

Variations of zooplankton in the frontal area of the Alboran sea (Mediterranean sea) in winter 1997

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Abstract – Zooplankton from the upper 200 m of the Almeria-Oran frontal region, (east of the Alboran sea, western Mediterranean) was sampled during winter 1997, using two nets equipped with 200 and 80 μ m mesh. Eight sites representative of the different hydrodynamic structures (Mediterranean water, geostrophic Atlantic jet, associated anticyclonic gyre) were investigated over 2 d, using two day- and two night-samples per site. Zooplankton biomass was correlated to chlorophyll abundance, with lowest values in the oligotrophic Mediterranean water and highest in Atlantic water. The high biomass resulted from the enhancement of the secondary production, as indicated by the greater proportion of nauplii and the increase of zooplankton metabolism and feeding. Total abundance and biovolume of organisms varied like their biomass. Maximum quantitative values were recorded in the material collected by the 80- μ m net which sampled more efficiently young developmental stages such as nauplii. Copepods accounted for 60–71 % of the zooplankton, and their nauplii, scarce in the 200- μ m net material, up to 33 % in the 80- μ m samples. Compared to the average repartition of total zooplankton at the different sites, nauplii, siphonophora, chaetognatha, ostracoda and meroplankton were preferentially distributed in the Atlantic sites. The general aspect of the copepods assemblage was homogeneous, the bulk of the population being constituted of *Clausocalanus* and *Oithona* spp. Nevertheless, the specific diversity was greater in the Atlantic waters, with the addition of some scarce species absent from the Mediterranean water. Several other species, present at every site were significantly more abundant in the Atlantic waters, e.g. *Pleuromamma borealis* and *Eucalanus crassus*. The distribution of *Centropages typicus* and *Clausocalanus furcatus* was more specifically linked to the front limit where these species could find favourable feeding conditions. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Résumé – Variations du zooplancton dans la région frontale de la mer d'Alboran (mer Méditerranée) en hiver 1997. Le zooplancton des deux cents premiers mètres de la région du front Almeria-Oran (à l'est de la mer d'Alboran, Méditerranée occidentale) a été échantillonné pendant l'hiver 1997, à l'aide de deux filets couplés équipés de mailles de 200 et de 80 μ m. Huit sites représentatifs des différentes structures hydrodynamiques (eaux méditerranéennes, jet géostrophique atlantique, tourbillon anticyclonique associé) ont été étudiés pendant 2 j chacun, à partir de deux prélèvements diurnes et deux prélèvements nocturnes. La biomasse du zooplancton était corrélée à l'abondance de chlorophylle, avec ses plus basses valeurs dans les eaux oligotrophes méditerranéennes, et ses plus hautes dans les eaux atlantiques. Les biomasses élevées résultent d'une activation de la production secondaire, comme l'indiquent par ailleurs la plus grande proportion de nauplii et l'accroissement du métabolisme et de la nutrition du zooplancton. L'abondance totale et le biovolume des organismes varient comme leur biomasse. Les valeurs quantitatives sont plus élevées avec le

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matériel recueilli par le filet de 80 μm , qui échantillonne plus efficacement les jeunes stades de développement tels que les nauplii. Les copépodes constituent 60 à 71 % du zooplancton, et leurs nauplii, rares dans le matériel du filet de 200 μm , atteignent jusqu'à 33 % dans les échantillons du filet de 80 μm . Par comparaison avec la distribution du zooplancton aux différents sites, les nauplii, siphonophores, chaetognathes, ostracodes et le meroplancton sont préférentiellement distribués dans les sites atlantiques. L'aspect général de l'assemblage de copépodes est homogène dans toute la région, l'essentiel de la population étant constitué par *Clausocalanus* et *Oithona* spp. Cependant la diversité spécifique est plus grande dans les eaux atlantiques, en raison de l'addition des quelques espèces rares absentes des eaux méditerranéennes. D'autres espèces, présentes à chaque site, étaient significativement plus abondantes dans les eaux atlantiques, e.g. *Pleuromamma borealis* et *Eucalanus crassus*. La distribution de *Centropages typicus* et de *Clausocalanus furcatus* était plus spécialement liée à la limite frontale où ces espèces peuvent rencontrer des conditions trophiques favorables à leur production. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Alboran sea / distribution / front / zooplankton

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1. INTRODUCTION

Hydrological fronts constitute areas of active exchanges of energy and matter where the primary production is enhanced, when compared to adjacent waters (Priour et al., 1993). Geostrophic fronts exhibit complex structures where the primary current circulation (related to the geostrophic situation) is accompanied by a cross frontal secondary circulation associated with divergence and convergence areas, which usually promote primary production in the surface water. In the western Mediterranean, such a frontal structure is induced by the entrance of Atlantic water through the Gibraltar strait. It is characterised by its size (length 200 km) and its strong horizontal gradient of density ($> 0.4 \text{ kg} \cdot \text{m}^{-3}$ for 10 km; Priour and Sournia, 1994). The inflow of Atlantic water forms two anticyclonic gyres (a western and an eastern one), occupying all the Alboran sea. The eastern structure generally starts near the Cape Tres forcas, in Algeria, proceeds to the Spanish coasts, near Almeria, then constitutes a well defined jet flowing in the SE direction towards Cape Gata and Oran (Algeria), associated in its southern part with an anticyclonic gyre of Atlantic water (Tintore et al., 1988). The left side of the jet forms a well marked density gradient, clearly visible on the satellite images (Arnone et al., 1990; Folkard et al., 1994). This permanent geostrophic structure (Almeria-Oran front) probably plays a significant role in biological productivity at the regional scale.

The multidisciplinary cruise 'Almofront 2', in December 1997–January 1998, was planned to examine the influence of the internal hydrological structure and secondary

circulation on biological production and on the export of matter in the Almeria-Oran frontal area. It was a follow-up of the Almofront 1 cruise, carried out earlier in the same region, but during another season (spring 1991). During Almofront 1, the chlorophyll biomass was higher in the hydrological structures related to the frontal region (Atlantic jet and anticyclonic gyre) than in the surrounding Mediterranean oligotrophic waters (Claustre et al., 1994). The biomass of zooplankton was also the highest in the Atlantic water structures, as a consequence of the enhancement of its nutritional activity and metabolism (Gaudy et al., 1991; Thibault et al., 1994).

The present work is specifically devoted to the secondary level. It analyses the relationships between mesozooplankton quantitative and qualitative variations and the different hydrodynamic structures observed during Almofront 2. Other results dealing with physiological studies of zooplankton (respiration, excretion, food ingestion) carried out during the same cruise are used for the discussion (Gaudy, unpubl. results).

2. MATERIALS AND METHODS

2.1. Studied region, choice and characteristics of the sites

The Almofront 2 cruise was carried out in the eastern part of the Alboran sea, between 3–0° W and 36–35° N (figure 1). During the first leg (13–23 December 1997), two transects through the frontal region and the adjacent

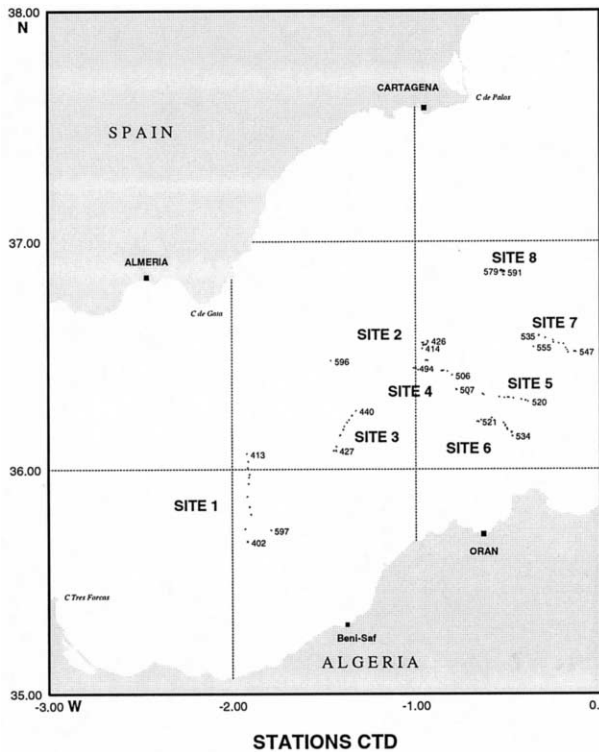


Figure 1. Study area (east of the Alboran sea). Location of the CTD stations during two successive days at each of the eight sites.

