JOURNAL OF PLANKTON RESEARCH | VOLUME 23 | NUMBER 3 | PAGES 319–331 | 2001

Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions

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Zooplankton abundance, biomass (biovolume) and taxonomic composition were studied within an annual cycle (August 1995–October 1996) in the Bay of Blanes (northwest Mediterranean). Weekly zooplankton sampling included oblique tows made with a 200 μm Juday–Bogorov net, and vertical tows made with a 53 μm net, to adequately sample both mesoplankton and the smaller zooplankton fractions. Total zooplankton abundance showed high variability, lacking any clear seasonal pattern. However, the different species within the zooplankton community displayed a clear succession throughout the year. In general, cyclopoid copepods (Oithona spp.) and cladocerans (Penilia avirostris) dominated the summer and autumn communities, whereas in winter and spring, calanoid copepods (Clausocalanus spp., Paracalanus sp. and Centropages typicus) were predominant. The zooplankton annual cycle in the Bay of Blanes does not resemble those of other Mediterranean littoral areas, probably due to the inherent particularity and variability associated with open coastal environments. On average, the abundance of organisms estimated with a traditional 200 μm Juday–Bogorov net was 8.1 times lower than the values obtained with a 53 μm net. Even if only organisms >200 μm collected in the 53 μm tows were considered, the total abundance within the 53 μm net was still 4.4 times higher than the estimates from the Juday–Bogorov net. These results suggest the need for accurate samplings of the entire zooplankton assemblage when characterizing the structure and dynamics of zooplanktonic communities.

INTRODUCTION

Coastal marine areas are of great ecological, economic and social interest. They are highly variable systems, where changes in the water circulation patterns, and fluctuations of land influences (e.g. rivers, sewage flow) induce high temporal variability on scales ranging from hours to seasons (Walsh, 1988). This variability may be reflected in the dynamics of the populations, particularly planktonic ones, thriving in coastal systems. Such variability may hide the underlying seasonal patterns of organism abundance and biomass.

Elucidation of the zooplankton community structure and dynamics requires the use of sampling methods that provide representative capture of the populations. For many groups of organisms, this problem has been reasonably solved. However, for the smaller size classes (juvenile and small zooplankters), which can comprise the bulk of the zooplankton community, especially in oligotrophic seas like the Mediterranean (Fulton, 1984; White and Roman, 1992; Kouwenberg, 1993) sampling issues have not been clearly addressed. Even though there is evidence of the bias produced in the collection of organisms with large-pore mesh nets (Krsinic and Lucic, 1994), data on the structure of the planktonic community corresponding to the smaller size fractions are still rather scarce. This is mainly because most studies have focused on the larger size classes of zooplankton (Vives, 1966; Dauby, 1980; Seguin, 1981; Sabatés *et al.*, 1989; Lakkis, 1990; Kouwenberg, 1993; Razouls and Kouwenberg, 1993; Mazzocchi and Ribera d'Alcalà, 1995; Siokou-Frangou, 1996; Christou, 1998), probably due to the reasoning that smaller organisms may be important in number, but their contribution to the total community in terms of biomass may be small. However, recent studies have shown the importance of small copepod species, along with juvenile stages, as a trophic link between classical and microbial food webs (Roff *et al.*, 1995; Wickham, 1995, Calbet *et al.*, 2000).

This role may be especially important in oligotrophic systems, where the relative size of primary consumers is expected to be smaller (Chisholm, 1992; Agawin *et al.*, 2000) and the microbial components dominant (Gasol *et al.*, 1997).

In this work, we report the succession of the zooplankton community in a coastal area of the northwestern Mediterranean throughout an annual cycle (from August 1995 to October 1996). We compare the data obtained with two plankton nets fitted with mesh sizes adequate for the collection of meso- and microplankton metazoans. The results are discussed in relation with seasonal clues in the environment, best characterized by temperature (Duarte *et al.* 1999) and changes in the autotrophic components of the food web (chlorophyll *a*). Data are compared with previous results obtained in other Mediterranean coastal areas.

METHOD

The study took place in the coastal zone off Blanes (northwest Mediterranean), a tourist village approximately 60 km north of Barcelona. The area is an open bay which receives some urban sewage, particularly during the tourist season [July and August (Duarte *et al.*, 1999)]. The sampling station (41°39.9′N, 2°48.03′E), half a mile offshore and of 20–25 m depth, was sampled weekly from August 1995 to October 1996. For further details on hydrographic characteristics of the study area, see (Cebrián *et al.*, 1996).

Surface water samples for temperature measurement and chlorophyll *a* (Chl *a*) determination were collected weekly (except for December and January) between 09:00 and 12:00 h. Chl *a* was measured by filtering 500 ml of surface water onto GF/F Whatman filters, and further fluorimetric analyses of the acetone extracts following the protocol of Parsons *et al.* (Parsons *et al.*, 1984).

Two sampling methods were used for the estimation of zooplankton abundance: vertical tows from near the bottom to the surface with a microplankton net (53 μm mesh, 25 cm mouth diameter), and 4 minute oblique tows with a Juday–Bogorov net (200 μm mesh, 50 cm diameter). The volume filtered for both nets was ~1 m^3 for the microplankton net and ~60 m^3 for the Juday–Bogorov. The contents of the cod ends were preserved with formalin (4% final concentration) for further analysis. Once in the laboratory, samples from the microplankton net were divided into two nominal size fractions (53–200 μm and >200 μm) by filtering through a 200 μm sieve. Both fractions were counted and sized separately under the stereomicroscope. At least 300 organisms were counted per fraction, which represented 4–16% of the entire sample. Cladocerans and copepods were identified to species or genus level (except for the copepods *Paracalanus* sp. and *Clausocalanus* spp., which were grouped together due to high morphological resemblance of juveniles). In addition, copepod data were separated into nauplii and copepodite (including adults) stages. All other taxa were identified to the phylum, class or order levels.

To estimate biomass as biovolume, video pictures of 150 organisms for each size fraction (53–200 μm, >200 μm) of the microplankton tows were digitized with a Power Macintosh computer provided with a frame grabber and NIH Image analysis software. The silhouette of the entire organism in ventral view was outlined and major and minor axes were automatically calculated. This procedure allowed accurate measurements of the organisms which were converted into volumetric estimates by assuming an ellipsoidal shape.

