

Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 1. Abundance and specific composition

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*Short-term changes in the zooplankton community were investigated at a time-series station in the open NW Mediterranean during the DYNAPROC cruise programme (May 1995). Based on the samples obtained with three devices (12 l bottle, 200 µm and 500 µm mesh nets), the abundance and specific composition are presented for mesozooplankton (copepods mainly), macroplankton and micronekton. Over the 3 week sampling period, overall density of the copepod community decreased and changes in the specific composition occurred. The decline was also observed in nauplii and was more marked in small-sized copepod species than in larger ones; one species, *Centropages typicus*, even disappeared. An increase in the proportion of carnivorous organisms appeared in both copepods (*Euchaeta acuta*, *Heterorhabdus* spp.) and euphausiids (*Nematoscelis megalops*, *Stylocheiron longicorne*). These changes are discussed in relation to environmental features and in the context of seasonal variability, the observational period coinciding with the transition from spring bloom to oligotrophy in this area. Effects of a major wind event that appeared to have induced long-lasting changes are also explored.*

INTRODUCTION

The vertical flux of particulate organic matter depends on biological, chemical and physical processes (e.g. primary production, grazing of zooplankton, wind event) that vary on short time scales, of 1 h to a few days. Several studies have provided evidence of the short-term changes in biological variables, and downward flux of matter, in response to physical forcing and particularly wind-induced mixing [e.g. (Taylor, 1989; Marra *et al.*, 1990)]. For example, wind events have been shown to enhance availability of nutrients in the euphotic zone and subsequently, to initiate increases in phytoplankton production, with development of short-lived blooms of diatoms [see the review of Kiørboe (Kiørboe, 1993)]. However, the

possible influence of wind events on the zooplankton community is far less documented, particularly in the open sea; in fact, most of the available observations are for nearshore environments or in areas occasionally subjected to horizontal advection [e.g. (Ortner *et al.*, 1984; Nielsen and Kiørboe, 1991)]. On the other hand, although seasonal variability in abundance and specific composition of the zooplankton community is now relatively well documented for the western Mediterranean Sea, available data are mainly based on monthly sampling and do not address short-term changes [e.g. (Vives, 1963; Hure and Scotto di Carlo, 1968; Franqueville, 1971; Sardou *et al.*, 1996)].

The multidisciplinary cruise DYNAPROC, devoted to the study of the DYNAMics of the rapid PROCesses that control the vertical flux of matter on short time scales, was

carried out in May 1995 in the northwestern Mediterranean. The study was conducted in the open central zone of the Ligurian Sea where currents are weak and horizontal advection negligible. The purpose of this paper is to present data on the abundance and specific composition of the zooplankton community (meso- and macroplankton, micronekton). Short-term changes in this community structure are discussed in relation to environmental features and, particularly, in relation to the major wind event that occurred during the cruise. Vertical distributions and diel migrations of the organisms are presented in the following paper (Andersen *et al.*, 2001).

METHOD

The DYNAPROC cruise was conducted over a 1 month period (1 May–1 June 1995) in the open northwestern Mediterranean (Figure 1). It was divided into four legs. Most of the multidisciplinary measurements were performed at the JGOFS-France time-series station DYFAMED [e.g. (Buat-Ménard and Lambert, 1993)], 28 nautical miles offshore ($43^{\circ}25.2'N$, $7^{\circ}51.8'E$, depth of 2600 m) and called herein TSS. In addition, a 16 station grid centred on TSS (Figure 1) was occupied four times

during the cruise to check for weakness in any horizontal gradients. A detailed description of the study site and the sampling strategy is given in Andersen and Prieur (Andersen and Prieur, 2000).

The biomass and faunistic composition of zooplankton and micronekton were investigated in the day time and at night time during leg 2 (10–16 May) and leg 4 (26 May–1 June) of the DYNAPROC cruise. Sampling of the small-sized organisms was performed at the time-series station with a 12 bottle rosette at 9–12 depth levels in the upper 100 m; water samples of 12 l were filtered through 50 μm . Vertical hauls were carried out with a WP-II net (200 μm mesh) in the upper 200 m (filtered volume of 48 m³). Larger zooplankton were sampled with the BIONEISS (Sameoto *et al.*, 1980), a multiple opening and closing net equipped with 500 μm mesh nets of a mouth area of 1 m². Oblique hauls were performed in the 0–980 m water column, divided into nine strata; the volume of water filtered in each layer varied from 257 to 1101 m³. The sampling data are summarized in Table I. Note that the daytime hauls on 1 June are referred to as D32. The series of WP-II hauls and BIONEISS hauls were achieved within less than 1 or 3 miles from the TSS, respectively (Figure 1).

Samples were preserved in 5% borax-buffered formalin seawater for further analysis. In this paper, we present density estimates of the organisms standardized to number of individuals m⁻² for the entire water column explored, 0–100 m, 0–200 m or 0–980 m, depending on the device used. For copepod taxonomy, we have followed the inventory of Razouls and Durand (Razouls and Durand, 1991) for the Mediterranean Sea. Copepodite stages have been identified for the most abundant species.

RESULTS

Meteorological and environmental conditions

From several types of observations, such as continuous measures of Doppler-based currents and CTD casts on the 16 station grid, it was shown that horizontal advective movements at the TSS, and in its vicinity, remained weak throughout the cruise (Andersen and Prieur, 2000). Time-course of wind speed and time-depth distributions of temperature, salinity, nitrates and chlorophyll *a* are presented in Figure 2; more details on environmental conditions are given in Andersen and Prieur (Andersen and Prieur, 2000). Briefly, temporal variation of wind speed was characterized first by a major wind event on 13 May, associated with a low pressure system, then by several successive wind events of smaller amplitude until 25 May (Figure 2a). During the first wind event, an

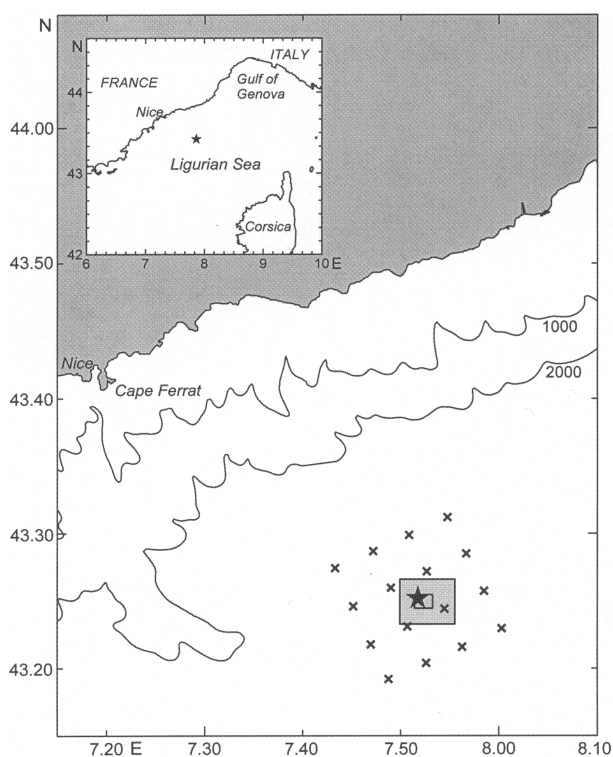


Fig. 1. Station locations: time-series station (★), area of WP-II and BIONEISS hauls (small and large shaded rectangles respectively), grid of 16 stations 3 miles apart (×) [after (Andersen and Prieur, 2000)].

