Copepod Distribution in Relation to Seasonal Hydrographics and Spatial Structure in the North-western Mediterranean (Golfe du Lion)

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Copepod abundance and hydrography from the upper 50 m in the Golfe du Lion (NW Mediterranean) were studied during 1986–88. Seasonal distributions of eight genera and 35 species at 87 stations were analysed by means of numerical classification. An obvious distinction can be observed between near-coastal/neritic stations and oceanic stations. Most abundant copepods were epipelagic and non-migrating like: Clausocalanidae, Oithonidae, *Paracalanus parvus*, Oncaeidae, *Centropages typicus* and *Temora stylifera*. Inverse analysis demonstrated (1) High densities for the epipelagic, non-migrating Clausocalanidae and Oithonidae over many clustered station groups. *Paracalanus parvus* and *C. typicus* were abundant during the summer sampling periods whereas *T. stylifera* was abundant in September. Common were some vertical migrators like: *Calanus helgolandicus*, *Pleuromamma gracilis*, *Candacia armata* and *Euchaeta marina*. (2) Rare, bathypelagic species were collected during the February and July sampling periods in the upper 50 m. In February this synchronized with vertical mixing of the water column, in July with locally upwelled deep intermediate water, remaining below the thermocline. Relatively high mean subsurface temperatures were measured in December and February. Salinities showed a considerable variation in Rhône influence between the different seasons. Species with mainly herbivorous feeding habits were more abundant than those of more diverse omnivorous or carnivorous feeding habits.

Introduction

The Golfe du Lion in the north-western Mediterranean has distinct hydrographical and geological characteristics. The wide continental shelf (down to 200 m depth) changes rapidly into an oceanic part with more than 2000 m depth. The waters in this basin originate from: (1) the Atlantic (≈ 50 m depth). This water is considerably modified after entering the Strait of Gibraltar (Millot, 1987), but is still influenced by the Atlantic, since species characteristic for Atlantic waters occasionally show up (Gaudy, 1963, 1985; Mazza, 1967; Estrada *et al.*, 1985); (2) the eastern Mediterranean (≈ 200 –400 m depth);

Figure 1. Schematic presentation of some current patterns, surface transport and coastal processes with Rhône influence and dominating wind-regimes in the Golfe du Lion.

→, Assumed circulation during Tramontane (Millot, 1976); , strongly mixed and modified water of Atlantic origin (Furnestin & Allain, 1962); , eastern Mediterranean water (Furnestin & Allain, 1962); , Rhône current (Furnestin & Allain, 1962).

and (3) the River Rhône. A thin layer of fresh, nutrient-rich Rhône water (plume) covers the saline water. The surface waters mix in a cyclonic current pattern (Figure 1) as described by Furnestin and Allain (1962), Millot (1976), Nihoul and Beckers (1989), Nihoul *et al.* (1990), Salat *et al.* (1990) and Brasseur (1992). Mean surface salinities range from 33 in the Rhône delta up to 38.2 in the south-eastern part of the gulf (Furnestin, 1960; Brasseur, 1992). Two wind-regimes, the northern 'Mistral' (Rhône valley) and the north-western 'Tramontane' dominate water movements. They strongly influence coastal upwellings, mixing of fresh and saline water (Cruzado & Velasquez, 1990), and surface current directions (Millot, 1979, 1981).

Zooplankton distribution is closely related to the (seasonal) changes in hydrodynamic features and circulation patterns. Copepods are important contributors to zooplankton biomass in the Golfe du Lion (Razouls, C., 1972) and extensive research has been done on the copepod fauna during the last 30 years (Furnestin, M.L., 1960, 1979; Vives, 1963; Thiriot, 1965; Mazza, 1966, 1967; Gaudy, 1970, 1971; Razouls, C., 1972, 1973; Estrada *et al.*, 1985; Kouwenberg & Razouls, 1990; Kouwenberg, 1993a). Most common copepods in the Mediterranean are cosmopolitan; many have an Atlantic, and some an Indo-Pacific origin. Less common species are of Boreo-Arctic and tropical origin (Vervoort, 1946, 1963, 1965; Sewell, 1948; Mazza, 1967). Copepod species diversity in the Mediterranean

is considerable with 469 species (Razouls & Durand, 1991); 186 species occur in the Golfe du Lion, but only 25 are important in secondary production (Furnestin, 1979).

The biology and ecology of individual copepod species from the Golfe du Lion were studied by Gaudy (1970, 1972), Razouls, C. (1972), Razouls, S. (1972), Razouls and Guinness (1973), and Razouls and Razouls (1976), but little attention has been given to the distribution of copepod assemblages in relation to seasonal and hydrodynamical characteristics.