waters, using CTD, ADCP and TOW-YO device were analysed to describe the whole area and identify the location of the main hydrodynamic structures. The second leg (24 December 1997–4 January 1998) was devoted to the study of the biological processes, at eight different sites (figure 2) representative of the various zones of the frontal system, selected from the information obtained during the first part of the cruise. The denomination of the sites (1 to 8) corresponds to their chronological approach. The location of each site was not fixed, but followed the position of a buoy sustaining two sediment traps, at 100 and 300 m depth, and drifting in the currents for 2 d. At each site, ten to twelve CTD profiles were realised at regular intervals to check the stability of the hydrological features and to be sure that the successive samplings were performed in the same structure. Site 1 was at the most western position, in the left part of the gyre, close to the right limit of the cyclonic meander of the Atlantic jet. Sites 3 and 6 were placed in the core of the gyre, upstream and downstream, respectively. Sites 4 and 5, where there is a relatively rapid current, were representative of the jet. Sites 8 and 2 were

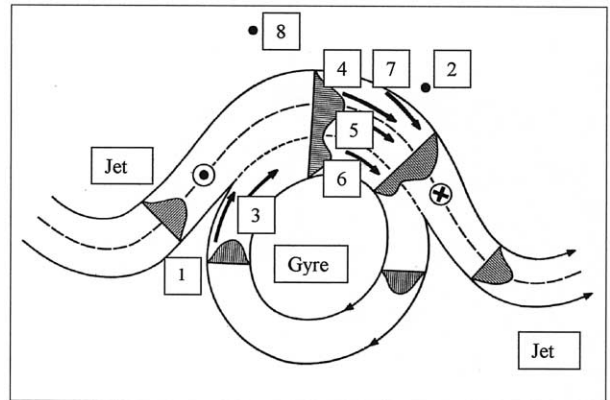


Figure 2. Location of the sites with respect to the schematic structure of the Almeria-Oran front. Current velocity is indicated by the shadow areas. The arrows represent the shift of the position of the sampling stations drifting in the current during the time of study of each site. Sites 8 and 2 are located in the Mediterranean water.

located in Mediterranean waters. The first was influenced by a secondary hydrodynamic structure characterised by a current flowing northward, contrary to site 2 which was closer to the front. Site 7 was at the front limit, where the maximum horizontal density gradient was observed. At these different sites, the CTD profiles of temperature, salinity and fluorescence, performed between 0 and 200 m, differed according to the degree of Mediterranean or Atlantic water influence. Mediterranean sites displayed colder, saltier and poorer water than Atlantic sites. Time variability occurred between the CTD profiles performed successively at each site, but this intra-site variability was lower than the hydrologic differences between sites, justifying their separation according to their hydrological characters (Prieur, pers. comm.). Specifically, the water density (figure 3) allows to separate clearly the denser Mediterranean waters (sites 8 and 2) from the lighter waters of the jet and gyre sites. At the frontal limit (site 7), some differences appeared between the first day, when density values approached the Mediterranean ones, and the second day of investigation, with values closer to the jet water density. Nevertheless, as no evident difference appeared in zooplankton quantitative and qualitative data between the 2 d, we did not try to consider separately the results of days 1 and 2. Therefore, the results obtained at the different sites are presented according to a Mediterranean-Atlantic gradient, based on the density of surface water and the depth of the pycnocline, (the deepest being observed in the gyre), in the following

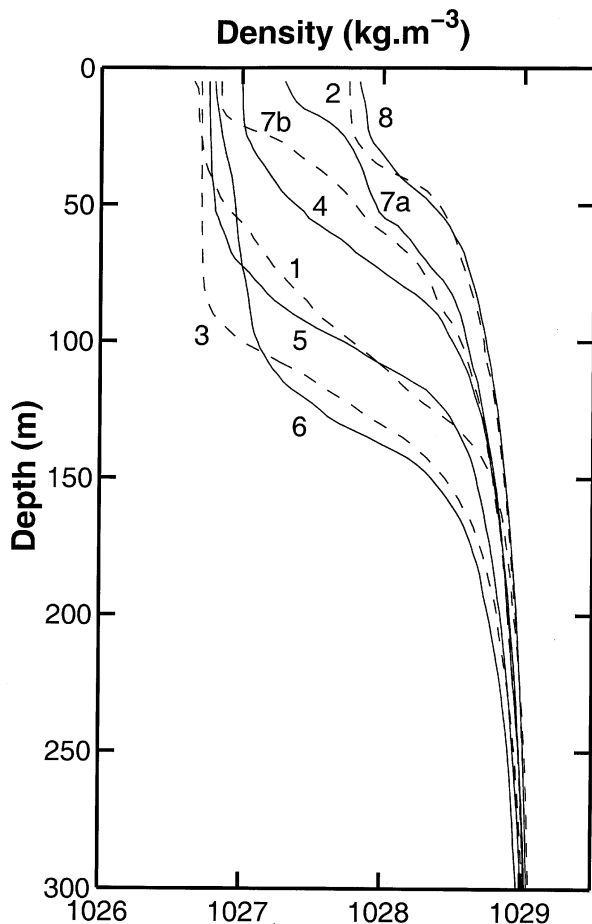


Figure 3. Vertical profiles of the density of water at the eight sites. Site 7 is separated into two profiles (a and b) corresponding to days 1 and 2.

order: 8, 2 (Mediterranean water), 7 (front limit), 4, 5 (core of the jet) and 1, 6, 3 (anticyclonic gyre).

2.2. Sampling and treatment of biological material

At each site, four plankton samples (corresponding to four different CTD stations) were taken, at night (04:00 hours) and during the day (11:00 hours), on two successive days. Zooplankton was sampled vertically between 200 m and the surface with two WP2 nets (UNESCO, 1968) fitted on a common frame. One of the nets was equipped with 200- μ m mesh size silk, according to the Mediterranean international standard, and the other, with

a smaller mesh (80 μ m) in view of sampling correctly tiny species and larval stages such as nauplii, generally poorly sampled with a conventional 200- μ m mesh. Each of the two samples was fractionated with a Motoda box. A quarter was filtered on a pre-weighed filtering disk of the same porosity as the silk of the net used for the sample. The filter with the retained zooplankton was rapidly rinsed with distilled water and then frozen. Later, at the land laboratory, samples were defrosted, dried in an oven (60 °C, 3 d) and then weighed. Dry-weight biomass was estimated from the difference between the final weight and the weight of the disk and normalised to the volume of water filtered in situ. An aliquot of the desiccated plankton retrieved from the disk was used to analyse the chemical elemental composition, using a Leco 800 autoanalyser.

Another quarter of the sample was stored in flasks using 4 % formaldehyde for preservation and borax as buffer. This part was reserved for the measurement of biovolume and for the determination and counting of organisms. Biovolume was deduced from the displacement volume of a fraction of the sample, retained on a filtering disk of the same mesh width as the relevant net and of pre-measured volume. This disk was then rolled to form a small cylinder, then immersed in a measuring cylinder containing 25 or 50 mL sea water. The volume of the sample, obtained from the difference between the increase of volume in the measuring cylinder and the volume of the disk, was then extrapolated to the water column. Identification and counting of the organisms were realised on sub-samples placed in Dollfus cuves using a dissecting microscope. Two stations per site (a day and a night one) were examined for abundance estimates. Main holoplankton and meroplankton groups were counted in the material collected by each type of net. Copepods were considered at the specific level, using the 200- μ m net samples only. The rest of the sample was reserved for gut fluorescence measurements and experiments on board the ship (results not reported here).