Table I: Sampling data by day (*D*) and at night (*N*)

Leg 2			Leg 4		
Date 1995	Time (UTC)	Haul no.	Date 1995	Time (UTC)	Haul no.
12 l bottle (0–100 m)					
12/05	0.536	D	26/05	12.56	D
12/05	14.29	D	27/05	10.19	D
13/05	01.01	N	29/05	00.53	N
13/05	06.42	D	29/05	14.32	D
14/05	14.14	D ^a	29/05	23.57	N
15/05	10.17	D	30/05	13.50	D
16/05	12.40	D	31/05	14.29	D
			31/05	18.37	sunset
			01/06	01.23	N
WP-II (0–200 m)					
13/05	20.55	N13	27/05	14.39	D27
14/05	15.07	D14	28/05	11.03	D28
14/05	23.36	N14	30/05	01.48	N29
16/05	00.47	N16	30/05	23.09	N30a
16/05	05.30	D16	30/05	23.45	N30b
			01/06	11.33	D32
Bioness (0–980 m)					
13/05	12.48–13.37	D13	26/05	11.45–12.34	D26
15/05	22.02–22.50	N15	26–27/05	23.18–00.15	N26
16/05	08.45–09.32	D16 ^b	29/05	08.30–09.29	D29
			01/06	08.17–09.18	D32

Time for 12 l bottle and WP-II corresponds to the beginning of the ascent of the rosette or net, ascent lasting about 7 and 10 min, respectively. Sunrise around 03.55–04.15 h and sunset around 18.40–19.05 h during this period. ^a, Down to 90 m; ^b, results of the 75–150 m stratum have been discarded due to malfunctioning of the net.

upward advective shift of deeper layers, related to Ekman pumping, was superimposed upon the wind-induced mixing of the superficial layers (Figure 2b); the thermocline slightly deepened, but became stronger. In contrast, direct wind-induced mixing of the upper layer occurred as a result of the wind event of 24–25 May, with a significant increase in depth of the thermocline. The salinity structure remained fairly constant throughout the observational period (Figure 2c), as expected for weak horizontal advection; the relatively low salinity values recorded on 2 May and 12–13 May resulted from significant precipitation. At the beginning of the cruise, nitrate was undetectable ($<0.1 \mu\text{mol l}^{-1}$) in the upper 20–25 m (Figure 2d). Shoaling of deep nitrate surfaces was observed during the wind event of 13 May, then the depth distribution of nitrates remained fairly constant until the end of the cruise. Phytoplankton biomass exhibited a very clear decrease throughout the study (Figure

2e), despite the enhanced availability of nutrients in the euphotic layer induced by the major wind event.

Major mesozooplankton groups and species

The small-sized zooplankton ($>50 \mu\text{m}$), recorded in the bottle samples in the upper 100 m, consisted essentially of copepods (Table II), i.e. nauplii (71% of the total standing stock), then *Oithona* spp. and calanoid copepodites (10–13% each), and then *Microsetella* spp. (1%). The other individuals consisted of euphausiid nauplii and radiolarians (microplankton). Copepods were also numerically dominant in the haul samples, i.e. 87–98% of the total community for WP-II and about 92% for BIONESS. The numbers of copepod taxa identified in the hauls were 32 species and six genera of undetermined species for WP-II, and 45 species and four genera for BIONESS. In this paper we present only the major species or genera; each of them represented more than 1% (WP-II) or 2.5%

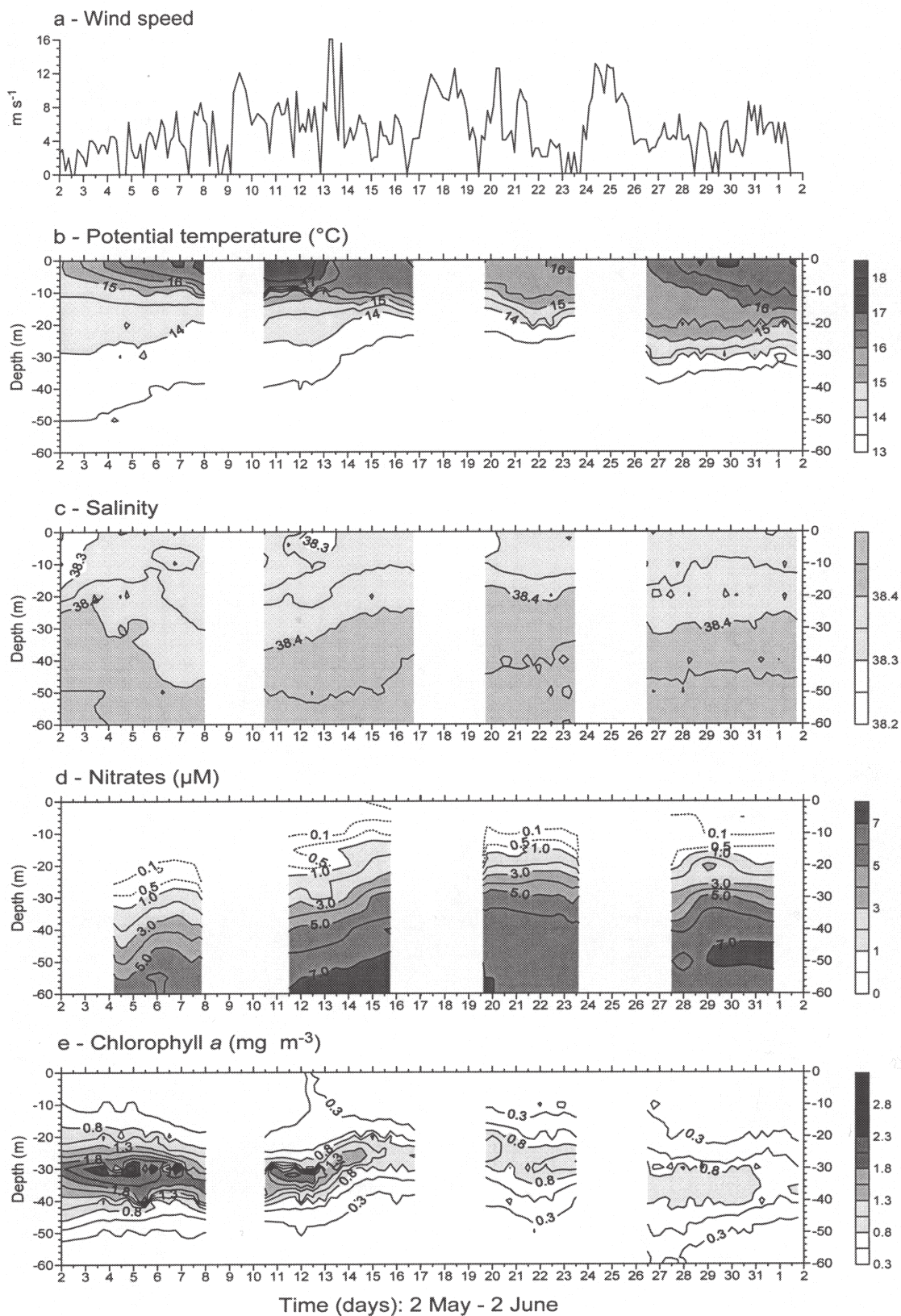


Table II: Bottle samples in the upper 100 m. Average number of individuals m^{-2}

Categories	Total		Leg 2 no. m^{-2}	Leg 4 no. m^{-2}
	no. m^{-2}	%		
Copepod nauplii	544 200	70.6	755 600	379 750*
Cyclopoids (<i>Oithona</i> spp.)	98 150	12.8	167 800	43 950*
Calanoids (copepodites)	75 500	9.8	95 700	59 750
Harpacticoids (<i>Microsetella</i> spp.)	7150	0.9	5700	8250
Euphausiid nauplii	25 750	3.3	44 500	11 150*
Radiolarians	19 700	2.6	14 050	24 100*

Values are given as numbers to the nearest 50. * t-test of leg 2/leg 4, difference significant at the 0.05 level.

(BIONESS) of the total copepod number (TN) for at least one of the two sampling periods.

In WP-II hauls (Table III), dominant taxa were *Oithona helgolandica* (41% of TN) and *Clausocalanus* spp. (essentially females of *Clausocalanus pergens/parapergens*, and copepodites and males of undetermined species), then *Centropages typicus* and *Pleuromamma gracilis* (3–4% each). It should be noted that the genus *Oithona* was also abundant in the bottle samples. Copepodites C5 and the adults of Euchaetidae, identified at the species level, corresponded to only one species, *Euchaeta acuta*.