RESULTS

Annual cycle in the Bay of Blanes

The seasonal patterns of surface Chl *a* concentration and temperature are presented in Figure 1. Temperature ranged from 12 to 25°C, reaching minimum and maximum values during winter and summer, respectively.

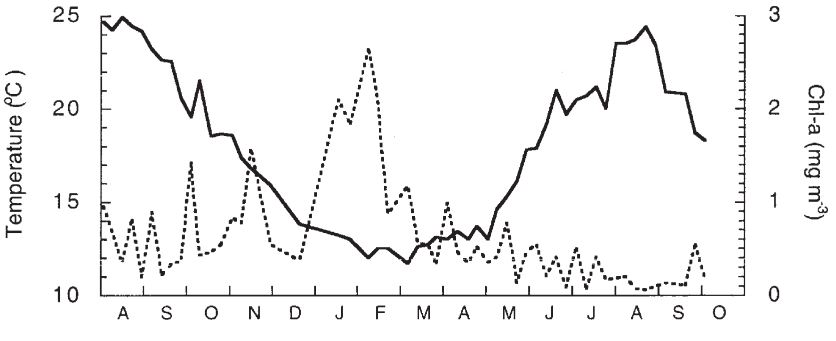

Fig. 1. Seasonal patterns of surface temperature (solid line) and chlorophyll *a* (dashed line) during the study in the Bay of Blanes. August 1995–October 1996.

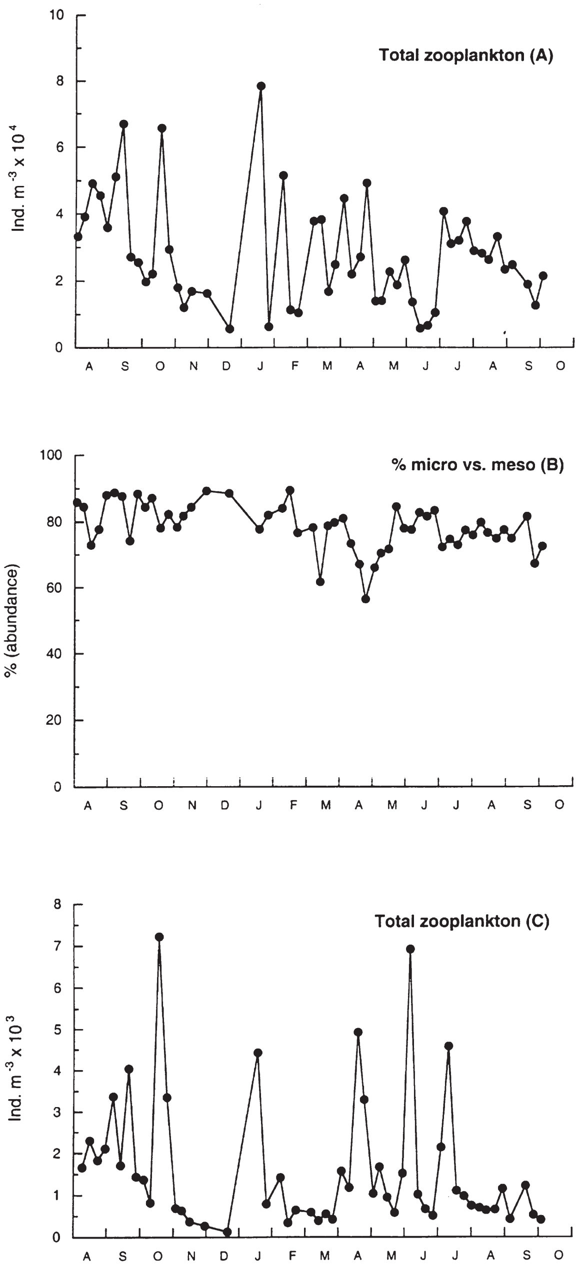

Fig. 2. (**A**) Annual pattern of abundance of zooplankton (53–200 μm + >200 μm) from microplankton net tows. (**B**) Percentage (in abundance) of the zooplankton community represented by microzooplankton (53–200 μm). (**C**) Annual cycle in total abundance of zooplankton from Juday–Bogorov net estimates. Note different scale between plots A and C. August 1995–October, 1996.

Chl *a* concentration was very variable and notably different between the two years studied. However, in general, trends followed an opposite pattern to that of temperature, with highest values in late winter 1995 and lowest values in summer 1996. Sporadic secondary peaks were also found throughout the year, especially during autumn 1995.

Even though data on total zooplankton abundance for the Juday–Bogorov net are given in the study, we will describe the patterns of zooplankton variability in the Bay of Blanes using the values obtained from the microplankton tows as both fractions together, i.e. 53–200 μm and >200 μm. These values provide better estimations of the absolute abundance of organisms than those obtained from the Juday–Bogorov net, as will be shown later.

Total zooplankton abundance was highly variable within the study period (Figure 2), ranging between 5635 and 78 473 ind. m^{-3}, with an average of 28 111 ind. m^{-3} (16 197.6 S.D.). The highest value was recorded in January, but several peaks occurred throughout the year, with no evidence of clear seasonality (Figure 2A). The 53–200 μm size category (microzooplankton) represented a fairly uniform fraction throughout the year, with an average of 78.5% (7.11 S.D.) of total zooplankton abundance (Figure 2B). The highest proportion of microzooplankton was observed in late November and February (89%) and the lowest in April (56.5%). Zooplankton abundance from the Juday–Bogorov estimates was also very variable throughout the study, lacking any seasonal pattern (Figure 2C). Zooplankton biomass (biovolume, Figure 3A) showed a clear peak in January, mostly due to cirriped larvae and large copepods. Microzooplankton (numerically dominated by copepod nauplii) represented, on average, 21% of the total biovolume of the community. A maximum volumetric contribution of microzooplankton in June (97%) was found, corresponding to a minimum in mesozooplankton abundance (Figure 3B).