3. RESULTS

3.1. Space variations

The biomass of the zooplankton collected with the 200- μ m net is always lower than in the 80- μ m net

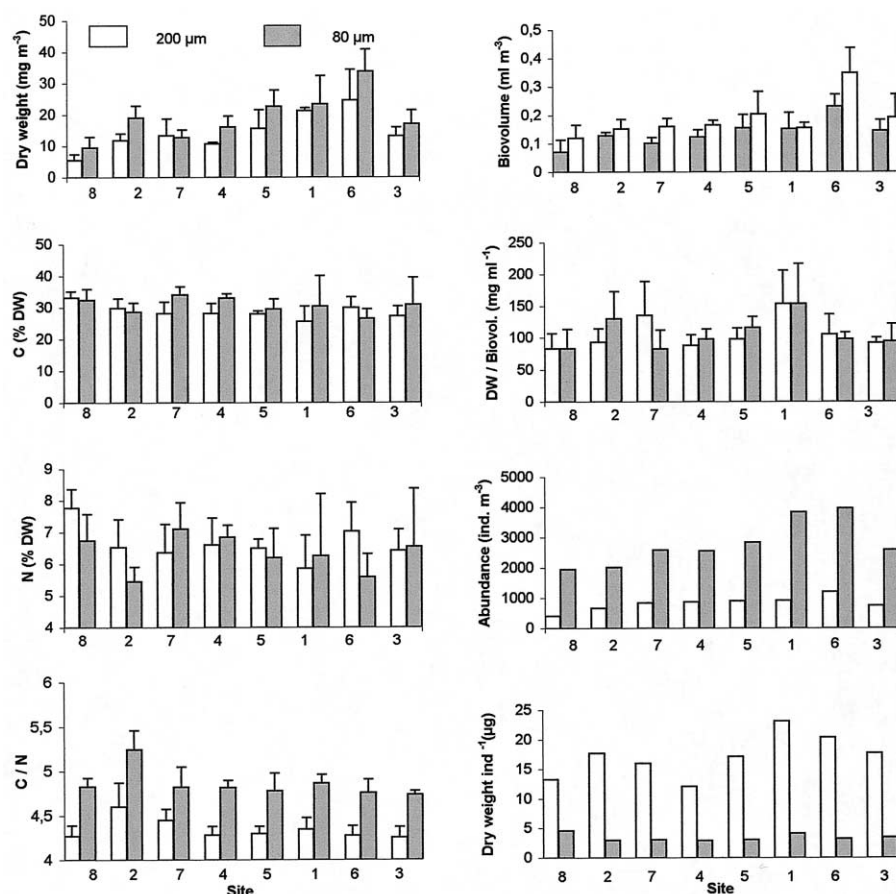


Figure 4. Variation of standing stock (dry weight), body carbon, body nitrogen (% dry weight), C:N ratio, biovolume, dry weight:biovolume ratio (body density), abundance, dry weight:abundance ratio (mean individual body weight) at the different sites. White columns correspond to 200- μm net samples and dark ones to 80- μm net samples.

samples, except at site 7 (figure 4). This is the consequence of a better capture of the very numerous tiny organisms in the water column by the finer net but poorly retained by the 200- μm net. Using the coarse net, significant higher biomass values (15 to $25 \text{ mg} \cdot \text{m}^{-3}$) are found at sites 6, 1 and 5 of the gyre and the jet (SNK test). The minimum value ($5.5 \text{ mg} \cdot \text{m}^{-3}$) were found at Mediterranean site 8. With the fine net (80 μm), three groups of sites differing in biomass can be distinguished, according to the SNK: site 6 where the maximum value occurs; the group formed by sites 5 and 1; and the group of sites 8, 7, 4, 3 and 2, where the lowest values are observed.

Carbon and nitrogen, expressed as percentages of zooplankton dry weight, do not show any significant differences between the different sites or the two types of net. Nevertheless, C:N values (figure 4) are significantly lower (ANOVA: $F = 194$, $P < 0.001$, $\text{df} = 30$) in the

material collected by the 200- μm net (average 4.34) compared to the 80- μm net (average 4.86). This ratio also varies according to the sites (ANOVA: $F = 7$, $P < 0.001$); the SNK test shows that zooplankton at sites 3 and 8 display significantly lower C:N values than at the other sites. With the material of the 80- μm net, C:N is significantly higher at site 2 than at the other sites.

As for dry weight, highest zooplankton biovolumes are found in the material collected by the fine net (figure 4). Biovolume varies like biomass, according to the sites. The average body density of organisms (biomass:biovolume ratio) is similar whatever the net used but varies according to the sites (ANOVA 200 μm : $F = 2.68$, $P < 0.033^*$, $\text{df} = 30$; 80 μm : $F = 2.66$, $P < 0.035^*$, $\text{df} = 30$), with maximum values at site 1 (both nets), then at site 7 (200- μm net), indicating a greater proportion of heavy organisms in the core of the jet and at its frontal limit.

The abundance of organisms is 5 to 9 times lower using the 200- μm net, compared to the 80- μm net (*figure 4*). Using the material collected by the 200- μm net, the SNK test indicates that the zooplankton of sites 6, 7, 4 and 5 is significantly more numerous than at the other sites. Maximum abundance is noted at site 6 (1 208 ind·m⁻³) and the minimum value, at Mediterranean site 8 (417 ind·m⁻³). With the 80- μm net, the zooplankton of both Mediterranean sites (8 and 2) is significantly poorer (SNK test) than at the other sites.

The mean individual weight (dry weight: number ratio) is 3 to 4 times lower in the samples collected by the 80- μm net than with the other net (*figure 4*), due to the more efficient catch of small organisms by the finer mesh. With the 200- μm net, ANOVA test shows significant differences between the sites ($F = 5.55$, $P < 0.05$, $df = 30$) with the highest value (23 μg) at site 1 and the lowest (9.4 μg) at site 4. No significant difference appears considering the material collected by the 80- μm net ($F = 1.76$, $P < 0.22$, $df = 30$).

Table I shows the proportion of the main components of the mesozooplankton (copepods, nauplii, other holoplankton and meroplankton) in the samples collected by the two types of nets. With the 200- μm net, the bulk of the population is made of copepods (66 to 71 % of total number), their nauplii account for 1 to 7 %, the rest of holoplankton at 25 to 27 % and meroplankton at only 1 to 3.5 %. This proportion remains relatively constant at the

different sites, except for meroplankton which displays significant differences with a minimum percentage at site 8 and higher values at the Atlantic water-influenced sites (SNK test). With the 80- μm net, copepods constitute 54 to 62 % of total zooplankton and their nauplii, more efficiently retained, are proportionally more abundant (30 to 39 %). As for biomass and total number, the abundance of the main holoplankton taxa is always higher in Atlantic water sites than in Mediterranean sites (*figure 5*). The relative distribution of the main zooplankton taxa at the different sites was compared to the distribution of total zooplankton, using the χ^2 test (*table II*). In the material sampled with the 200- μm net, due to their strong numerical dominance, copepods show a distribution similar to total zooplankton. Only nauplii, siphonophora, ostracoda and chaetognatha display significant distribution differences. Siphonophora are relatively more abundant in Atlantic water sites (5, 6 and 3) than in Mediterranean waters. Chaetognatha are proportionally more numerous at sites 1 and 3, and Ostracoda at sites 7 and 3. In the material collected by the 80- μm net, all taxa except siphonophora show a significantly different distribution per site, referring to total zooplankton distribution. This is the consequence of the different distribution of copepods and of their nauplii, peaking at site 1, while the rest of zooplankton showed its maximum abundance at site 6. This diverges from the results obtained in the 200- μm samples where the distribution of copepods was similar to total zooplankton distribution.

Table I. Relative abundance of the main zooplankton taxa (% of total number per site).