WP hauls and BIONESS hauls did not sample the

same part of the copepod population, due to the different mesh size (200 μm compared with 500 μm) and also, to the different portion of the water column explored (0–200 m compared with 0–980 m). Total numbers of individuals were about eight times lower in the BIONESS samples than in the WP (3500 compared with 28 300 ind m^{-2}). The BIONESS results integrated deep-living species (such as *Calanus helgolandicus*, *Monacilla typica*) or diel migrating species (e.g. *Pleuromamma gracilis*), with *C. helgolandicus* and *P. gracilis* largely dominant (27–29% of TN each, Table IV). They were followed by *Euchaeta acuta* (>90% of the Euchaetidae), *Heterorhabdus* spp. (one

Table III: WP-II hauls in the upper 200 m. Average number of individuals m^{-2} and per cent contribution of stages, recorded for the major taxa of copepods

Family, genus or species	Total		Leg 2 no. m^{-2}	Leg 4 no. m^{-2}	Stages (%)			
	no. m^{-2}	%			C1–C3	C4	C5	f-m
Total copepods	28 278		38 459	19 793*				
<i>Calanus helgolandicus</i> ^a	136	0.5	295	3*	1	6	77	16
<i>Centropages typicus</i>	1067	3.8	2287	50*	4	12	16	68
<i>Clausocalanus</i> spp. (<i>C. pergens/parapergens</i>)	10 298	36.4	13 136	7934	←	53	→	47
Euchaetidae (<i>Euchaeta acuta</i>)	421	1.5	353	478	71	14	11	4
<i>Neocalanus gracilis</i>	363	1.3	323	396	47	14	25	14
<i>Oithona atlantica</i>	409	1.4	483	347	–	–	–	100
<i>Oithona helgolandica</i>	11 468	40.6	17 000	6858*	←	35	→	65
<i>Pleuromamma gracilis</i>	883	3.1	1290	543*	16	20	22	42
Undetermined Calanoida	1844	6.5	1703	1962	←	100	→	–

C, copepodite; f-m, adult; ^a, not a major species, but recorded in BIONESS hauls also; * t-test of leg 2/leg 4, difference significant at the 0.05 level.

Fig. 2. Wind speed (a) and time–depth distributions of temperature (b), salinity (c), nitrates (d) and chlorophyll a (e) recorded in the 0–60 m water column at the time-series station throughout the cruise. Periods with no data correspond to occupations of the 16 station grid and to port calls between the four legs of the cruise; wind speeds during port calls correspond to output of a meteorological model [after (Andersen and Prieur, 2000)].

Table IV: BIONESS hauls in the 0–980 m water column. Average number of individuals m^{-2} and per cent contribution of stages, recorded for the major taxa of copepods

Family, genus or species	Total		Leg 2 no. m^{-2}	Leg 4 no. m^{-2}	Stages (%)			
	no. m^{-2}	%			C1–C3	C4	C5	f-m
Total copepods	3546		3757	3388				
<i>Calanus helgolandicus</i>	1012	28.5	777	1189	–	+	96	4
<i>Centropages typicus</i>	45	1.3	103	1	–	–	+	100
Euchaetidae (<i>Euchaeta acuta</i>)	375	10.6	429	335	21	31	28	20
<i>Euchirella</i> spp.	107	3.0	117	100	17	19	12	52
<i>Heterorhabdus</i> spp.	225	6.3	214	233	–	3	14	83
<i>Monacilla typica</i>	159	4.5	92	209	–	+	91	9
<i>Neocalanus gracilis</i>	235	6.6	308	180	8	25	40	27
<i>Pleuromamma abdominalis</i>	145	4.1	179	120	–	40	35	25
<i>Pleuromamma gracilis</i>	949	26.8	1242	729	–	+	4	96

C, copepodite; f-m, adult.

species identified, *Heterorhabdus papilliger*) and *Neocalanus gracilis* (6–11% each).

Changes in mesozooplankton abundance and composition over the sampling periods

Four of the six taxonomic categories sampled with the bottles showed lower densities during leg 4 than during leg 2 (Figure 3 and Table II), with significant differences by factors of 2–4 for the copepod nauplii, *Oithona* spp. and the euphausiid nauplii, and a similar trend for calanoids (Figure 3a–d). In contrast, the two other taxa showed an increased average density during leg 4 compared with leg 2 (significant increase for radiolarians, and a similar trend in *Microsetella* spp., Figure 3e–f). No obvious difference occurred between day and night samples for the six taxa. The decrease in density of *Oithona* spp. could have started during leg 2; in fact, numbers of individuals were about two times lower on 15–16 May than on 12–14 May. The short-term variability observed, for example in the three successive samples on 31 May–1 June for *Microsetella* spp. and radiolarians, could be related to the type of sampling. In fact, sampling with bottles is made at discrete depths, in contrast to haul sampling, and patches of organisms can be caught or missed. For example, from these samples, *Microsetella* spp. appeared evenly distributed in the water column (Andersen *et al.*, 2001).

Copepod density recorded with the WP-II hauls clearly decreased by a factor of about two between legs 2 and 4 (Figure 4, Table III). A significant decrease was observed in several species such as *O. helgolandica*, *P. gracilis* and *C. typicus*, but only *C. typicus* quasi-disappeared, the density of *Clausocalanus* spp. also tended to decrease. Changes in

stage composition were also observed. In *O. helgolandica*, the most abundant species, and in *P. gracilis*, the lower density during leg 4 essentially resulted from the decrease in copepodites (Figure 4b,e). In contrast, the abundance of copepodites of *Clausocalanus* spp. appeared similar over the two sampling periods, while that of adults was clearly lower during leg 4 (Figure 4c).

Night catches did not appear obviously higher than day catches for the major taxa, except for the C4–C5 and adults of the migrant species, *P. gracilis*, for which the density tended to be higher at night than by day in the upper 200 m (Figure 4e). Density values recorded during leg 2 can therefore be compared, independently of the time of the day, for most of the major species. A gradual decrease from 14 to 15 May, then to 16 May, appeared in the density of the total copepod population, *Clausocalanus* spp. and *C. typicus* (Figure 4a,c,d). *Pleuromamma gracilis* showed some inverse trend, a higher density being recorded at the end of leg 2 (Figure 4e).

Copepods from BIONESS hauls showed an increase in density between the beginning and end of leg 2 (Figure 5a), as did *P. gracilis* for WP hauls. BIONESS copepods were of a greater size than those found in WP-II hauls, and this could explain why changes in density in BIONESS copepods resembled changes in one of the largest species recorded in the WP hauls. This also suggests that the low density observed in the BIONESS haul D13 was not an artefact. Results of the 75–150 m stratum of D16 have not been considered in the total density value (Table I); however, as this stratum was relatively poor in copepods (Andersen *et al.*, 2001), the results of D16 can be compared with the results of the other hauls.