In this paper only the copepods from the upper 50 m layer and at shallower depth (≈ 20 m) at the near-coastal stations are considered. This represents the subsurface and euphotic upper layer in most seasons and facilitates comparison of near-coastal, neritic and oceanic stations. In addition, hydrographical and climatic effects, characteristic for the region, are most pronounced at these shallower depths.

Material and methods

Zooplankton samples were collected with a triple-WP2 vertical sampling net (Unesco, 1968), of mesh size 200 μm , in the near-coastal, neritic and oceanic region in the Golfe du Lion during five cruises of the multidisciplinary French/Spanish Pélagolion and Leopol programmes. Depth permitting, a total of 87 stations were alternately sampled by day and by night in vertical hauls at different depths. This paper is based on the 50–0 m samples. The five cruises (Figure 2) provided a good degree of seasonal coverage. At every station CTD data (bottom depth, salinity, temperature) were recorded. Geographical position, wind speed, cloud cover, time and date were noted. On board ship the sampled zooplankton was preserved in 4% neutralized formaldehyde.

After subsampling with a planktonsplitter (Razouls, C., 1972), about one thousand copepods per sample were identified and counted under a stereo-microscope. Most copepods were identified to species level (Rose, 1933), except for the Clausocalanidae, Oithonidae, Oncaecidae and Corycaecidae which were identified to genus level. According to Furnestin, M.L. (1960) *Clausocalanus arcuicornis* Dana, 1849 and *C. furcatus* Brady, 1883, occur abundantly in the Golfe du Lion, *C. arcuicornis* being the most abundant. Among Oithona, the most abundant species are *O. nana* Giesbrecht, 1892 and *O. helgolandica* Claus, 1863. The most important species in Oncaea are *O. media* Giesbrecht, 1891 and *O. venusta* Philippi, 1843. Eleven species represent the Corycaecidae (Razouls, 1973), the most common being *Corycaeus ovalis* Claus, 1863 and *Farranula rostrata* (Claus, 1863). The number and relative abundance of species and genera were calculated per m^2 for each station in every season.

A difference in copepod densities between day and night was expected due to the diurnal vertical migration of some 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.

In order to classify the samples, the collected data were analysed by means of numerical classification. The data for all 87 sampling stations, comprising the abundance of 35 species and eight genera were combined into one large data table and analysed by cluster analysis. The average linkage method (Sokal & Mitcheener, 1958) combined with the Bray–Curtis dissimilarity coefficient was chosen for clustering (Longhurst, 1985; Kaandorp, 1986; de Kluijver, 1989; Gowing & Garrison, 1991). This approach has the

Figure 2. Location of sampling stations over the period 1986-88.

advantage of integrating sample results and species results. Field *et al.* (1982) formulated the Bray-Curtis equation as:

$$\partial_{jk} = \frac{\sum_{i=1}^s |Y_{ij} - Y_{ik}|}{\sum_{i=1}^s (Y_{ij} + Y_{ik})} \quad (1)$$

where Y_{ij} is the number of the i th species in the j th sample; Y_{ik} is the number of the i th species in the k th sample; ∂_{jk} ranges from 0 (identical scores for all species) to 1 (no species in common). A logarithmic transformation of the data set was chosen in order to give less weight to the dominant species and to give more weight to qualitative aspects of the data (van Tongeren, 1987).

$$\begin{aligned} x=0.0 & \quad T(x)=0 \\ 10 \leq x \leq 100.000 & \quad T(x)=\log(0.1x+1) \end{aligned} \quad (2)$$

in which x is the number of individuals m^{-2} and $T(x)$ the corresponding transformed value. Using the log transformation it is necessary that the minimal value of presence (which is not 0) is transformed to 1. The lowest value from this data set was 10 copepods m^{-2} . In order to transform this to 1, all values were converted to $0.1x$. The use of $\log(0.1x)+1$ was necessary because the minimum values were as low as 10 copepods m^{-2} .

After classification of all samples (the normal cluster analysis), a classification of the species in an inverse analysis was performed using the program SRTORD (Kaandorp, 1986). This inverse analysis reveals the species abundance and combinations, responsible for the separation of the different clusters. Species groups were identified using the 'variable stopping rule' which is based on the perception that individual groups with relative internal homogeneity may cluster at different levels of resemblance (Boesch, 1977). Stations with a low species diversity do always cluster at a lower similarity level with the group having the same dominant species and characteristics. Using the 'fixed stopping rule' these stations would be isolated, but now they join the station group with the same species dominance. The inverse analysis will show which species are responsible for clustering of a station at a lower similarity level. The data set includes both common and rare species. It seems reasonable to require higher intra-group resemblance in groups of common species than in groups of rare species for which the probability of co-occurrence is low. In data interpretation, however, attention is also paid to the value of the rare species.

Results

All species and genera collected during the sampling periods are listed in Table 1 in order of ubiquity together with a classification of main feeding strategies (mainly herbivorous, carnivorous, omnivorous).

