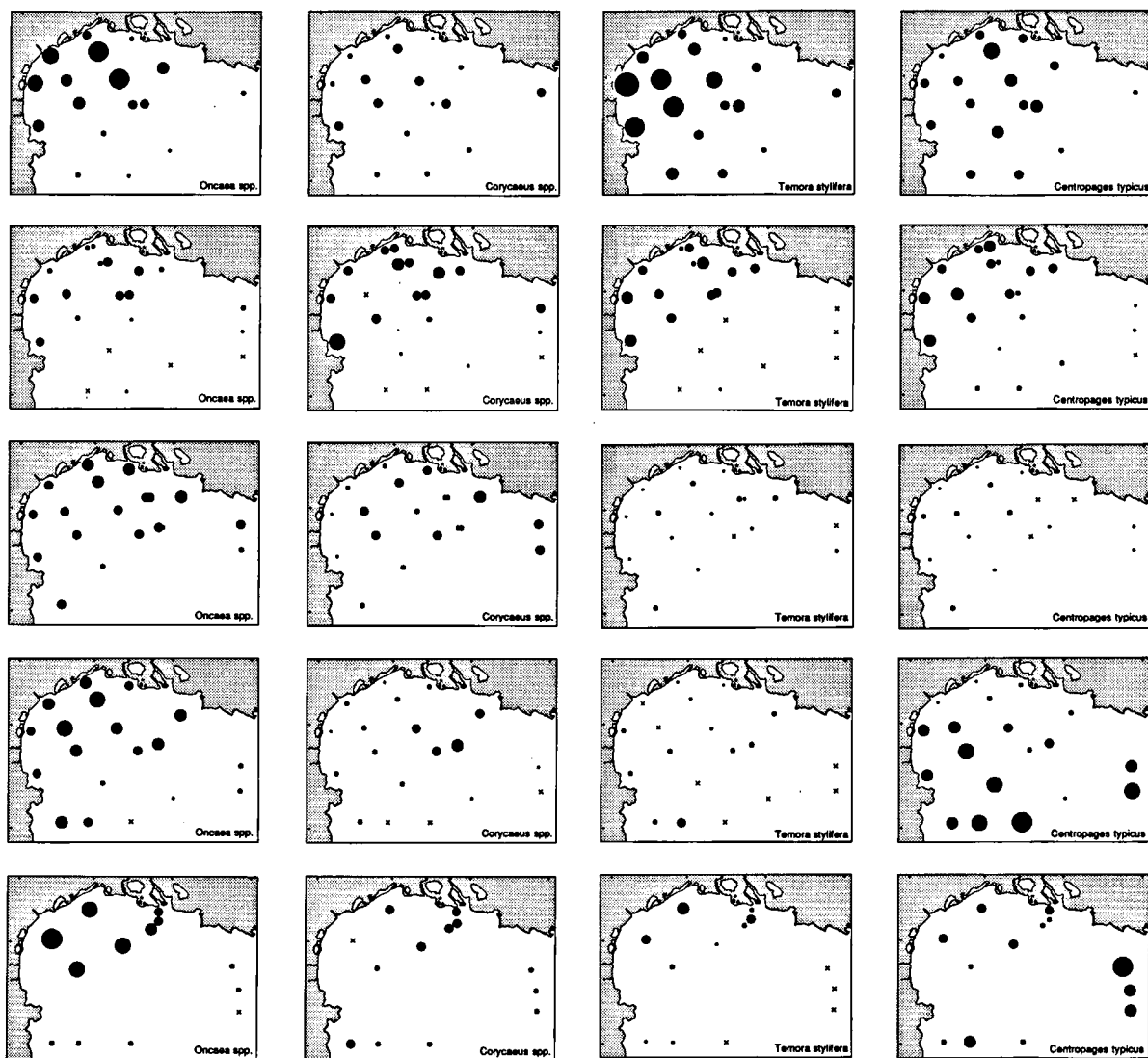


Fig. 3. Seasonal abundance in numbers m^{-2} at each sampled station for the eight most important copepod species and/or genera in the upper 50 m of the Golfe du Lion and adjacent waters.

In order to test the difference in adult-to-juvenile proportions between the neritic stations and the oceanic stations (Fig. 4), a two-way Wilcoxon inversion test for population homogeneity between two populations was carried out (Zijp, 1974). The null hypothesis was formulated as:

$$\frac{\text{Juveniles oceanic}}{\text{Adults oceanic}} = \frac{\text{Juveniles neritic}}{\text{Adults neritic}}$$

This null hypothesis had to be rejected in all sampling periods ($\alpha = 0.05$). This means that there were significantly more juveniles than adults at the oceanic stations compared to the neritic stations.