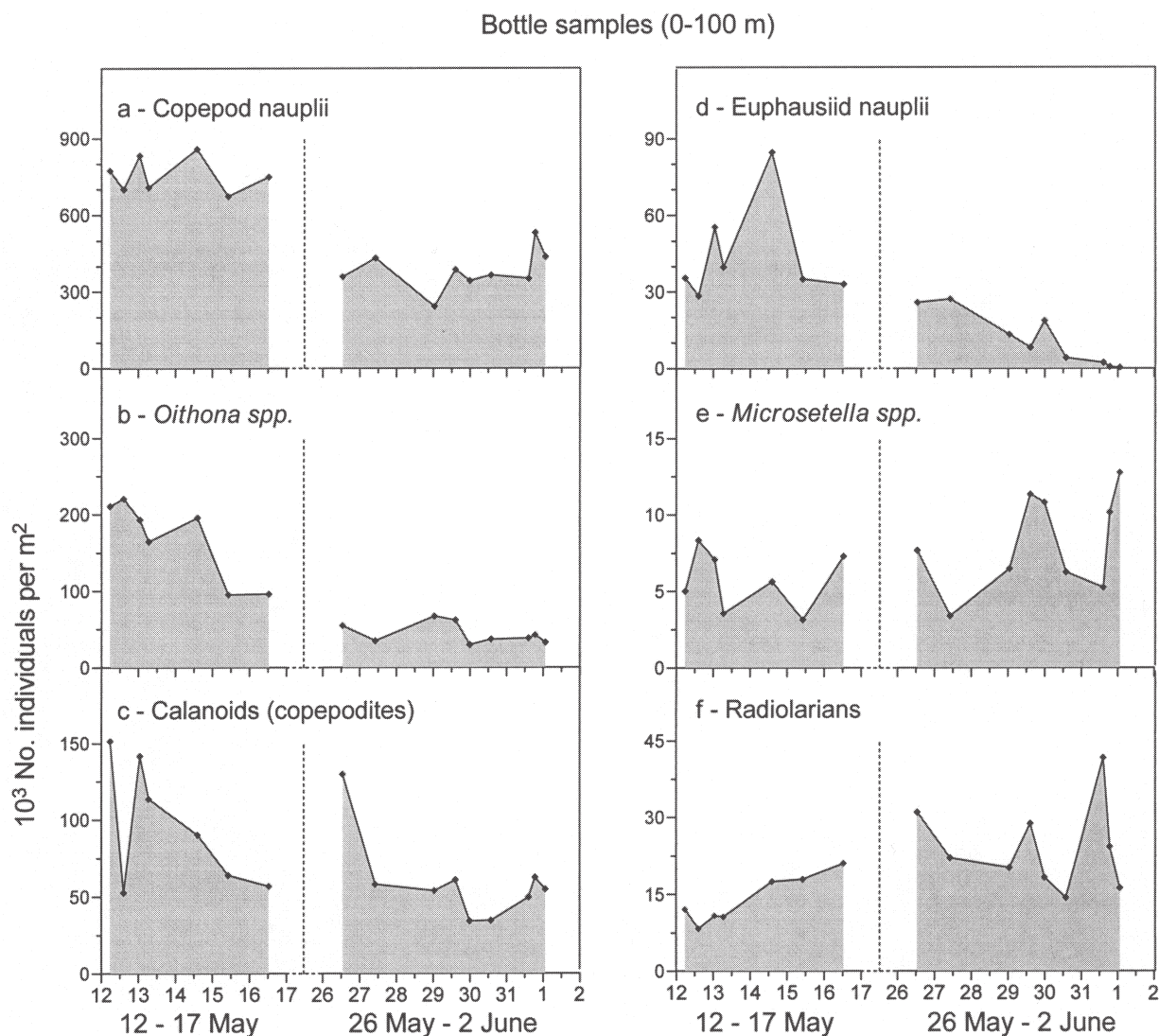


Fig. 3. Bottle samples in the upper 100 m. Density of the zooplankton categories recorded during the two sampling periods, 12–17 May and 26 May–2 June.

A large increase in density between the beginning and end of leg 2 was observed in most of the major species or genera caught by the BIONESS. During leg 4, these taxa showed (i) reduced density compared with the end of leg 2, as was the case for *P. gracilis*, *P. abdominalis*, *E. acuta*, *N. gracilis* (Figure 5b–e) and *C. typicus*, which was nearly absent during leg 4, as observed with WP hauls (Table IV), and (ii) similar or slightly higher densities for *C. helgolandicus*, *Heterorhabdus* spp. and *Monacilla typica* (Figure 5f–h). As for the WP-II results, lower densities during leg 4 often resulted from a larger decrease in copepodites compared with adults (e.g. *P. abdominalis*, Euchaetidae, *N. gracilis*; Figure 5c–e). During leg 4, *C. helgolandicus* was recorded in

high numbers in BIONESS hauls (0–980 m), while it was nearly absent from WP-II hauls (0–200 m). In fact, *C. helgolandicus* occurred mainly below 450 m and disappeared from the surface waters between the two sampling periods (Andersen *et al.*, 2001).

Major species of macroplankton and micronekton

Total numbers (TN) of macroplankton and micronekton recorded in the 0–980 m water column remained fairly constant over the two sampling periods (Figure 6a). However, night catches were ~1.7 times higher than day catches; this difference will be discussed later at the species

WP-II hauls (0–200 m)

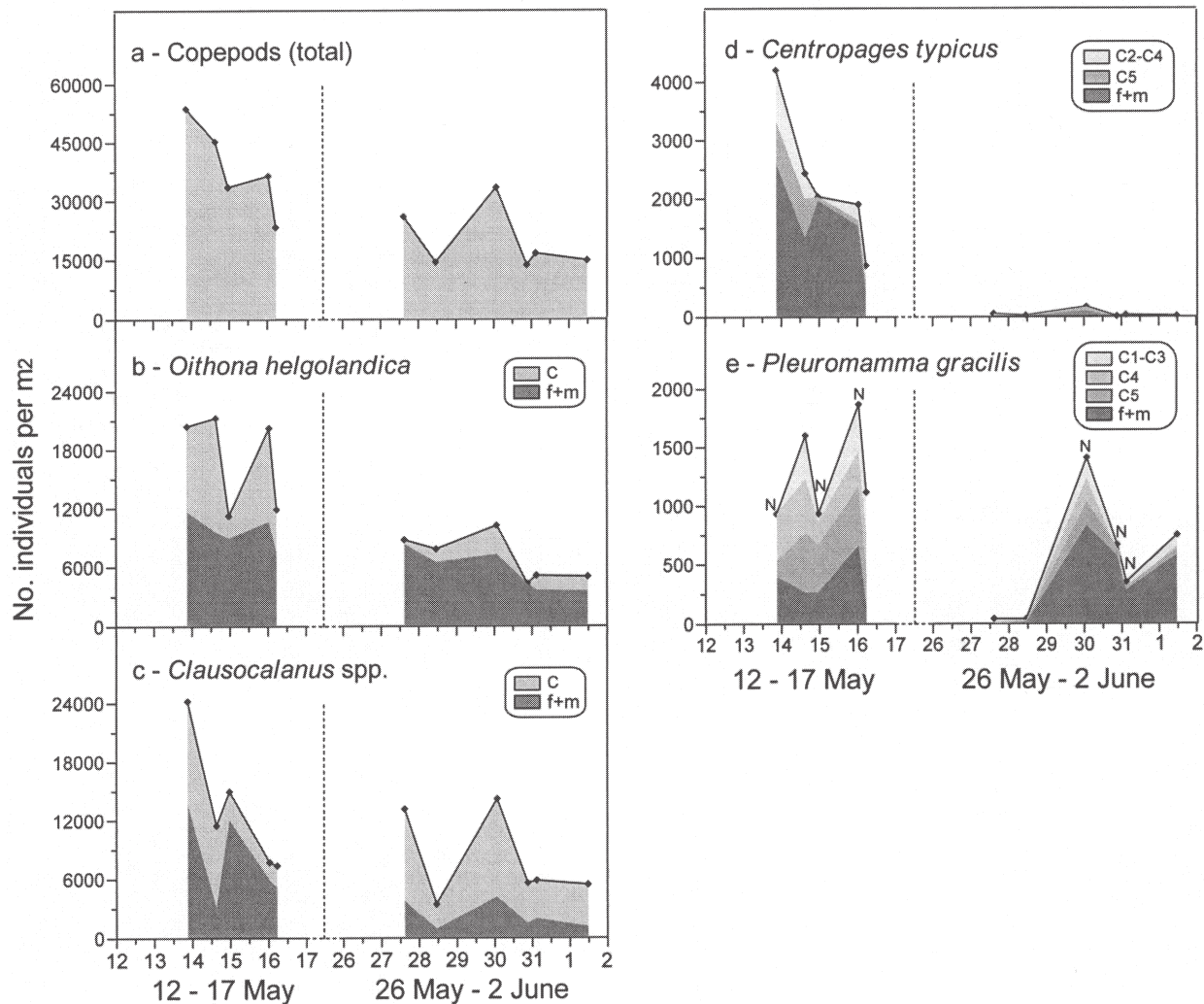


Fig. 4. WP-II hauls in the upper 200 m. Density of the major species or genera of copepods recorded during the two sampling periods, 12–17 May and 26 May–2 June. C, coepodite; f + m, adults; N, night hauls (indicated on e).

level. Catches essentially consisted of five groups (Table V): fishes and siphonophores (26–28% of TN each), followed by euphausiids and amphipods (15–19%), then pteropods (7%). In each group, a small number of species were numerically abundant (>3% of TN for at least one of the two sampling periods); these 10 species, among the 52 identified in the hauls, represented 89% of TN.