Cluster analysis

The dendrogram resulting from the cluster analysis of all data (Figure 3) shows the dissimilarity of the stations based on the quantities of the different copepod species. In Figure 4 the clustered station groups are geographically presented. The stations, grouped in the sub-clusters A1–A5 overlap mainly the September, December and July sampling periods. The stations, grouped in the sub-clusters B1–B4 were sampled during February (B1–B2) and May/June (B3–B4). The stations, grouped in the clusters, C, D and E were sampled during the summer, and those grouped in the F cluster were sampled during December.

Inverse analysis

Table 2 shows the distribution of species over all clustered station groups. Some species are common, others are restricted to one or a few (sub)clusters at a concentration level of 90%.

Sub-cluster characteristics based on species abundance and diversity. The vertical structure in the inverse analysis (Table 2) shows that the station groups (clusters and sub-clusters in A–F) can be distinguished by a number of characteristics.

Sub-cluster A1 (Rhône-plume environment in September and December, Figure 4) is characterized by highly dominating *Clausocalanus* spp., with the highest mean abundance of all clusters and sub-clusters ($36.5 \times 1000 \text{ m}^{-2}$). Other important species in this sub-cluster are *Oithona* spp. and *Temora stylifera*. Well represented, but not so abundant are *Centropages typicus*, *Oncaea* spp. and *Pleuromamma gracilis*.

Sub-cluster A2 (neritic, outside the Rhône plume in December and February, Figure 4) is also dominated by *Clausocalanus* spp. and secondly by *Oithona* spp. but mean numbers

TABLE 1. All species and genera collected during the different sampling periods in the upper 50 m with main feeding strategies. Sources: Wickstead (1959, 1962), Corner (1961), Anraku and Omori (1963), Arashkevich and Timonin (1970), Nassogne (1970), Timonin (1971), Harding (1974), Bennet and Hopkins (1989)

Species/genera	Main feeding strategy
Abundant and frequent	
<i>Clausocalanus</i> spp.	Herbivorous (fine filter-feeders)
<i>Oithona</i> spp.	Carnivorous (piercing and sucking)
<i>Paracalanus parvus</i> (Claus, 1863)	Herbivorous (fine filter-feeders)
<i>Oncaea</i> spp.	Carnivorous (piercing and sucking)
<i>Centropages typicus</i> Krøyer, 1849	Omnivorous
<i>Temora stylifera</i> (Dana, 1849)	Herbivorous
<i>Calanus helgolandicus</i> (Claus, 1863)	Herbivorous
<i>Corycaeus</i> spp.	Carnivorous (piercing and sucking)
<i>Acartia clausi</i> Giesbrecht, 1889	Omnivorous
<i>Ctenocalanus vanus</i> Giesbrecht, 1888	Herbivorous
<i>Pleuromamma gracilis</i> (Claus, 1863)	Omnivorous, carnivorous
<i>Calocalanus</i> spp.	Herbivorous (fine filter-feeders)
<i>Candacia armata</i> (Boeck, 1872)	Carnivorous (piercing and sucking)
Frequent, not abundant	
<i>Euterpina acutifrons</i> (Dana, 1847)	Herbivorous
<i>Euchaeta marina</i> (Prestandrea, 1833)	Carnivorous (seizing and masticating)
<i>Neocalanus tenuicornis</i> Dana, 1847	Herbivorous
<i>Heterorhabdus papilliger</i> (Claus, 1863)	Carnivorous (piercing and sucking)
<i>Clytemnestra rostrata</i> (Brady, 1883)	Herbivorous
<i>Nannocalanus minor</i> (Claus, 1863)	Herbivorous (fine filter-feeders)
<i>Neocalanus gracilis</i> (Dana, 1849)	Herbivorous (coarse filter-feeders)
<i>Macrosetella gracilis</i> (Dana, 1848)	Herbivorous
<i>Microsetella</i> spp.	Herbivorous
Rare, moderate in summer	
<i>Eucalanus elongatus</i> (Dana, 1849)	Herbivorous (coarse filter-feeders)
<i>Euchirella rostrata</i> (Claus, 1866)	Omnivorous
<i>Sapphirina</i> spp.	Carnivorous
<i>Monacilla typica</i> Sars, 1905	Carnivorous
Rare	
<i>Oithona plumifera</i> Baird, 1843	Carnivorous (piercing and sucking)
<i>Haloptilus</i> spp.	Carnivorous (piercing and sucking)
<i>Centropages violaceus</i> (Claus, 1863)	Omnivorous
<i>Lucicutia flavicornis</i> (Claus, 1863)	Herbivorous (coarse filter-feeders)
<i>Aetideopsis rostrata</i> Sars, 1903	Carnivorous
<i>Aetideus armatus</i> (Boeck, 1872)	Carnivorous
<i>Anomalocera patersonii</i> Templeton, 1837	Carnivorous
<i>Candacia simplex</i> Giesbrecht, 1889	Carnivorous (piercing and sucking)
<i>Isias clavipes</i> Boeck, 1864	Omnivorous
<i>Pleuromamma abdominalis</i> (Lubbock, 1856)	Omnivorous
<i>Heterorhabdus spinifrons</i> (Claus, 1863)	Carnivorous (piercing and sucking)
<i>Mecynocera clausi</i> I. C. Thompson, 1888	Herbivorous
<i>Parapontella brevicornis</i> (Lubbock, 1857)	Carnivorous
<i>Euchaeta acuta</i> Giesbrecht, 1892	Carnivorous (seizing and masticating)
<i>Oncaea conifera</i> Giesbrecht, 1891	Carnivorous (piercing and sucking)
<i>Scolecithricella dentata</i> (Giesbrecht, 1892)	Omnivorous
<i>Mormonilla phasma</i> Giesbrecht, 1891	Herbivorous