Copepods (from nauplii to adults) dominated the zooplankton community throughout the year (Figure 4), averaging 91% of the total zooplankton (range: 76–99%). Copepod nauplii constituted the bulk of the community, representing 59% of total zooplankton abundance (range: 40–74%). The most abundant zooplankton groups, other than copepods, were cladocerans (average: 821; maximum: 5737 ind. m^{-3}), appendicularians (773 and 3713 ind. m^{-3}, respectively) and cirripeda (345 and 4726 ind. m^{-3}) (Figures 4 and 5). Other groups included mollusc larvae (average: 217; maximum: 1337 ind. m^{-3}), polychaete larvae (181 and 2613 ind. m^{-3}) and chaetognaths (43 and 263 ind. m^{-3}). Despite the highly variable temporal pattern displayed by zooplankton as a whole, which tended to mask any clear seasonal signal, most of the above-mentioned groups exhibited evident seasonality. This was especially apparent for cladocerans and appendicularians, which occurred in summer, and for meroplankton (cirriped, mollusc and polychaete larvae), which were more important during the winter months. Chaetognaths showed a summer–autumn distribution which closely coincided with the pattern of appendicularians

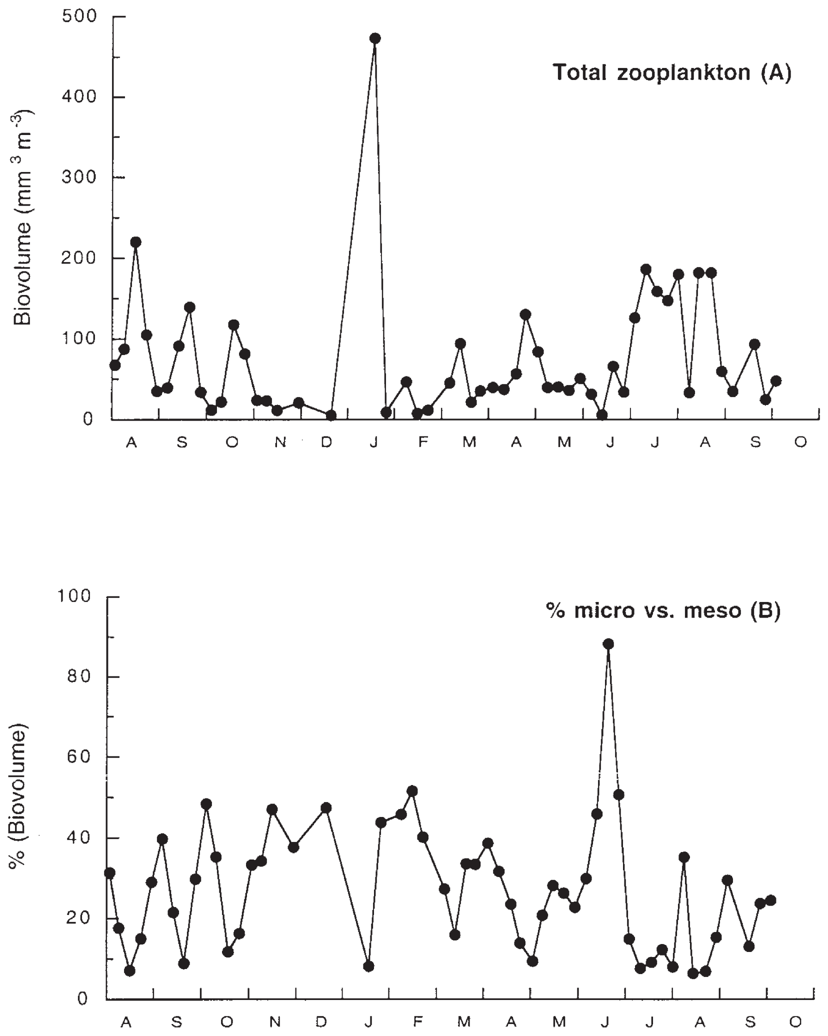

Fig. 3. (**A**) Annual pattern of zooplankton biovolume (53–200 μm + >200 μm) from microplankton net tows. (**B**) Percentage (in biovolume) of the zooplankton community represented by microzooplankton (53–200 μm). August 1995–October 1996.

and cladocerans. Amongst cladocerans, *Penilia avirostris* was dominant during the summer and early autumn (Figure 6). Another genus, *Evadne*, appeared in the plankton earlier in the year (i.e. spring), although its contribution was small (<100 ind. m^{-3}).

Nine copepod genera were identified which contributed 98% of the copepodite and adult copepod abundance (Table I and Figure 7). The calanoids were composed predominantly of *Paracalanus* sp. and *Clausocalanus* spp. (hereafter *Para./Clauso.*), *Centropages typicus*, *Temora stylifera* and *Acartia clausi*. The cyclopoids (including poecilostomatoids) were represented mostly by *Oithona* spp. and *Oncaea* spp., and the harpacticoids by *Euterpina acutifrons* and *Microsetella* sp. The *Para./Clauso.* group and *C. typicus* were the most important contributors to the copepod community during winter and spring (Figure 7). Even though these genera were present throughout the year, their abundance declined during summer and autumn. During these seasons (especially in summer), cyclopoids (*Oithona* spp.) and harpacticoids (*E. acutifrons*) dominated the copepod assemblages (Figure 7). Other copepods, i.e. *T. stylifera*, displayed a pattern similar to the one exhibited by *Oithona* spp. and *E. acutifrons* but peaked in abundance later in the season. The rest of the genera were only a small component of the copepod community and had no clear seasonal pattern. For example, *A. clausi* was present all year with irregular oscillations of abundance.

The annual succession of the main components of the zooplankton community in the Bay of Blanes for the period considered is summarized as follows. The spring community was mostly dominated by *C. typicus*, followed by the group of *Para./Clauso.*, *Oithona* spp. (both groups