Mesh size of the net	Site	Copepoda	Nauplii	Other holoplankton	Meroplankton
200 μm	8	71.3	1.1	26.7	0.9
	2	70.1	1.6	26.1	2.1
	7	69.2	3.2	26.3	1.3
	4	65.7	5.7	26.1	2.5
	5	66.9	4.9	25.1	3.1
	1	68.7	1.7	26.2	3.5
	6	66.0	7.2	24.5	2.3
	3	67.7	1.9	27.1	3.4
80 μm	8	60.5	32.3	6.7	0.6
	2	60.2	32.9	6.3	0.6
	7	62.3	30.3	7.0	0.5
	4	59.2	32.6	7.6	0.7
	5	61.0	29.6	8.5	0.9
	1	55.2	36.8	7.2	0.8
	6	53.7	38.9	6.7	0.6
	3	57.2	33.4	8.4	1.0

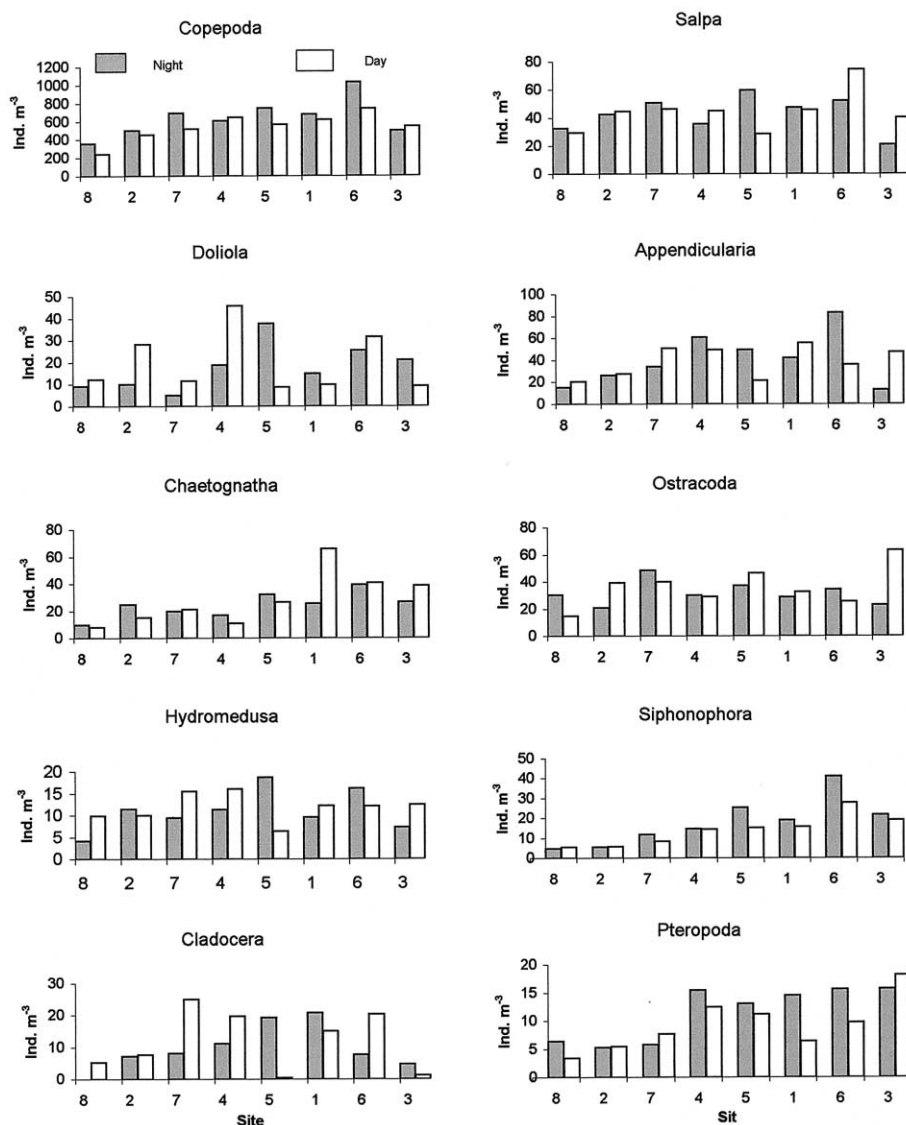


Figure 5. Abundance of the main holoplankton taxa at the different sites (200-µm net). Dark columns correspond to night samples, white columns to day samples.

The discrepancy between the two sets of results is the consequence of the particular abundance of young copepodite stages and nauplii in the 80-µm samples, in contrast to their scarcity in the 200-µm net samples.

In order to obtain synthetic information on the interaction between environmental factors and zoological taxa distribution, a correspondence analysis was performed using 'chlorophyll' as the trophic variable and 'density' of water, as the physical variable, resulting from the combination of temperature and salinity (figure 6). A large part of the variance (75.4 %) is explained by axis 1 which

expresses the opposition between the Mediterranean characteristics (oligotrophy and high water density), with a relative abundance of salps, hydromedusa, doliola, ostracoda and copepoda, and the features of Atlantic waters (chlorophyll richness and low water density). Axis 2 (10.2 % of the variance) expresses the gradient of thickness of the Atlantic water layer (figure 4) from the frontal limit (site 7), where cladocera and appendicularia are abundant, to the core of the anticyclonic gyre (sites 1, 3), where chaetognatha and siphonophora are relatively well represented. Axis 3 (6.6 % of the variance) is linked to a single site (site 1). Chaetognatha and cladocera are posi

Table II. Comparison of the distribution of the main zooplankton taxa at the different sites with the distribution of total zooplankton; results of the χ^2 test (* significant at $P < 0.05$; ** significant at $P < 0.01$).

Mesh size of the net	200 μm	80 μm	200 μm
Holoplankton			
Main taxa			(Copepoda, contd)
Chaetognatha	21.61**	27.51**	<i>Calocalanus styliremis</i> 7.36
Ostracoda	18.99**	126.74**	<i>Corycaeus speciosus</i> 7.02
Siphonophora	15.41*	12.83	<i>Pleuromamma gracilis</i> 6.84
Cladocera	13.68	33.61**	<i>Calanus helgolandicus</i> 6.83
Doliola	13.1	35.35**	<i>Calocalanus contractus</i> 6.41
Pteropoda	9.88	120.1**	<i>Eucalanus elongatus</i> 6.35
Salpa	7.6	44.55**	<i>Candacia varicans</i> 5.86
Appendicularia	7.33	40.69**	<i>Calocalanus tenuis</i> 5.68
Hydromedusa	1.35	31.1**	<i>Pleuromamma abdominalis</i> 5.64
Copepoda	0.23	19.64**	<i>Clytemnestra scutellata</i> 5.24
Nauplii	90.73**	75.4**	<i>Oithona helgolandica</i> 4.96
			<i>Temora stylifera</i> 4.82
Copepoda			<i>Centropages chierchiae</i> 4.47
<i>Centropages typicus</i>	63.7**		<i>Oithona plumifera</i> 4.17
<i>Oncaea media</i>	24.5**		<i>Clausocalanus pergens</i> 4.34
<i>Pleuromamma borealis</i>	17.82*		<i>Oncaea conifera</i> 3.99
<i>Clausocalanus furcatus</i>	16.86*		<i>Corycaeus limbatus</i> 3.59
<i>Eucalanus crassus</i>	13.45		<i>Clausocalanus arcuicornis</i> 3.63
<i>Oncaea dentipes</i>	11.13		<i>Phaenna spinifera</i> 2.69
<i>Microsetella norvegica</i>	9.46		<i>Acartia danae</i> 2.64
<i>Mecynocera clausi</i>	9.76		<i>Lucicutia flavicornis</i> 2.38
<i>Oncaea venusta</i>	8.89		<i>Euterpina acutifrons</i> 1.92
<i>Acartia clausi</i>	7.97		
Meroplankton			
Actinotrocha	37.1**	17.89*	
Plutei	20.41**	9.19	
Tornaria	13.09	8.82	
Mysis	11.71	2.54	
Polychaeta	11.11	20.87**	
Protozoae	4.96	277.7**	
Fish	1.44	677.5***	

tively related to this axis, and pteropods, negatively. This axis may express the influence of the Algerian coast where some neritic organisms could be carried by the southern part of the gyre towards site 1 (see later).