are lower per m². This is also true for *T. stylifera* and *C. typicus*, whereas mean *Oncaea* spp. numbers remain about the same. On the other hand, *Corycaeus* spp. shows its maximum abundance in this sub-cluster with mean numbers of $2.5 \times 1000 \text{ m}^{-2}$.

In sub-cluster A3 (coastal and oceanic stations in September, coastal in December, Figure 4) a sharp decline can be observed in the still dominating Clausocalanidae and

Figure 3. Dendrogram showing classification of 87 stations, comprising all combined data. The distinguished clusters are marked with letters (A-F), the sub-clusters with A1-A5 and B1-B4.

Oithonidae to less than half the mean numbers m^{-2} of sub-cluster A1. Mean numbers of *C. typicus* and *T. stylifera* are somewhat higher than in sub-cluster A2, but lower than in sub-cluster A1.

Sub-cluster A4 (neritic and coastal stations, north-west of the Rhône plume in September and December, Figure 4) is characterized by: (a) higher quantities of *Acartia clausi*, *Calanus helgolandicus* and *Paracalanus parvus*, which were of low importance in sub-clusters A1-A3; (b) species diversity is higher (20) in comparison with sub-cluster A3 (13); (c) *Clausocalanus* spp., *Oncaea* spp. and *Oithona* spp. dominate and (d) *C. typicus* and *T. stylifera* show maximum mean values of all A sub-clusters.

Sub-cluster A5 (neritic stations in July, Figure 4) is characterized by a highly dominating *P. parvus* with a mean abundance of $33.3 \times 1000 m^{-2}$ over this station group. It is the only sub-cluster in which *P. parvus* shows these high abundances. Mean numbers of *Clausocalanus* spp. are much reduced ($15.6 \times 1000 m^{-2}$). Oithonidae, Oncaeidae and *C. helgolandicus* show the maximum values of all clusters. Vertical migrators, like *Euchaeta marina* and *Neocalanus gracilis* are present. Furthermore, some rare species, like *Aetideus armatus*, *Aetideopsis rostrata*, *Eucalanus elongatus*, *Sapphirina* spp. and *Anomalocera patersonii* concentrate in this sub-cluster.

Sub-cluster B1 (near-coastal stations in February, Figure 4) shows very low mean values of all important species. *Clausocalanus* spp. and *Oithona* spp. dominate with 4.9 and $1.8 \times 1000 m^{-2}$, respectively.

In sub-cluster B2 (neritic and oceanic stations in February, Figure 4) *Clausocalanus* spp. and *Oithona* spp. dominate with considerably higher mean values than in sub-cluster B1. *Calanus helgolandicus* shows relatively high values in comparison with the other clusters. Rare species, like *Lucicutia flavicornis*, *Monacilla typica*, *Aetideopsis rostrata*, *Neocalanus gracilis*, *Aetideus armatus*, *Isias clavipes*, *Mecynocera clausi*, *Candacia simplex* and *Parapontella brevicornis* were concentrated here, as was also observed in sub-cluster A5.

Sub-cluster B3 (neritic stations near Rhône plume and south-west in May/June, Figure 4) is characterized by dominating *P. parvus* and *Oithona* spp. with low mean values for the Clausocalanidae. It is the only sub-cluster in which *Nannocalanus minor* is of some

Figure 4. Geographical location of the by cluster analysis grouped stations. (a) September 1986, (b) December 1986, (c) July 1987, (d) February 1988, and (e) May/June 1988.

importance; *Ctenocalanus vanus* has its maximum mean values here with $1.8 \times 1000 \text{ m}^{-2}$.

In sub-cluster B4 (near coastal-stations in May/June, Figure 4) the generally dominant Clausocalanidae show their minimum values. The Oithonidae dominate and *P. parvus* is second in abundance. Species diversity is very low.