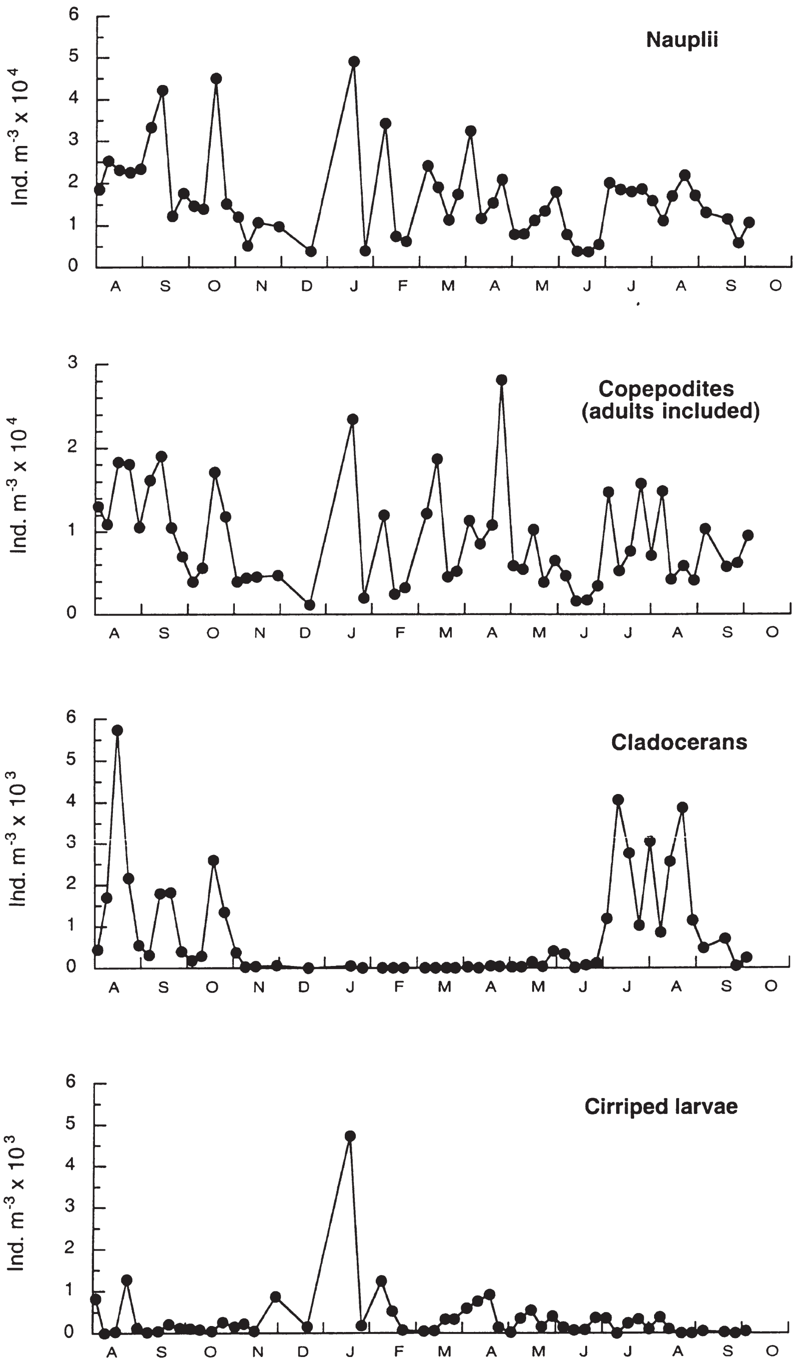

Fig. 4. Annual cycle in abundance of crustacean zooplankton (53–200 μm + >200 μm) from microplankton net tows. August 1995–October, 1996.

were present during the whole study) and *Evadne* spp. In summer, fine particle filter feeders, i.e. cladocerans (especially *P. avirostris*), and appendicularians dominated the zooplanktonic community. During this season, *Oithona* spp. and *E. acutifrons* were the dominant copepods. Other zooplankters, such as *T. stylifera*, *A. clausi*, *Oncaea* spp., *Podon* spp., *Evadne* spp., mollusc larvae and chaetognaths, also occurred, but in much lower abundance. In autumn, zooplankton were still numerically dominated by *Oithona* spp. and a smaller component of *P. avirostris*. New contributions