Results

Seasonal fluctuations in the dominating species

Clausocalanus spp. were the most abundant during all sampling periods (Fig. 3). During September, December, and February the distribution pattern and numbers per m^2 were similar. During May/June high densities were found in the oceanic region and low densities in the neritic and coastal region. During July densities were higher in the neritic region and lower in the oceanic region.

Generally, *Paracalanus parvus* showed low densities during September, December, and February. In May/June densities increased, especially in the neritic region. In July very high densities were found in the neritic region.

Vertically migrating *Calanus helgolandicus* showed rather low densities in general in the upper 50 m, but was frequently found at neritic stations. Highest densities were found during February, when vertical mixing occurred. During July the species was well represented at the neritic stations, but hardly found at the oceanic stations.

The Oithonidae have a very regular distribution pattern; neither high fluctuations nor variations were found. Lowest densities occurred during December.

Oncaea spp. and *Corycaeus* spp. have a neritic and coastal distribution; they were very rare in the oceanic region. Lowest densities for *Oncaea* spp. occurred during December, and for *Corycaeus* spp. during May/June and July, except around the Rhone mouth.

Temora stylifera showed rather high densities during September, especially in the neritic and coastal region. During December the species was present at the coastal and neritic stations, not at the oceanic ones. During February and May/June it showed very low densities and during July it was present in the neritic region and the Rhone mouth.

During September, December, and February *Centropages typicus* showed a distribution pattern similar to that of *T. stylifera*: rather high densities during September, only coastal and neritic distributions during December, and almost absent during February. During May/June, however, high densities were found for *C. typicus* in the oceanic and neritic regions (southern and western part of the Gulf). During July rather high densities were found in the oceanic region.

Abundance and distribution of adults and copepodids

Generally, copepodids outnumbered the adults during all seasons. The proportion juveniles-to-adults was significantly higher at the oceanic sta-

tions (2–3 times as high) compared with the neritic and coastal stations (Fig. 4), except for February, during vertical mixing, and July, with very high juvenile proportions at some neritic stations.

During September, *Clausocalanus* spp., *Oithona* spp., *Temora stylifera*, and *Oncaea* spp. were largely responsible for the high numbers in the neritic region (average: 65,364 m⁻²) (Fig. 3), with high adult means (28,507 m⁻²), compared to the near-coastal (14,420 m⁻²) and oceanic region (11,140 m⁻²). Mean numbers of juveniles were about equal in both the neritic (36,857 m⁻²) and oceanic region (36,604 m⁻²), but adult mean numbers were much lower in the oceanic region (Fig. 4).

Copepod abundance in December was lower than in September in all regions, and minimum numbers were recorded in the oceanic region (Fig. 4). The dominating species in the neritic region were the same as in September, with *Clausocalanus* spp. having the same abundance, and the other species decreasing considerably (Fig. 3).

Low abundances were also found in the near-coastal region in February. The most abundant species present at the coastal stations were *Clausocalanus* spp., *Oithona* spp., and *Oncaea* spp. (Fig. 3). In the oceanic region mean numbers were slightly higher than in the neritic region for both adults and juveniles. *Clausocalanus* spp. dominated, and *Oithona* spp., *Oncaea* spp., *Calanus helgolandicus*, and *Paracalanus parvus* were well represented at most neritic and oceanic stations. *Centropages typicus* and *Temora stylifera* were hardly present during this sampling period (Fig. 3).

In general, during May/June adult means were somewhat lower compared with February, and juvenile mean numbers were similar (Fig. 4). The dominating species, however, changed. In the neritic region *Clausocalanus* spp. decreased, but *Paracalanus parvus*, *Centropages typicus*, and *Oncaea* spp. increased. In the oceanic region, *Clausocalanus* spp., *Oithona* spp., and *Centropages typicus* were more abundant than in the neritic region (Fig. 3). During both months low means were found in the near-coastal region.