Cluster C (oceanic stations in June/July, Figure 4) shows high dominance of *Clausocalanus* spp. and *Oithona* spp. Maximum mean values were measured here for *C. typicus* ($6.5 \times 1000 \text{ m}^{-2}$), *Oithona* spp. ($12.0 \times 1000 \text{ m}^{-2}$) and *Pleuromamma gracilis* ($1.6 \times 1000 \text{ m}^{-2}$). Two rarely encountered species in the upper 50 m are restricted to this cluster, namely *Oncaea conifera* and *Euchirella rostrata*.

Cluster D (oceanic stations in July, Figure 4) comprises only two stations, showing low species diversity and low mean values for the otherwise abundant species. *Clausocalanus* spp. dominate slightly; other species, even *Oithona* spp. are of minor importance.

Cluster E (oceanic stations in June, Figure 4) comprises three stations. Here again low species diversity occurs, but *Clausocalanus* spp. dominates with much higher mean values than in cluster D. Higher values are also apparent for *C. typicus* and *Oithona* spp.

Finally in cluster F (oceanic stations in December, Figure 4) only the Clausocalanidae are of some importance; other species show very low values or are absent.

Copepod assemblages. Horizontally, 15 different assemblages can be distinguished in Table 2. (1) Species that occurred most clustered at station groups from A to F. However, except for the Clausocalanidae, which were present at all station groups, all other species in this assemblage were absent in clusters D and E, representing the oceanic stations in early and mid-summer. *Euchaeta marina*, *Neocalanus gracilis* and *Lucicutia flavicornis* were never found at near-coastal stations, grouped in sub-clusters B1 (February) and B4 (May/June). (2) Two rare species, *Scolicithricella dentata* and *Mormonilla phasma* were restricted to cluster F, representing the oceanic region in December. (3) The species that were for 90% spread over the clusters A to E, and not in cluster F. The most frequent and abundant species here were *C. typicus*, *Acartia clausi* and *Oithona* spp. (4) *Microsetella* spp., occurring rather frequently but very low in numbers, was the only species, spread over the stations, grouped in clusters A to D. (5) A large assemblage was spread over clusters A to C, thus restricted to the coastal and neritic region, with the most important species being: *C. helgolandicus*, *C. vanus*, *P. gracilis* and *Candacia armata*. (6) *Oncaea conifera* and *Euchirella rostrata* were restricted to the stations, grouped in cluster C. (7) The most important species spread for 90% over the stations, grouped in clusters A to B were *P. parvus*, *Oncaea* spp., *Euterpina acutifrons* and *Corycaeus* spp. (8–15) *Temora stylifera* is the only important species which was restricted for 90% to the stations grouped in the sub-clusters A1–A4, the other assemblages consist of rarely encountered species which were restricted to sub-clusters from the A and B clusters.

Salinities and temperatures

Surface salinities and salinities at 50 m depth are presented in Figure 5(a,b). Rhône river outflow results in a considerable influence zone at the surface during September, December and May/June. In February this influence was less pronounced. During May/June variability in surface salinities was highest; during September lowest. At 50 m depth salinities were higher and less variable during each season. During December, February and May/June bottom salinities were lower at the near-coastal stations (± 20 m depth) than at the neritic and oceanic stations at 20 m (Table 3) and 50 m. Table 3 shows the mean salinities and temperatures for the stations, grouped by cluster analysis at three different depths; surface, 20 m depth and 50 m depth. Between the different clusters there are no significant differences in salinities or temperatures, except for the stations grouped in cluster D (July).

Discussion

The copepod groups showing a similar distribution pattern (Table 2 and Figure 4) are a mixture of surface and subsurface dwellers and strong migrators. The vertical migrators, like *Calanus helgolandicus*, *Pleuromamma gracilis*, *Candacia armata*, *Euchaeta marina* and *Heterorhabdus papilliger* are common but not abundant and the epiplanktonic copepods outnumber them greatly. This is why the difference in sample means between day and night is not significant.

Figure 5. (a) Surface salinities in each sampling period and (b) salinities at 50 m depth and bottom salinities at the shallower (≈ 20 m) near-coastal stations.

TABLE 3. Mean salinities and temperatures for surface, 20 and 50 m depths for the stations grouped in clusters A to F