Dominant species were *Cyclothone braueri* and *C. pygmaea* for the fish population (13–14% of TN each), *Leusie conoidea* (22%) and, to a lesser extent, *Chelophyes appendiculata* for siphonophores. The hyperiid amphipod *Vibilia armata* was also abundant (12% of TN). Most hyperiid

amphipods are parasitoids of gelatinous zooplankton, and associations of members of the genus *Vibilia* are only known to occur with salps (Laval, 1980). Salps were nearly absent from the catches (Thaliacea <0.3% of TN) during the period of the hauls (legs 2 and 4), but they occurred in huge swarms during leg 1 (personal observation on board on 2–4 May), i.e. at least 9 days before. High densities of *Vibilia* sp. in the absence of salps, but 13–15 days after the occurrence of salp swarms, have also been recorded from BIONESS hauls by Andersen *et al.* (Andersen *et al.*, 1997) in the northeast tropical Atlantic. As salps do not appear broken up and lost in the nets, the behaviour of *Vibilia* spp.

BIONESS hauls (0-980 m)

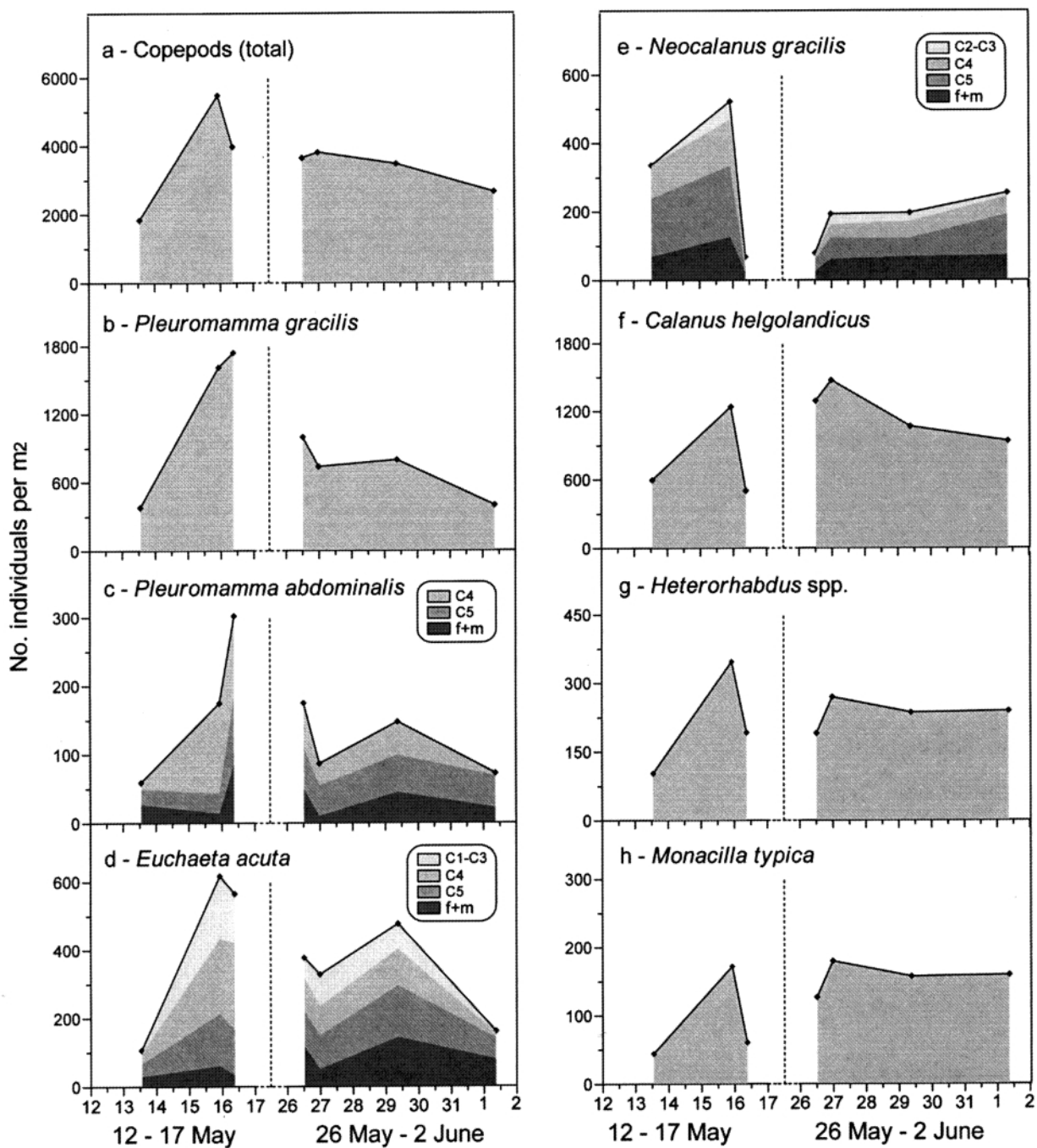


Fig. 5. BIONESS hauls in the 0-980 m water column. Density of the major copepod taxa recorded during the two sampling periods, 12-17 May and 26 May-2 June. C, copepodite; f + m, adults.

Table V: BIONESS hauls in the 0–980 m water column. Average number of individuals m^{-2} and percent of contribution, recorded for the major species of macroplankton and micronekton

Species	Total		Leg 2 no. m^{-2}	Leg 4 no. m^{-2}
	no. m^{-2}	%		
Total	317.5		290.1 ^a	251.6 ^a
day time	267.0			
night time	445.9			
Siphonophores	80.9	25.5		
<i>Chelophyes appendiculata</i>	11.0	3.5	11.1	10.9
<i>Lensia conoidea</i>	68.6	21.6	77.0 ^a	38.3 ^a
Pteropods	22.7	7.2		
<i>Cavolinia inflexa</i>	19.9	6.3	9.2 ^a	9.0 ^a
Amphipods	47.7	15.0		
<i>Vibilia armata</i>	39.4	12.4	31.1	45.6
Euphausiids	59.5	18.7		
<i>Euphausia krohni</i>	10.0	3.1	13.4	7.4
<i>Meganctiphanes norvegica</i>				
small	11.8	3.7	27.3	0.2
large	7.5	2.4	14.9	1.9
<i>Nematoscelis megalops</i>				
small	8.1	2.6	3.9	11.3
large	16.0	5.0	7.5 ^a	9.6 ^a
<i>Stylocheiron longicorne</i>	4.3	1.4	2.8	5.5
Fishes	87.6	27.6		
<i>Cyclothone braueri</i>	45.1	14.2	36.1	51.8
<i>Cyclothone pygmaea</i>	40.5	12.7	47.5	35.2

^aCalculated from daytime hauls only, as night numbers differ greatly from day numbers.

needs to be further investigated. Cornet and Gili also reported high densities of *V. armata* in the presence of low salp abundance in the southeast tropical Atlantic (Cornet and Gili, 1993).

The euphausiid population was essentially represented by *Nematoscelis megalops* and *Meganctiphanes norvegica* (6–8% of TN each), *Euphausia krohni* and *Stylocheiron longicorne*. Two size classes were distinguished for *N. megalops* and *M. norvegica*: (i) small individuals with a total length ≤ 11 mm and ≤ 7 mm, respectively, and (ii) large individuals of greater size, as the migrating behaviour of these species has been shown to vary according to these size classes (Andersen and Sardou, 1992; Sardou and Andersen, 1993). Pteropods consisted essentially of *Cavolinia inflexa*.