Highest abundances for both adults and copepodids were found in the neritic region in July, consisting for a considerable part of *Paracalanus*

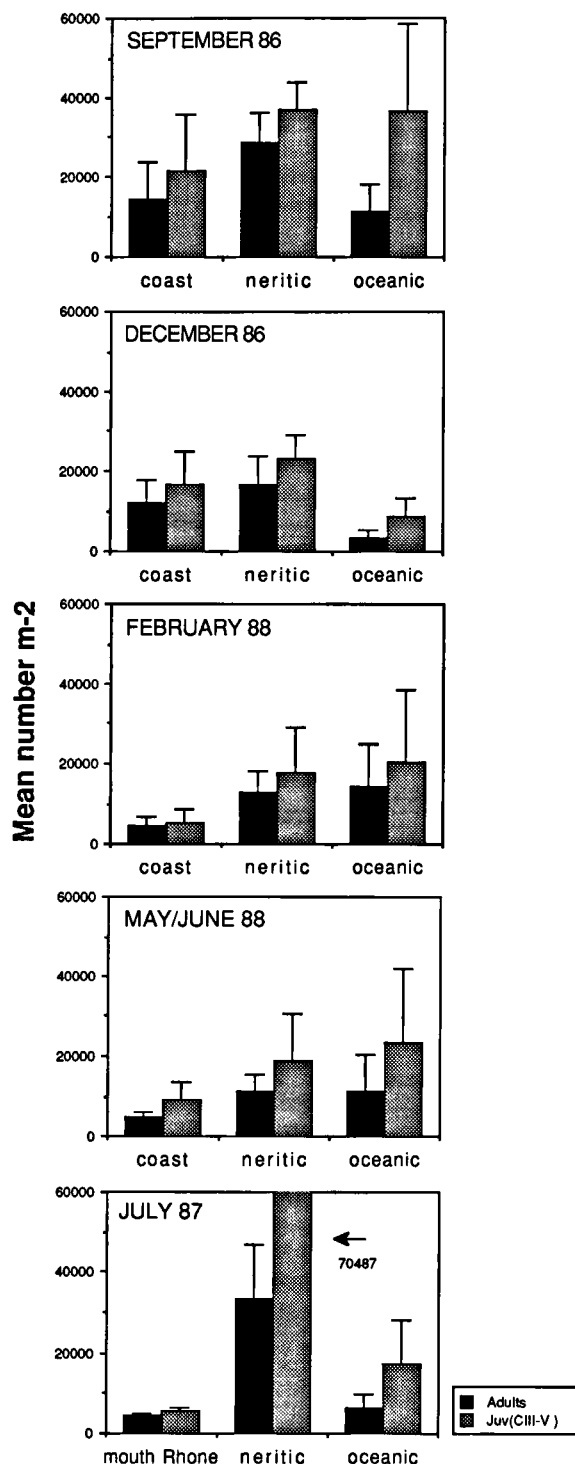


Fig. 4. Mean numbers m⁻² of adult and juvenile copepods \pm S.D. for each sampling period at the near-coastal, neritic, and oceanic stations from the upper 50 m (or shallower at limiting depths).

parvus (Fig. 3), while *Clausocalanus* spp., *Oithona* spp., and *Oncaea* spp. were the other dominating species. In the Rhone mouth and the oceanic region these species were not abundant. *Centropages typicus* was more abundant in the oceanic region than in the neritic region.

Copepod dominance in relation to total zooplankton biomass

Table I gives an overview of the mean mesozooplankton biomass and the dominating zooplanktonic groups in the upper 50 m during all sampling periods.

During September, December, and February, copepods were the dominating zooplanktonic group in all regions. During May/June and July, copepods were less important. Total mesozooplankton biomass, however, was higher during these months, containing high concentrations of other groups.

Discussion

The Clausocalanidae, Oithonidae, Oncaeidae, and Corycaidae were only identified to genus level, because of the high species diversity and high morphologic resemblance of juveniles belonging to these genera. According to Furnestin (1960), *Clausocalanus arcuicornis* (Dana, 1849) and *C. furcatus* (Brady, 1883) occur abundantly in the Golfe du Lion, the former being the most abundant. Among the Oithonidae, the most abundant species are *Oithona nana* Giesbrecht, 1892 and *O. helgolandica* Claus, 1863. The most important species in the Oncaeidae are *Oncaea media* Giesbrecht, 1891 and *O. venusta* Philippi, 1843. The Corycaidae are represented by eleven species (Razouls, 1972), the most common being *Corycaeus ovalis* Claus, 1863 and *Farranula rostrata* (Claus, 1863).

The most abundant copepod species were all (sub)surface dwellers, staying within the sampled 50 m depth range and showing no, or only slight, diurnal vertical migration. It is obvious that no significant differences were found in total

Table 1. Mean mesozooplankton biomass in mg dry weight $m^{-2} \pm$ S.D. for the upper 50 m (or shallower at limiting depth) with dominating zooplanktonic groups for the near-coastal, neritic, and oceanic region.