Sampling period	Clusters	n	Salinity			SD			Temperature (°C)			SD		
			surface	-20 m	-50 m	surface	-20 m	-50 m	surface	-20 m	-50 m	surface	-20 m	-50 m
Sep./Dec.	A1	9	37.29	38.02	38.13	1.30	0.07	0.11	18.50	17.35	14.63	2.30	2.25	1.03
Dec./Feb.	A2	8	37.84	37.92	38.05	0.31	0.18	0.12	15.60	15.60	14.85	2.50	2.35	1.13
Sep./Dec.	A3	9	37.67	38.04	38.07	0.82	0.20	0.22	18.72	16.87	14.02	2.70	2.83	0.43
Sep./Dec.	A4	6	37.86	37.86	38.08	0.36	0.38	0.16	17.36	15.46	14.22	2.90	2.32	0.81
Jul.	A5	6	ND	ND	ND	ND	ND	ND	21.91	17.51	13.82	1.40	2.18	0.43
Feb.	B1	6	37.31	37.65	37.80	0.53	0.18	0.41	12.77	13.02	13.14	0.31	0.34	0.36
Feb.	B2	10	38.06	38.08	38.12	0.13	0.10	0.08	13.29	13.34	13.36	0.16	0.13	0.12
May/Jun.	B3	7	36.95	37.80	37.89	0.68	0.33	0.40	17.50	15.81	13.54	0.49	0.89	0.26
May/Jun.	B4	5	37.01	37.88	38.00	0.75	0.23	0.07	17.10	4.75	13.40	1.17	0.78	—
Jun./Jul.	C	5	37.83	38.21	38.31	0.58	0.13	0.14	19.92	16.70	13.71	2.70	1.50	0.57
Jul.	D	2	38.40	38.36	—	—	—	—	22.10	18.70	16.73	1.50	3.20	3.00
Jun.	E	3	38.17	38.18	38.30	0.08	0.09	0.00	17.63	17.10	13.30	0.50	0.17	0.17
Dec.	F	7	37.98	38.11	38.18	0.15	0.11	0.09	14.96	14.73	14.15	0.72	0.81	0.65

Abundance and distribution pattern in relation to feeding habits

Many copepods occurring at the stations grouped in the same clusters have different feeding strategies. Wickstead (1962) divided pelagic copepods into three main groups, based on feeding habits: mainly herbivorous forms (selective and random), mixed feeders (true and facultative) and mainly carnivorous forms (selective and random). Studies on the feeding mechanisms of pelagic copepods, which traditionally were called herbivores reveal that many of them are mixed feeders, their diet including a variety of animal food (Anraku & Omori, 1963; Gaudy, 1974; Poulet, 1978; Paffenhöfer & Knowles, 1980; Wiadnyana & Rassoulzadegan, 1989). Daan *et al.* (1988) observed a tendency for increased predatory behaviour in the absence of other food. In clusters where copepods with mainly herbivorous feeding strategies were abundant, carnivores were also well represented. This confirms the findings of Longhurst (1985), who analysed zooplankton communities in the eastern tropical Pacific Ocean. For example, when the mainly herbivorous Clausocalanidae or Paracalanidae (Frost & Fleminger, 1968; Timonin, 1971; Paffenhöfer, 1984) were present in high quantities (Table 2), the mainly carnivorous Oithonidae (Lampitt, 1978; Davis, 1984) were also well represented. On the other hand, when the mainly herbivorous forms were low in number, the Oithonidae also showed their minimum abundance. Possibly the Oithonidae feed on the younger stages of *Clausocalanus* spp. and *Paracalanus parvus*.

Taking into account that among the most important species in the Golfe du Lion indicated in Table 1, there are two species of mainly herbivorous Clausocalanidae (*Clausocalanus arcuicornis* and *C. furcatus*), two species of mainly carnivorous Oithonidae (*Oithona helgolandica* and *O. nana*), three species of mainly carnivorous (Wickstead, 1962; Timonin, 1971; Davis, 1984) Corycaidae (*Corycaeus ovalis*, *C. latus* and *Corycella rostrata*) and two species of mainly carnivorous (Wickstead, 1962; Timonin, 1971; Davis, 1984) Oncaidae (*Oncaea media* and *O. venusta*) (Furnestin, M.L., 1960; Mazza, 1966), it appears that the species diversity of abundant carnivores and omnivores is higher than that encountered among the mainly herbivorous copepods. However, the latter show overall higher abundance (Figure 6). In total, there were 18 mainly herbivorous species and 30 omnivorous carnivorous species (Table 1).

The geographic shape of the sub-clusters A1, A2, A4, A5 and C, representing the station groups where high quantities of the mainly herbivorous copepods *Clausocalanus* spp. (A1, A2, A4, C) and of *Paracalanus parvus* (A5) were concentrated is probably more related to the typical areas of seasonally high phytoplankton production, resulting from the high nutrient input by the Rhône River (Cruzada & Velasquez, 1990) and the seasonal current and wind patterns, revealed on CZCS images (Morel *et al.*, 1990), than to the surface and subsurface salinities at the moment of sampling [see Figure 5(a,b)]. The shapes of the different salinity zones do not correspond at all with the shape of the sub-clusters. Most epipelagic copepod species in the Golfe du Lion are bound to be euryhaline and eurythermic, because of the high and rapid fluctuations due to climate.