The qualitative composition of the copepod community was analysed (table III). A total of 55 species were identified. Several species, belonging to *Clausocalanus*, *Ctenocalanus*, *Paracalanus* and *Calocalanus* genera, were only present as immature copepodite stages and could not be distinguished. Thus, the number of species reported in table III must be underestimated. Diversity is

lowest in Mediterranean waters and reaches its maximum value (49) at site 6. In the overall studied area, 72 % of the individuals belong to four genera only. *Clausocalanus* predominates (43 %); it is followed by *Oithona* (10.5 %) and by *Pleuromamma* (9.3 %). The fourth genera, *Oncaea*, accounts for 9 % of the individuals. The relative distribution of the most abundant species according to the sites does not show any particular difference with the distribution of total zooplankton (table III). On the contrary, some scarce species display a special affinity for particular sites. For example, *Centropages typicus*, *Clausocalanus furcatus*, *Temora*

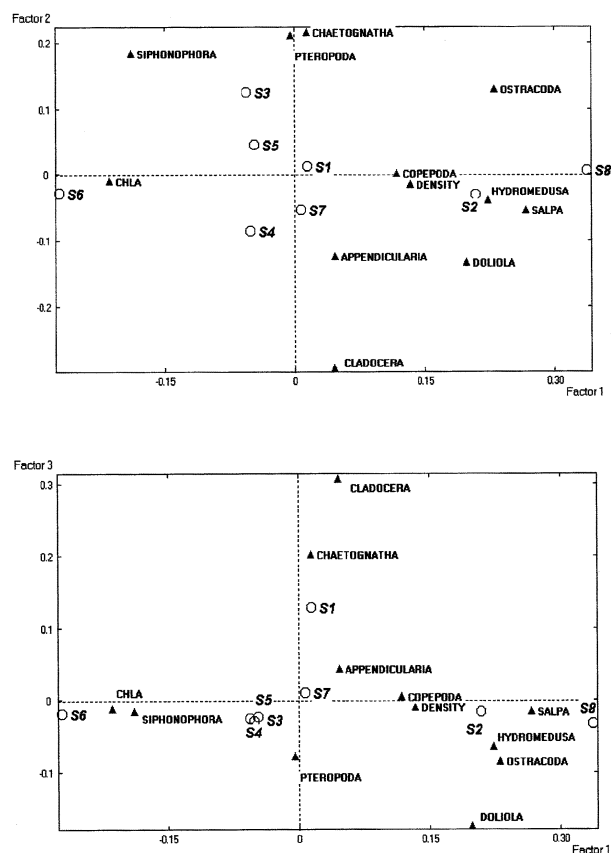


Figure 6. Correspondence analysis performed for main holoplankton taxa.

stylifera and *Acartia clausi* show a higher relative abundance at the left border of the jet (site 7), where the strongest horizontal density gradient (frontal limit) is located. The χ^2 test shows that this difference of 'preference' is significant at $P < 0.05$ only for the first two species (table II). Another group of species seems more particularly linked to Atlantic waters (*Pleuromamma borealis*, *Eucalanus crassus*, *E. elongatus*, *Oncaea dentipes*). The difference in distribution compared to total zooplankton is significant only for *P. borealis*, while the χ^2 value approaches the significant threshold for *E. crassus*.

The correspondence analysis carried out for the main copepod species (figure 7) shows that axis 1 provides most of the information (45.3 % of the variance). It expresses the opposition between Atlantic waters (sites 5, 3 and 6) and Mediterranean (site 8) and front (site 7). *Centropages typicus* occupies an utmost position in

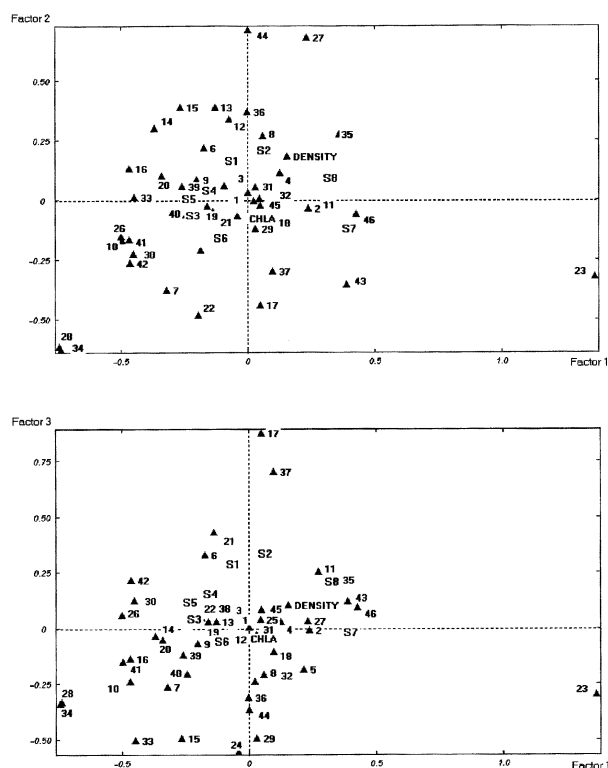


Figure 7. Correspondence analysis performed for copepod species. The code of the different species (numbers) refers to those in table III.

relation to its special abundance at the front. *Oncaea dentipes*, *Pleuromamma borealis*, *Oithona setigera* and *Oncaea conifera* mark the Atlantic influence in the negative part of the axis. Axis 2 (14.6 % of the variance) is negatively related to chlorophyll richness, and positively, to water density. Site 2, in the positive part, is clearly separated from the other Mediterranean site (site 8). These two oligotrophic Mediterranean sites differ by their hydrodynamic conditions: site 2, closer to the jet meander could be influenced by the front convergence area, in contrast to site 8 which is affected by a current flowing northwards, moving away from the front. Thus, axis 2 represents the contrast between convergence water (presence of *Calanus helgolandicus* and several other Mediterranean species) and waters of Atlantic origin (*Pleuromamma abdominalis*, *Phaenna spinifera*, *Clytemnestra scutellata*). Axis 3 (12.6 % of the variance) expresses the character of the usual habitat of the species: neritic in its negative part, with the presence of epipelagic coastal species (*Centropages chierchiae*, *Acartia clausi*), and oceanic in its positive part, with open sea or

Table III. Copepod species percentages of total zooplankton number per site, the total number of identified species and their correspondence analysis code.