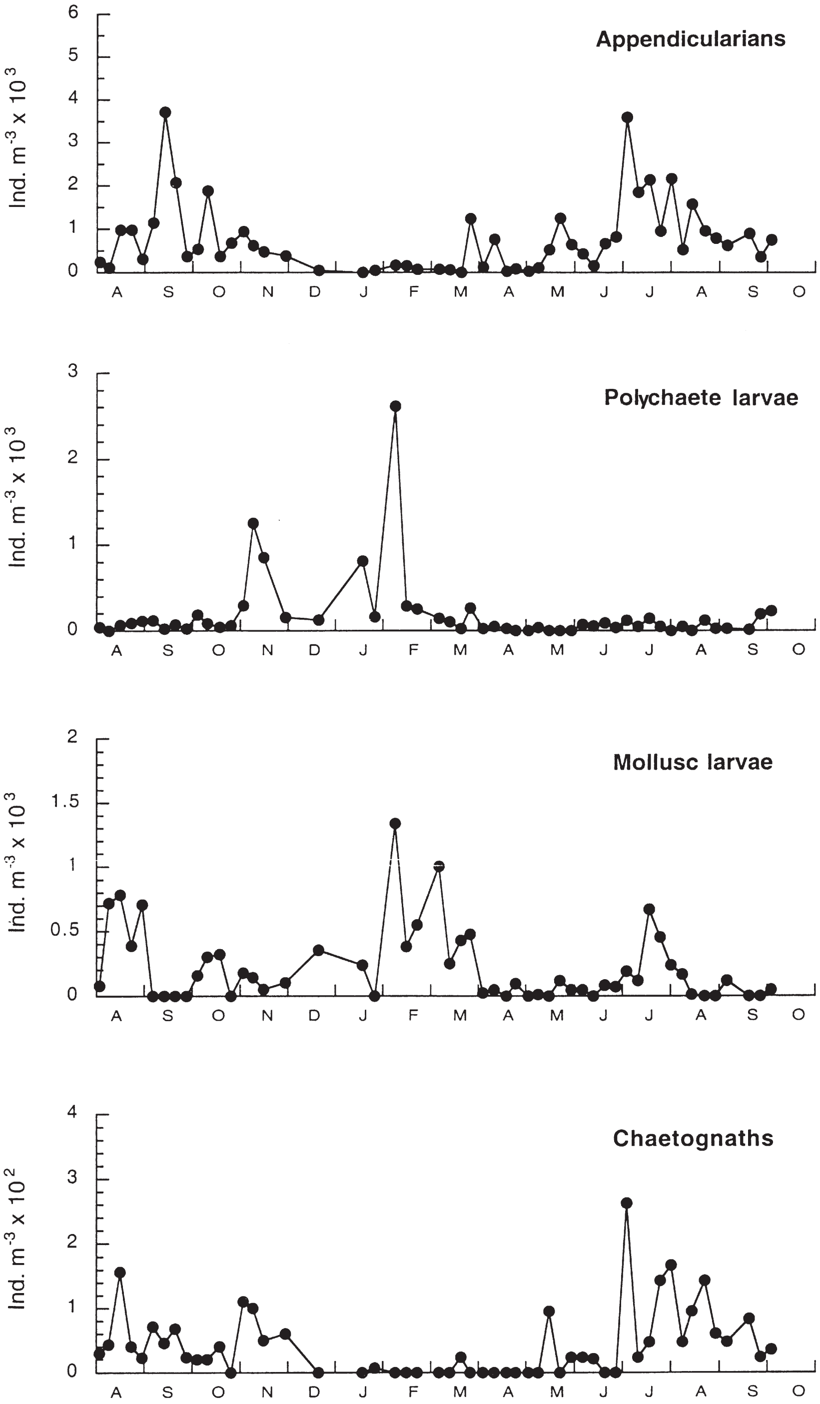

Fig. 5. Annual cycle in abundance of non-crustacean zooplankton (53–200 μm + >200 μm) from microplankton net tows. August 1995–October, 1996.

to the community were the harpacticoid *Microsetella* sp. and planktonic polychaetes. Finally, in winter, the zooplankton community was once again dominated by calanoid copepods, mostly *Para./Clauso.*, but also some *C. typicus* and *A. clausi*. *Microsetella* sp. and *Oithona* spp. were still present in the water column, simultaneously with new groups such as cirriped larvae. If data on copepod abundance are gathered into seasons, it is worth noting the

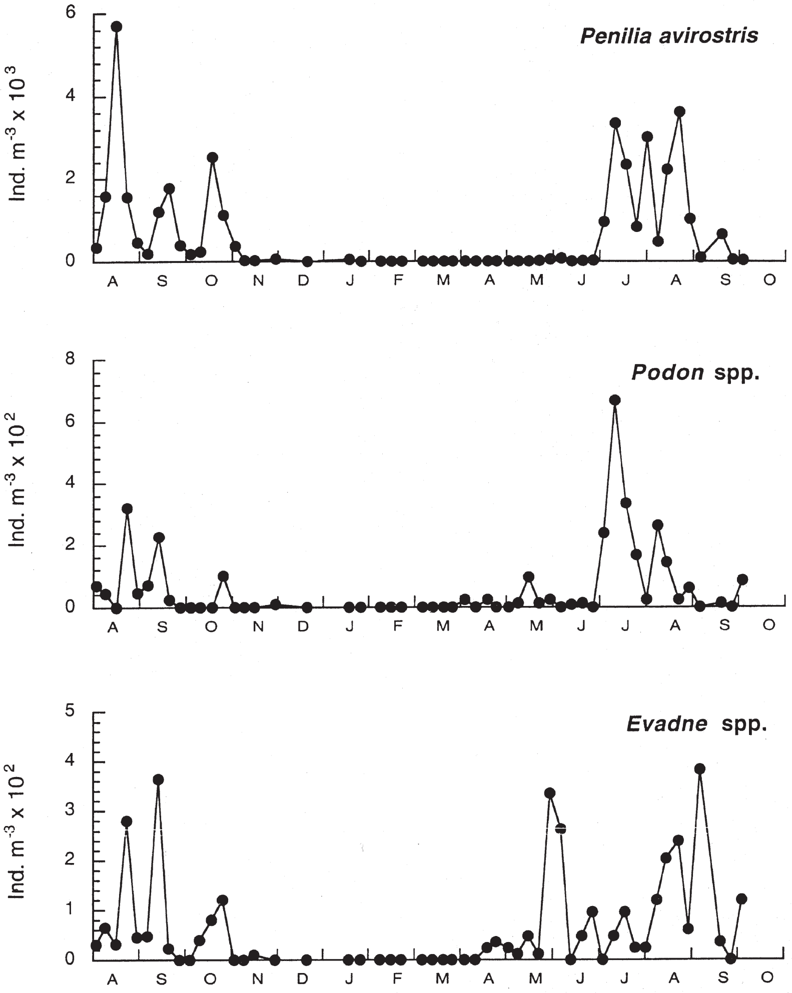

Fig. 6. Annual cycle in abundance of the most abundant cladoceran genera (53–200 μm + >200 μm) from microplankton net tows. August 1995–October 1996.

relationships existing amongst groups (Figure 8). In general, calanoid copepods dominated in abundance during spring and winter, whereas cyclopoids were more abundant during summer and autumn.

Relationships between zooplankton and environmental variables

Total zooplankton abundance was correlated neither with temperature nor with Chl *a*. With regard to the different zooplankton groups, temperature was significantly correlated ($P < 0.01$) with cladocerans ($r = 0.62$), especially *P. avirostris* ($r = 0.59$), but also *Evadne* spp. ($r = 0.41$) and *Podon* spp. ($r = 0.36$). Other significant correlations with temperature were also found for chaetognaths ($r = 0.52$), appendicularians ($r = 0.49$) and the copepods *E. acutifrons* ($r = 0.40$), *T. stylifera* ($r = 0.48$) and *Oithona* spp. ($r = 0.48$). *Centropages typicus* displayed a weak, but significant ($P < 0.01$), negative correlation with temperature ($r = -0.40$). With regard to Chl *a*, only polychaetes ($r = 0.66$, $P < 0.001$) and cirripedes ($r = 0.49$, $P < 0.01$) showed significant positive correlations. Appendicularians and cladocerans, on the other hand, exhibited negative correlations with Chl *a* (both $r = 0.34$, $P < 0.001$). Other groups did not show any clear relationship with either temperature or Chl *a*.