As copepods are able to detect amino acids secreted by phytoplankton cells (Poulet & Ouellet, 1982) often at long distances (Paffenhöfer, 1991), food conditions may be the most important parameter in the distribution pattern of the mainly herbivorous copepods, which are by far the most abundant in this region, attracting the carnivores which feed on them.

Subsurface winter situation and watermass characteristics

During December, the Clausocalanidae were the only abundant, mainly herbivorous copepods in the oceanic region. The oceanic stations, grouped in the F cluster are

Figure 6. Mean numbers $\pm$ SD of (a) the most abundant mainly herbivorous ($\blacksquare$, *Clausocalanus*; $\square$, *Paracalanus*; $\boxtimes$, *Ctenocalanus*; $\boxplus$, *Temora*) and (b) the most abundant omnivorous/carnivorous copepods ($\blacksquare$, *Oithona*; $\boxtimes$, *Corycaeus*; $\square$, *Oncaea*; $\boxplus$, *Pleuromamma*; $\boxminus$, *Centropages*) in the near-coastal, neritic and oceanic region over all sampled periods.

characterized by low copepod abundance and low species diversity (Figure 7). In this period nutrients are exhausted and phytoplankton production is low; mean chlorophyll *a* values in the oceanic region during the December sampling period for surface, 20 m depth and 50 m depth, were 0.310, 0.424, and 0.225 $\mu g\ l^{-1}$ respectively. The Clausocalanidae seem to have the most successful competitive strategy for the remaining food. The other species recorded here are mainly carnivorous, for example *Euchaeta marina* and *Heterorhabdus papilliger* (Timonin, 1971).

Compared to previous years, mean water temperatures in December 1986 and February 1988 were relatively high. During the February sampling period in 1988, mean surface temperatures were 12.98 $^{\circ}C$ and at 50 m depth 13.37 $^{\circ}C$ (Kouwenberg & Razouls, 1990). However, mean surface temperatures in February during the years 1965–68 were 10.62 $^{\circ}C$

Figure 7. Mean zooplankton biomass from the upper 50 m $\pm$ SD for each station group forming the clusters A to F.

(Jacques *et al.*, 1969) and mean temperatures at a depth of 50 m were 11.87 °C in February 1969 (Fieux, 1971).

During February, species like *Paracalanus parvus*, *Calanus helgolandicus*, and *Oithona* spp. were more abundant than during December (Kouwenberg, 1993b). Most of the rarely encountered species were concentrated at stations grouped by cluster B2 in February as well (Table 2). They are mesopelagic or bathypelagic, like *Lucicutia flavicornis*, *Monacilla typica*, *Aetideopsis rostrata*, *Aetideus armata*, *Candacia simplex*, *Isias clavipes*, *heterorhabdus spinifrons* and *Mecynocera clausi* (Vervoort, 1963, 1965; Vives, 1963). In February in the neritic area mean salinities and temperatures down to 60 m depth were similar [Table 2, Figure 8(a)]; mean temperatures remained uniform to a depth of 200 m (13.29 °C $\pm$ 0.15, unpubl. data). This uniformity is a consequence of frequent vertical mixing movements in January and February, sometimes reaching depths down to 2000 m (Jacques & Tréguer, 1986). It results in nutrient transport from deeper layers into the euphotic upper layer. During vertical mixing, a part of the bathypelagic copepod population also appears to rise into the upper 50 m. The nutrient enrichment during vertical mixing is responsible for phytoplankton growth (Jacques *et al.*, 1973). Phytoplankton maxima (and indirectly zooplankton maxima) depend on the importance of the vertical mixing, varying according to the periodicity of cold and mild winters. Margalef (1984) observed that coldest winters precede high primary production.

Subsurface summer situation and watermass characteristics

Herbivorous *Paracalanus parvus* is amongst the most abundant species in the summer period (Table 2). It shows highest numbers in summer at the neritic stations grouped in cluster C2 (> 100 000 ind. m⁻²). Like the Clausocalanidae with which it successfully competes in summer it is a strongly euryhaline and eurythermic species (Vervoort, 1946).

Not only in February but also in July some meso- and bathypelagic species, like *Aetideopsis rostrata*, *Eucalanus elongatus*, *Aetideus armatus*, *Euchirella rostrata*, *Sapphirina* spp. and *Oncaea conifera* (Vervoort, 1963, 1965) were present in the 50–0 m samples (Table 2, sub-cluster A5). In summer the surface layer of the neritic and the oceanic region is characterized by nutrient exhaustion. However, during the summer, local and short-lived upwellings induce a phytoplankton-rich layer below the thermocline which occurs at $\approx$ 30–40 m depth (Cahet *et al.*, 1972). Thus, the thermocline separates two different watermasses: an oligotrophic surface layer (less than 0.1 μ g chlorophyll a l⁻¹) and a

Figure 8. CTD profiles down to 60 m. (a) The stations grouped in cluster B2 (February) and (b) the stations grouped in cluster C (June/July). (c) Fluorescence profile down to 70 m of the stations grouped in cluster E (June 1988).

eutrophic subsurface layer. The summer stations, grouped in sub-cluster A5 (neritic) and cluster C (oceanic) show a high zooplankton biomass (Figure 7) and the species encountered here probably feed on organisms accumulating at the thermocline, between

15 and 25 m depth at most stations [Figure 8(b)]. According to Vives (1963) *Centropages typicus*, *Calanus helgolandicus*, *Ctenocalanus vanus*, and *Candacia armata* are common winter species that remain under the thermocline in summer. The meso- and bathypelagic species that were found at the stations, grouped by sub-cluster A5 and cluster C (Figure 4) were probably carried along with local upwellings of intermediate waters.