Species	Site								Code
	8	2	7	4	5	1	6	3	
<i>Clausocalanus arcuicornis</i>	37.3	31.80	31.96	33.87	30.08	28.26	31.23	31.89	1
<i>C. pergens</i>	1.06	2.37	1.63	1.68	1.75	2.07	1.61	2.73	3
<i>C. furcatus</i>	11.38	8.77	13.10	7.28	7.11	7.61	8.22	7.53	2
<i>Calocalanus contractus</i>	3.95	5.46	4.17	3.35	2.39	3.44	3.51	3.72	4
<i>C. pavo</i>	0.53	1.14	1.05	0.42	0.64	0.86	0.40	0.49	5
<i>C. styliremis</i>	0.65	1.07	0.13	0.90	0.29	0.42	0.59	1.10	6
<i>C. tenuis</i>	0.00	0.16	0.13	0.06	0.30	0.06	0.46	0.05	7
<i>Calanus helgolandicus</i>	0.84	1.30	0.97	0.50	1.09	1.63	0.50	0.35	8
<i>Eucalanus elongatus</i>	0.93	1.22	0.90	1.38	2.07	2.11	0.95	1.65	9
<i>E. crassus</i>	0.00	0.08	0.24	0.86	1.11	1.33	1.23	0.72	10
<i>E. attenuatus</i>	0.22	0.00	0.11	0.12	0.05	0.12	0.04	0.13	11
<i>E. monachus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.05	
<i>Rhincalanus nasutus</i>	0.00	0.00	0.06	0.00	0.05	0.00	0.00	0.00	
<i>Mecynocera clausi</i>	1.06	3.10	0.92	1.24	1.41	1.71	1.15	1.46	12
<i>Chiridius poppei</i>	0.22	0.08	0.00	0.10	0.10	0.25	0.07	0.05	13
<i>Aetideus armatus</i>	0.00	0.00	0.00	0.00	0.06	0.25	0.07	0.05	
<i>Euchirella messinensis</i>	0.00	0.16	0.00	0.00	0.05	0.06	0.12	0.05	14
<i>E. rostrata</i>	0.00	0.23	0.06	0.12	0.21	0.23	0.12	0.00	15
<i>E. intermedia</i>	0.00	0.00	0.06	0.00	0.00	0.00	0.04	0.00	
<i>Euchaeta marina</i>	0.40	0.23	0.24	0.00	0.05	0.12	0.15	0.05	
<i>E. acuta</i>	0.00	0.42	0.00	0.00	0.42	0.06	0.27	0.13	16
<i>E. media</i>	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	
<i>E. hebes</i>	0.00	0.08	0.00	0.10	0.00	0.00	0.00	0.07	
<i>Phaenna spinifera</i>	0.12	0.00	0.06	0.00	0.05	0.00	0.04	0.18	17
<i>Temora stylifera</i>	1.59	2.45	3.89	2.91	2.55	2.42	2.37	2.75	18
<i>Pleuromamma</i> sp.	5.16	5.15	3.89	6.45	7.74	5.70	6.35	6.85	
<i>P. borealis</i>	0.68	3.70	0.88	3.43	3.21	4.05	3.61	6.84	19
<i>P. gracilis</i>	0.87	0.00	0.00	0.24	0.48	0.29	0.31	0.36	20
<i>P. abdominalis</i>	0.22	0.00	0.06	0.06	0.18	0.06	0.44	0.05	21
<i>Centropages</i> sp.	0.50	0.57	1.44	0.16	0.11	0.00	0.22	0.00	
<i>C. typicus</i>	1.52	0.49	3.48	0.46	0.06	0.36	0.22	0.05	22
<i>C. chierchiae</i>	0.00	0.00	0.06	0.24	0.00	0.12	0.03	0.00	23
<i>Lucicutia flavicornis</i>	1.71	2.42	1.92	2.00	1.36	2.06	2.41	2.17	24
<i>Haloptilus acutifrons</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	
<i>Candacia</i> sp.	0.71	0.16	0.73	0.78	0.59	0.25	1.08	0.25	
<i>C. varicans</i>	0.00	0.08	0.06	0.56	0.47	0.19	0.21	0.49	25
<i>C. longimana</i>	0.09	0.16	0.06	0.00	0.05	0.12	0.00	0.05	26
<i>C. bipinnata</i>	0.00	0.00	0.00	0.00	0.06	0.00	0.04	0.00	27
<i>Acartia clausi</i>	0.22	0.23	0.92	0.58	0.72	1.11	0.86	0.05	28
<i>A. danae</i>	0.00	0.00	0.06	0.12	0.16	0.19	0.12	0.31	29
<i>Oithona plumifera</i>	10.13	9.19	8.05	9.76	8.94	8.41	8.73	6.47	20
<i>O. helgolandica</i>	0.62	1.80	1.79	1.74	1.69	1.254	1.63	0.74	31
<i>O. setigera</i>	0.00	0.00	0.00	0.10	0.00	0.13	0.12	0.00	32
<i>O. nana</i>	0.00	0.00	0.00	0.00	0.05	0.00	0.04	0.00	33
<i>Euterpina acutifrons</i>	0.00	0.24	0.12	0.21	0.11	0.11	0.04	0.05	35
<i>Microsetella norvegica</i>	1.83	0.88	0.65	0.36	0.42	0.81	0.52	0.36	34
<i>Clytemnestra scutellata</i>	0.40	0.00	0.17	0.12	0.14	0.06	0.12	0.49	36
<i>Oncaea media</i>	3.51	4.01	5.44	5.11	7.59	5.63	9.22	9.72	37
<i>O. dentipes</i>	1.18	1.80	1.21	2.79	2.94	3.80	2.38	2.48	38
<i>O. conifera</i>	0.12	0.65	0.62	1.06	1.20	0.90	0.90	0.72	39
<i>O. venusta</i>	0.00	0.16	0.19	0.60	1.20	0.67	0.59	0.66	40
<i>Sapphirina scarlata</i>	0.00	0.08	0.06	0.16	0.30	0.00	0.07	0.31	41
<i>S. nigromaculata</i>	0.12	0.00	0.06	0.00	0.10	0.00	0.03	0.00	42
<i>Copilia mediterranea</i>	0.00	0.16	0.06	0.00	0.05	0.17	0.00	0.05	43
<i>Corycaeus limbatus</i>	2.30	2.03	2.54	1.70	1.99	2.40	1.85	3.6	44
<i>C. speciosus</i>	1.40	0.57	1.44	0.44	0.40	0.83	0.55	0.84	45
<i>Pachos punctatum</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	
Others	6.47	5.62	4.54	5.89	5.99	7.43	4.08	4.13	
Number of identified species	30	36	40	39	46	42	49	42	

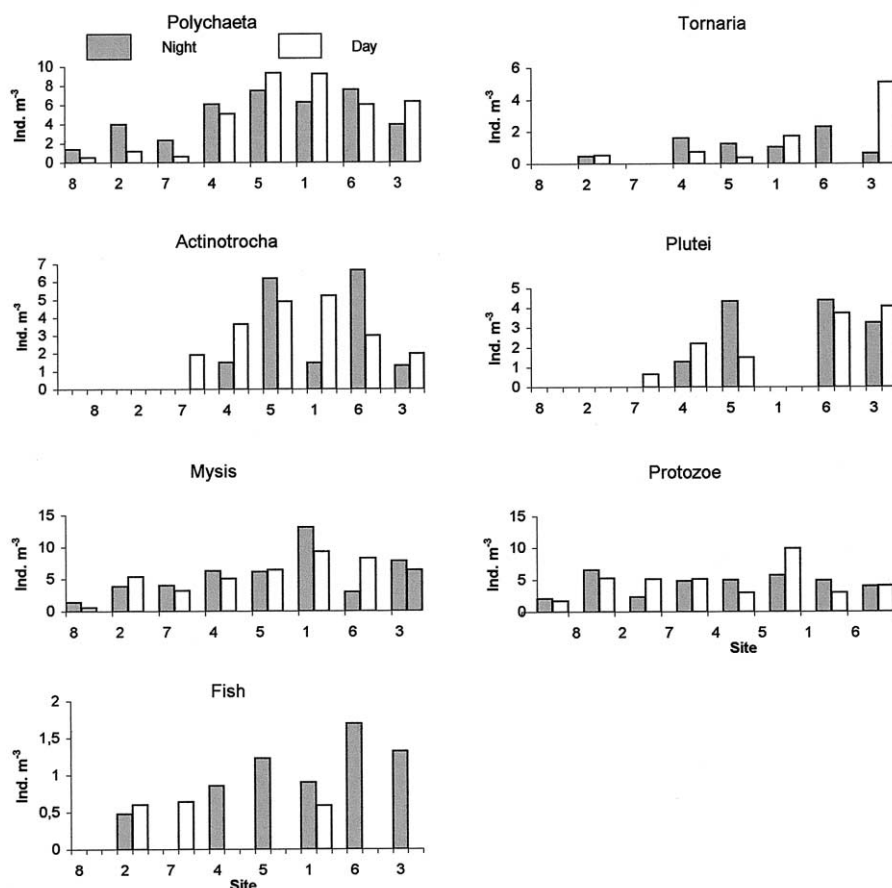


Figure 8. Abundance of the main meroplankton taxa at the different sites (200- μ m net). Dark columns correspond to night samples, white columns to day samples.

mesopelagic species such as *Phaenna spinifera*, *Clytemnestra scutellata*, *Calocalanus tenuis*, *Pleuromamma gracilis*, *Microsetella norvegica* or *Eucalanus attenuatus*.

Concerning meroplankton, the distribution of some identified larvae (figure 8) is linked to particular sites, differing from the tendency observed for total zooplankton. Tornaria (enteropneust larvae) are seen only at site 7. In Mediterranean waters, larvae such as plutei or actinotrocha are scarce or absent, while they are proportionally more abundant than total zooplankton at the sites influenced by Atlantic waters (5, 6 and mainly 3, in the core of the gyre). At this last site, the proportion of plutei, toranaria and actinotrocha is 4- to 5-fold higher than the proportion of total zooplankton. The χ^2 test confirms that actinotrocha and plutei distributions according to the sites are significantly different from total zooplankton distribution while the χ^2 value for Tornaria distribution is close to the threshold value, with $P < 0.05$ (table II).