Juday–Bogorov versus microplankton net tows

There were significant differences in the number of organisms collected with both nets (Table II). The annual mean abundance of copepods (adults + copepodites) estimated from the microplankton net for both fractions together (i.e., 53–200 μm + >200 μm), or estimated from the >200 μm fraction alone, were, respectively, ~10 times

Table I: Mean and maximum abundance (ind. m^{-3}) from the microplankton net samples (both fractions together, 53–200 µm + >200 µm) of the most important genera of copepods (CI to CVI) during the study. The month at which maximum abundance was reached is also indicated

Genus	Mean (S.D.)	Maximum	Month
Para./Clauso.	1722 (2476)	11742	January
Centropages	1496 (1864)	11205	April
Temora	212 (311)	1549	September
Acartia	393 (479)	2649	July
Oithona	3775 (3331)	13216	August
Euterpina	448 (717)	3986	July
Oncaea	424 (641)	3312	August
Microsetella	344 (518)	3007	November
Other copepods	187 (229)	1074	February

and ~five times higher than those obtained with the Juday–Bogorov net. For total cladocerans, the abundance obtained with the 53 µm net was ~two times higher. On average, for all the groups, the values given by the 53 µm net were 8.1 times higher than Juday–Bogorov's net estimations. Maximum differences were found for *E. acutifrons* and *Oithona* spp., which showed values 24 and 25 times higher, respectively, when using the microplankton net. Only mollusc larvae and the cladoceran *Evadne* spp. were slightly underestimated using this net. The coefficients of correlation between estimates obtained with the Juday–Bogorov net and the different size-fractions of the microplankton net were significant for most of the groups (Table III). This indicates that in general, the seasonal pattern shown with both nets was comparable. Exceptions to this were small copepods such as *Oithona* spp. and *E. acutifrons*, and rare groups such as mollusc larvae.

DISCUSSION

Annual cycle in the Bay of Blanes

The Bay of Blanes has been a site of regular biological sampling since 1992 (Andreu and Duarte, 1996; Cebrián *et al.*, 1996; Gracia *et al.*, 1996; Mura *et al.*, 1996a,b; Palomera and Olivar, 1996; Pinedo *et al.*, 1996; Satta *et al.*, 1996; Vaqué, 1996; Vaqué *et al.*, 1997; Agawin *et al.*, 1998; Duarte *et al.*, 1999). A common feature of the planktonic compartments in this bay, and also in other Mediterranean areas, is the recurrence of an annual phytoplankton bloom in late winter (Cacciamani *et al.*, 1992; Modigh *et al.*, 1996; Mura *et al.*, 1996a; Fernández de Puelles *et al.*, 1997; Duarte *et al.*, 1999). This phenomenon, which is associated with periods of high atmospheric pressure, may be triggered by a combination of decreasing water column stability and an increase in irradiance due to clear skies (Duarte *et al.*, 1999). The presence of this phytoplankton bloom appears to have had little effect on the abundance of zooplankton during our study, as abundance did not show a clear seasonal pattern following the phytoplankton bloom. In February, when maximum values of Chl *a* were reached, zooplankton abundance and biovolume were minimal. The presence of sardine larvae (active predators of zooplankton) during the winter months (Palomera and Olivar, 1996) may be one of the main causes of the decrease in zooplankters, preventing the settling of a more numerous zooplankton community. Conversely, other Mediterranean coastal areas show a spring–summer increase in zooplankton, following on most occasions, a phytoplankton bloom (Dauby, 1980; Seguin, 1981; Lakkis, 1990; Mazzocchi and Ribera d'Alcalà, 1995; Fernández de Puelles *et al.*, 1997; Siokou-Frangou, 1996). However, a lack of seasonality (Christou, 1998) or multiple peaks in zooplankton abundance

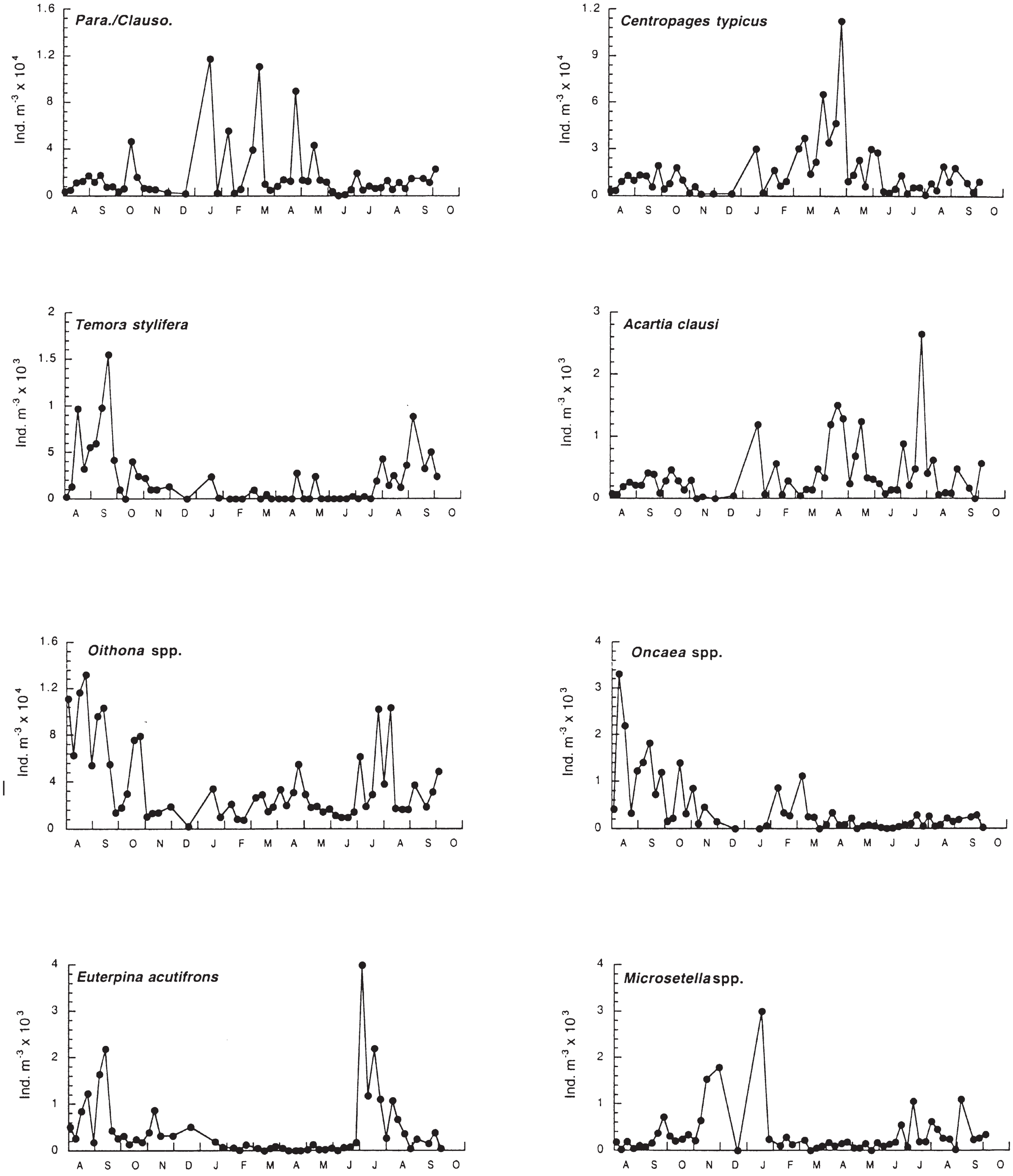

Fig. 7. Annual cycle in abundance of the most abundant copepod genera (53–200 μm + >200 μm) from microplankton net tows. August 1995–October 1996.