Higher night than day catches were recorded for large *N. megalops*, *Lensia conoidea* and *Cavolinia inflexa* (Figure 6b,e,g). Catches of *M. norvegica* also tended to be higher at night than by day. These differences can be related to (i)

daytime avoidance of the net for *N. megalops* and *M. norvegica* [e.g. (Wiebe *et al.*, 1982; Cochrane *et al.*, 1991)], (ii) swarming at night in the surface layers for *C. inflexa* and *M. norvegica* (Rampal, 1967; Casanova, 1970), and (iii) migration of part of the population down to below the lowest stratum sampled by day for *L. conoidea*, as would be suggested from its vertical distribution (Andersen *et al.*, 2001).

Changes in macroplankton community

An average lower density of siphonophores was recorded during leg 4 than leg 2, resulting from a decrease in abundance of the dominant siphonophore species, *L. conoidea*; this trend was very clear from day time hauls, and less pronounced, but based on only two hauls, at night (Figure 6e). Total numbers of euphausiids were also lower during leg 4 than during leg 2, but the different species did not show the same temporal variations in abundance (Figure 6c,d).

BIONESS hauls (0-980 m)

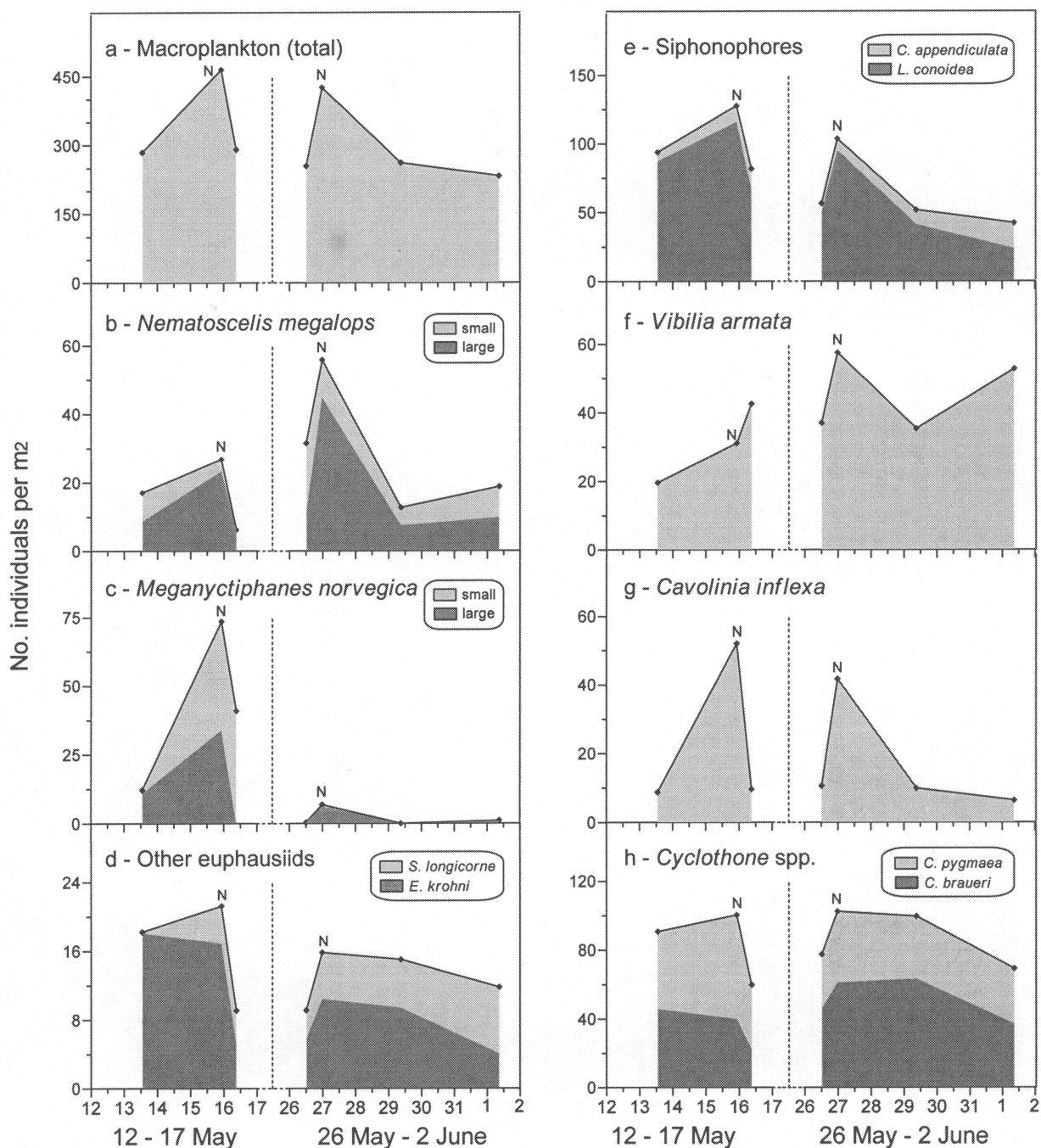


Fig. 6. BIONESS hauls in the 0–980 m water column. Density of the major species of macroplankton and micronekton recorded during the two sampling periods, 12–17 May and 26 May–2 June. N, night hauls.

Meganyctiphanes norvegica, the most common euphausiid species during leg 2, was rarely caught during leg 4; *Euphausia krohnii* showed a twofold decrease in density between legs 2 and 4. In contrast, *N. megalops* and *S. longicorne* were, on

average, more abundant during leg 4 than during leg 2. In haul D16, large *Nematoscelis* individuals were less present and no small individuals were caught, but this could be related to the absence of sampling of the 75–150 m stratum (Table

I). *Vibilia armata* was caught in higher numbers during leg 4 (Figure 6f). Pteropod and fish abundance did not show a particular trend (Figure 6g,h). The number of hauls was insufficient to detect changes throughout leg 2; however, there was an increase in density after D13 of the small *M. norvegica*, *S. longicorne* and *V. armata*.

DISCUSSION AND CONCLUSION

Transition in the abundance and composition of the community between the two sampling periods

To place in context the changes in the zooplankton community, data on copepod densities (previously presented) and on some characteristics of phytoplankton and vertical matter flux are summarized in Figure 7. A decline in copepod density was recorded between leg 2 and leg 4 with the three types of sampling; this decrease was more important among the small-sized copepods (average density divided by at least 2, Figure 7a,b) than in the larger ones (Figure 7c). One species, *Centropages typicus*, even disappeared from the catches as recorded from both WP and BIONESS hauls. The density of copepod nauplii also showed a twofold decrease between the two legs (Figure 7d). This general decline in copepod numbers agrees with the decrease by 30–40% in mesozooplankton biomass (dry weight from WP-2 hauls) reported between the same periods by Andersen and Prieur (Andersen and Prieur, 2000).

Some shift from small-sized copepod species to larger ones also appears to have occurred as time proceeded. The species for which density decreased markedly (such as *Centropages typicus*, *Clausocalanus* spp., *Oithona* spp. and *Pleuromamma gracilis*) are of relatively small size (prosoma length of adults <2 mm) compared with the species whose concentration remained more or less constant (*Calanus helgolandicus*, *Euchaeta acuta*, *Euchirella* spp., *Heterorhabdus* spp., *Monacilla typica* and *Pleuromamma abdominalis*). It may also be noted that among these last species, those that live mainly in the upper 250 m are generally reported to be omnivorous (*Euchirella* spp., *P. abdominalis*) or carnivorous, such as *E. acuta*, and *Heterorhabdus* spp. [e.g. (Mauchline, 1998)]. The composition of the phytoplankton community, consisting mainly of chromophyte nanoflagellates, diatoms and cyanobacteria, varied throughout the cruise (Vidussi *et al.*, 2000). The contribution of diatoms to total chlorophyll *a* content decreased from $27 \pm 5\%$ during leg 2 to $20 \pm 2\%$ during leg 4, while that of cyanobacteria increased from $12 \pm 2\%$ to $18 \pm 2\%$ (Figure 7f,g). The preferred food of herbivorous copepods therefore decreased, while the density of potential prey for

omnivorous and carnivorous copepods increased. In fact, between legs 2 and 4, the number of radiolarians increased significantly (Figure 3f) and the biomass of heterotrophic ciliates doubled (Pérez *et al.*, 2000).