3.2. Nycthemeral variations

Zooplankton biomass is slightly more elevated during the night than during the day at sites 7, 5, 6 and 3 using the 200- μ m net and at sites 8, 2 and 3 with the 80- μ m net, while the opposite is observed at the other sites (figure 9). Using the data obtained at all sites, no general tendency in the day-night behaviour can be drawn: ANOVA treatment shows that night and day values are not significantly different ($F = 0.69$, $P < 0.42$, $dl = 7$ for the 200- μ m net material; and $F = 0.09$, $P < 0.77$, $dl = 7$ for the 80- μ m net). Total abundance shows the same variability. With the 200- μ m net material, zooplankton is slightly more abundant during the night, except at sites 4 and 3. In the 80- μ m net samples, the tendency is reversed, with higher abundance during the day at six out of eight sites. Considering the main taxa, day-night variations differ according to groups or sites. In copepoda, pteropoda and

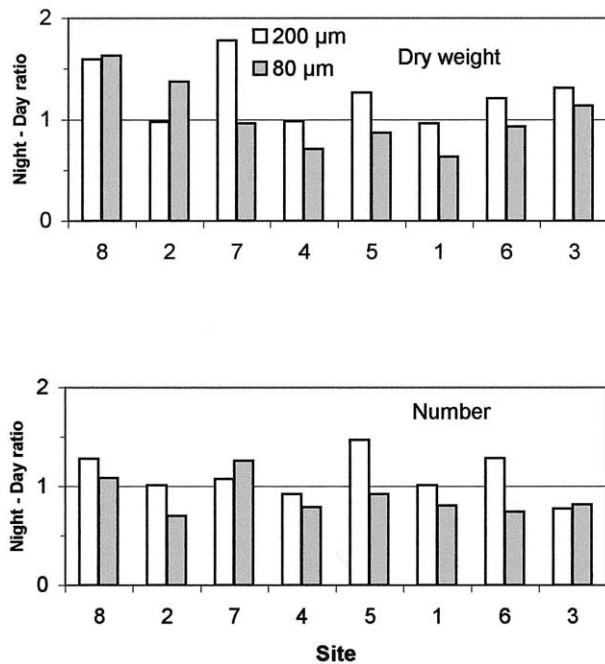


Figure 9. Night-day variations of biomass and abundance at the different sites and ratio between night and day values. White columns correspond to 200-µm net samples and dark columns to 80-µm samples.

siphonophora, nocturnal abundance is generally greater than diurnal (six of eight sites) while the results are more variable for the other holoplankton species, with a tendency for higher diurnal values in doliola, hydromedusa and ostracoda (figure 5). Nevertheless, taking into account the variability of responses at the different sites, the ANOVA test does not show any significant difference between day and night abundance for each groups. Results concerning the meroplankton are too fragmentary and variable to obtain clear information on their day-night distribution (figure 8).

4. DISCUSSION

4.1. Biomass and hydrological structure

Zooplankton biomass and abundance increased 3- to 4-fold at the sites influenced by Atlantic waters compared to Mediterranean waters. Biomass values exceed most of

the standing stock data recorded for the western Mediterranean, except in some coastal regions under upwelling influence such as the Malaga region (Estrada et al., 1985). In the open sea, biomass values usually range between 0.2 to 2 mg·m⁻³ (Estrada et al., 1985; Gaudy, 1985). These values are considerably lower than the maximum values of 15–25 mg·m⁻³ obtained at the Almeria-Oran front.

High zooplankton biomass often characterises the different types of oceanic or coastal fronts compared to the adjacent structures (Longhurst, 1967; Pingree et al., 1974; Gaudy et al., 1996). Several causes could explain the standing stock increase. The transportation of organisms towards the convergence zone could concentrate surface species at the front limit (Herman et al., 1981; Mackas and Louttit, 1988; Gaudy et al., 1996). In the area of study, this mechanism explains the preferential distribution of some epipelagic species at the limit of the front (see later) but not the location of maximum zooplankton densities and biomass inside the jet and the gyre. The high biomass found in Atlantic waters could result either from the passive accumulation of allochthonous fauna transported by the Atlantic current, or from a local increase in secondary production. According to the first hypothesis, Greze et al. (1985) suggested that the abundance of zooplankton at the east of Gibraltar strait was due to the permanent introduction of Atlantic fauna by the current entering the Mediterranean sea. This fauna would remain at the surface (0–50 m) in the east of Alboran sea, as a consequence of its vertical migrations, alternating from the Atlantic surface current flowing eastwards during the night to the westwards undercurrent during the day. According to these authors, this process could explain the doubling of zooplankton abundance west of the Alboran sea, compared to the Ibero-Moroccan bay. Nevertheless, Vives et al. (1975) in a previous synoptic study had not noticed such a difference in zooplankton richness, with the existence of similar values east and west of the Gibraltar strait. Moreover, they noted that zooplankton biomass was directly related to chlorophyll distribution at the different stations investigated in the whole western Alboran sea, which suggests a direct trophic link between secondary and primary levels, rather than passive transportation by currents.

In the eastern part of the Almeria-Oran front, our results also show that zooplankton enrichment can be associated with higher phytoplankton richness. During the first leg

of the cruise, Chl *a* concentrations ranged from 25 to 30 mg·m⁻² north of the Alboran sea (Mediterranean waters), and from 40 to 70 mg·m⁻² in its southern part (influenced by the Atlantic waters), with a sudden increase at the front limit (Vescovoli, unpubl. results). At the different sites, chlorophyll shows its minimum values at Mediterranean sites 2 and 8 (26 and 37 mg·m⁻², respectively), as compared to the sites influenced by Atlantic waters, where the maximum value reaches 91 mg·m⁻² (Claustre and Oubelkheir, unpubl. results). Biomass and abundance of zooplankton are positively correlated to chlorophyll concentration ($r = 0.73$ and 0.91 , respectively, using the 200- μ m net samples and $r = 0.81$ and 0.90 respectively, with the 80- μ m net). Maximum zooplankton biomass and abundance observed at site 6 corresponds to the highest concentration of chlorophyll and microphytoplankton (Claustre and Oubelkheir, unpubl. results).

In our results, several clues indicate that the higher zooplankton biomass found in the Atlantic waters is the consequence of local activation of the secondary production processes, benefiting from the high chlorophyll concentration prevailing in the frontal structures. Such enhancement of secondary production was also invoked by Herman et al. (1981) in the South of New Scotland, or by Scrope-Howe and Jones (1985) in a tidal front of the Irish sea, to explain the higher biomass observed. In the Almeria-Oran front, the activation of the reproduction process is indicated by the higher proportion of nauplii, in the jet and the gyre, as already observed during Almo-front 1 (Gaudy et al., unpubl. results). The qualitative value of phytoplankton probably plays a role in reproduction efficiency. According to Kiørboe and Nielsen (1994), the highest egg production rates are often related to the dominance of diatoms in the microphytoplankton. Diatoms were abundant in the frontal structures investigated during Almo-front 1 and 2, as the result of an active new production, fuelled by the advection of nutrients in the euphotic zone by the secondary circulation (Prieur et al., 1993; Fiala et al., 1994; and Claustre and Oubelkheir, Madec et al., and Morin, unpubl. results). Maximum copepod egg production may occur near the front boundary, due to the existence of qualitatively favourable feeding conditions. At the frontal limit, the C/Chl *a* ratio of particles is close to 50 (Claustre and Oubelkheir, unpubl. results), indicating a material mainly composed of freshly produced phytoplankton. During Almo-front 2, diatoms dominated the microphytoplankton at the front

limit (Striby and Goutx, and Vescovoli et al., unpubl. results), similarly to the situation observed during Almo-front 1 (Claustre et al., 1994; Fiala et al., 1994; Videau et al., 1994). In eutrophic conditions, diatoms are considered as the preferential food of copepods, according to the 'classic food chain' concept (Cushing, 1989). The effect of food quality on feeding intensity is demonstrated by the analysis of the organic material collected by the sediment traps: the highest proportion of phytol, a selective index of phytoplankton degradation, was found at the front (site 7), showing a maximum zooplankton grazing activity at this site (Striby and Goutx, unpubl. results), although highest chlorophyll abundance occurred at a different place (site 6). As an isopycnal down-welling transfer of primary and secondary production occurs from the left to the right side of the jet (Prieur et al., 1993; Gerin and Goux, 1994; Seguin et al., 1994; Pedrotti and Fenaux, 1996), the eggs produced at the left side of the jet (site 7) would develop during their transportation towards site 6 where the maximum proportion of nauplii was found. Another clue suggesting the local enhancement of secondary production is the increase in zooplankton metabolism (respiration, ammonia excretion) and feeding at the Atlantic sites compared to the neighbouring Mediterranean waters (Gaudy et al., unpubl. results), as previously observed during Almo-front 1 (Gaudy et al., 1991; Thibault et al., 1994).