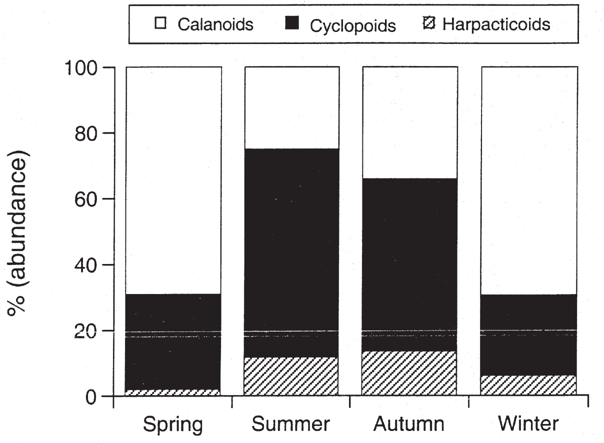

Fig. 8. Mean percentage per season of calanoid, cyclopoid and harpacticoid copepods during the study.

throughout the year has also been reported (Kimor and Berdugo, 1967; Regner, 1985). In the Bay of Blanes, primary production is highest in summer and lowest in spring (Satta *et al.*, 1996; Agawin *et al.*, 1998), opposite to the biomass pattern. This increase is due to more daylight and photon fluxes in summer, and to the much faster growth and turnover rate of the picoplankton that dominate the summer autotrophic community (Agawin *et al.*, 1998) compared with the low growth rate of the diatoms that dominate the winter population (Mura *et al.*, 1996b). The shift in size spectra of the autotrophic community leads to a change in the zooplankton community structure towards filter-feeding organisms, such as *Penilia avirostris* and appendicularians, that are able to consume the dominant *Synechoccocus* population efficiently.

The absence of clear seasonality in the total abundance of the zooplankton community of the Bay of Blanes resulted from the combination of populations of different components, each with a specific, but often contrasting, seasonal pattern. There was a succession of zooplankton species throughout the year. Changes in biomass or production of autotrophic food seem to play little role in determining the seasonal succession of planktonic metazoans in Mediterranean coastal waters (Mazzocchi and Ribera d'Alcalà, 1995; Siokou-Frangou; 1996; Christou, 1998). Other factors, such as salinity (Regner, 1985; Christou, 1998), temperature (Regner, 1985; Siokou-Frangou, 1996; the present study) and, possibly, food size-spectra may be more important in determining the seasonality of zooplankton species composition. In our study, only

Table II: Annual mean of different zooplankton abundance (ind. m^{-3}) estimated with a 200 μm Juday–Bogorov net (JB), and a 53 μm mesh microplankton net (M)

	JB	M (>200)	M (Total)	M (>200)/JB	M (Total)/JB
Total copepods	920	4432	8932	4.8	9.7
Para./Clauso.	398	1445	1747	3.6	4.4
C. typicus	119	875	1518	7.3	12.7
Oithona spp.	153	1068	3634	7.0	23.8
A. clausi	63	320	399	5.1	6.4
T. stylifera	93	200	215	2.1	2.3
Oncaea spp.	42	126	424	3.0	10.2
E.acutifrons	18	171	447	9.4	24.7
Total cladocerans	465	819	821	1.8	1.8
P. avirostris	259	696	697	2.7	2.7
Evadne spp.	200	64	64	0.3	0.3
Podon spp.	6	58	59	9.7	9.8
Appendicularians	81	372	773	4.6	9.5
Other tunicates	41	85	87	2.0	2.1
Mollusc larvae	71	40	123	0.6	1.7
Chaetognaths	6	41	43	6.4	6.7
Average				4.4	8.1

For the 53 μm net, the fraction retained by a 200 μm filter (>200) and the total value, including both size fractions (53–200 μm + >200 μm, i.e. Total) are given (see text).

Table III: Correlation coefficients (R) between zooplankton abundance estimated with a 200 μm Juday–Bogorov net (JB) and the 53 μm mesh microplankton net (M)

	JB versus M (>200)	JB versus M (Total)
Total copepods	0.61 ***	0.55 ***
Para./Clauso.	0.56 ***	0.54 ***
C. typicus	0.61 ***	0.35 **
Oithona spp.	0.50 ***	0.24 n.s.
A. clausi	0.51 ***	0.42 **
T. stylifera	0.77 ***	0.76 ***
Oncaea spp.	0.51 ***	0.34 *
E. acutifrons	0.19 n.s.	0.15 n.s.
Total cladocerans	0.41 **	0.41 **
P. avirostris	0.67 ***	0.67 ***
Evadne spp.	0.35 **	0.35 **
Podon spp.	0.38 **	0.38 **
Appendicularians	0.42 **	0.42 **
Other tunicates	0.81 ***	0.80 ***
Mollusc larvae	0.04 n.s.	0.00 n.s.
Chaetognaths	0.54 ***	0.59 ***

For the 53 μm net, both the fraction retained by a 200 μm filter (>200) and the total value including both fractions together (53–200 μm + >200 μm, i.e. Total) are compared with the Juday–Bogorov net values. Asterisks indicate the level of significance of the correlation: *$P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; n.s., not significant.