The DYNAPROC cruise showed that in this area, the month of May coincided with the transition period from a mesotrophic system to an oligotrophic one. Several types of observations support this idea, for example, decrease in the chlorophyll *a* content throughout the cruise (Figure 2e), changes in phytoplankton composition and ciliate biomass (detailed above), and higher fluxes of particulate organic carbon (POC) during leg 2 than during leg 4, with export production representing, respectively, 9.2 and 1.8% of primary production [Figure 7h (Goutx *et al.*, 2000)]. The results concerning the copepod community presented here are also consistent with this scenario.

To place the present results in the context of seasonal variability, we have presented schematically in Figure 8 (i) the observed trend during the DYNAPROC cruise for the major copepod species, and (ii) the periods of minimum and maximum abundance reported in the literature. It should be noted that the literature data on copepod annual cycles are often based on monthly sampling throughout one year and restricted to the superficial layer (sampling mainly shallower than 200 m depth). The disappearance or large decrease in density of several species observed between mid-May and the end of May 1995, concords with literature data, these species being generally reported as abundant in spring until May and at a minimum in June–September. Moreover, Hure and Scotto di Carlo (Hure and Scotto di Carlo, 1969) performed two cruises in May 1965 (7–9 May, 26–28 May) and observed, as in the present study, at least a twofold decrease in concentration of *Calanus helgolandicus*, *Centropages typicus*, *Clausocalanus pargens* and *Oithona helgolandica*. However, the time of maximum abundance sometimes differed (e.g. *C. typicus*, *C. arcuicornis*). The fairly constant or increased density observed over the present cruise for *Heterorhabdus* spp., *Euchaeta acuta* and *Monacilla typica* did not appear to contradict the rare available literature data.

Temporal changes in the macroplankton and micronekton community showed features similar to those in the copepod community. Marked changes were observed in the species composition of the euphausiid population, among which different species have different diets (Fowler *et al.*, 1971; Casanova, 1974; Mauchline, 1980; Barange *et al.*, 1991; Patrìti and Yoon, 1995). *Meganyctiphanes norvegica* and *Euphausia krohni*, reported as omnivorous species in the references cited above, decreased in abundance between legs 2 and 4, while *Nematoscelis megalops* and *Stylocheiron longicorne*, reported as carnivorous species, occurred in higher numbers during

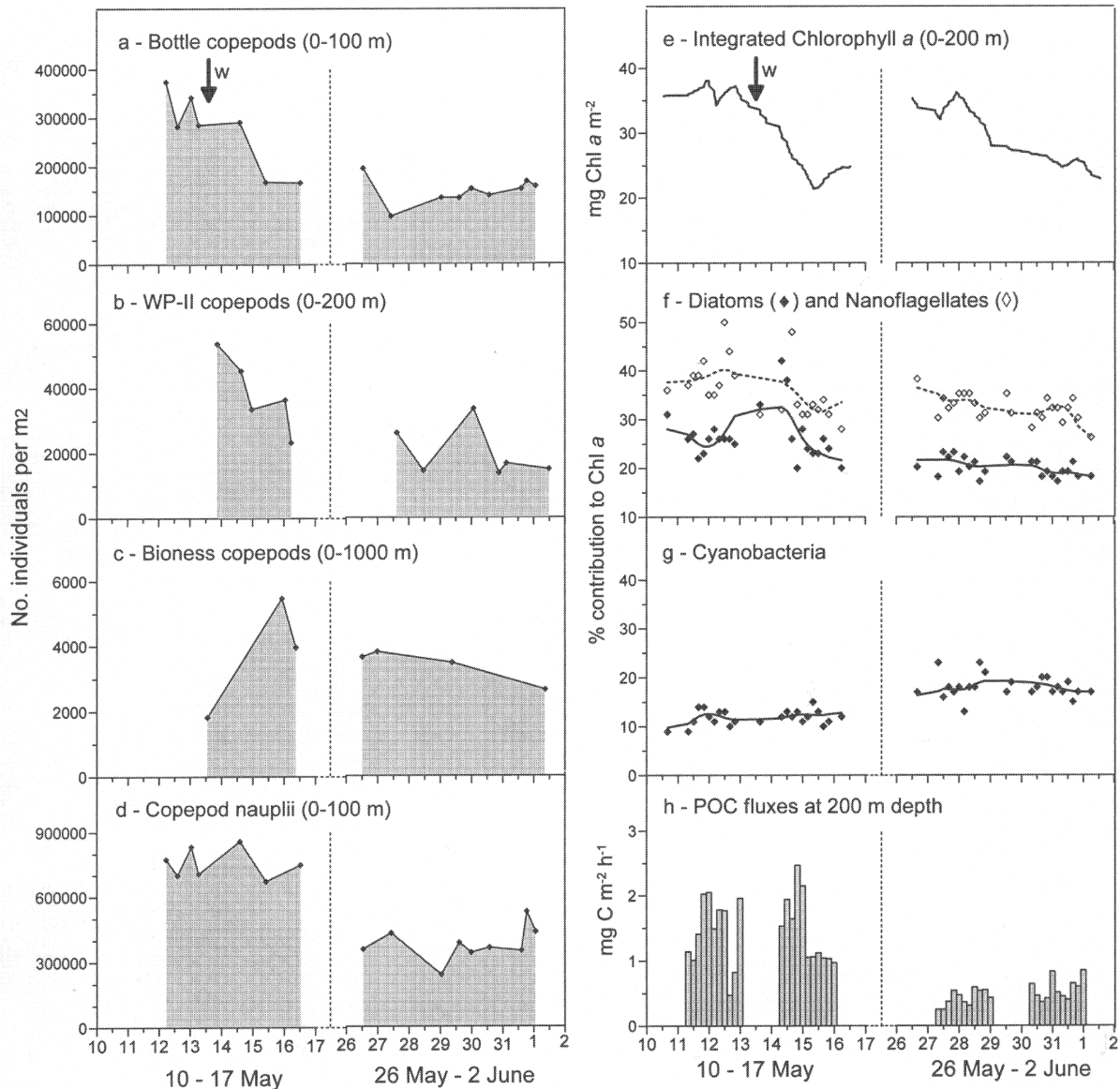


Fig. 7. Overview of the copepod densities and phytoplankton and vertical flux characteristics recorded at the time-series station during legs 2 and 4. (**a-c**) Densities of copepods recorded with the three types of sampling device, (**d**) density of copepod nauplii, (**e**) integrated chlorophyll *a* content [after (Andersen and Prieur, 2000)], (**f,g**) contribution of the three main phytoplankton groups to total integrated chlorophyll *a* [after (Vidussi *et al.*, 2000)], (**h**) flux of particulate organic carbon, recorded with free-floating sediment trap at 200 m depth with 4 h intervals for the samples [after (Goutx *et al.*, 2000)]; wind event (↓w).

leg 4 than leg 2 (Figure 6b,c,d). A shift to carnivorous species therefore appeared in both copepods and euphausiids. The increased impact of carnivorous zooplankton was also suggested by a greater contribution of storage lipids to particulate flux at 200 m depth during leg 4 than during leg 2 (Goutx *et al.*, 2000). The density of euphausiid nauplii showed a fourfold decrease throughout the cruise, while the density of the older organisms was

only reduced twofold. This would be in agreement with the period of egg laying reported for *N. megalops* and *M. norvegica* in spring and April, respectively (Casanova-Soulier, 1968; Franqueville, 1971). The disappearance of *M. norvegica*, and the decrease in *L. conoidea* and *N. megalops* observed over DYNAPROC, are in agreement with the periods of seasonal abundance reported in the literature (Figure 8). *Meganyctiphanes norvegica* and *L. conoidea* tend to