The correlation observed between chlorophyll concentration and zooplankton biomass suggests the maintenance of favourable trophic conditions, responsible for the reproduction increase, during a time long enough to allow an efficient growth of the larval stages. In copepods, a minimum period of 15–20 d is necessary for the achievement of the larval growth at the temperature conditions (14–17 °C) prevailing during the cruise (Landry, 1983; Hart, 1990). In density fronts, such as plume fronts, the scale of time variations of the enrichment phenomenon seems too short to allow local growth of zooplankton (Gaudy et al., 1991; Bianchi et al., 1993). In geostrophic fronts, such as the Almeria-Oran front, the minimum time necessary for zooplankton growth seems largely greatly exceeded due to the quasi permanence of hydrodynamic structures, as demonstrated by satellite observations (Tintore et al., 1988; Folkard et al., 1994). It is likely that the high zooplankton biomass, already observed at two periods of the year, are a permanent characteristic of the east Almeria sea.

4.2. Time variations

The comparison of the quantitative results obtained in the eastern Alboran sea in January (Almofront 2) and in March (Almofront 1; Thibault et al., 1994) reveals the existence of relatively large seasonal variations. In the jet, the biomass and density of zooplankton are two to three times lower in winter ($15\text{--}25\text{ mg}\cdot\text{m}^{-3}$, $643\text{ ind}\cdot\text{m}^{-3}$) than in spring ($40\text{--}73\text{ mg}\cdot\text{m}^{-3}$, $1\,020\text{ ind}\cdot\text{m}^{-3}$). These differences are related in particular to the richness of food conditions (spring bloom, winter scarcity) rather than to temperature, which had similar values during the two cruises (around $15\text{ }^{\circ}\text{C}$).

Day-night variations of total zooplankton were not significant, meaning that most of the vertical migration, if it occurs, must take place in the upper 200 m of the water column integrated by the vertical hauls. Using the same sampling technique, Boucher and Thiriot (1972) also observed the absence of extended zooplankton vertical migration in the central part of the western Mediterranean sea. Herman et al. (1981) also observed that copepods did not migrate in frontal waters contrary to shelf waters. Considering separately the different taxa, inverse migrations were observed in several cases, with the highest abundance during the day. More data would have been necessary to analyse this result unambiguously.

4.3. Qualitative variations

The main feature of the mesozooplankton community is its homogeneous character all over the investigated area. The relative abundance of the main holoplanktonic groups is similar at the different sites. The most numerous copepods, *Clausocalanus arcuicornis* and *Oithona helgolandica*, were also the dominant species during Almofront 1 (Seguin et al., 1993). The numerical importance of the genera *Clausocalanus* and *Oithona* is in agreement with most previous data for the Alboran sea (Giron, 1963; Vives et al., 1975; Greze et al., 1985). As a matter of fact, these copepods display an ubiquitous distribution in the whole Mediterranean. They abound in coastal waters, independently of their salinity conditions or food richness, but also in the open sea community (Estrada et al., 1985; Gaudy, 1985). However, in our data, some heterogeneity in zooplankton assemblage is suggested by significant changes in several global clues, such as the mean values of body density, individual weight and C:N ratio.

Body density of organisms is lower at Mediterranean sites than at Atlantic sites, probably expressing variable proportions of light organism such as gelatinous animals (hydromedusa, siphonophora, doliola and salps). Their total abundance at each site is inversely correlated with the average body density of zooplankton organisms ($r = -0.72$; $P < 0.05$). The variation of mean individual weights, (maximum value at site 1 and minimum at site 4) also suggests differences in proportion of big animals, such as chaetognaths, (that displayed maximum abundance at site 1 and minimum, at site 4), or some large-sized copepods such as *Aetideus armatus*, *Chiridius poppei* and *Pleuromamma borealis*. The variations of C:N could also indicate some fauna changes but minimum values at sites 3 and 8 could not be related to any particular change in zooplankton population.

Maximum diversity in copepod assemblage is found at the sites influenced by Atlantic waters, due in particular to the addition of several species absent from the neighbouring Mediterranean water. Nevertheless, some of these species are known in the Mediterranean western basin near the coast, such as *Centropages chierchiae* which are very numerous north of the Alboran sea (Giron, 1963; Durán, 1963) or *Oithona setigera*. Others species found in Atlantic waters are oceanic forms (*Acartia danae*, *Eucalanus monachus*, *Rhincalanus nasutus*, *Haloptilus longicornis* or *Candacia bipinnata*). Among these copepods, several species have been considered as indicator species of the Atlantic current entering the Mediterranean sea (Giron, 1963; Vives et al., 1975; Estrada et al., 1985; Seguin et al., 1993). *Pleuromamma borealis* and *Eucalanus crassus*, which are found at all sites but show a higher relative abundance in the Atlantic structures, also belong to the pool of species characterising the Atlantic water inflow. Two species, *Centropages typicus* and *Clausocalanus furcatus*, are significantly linked to the front limit. A similar tendency, although non-significant, is also observed for *Temora stylifera* and *Acartia clausi*. These neritic species, carried far from the coast, could benefit from the better food richness prevailing near the front, compared to oligotrophic open sea waters (Boucher et al., 1987). Similarly, in the Ligurian front, large concentrations of *Centropages typicus* located at the maximum salinity-temperature horizontal gradient were observed by Boucher (1984), independently of chlorophyll concentration. This confirms the importance of the qualitative nature of food for production processes in some zoo

plankton species. *Calanus helgolandicus* is present at the Atlantic jet and gyre during Almofront 2, but also appears at the frontal limit and in the Mediterranean waters. As the age structure of this species was not analysed, we do not know whether the population was homogeneous in the whole area or if a local development occurred in the Atlantic water. As a matter of fact, in the Ligurian sea, Boucher (1984) and Boucher et al. (1987) demonstrated that *C. helgolandicus* was directly linked to frontal waters, where a large proportion of larval stages indicated a local development. Among the other holoplanktonic groups, several cladocera and chaetognatha species (*Penilia avirostris*, *Evadne* spp., *Sagitta friderici*, *Sagitta enflata*), which present affinities for low salinity water, are relatively more numerous in the less-salted Atlantic waters. Carnivorous animals (siphonophora, ostracoda) are also linked to these Atlantic waters where they could find more abundant prey. The distribution of doliola, pteropoda and appendicularia is also related to Atlantic waters, from site 4 in the core of the jet to sites 6 or 3 (where pteropoda reach their maximum relative abundance). These microfeeder organisms could probably find suitable trophic conditions in Atlantic water structures, where the microbial food web must be enhanced by the increased bacteria production (Van Wambeke and Bianchi, unpubl. results). Concerning the meroplankton, highest proportion of larvae appears in Atlantic water sites. Some categories of larvae such as plutei and actinotrocha are totally absent from surrounding Mediterranean water. Larvae could have been produced locally in the Atlantic current (protozoa, mysis, fish larvae) or could originate from the reproduction of organisms located upstream in coastal areas near the Gibraltar strait, or finally, could have been extracted from the neritic zone by the anticyclonic gyre flowing close to the Algerian coast in its southern part. Such hypothesis was advanced for the same region by Pedrotti and Fenaux (1996) to explain the particular abundance of echinoderm larvae in the anticyclonic gyre. Whatever their origin, zooplankton organisms and fish larvae must find suitable trophic conditions for optimal growth in the Atlantic structures of the frontal area. This area would thus act as a nursery area, as evoked by Boucher and Thiriot (1972).

5. CONCLUSION

According to Legendre and Le Fèvre (1989) which stated that fronts, as other hydrodynamic singularities, have a

major impact on the global carbon cycle, the Almeria-Oran front appears as a place of enhancement of the biological production, at the primary but also at the secondary level. Zooplankton responds to the permanence of favourable quantitative and qualitative food conditions by increasing its secondary production, as indicated by the high proportion of nauplii and meroplankton larvae in the frontal system, and by the enhancement of its physiological activity. Although the general aspect of the zooplankton community is relatively monotonous, especially for the copepod assemblage, some taxa or species show a 'preference' for a given type of hydrological structure, such as the front limit, the jet or the gyre. This suggests the occurrence of several type of mechanisms. The maintenance of organisms in Atlantic sites characterised by strong currents or at the frontal limit supposes an active behavioural mechanism, probably via the diel vertical migrations through differently oriented currents (Boucher et al., 1987). Passive transportation by the Atlantic current entering the Mediterranean sea could be invoked for indicator species. Finally, advection by the anticyclonic gyre of the Algerian shelf water could explain the occurrence of several coastal species in the oceanic structures.

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