Polychaeta and Cirripeda showed significant (although weak) positive correlations with Chl *a*, whereas the abundance of many species was well correlated with temperature. The fact that the abundance of a given species is well correlated with an environmental factor, such as temperature, does not imply causality. There are many examples in which a given taxon exhibits a peak in abundance in different seasons under opposite regimes of temperature. For instance, in our study, the group *Para./Clauso.* peaked during the cold months, simultaneously with the phytoplankton bloom. The species *Clausocalanus furcatus* peaks during summer and autumn in Calvi's Bay (Dauby, 1980) and in Sarinokos Gulf (Siokou-Frangou, 1996). However, in the South Spanish littoral (Vives, 1966) and in Lebanese waters (Lakkis, 1990), this species reaches maximum abundance at the end of winter and in spring. On the other hand, in the Gulf of Naples, a succession of different *Clausocalanus* species appears throughout the year, with *C. furcatus* dominant during the fall, coinciding with *Paracalanus parvus* (Mazzocchi and Ribera d'Alcalà, 1995). Another dominant copepod in the Bay of Blanes, especially during the summer, was *Oithona* spp. Interestingly, most of the studies in the Mediterranean report a maximum abundance of this genus in the winter and beginning of spring (Vives, 1966; Seguin, 1981; Gaudy, 1984; Mazzocchi and Ribera d'Alcalà, 1995; Siokou-Frangou, 1996). Many studies also coincide in situating the seasonal peak of abundance of *Centropages typicus* in spring and that of *Temora stylifera* in the warmer months (Vives, 1966; Gaudy, 1984; Siokou-Frangou, 1996), although with exceptions (Mazzocchi and Ribera d'Alcalà, 1995; Christou, 1998). As the summer progresses, the combination of warm and calm waters with a higher abundance of prokaryotic picoplankton (Agawin *et al.*, 1998) may explain the dominance of fine particle filter feeders, such as cladocerans (especially *P. avirostris*) and appendicularians (Paffenhöfer and Orcutt, 1986; Turner and Graneli, 1992; Vanderploeg, 1994). Other important copepod genera (e.g. *Acartia*, *Oncaea*, *Calanus* and *Ctenocalanus*) show large differences in their annual distribution, depending on the area studied (Vives, 1966; Razouls, 1974; Seguin, 1981; Lakkis, 1990; Mazzocchi and Ribera d'Alcalà, 1995; Siokou-Frangou, 1996).

An explanation for the differences found in the seasonal succession of copepods in other Mediterranean areas could be the particular characteristics of coastal zones. Coastal environments are highly variable and complex (Walsh, 1976), and exposed to different intensities of anthropogenic and land-related influences (sewage discharges, rivers, etc.). The particular conditions of each location (oceanic currents, degree of enclosure, presence of submarine canyons, eddies, etc.) may strongly influence the phyto- and zooplankton annual distribution (Regner, 1985; Kouwenberg, 1993; Casotti *et al.*, 2000). The Catalan coast is characterized by a relatively narrow continental shelf that has a high degree of influence from more oceanic mesoscale activity (Sabatés *et al.*, 1989). Thus, sporadic episodes of open-sea water intrusions enhanced by the upwelling, and water exchange derived from the interaction between flow and the submarine canyons in the area (Cebrián e*t al.*, 1996; Granata *et al.*, 1999), can mask the zooplankton seasonal pattern by introducing super-imposed variability. This variability may also be the cause of differences between years in other environmental factors such as chlorophyll. In addition, other long-term agents such as global warming or a progressive increase in anthropogenic forcing (Duarte *et al.*, 1999) may influence the ecology of planktonic populations, especially in coastal areas. Hence, differences among studies may be associated with both the particular characteristics of the area surveyed and long-term ecological changes.

Juday–Bogorov versus microplankton net tows

Another aspect of our study that has revealed surprising results, and which may help to elucidate the variations in zooplankton seasonal succession among Mediterranean sites, has been the differences found between values of zooplankton abundance obtained with the 200 µm Juday–Bogorov net and the 53 µm microplankton net. Traditional undersampling of small copepod species may lead to a limited view of the ecology of planktonic systems and must be considered when comparing results. Even though in the present study the seasonal patterns of abundance for most of the zooplankton groups were similar for both net estimates, their relative importance as contributors to the bulk of organisms was highly biased, depending on the towing device. Logically, the differences between nets were higher for smaller groups. Our estimates of the genera *Euterpina* and *Oithona* using a 200 µm net were ~24 times lower than the ones obtained with a 53 µm net, whereas for molluscs and cladocerans, it was only ~two times lower. The bias generated in the collection of these groups with large-size meshes masks some seasonal patterns. For instance, the dominance of cyclopoids in the summer and autumn copepod assemblages was not evident when data from the Juday–Bogorov net were used, the values obtained indicating a constant superiority of calanoid abundance throughout the year (~75% of total copepod community). Therefore, the use of small pore-size meshes may partially explain the differences shown between the present study and the seasonal pattern of small copepod abundance in other Mediterranean areas. However, for larger groups well represented in 200 µm mesh nets samples the differences are most likely due to particular characteristics of the study sites.

The differences between nets may not be due only to the mesh size, but also to the different towing techniques. Sampling usually takes place during daylight hours, when most zooplankters are found in deeper waters. Thus, in relatively shallow areas, the bulk of organisms may be close to the bottom, which makes the accuracy of the sample extremely dependent on the skills of the sampler. With a bottom to surface vertical tow, sampling of the entire water column is guaranteed. However, using this technique with a small diameter net does involve the risk of inaccurate sampling of strong swimmers and rare organisms. In order to collect these zooplankters (e.g. large copepods, fish larvae, cnidaria) larger water volumes must be sampled.

In summary, the results presented here portray a complex and diverse zooplankton community. There is evidence of a successional pattern which may be related to previously reported shifts in the size class of the autotrophic community from winter diatoms to small summer cyanobacteria (Mura *et al.*, 1996a; Agawin *et al.*, 1998). This pattern in zooplankton distribution was apparent despite the large variability in overall zooplankton abundance. Changes in the seasonal succession and hence, the size-spectrum of phytoplankton play a key role in the structure of zooplankton communities.

ACKNOWLEDGEMENTS

This work was supported by grants AMB94-0746 and MAR98-0854. The authors are especially indebted to G. Carreras and the rest of the people involved in the weekly sampling in the Bay of Blanes. We also wish to thank M.G. Mazzocchi and C. Benitez-Nelson for helpful comments and suggestions on earlier versions of the manuscript.

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Received on August 12, 2000; accepted on December 14, 2000