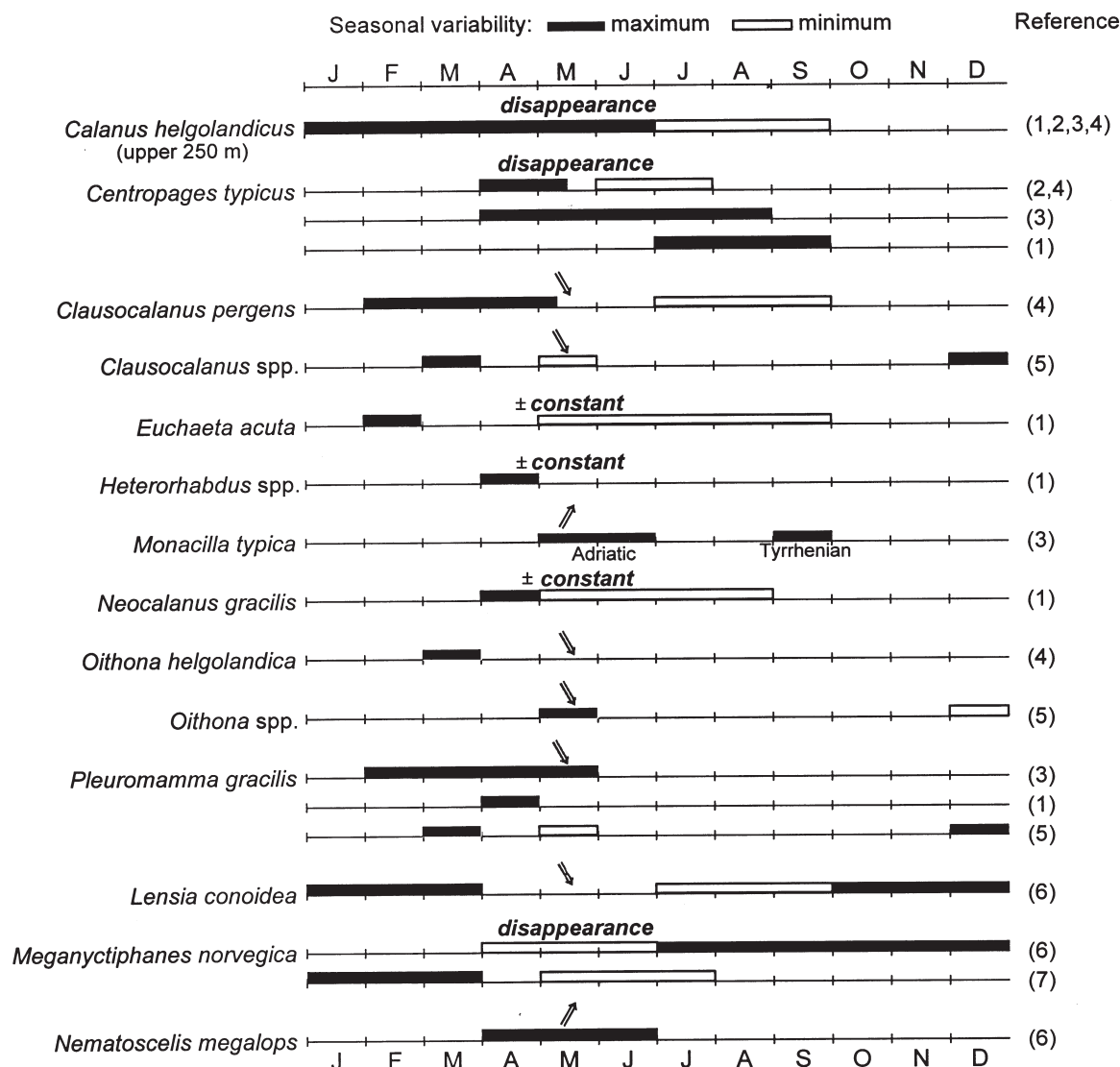


Fig. 8. Schematic view of the seasonal variability of the major species of copepods and macroplankton; periods of minimum and maximum abundance reported in the literature for the Mediterranean Sea and observed trend throughout the present cruise performed in May (disappearance, \pm constant, \searrow , \nearrow). The studies referred to were based on monthly sampling, except when indicated. 1. (Hure, 1955); 2. (Vives, 1963); 3. (Hure and Scotto di Carlo, 1968); 4. (Hure and Scotto di Carlo, 1969); 5. (Della Croce, 1959), four cruises; 6. (Franqueville, 1971), sampling between 0 and 1000 m, down to 1400 m occasionally; 7. (Sardou *et al.*, 1996), sampling between 0 and 1000 m.

go deeper at the end of the spring and to live below 500 and even 1000 m, 1000 m often being the deepest depth sampled (Franqueville, 1971; Casanova, 1974; Sardou *et al.*, 1996).

Effects of wind events

During the major wind event, an upwelling of deeper waters, related to Ekman pumping, occurred between 12 and 14 May. Despite the resulting enhanced availability of nutrients in the euphotic layer, total phytoplankton biomass decreased (Figure 7e; cf. Figure 2). Changes in phytoplankton composition were observed; diatoms

showed an increase in concentration and even became dominant, for a short period, compared with chromophyte nanoflagellates (Figure 7f). The obvious changes in density of copepods observed between 12 and 16 May could be related to this wind event. The density of the relatively small copepods (copepodites and adults) from bottle and WP samples was lower at the end of leg 2, on 15–16 May, while numbers of larger copepods caught by the BIONESS increased (Figure 7a–c); copepod numbers recorded with the BIONESS were much lower than those with bottles and WP-II (by about 10 and 50 times). This decrease could not be related to dilution resulting from a

deepening of the mixed layer as the thermocline was at 10–20 m depth, well above the deepest limits of the sampling (100 and 200 m). On the other hand, the number of nauplii remained rather constant during leg 2 (Figure 7d). As the density of adults decreased, this would suggest that egg production had increased during this period. This would agree with previous studies reporting an increase in abundance of copepod nauplii or in female egg production subsequent to a wind event [e.g. (Cowles *et al.*, 1987; Nielsen and Kiørboe, 1991; Kiørboe, 1993)].

According to Kiørboe (Kiørboe, 1993), an immediate functional response (feeding or production rate) of copepods to changes in food availability would be expected, while the numerical response in mesozooplankton biomass would lag. Kiørboe gave several examples of temporarily elevated mesozooplankton productivity subsequent to a bloom of large phytoplankton cells, but without obvious numerical responses in terms of biomass (Kiørboe, 1993). Highest ingestion rates of copepods, subsequent to a storm event and accompanied by a decrease in copepod biomass, have also been observed by Roman *et al.* (Roman *et al.*, 1993). In the present study, the short-term dominance of diatoms subsequent to the wind event could have induced a higher ingestion rate. At the time of the decline in phytoplankton biomass, primary production did not show any decrease (Vidussi *et al.*, 2000) and copepod numbers were still high. The increase in the flux of several tracers of the organic matter flux, such as POC (Figure 7h), glucosamine, proteins and chloroplast lipids, observed just after the wind event suggested that zooplankton rapidly responded to the development of diatoms in the upper layer (Goutx *et al.*, 2000). It seems, therefore, that increase in grazing pressure could be considered as a main factor responsible for the decline in phytoplankton standing stock, although the present study deals with densities and not biomass. From mesoplankton, macroplankton and ciliate biomass, Andersen and Prieur (Andersen and Prieur, 2000) estimated a grazing pressure of $0.39\text{--}0.86\text{ g C m}^{-2}\text{ day}^{-1}$, which was in the range of primary production ($0.25\text{--}0.73\text{ g C m}^{-2}\text{ day}^{-1}$, mean $0.48\text{ g C m}^{-2}\text{ day}^{-1}$).

The major wind event of 13 May appears to have induced long-lasting changes, at least until the end of the month when the community structure appeared rather stable. This study allowed documentation of the transition in the seasonal abundance and composition of the zooplankton community. We underline the need for short-term sampling of zooplankton, with estimates of specific composition and with several types of devices.

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