The oceanic summer stations grouped in clusters D and E were very poor in zooplankton biomass, at $357 \text{ mg} \pm 127 \text{ m}^{-2}$ (Figure 7), and copepod numbers, as well as species diversity, were low (Table 2). The only well-represented species here were *Oithona* spp., *C. typicus* and *N. minor*. At these stations a fluorescence peak occurred indicating a high chlorophyll content between 50 and 60 m depth [Figure 8(c)]. Saiz and Alcaraz (1990) found *C. typicus* maxima at the deep chlorophyll maximum (DCM) at the same depth during the summer stratification period between Barcelona and Mallorca. Probably zooplankton maxima were concentrated in and near this chlorophyll-rich layer and not captured with the 50–0 m hauls. In support of this, the zooplankton biomass at these stations in the upper 100 m was much higher, namely $878 \text{ mg} \pm 266 \text{ m}^{-2}$.

Indicator species for waters from different origin

The Rhône River covers the saline subsurface layer with a thin layer of freshwater, not more than the upper 2–10 m during calm weather conditions (Cruzado & Velasquez, 1990). Its dilution zone and area of influence strongly depend on the strength of the 'Mistral' and 'Tramontane', and the direction of other winds. As sampling was done vertically in the upper 50 m, the species composition in the samples of Rhône dilution zone consisted of both euryhaline surface species, tolerating low salinities, and less euryhaline subsurface species. Therefore, species collected by the above-mentioned sampling method cannot be considered indicator species for the freshwater Rhône plume, though indirect influence of the nutrient-rich Rhône outflow can be observed in the high quantities of the mainly herbivorous copepods, feeding in the phytoplankton rich area.

Isias clavipes and *Parapontella brevicornis*, characteristic for Atlantic influence (Gaudy, 1963, 1985) were collected incidentally at stations that form clusters B1 and B2 (February), during the period of vertical mixing.

An indicator species of eastern Mediterranean waters, *Monacilla typica*, (Mazza, 1967) was only found at stations grouped in cluster B2 in February and at stations grouped in clusters C and E in the oceanic region in summer. This may indicate that some eastern Mediterranean water (200–400 m deep Levantine current) is involved in the vertical mixing process during February, and that in summer the local, short-lived upwellings, responsible for the presence of deep-living copepods in the 50–0 m samples, also contain eastern Mediterranean water. These species, however, appear too infrequently to be considered reliable indicators of waters of different origin.

Conclusions

The results of the cluster analysis and the inverse analysis reflect the geographical distribution of the species studied, separating the oceanic region from the neritic and near-coastal region, during the appropriate season. The A and B clusters grouped the stations, based on the abundance and species composition, into near-coastal and neritic regions during the September, December, February and July sampling periods. The stations grouped in the C, D and E clusters reflect the abundance and species composition in the oceanic region during early and mid-summer and the F cluster grouped stations with species composition characteristic for the oceanic region in December.

Cluster analysis showed an obvious distinction between near-coastal/neritic stations with high copepod densities, and oceanic stations, with low densities and low species diversity. In winter this is due to a very low phytoplankton production, and in summer to zooplankton maxima deeper than 50 m.

No sharp boundaries in copepod number, species composition, salinities and temperatures exist between the September, December and February sampling periods. The June and July sampling periods were different from the others.

Vertical mixing in February could be determined by: (a) presence of meso- and bathypelagic copepods in the 50–0 m samples and (b) uniform temperatures and salinities down to great depths. Local intermediate upwellings in summer, remaining below the thermocline, could be determined by: (i) the presence of meso- and bathypelagic copepods in the 50–0 m samples; (ii) a deep chlorophyll-rich layer, resulting from nutrient input from below; and (iii) high zooplankton biomass in the upper 100 m compared to the upper 50 m.

Copepods with mainly herbivorous feeding strategies were highest in abundance but lowest in species diversity.

Paracalanus parvus replaced *Clausocalanus* spp. as the dominating species in the neritic region during the summer period.

The occasional appearance of indicator species of waters originating from the Atlantic and eastern Mediterranean is not enough to discuss the influence of these waters in the upper 50 m.

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