	Biomass	S.D.	Dominating groups
<i>September</i>			
near-coastal	411	304	Copepoda, Appendicularia, Euphausiacea, Doliolida
neritic	665	302	Copepoda
oceanic	435	190	Copepoda
<i>December</i>			
near-coastal	697	226	Copepoda, Cladocera, Appendicularia, Mysidacea
neritic	532	199	Copepoda, Appendicularia
oceanic	395	190	Copepoda, Pteropoda
<i>February</i>			
near-coastal	201	107	Copepoda (nauplii), Siphonophora, echinoderm larvae
neritic	888	547	Copepoda, Siphonophora, Salpidae, jellyfish
oceanic	460	218	Copepoda (nauplii)
<i>May/June</i>			
near-coastal	711	275	<i>Noctiluca</i> , Copepoda, Cladocera, decapod zoeae
neritic	1066	200	<i>Noctiluca</i> , Copepoda, Cladocera, Siphonophora, Ostracoda
oceanic	1773	832	Copepoda, Appendicularia, Siphonophora, Salpidae
<i>July</i>			
near-coastal	1121	264	Cladocera, Salpidae, <i>Noctiluca</i> , decapod zoeae
neritic	2028	512	Copepoda, Cladocera, Salpidae
oceanic	492	253	Salpidae, Pteropoda, Cladocera

copepod means between the day and night samples.

Although mean copepod number was highest during September, considering all three regions together, mean zooplankton biomass values were highest during May/June and July. Most Mediterranean (sub)surface copepods are small (≤ 3 mm), but very abundant. They contribute less to biomass than other, less abundant, but bigger mesozoo-

plankters, which was the case during May/June and July (Rhône mouth and oceanic) in the upper 50 m.

The near-coastal region

The low copepod abundance per m^2 at the near-coastal stations and the low zooplankton biomass, especially in February and May/June (Fig. 4, Table 1) is probably related to three factors: (1) Depth limitation (less than 25 m). (2) Low surface salinities in these months, due to freshwater inflow. (3) Strong Tramontane (mean wind speed 17 ± 5 knots during February) may have been unfavourable for the copepods and other zooplanktonic groups. The other groups during February and May/June were Siphonophora (Eudoxia), echinoderm larvae, *Noctiluca*, Cladocera, and decapod zoeae. The few copepod species of some importance were the euryhaline and potentially herbivorous *Clausocalanus* spp. and the carnivorous *Oithona* spp. and *Oncaea* spp. (Petipa et al., 1970; Timonin, 1971), probably also feeding on *Clausocalanus* nauplii and copepodids.

Furthermore, the possibility exists that swarming of copepods occurred on or a little above the bottom, as described by Ueda et al. (1983) for e.g. *Acartia* spp. and *Oithona* spp. along the Japanese coast. Bottom swarming may have occurred, as this phenomenon is considered to be common in temperate shallow and neritic waters (Emery, 1968; Hamner & Carleton, 1979). Many copepods may not have been sampled with the vertical WP-2 sampling net, being 3 m high, and not touching the sea bottom. Capturing bottom-swarming copepods demands other, more specialized sampling methods.

The neritic region

In the neritic region copepod abundance was high throughout the year, compared to the near-coastal and the oceanic region. During February and May/June, however, copepod abundance is about similar in the neritic and oceanic region (Fig. 4). In February this is due to vertical mixing, and in May/

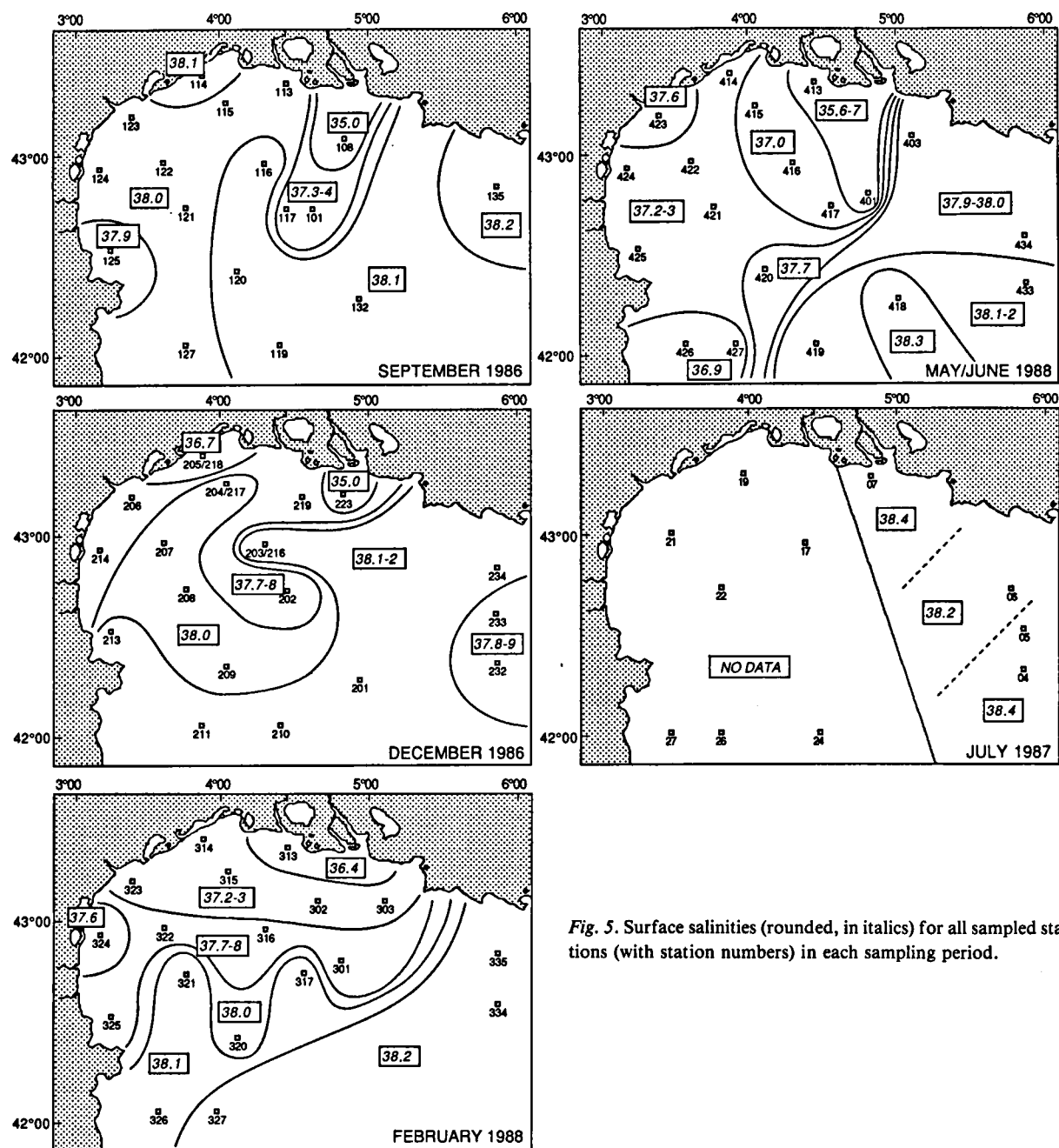


Fig. 5. Surface salinities (rounded, in *italics*) for all sampled stations (with station numbers) in each sampling period.

June to summer stratification, which forms an overlap of the ecological environment in both regions during these periods. Highest copepod abundance occurred during the months September and July. Adult means were about equal, but copepodid means were nearly twice as high during July ($70,487 \text{ m}^{-2}$) as during September

($36,857 \text{ m}^{-2}$). Mean biomass was also high during July in this region (Table I), while in summer the surface layer of the neritic and the oceanic region is characterized by nutrient exhaustion and low phytoplankton production. Cahet et al. (1972) described local upwellings of nutrient-rich intermediate waters during summer – not passing

beyond the thermocline – inducing a phytoplankton-rich layer below it. Around this layer many zooplankters may find sufficient food. Besides the high zooplankton biomass, another reason to assume that these local upwellings occurred during July is the record of *Eucalanus elongatus* (Dana, 1849), *Aetideus armatus* (Boeck, 1872) and *Euchirella rostrata* (Claus, 1866) in the upper 50 m, which are normally meso- and bathypelagic species with varying migration patterns, not coming to the (sub)surface (Vervoort, 1963, 1965).

High surface temperatures during July (22–24°C) generate short egg-development times for surface-dwelling copepods, with a high reproductive rate (female⁻¹ day⁻¹) as a result, at sufficient food concentrations. The dominating species in July was *Paracalanus parvus*, a typically neritic species, swarming at the surface (Vives, 1963; Mazza, 1967; Furnestin, 1979) and most probably responsible for the high copepodid concentration.

The oceanic region

The ratio juveniles/adults was much higher in the oceanic region than in the neritic and near-coastal regions in all periods (Fig. 4). In February the difference with the neritic region was less pronounced because of vertical mixing of the water column in both regions. During the other seasons the oceanic region is less exposed to strong water movements and fluctuations in temperature and salinity. In all seasons mean salinities were higher in the oceanic region, especially at 50 m depth (Kouwenberg & Razouls, 1990), except in July when mean surface salinities in the neritic and the oceanic region were as high as 38.4‰ S (Fig. 5). Juveniles may possibly be more stenohaline than adults and thrive better in warmer, more saline waters. Another possibility could be that adults undergo higher predation pressure in the oceanic region than juveniles, being of more interest to visual predators and predatory zooplankton.

Ambler & Miller (1987) found that adults have a deeper daytime distribution than juveniles in subtropical oceanic copepods. The recent results from the bottom-to-surface (100–200–0 m) and the

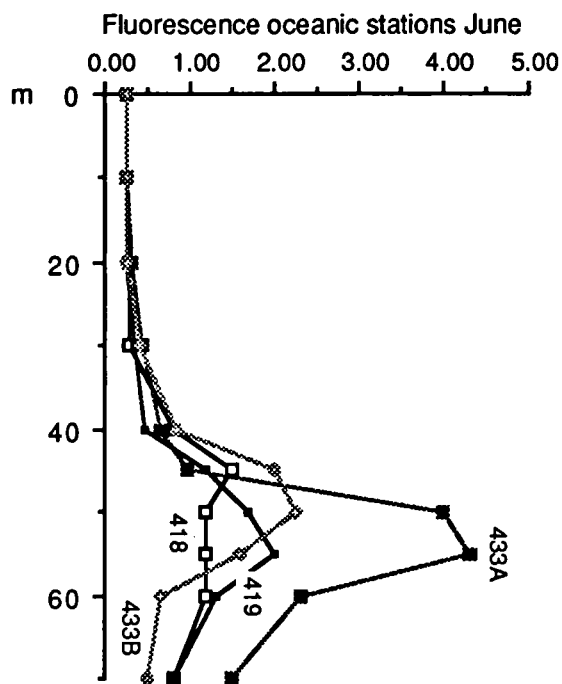


Fig. 6. Fluorescence profile (μg chlorophyll l^{-1}) down to 70 m at the oceanic stations in June 1988.

600–0 m samples from the September sampling period show proportions of juveniles/adults not different from those from the upper 50 m. At the oceanic stations proportions were: 2.13, 2.31, 1.66, 2.74, 1.74, 2.43, and 2.87; at the neritic stations: 1.84 and 1.66 (Kouwenberg, unpubl. data), resulting in similar proportions of juveniles/adults as in the upper 50 m, thus no deeper distribution patterns for adults were found in the northwestern Mediterranean.

The low copepod abundance at the oceanic stations and the low zooplankton biomass at the oceanic stations in December coincide with low phytoplankton production ($0.3 \mu\text{g l}^{-1}$ for surface; $0.4 \mu\text{g l}^{-1}$ for –20 m; $0.2 \mu\text{g l}^{-1}$ for –50 m (Kouwenberg, unpubl. data). In summer the thermocline separated two different water masses: an oligotrophic surface layer (less than $0.1 \mu\text{g}$ chlorophyll l^{-1}) and an eutrophic subsurface layer with deep chlorophyll maxima near and below 50 m depth (Fig. 6). Most copepods concentrating in this layer may not be captured with the 50–0 m hauls, which is supported by the much higher mean bio-

mass for the oceanic stations in the 100–0 m samples ($878 \text{ mg} \pm 266 \text{ m}^{-2}$; Kouwenberg, unpubl. data) compared to the 50–0 m samples ($357 \text{ mg} \pm 127 \text{ m}^{-2}$).

General conclusions

1. Copepodids have a distribution pattern different from adults, in view of the much higher ratio copepodids/adults in the oceanic region, compared to the near-coastal and neritic regions.
2. Copepods avoid the surface layer of the near-coastal region during periods of strong hydrodynamical mixing (Tramontane and Mistral), high freshwater inflow and low salinities.
3. The small-sized epipelagic copepods in the north-western Mediterranean do not contribute as much to the zooplankton biomass as do other planktonic groups together, in spite of the high numbers m^{-2} the whole year round (Clausocalanidae being the most abundant). Other groups have their population maxima during a short period in the upper 50 m, decreasing to very low numbers afterwards.

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