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Influence of organic matter and climatic factors on the harpacticoid copepod (Crustacea) population from the well sorted fine sands of Banyuls Bay

J. Y. Bodiou, D. Delille & L. Tito de Morais

Laboratoire Arago, Université P. et M. Curie, CNRS URA 117; F-66650 Banyuls-sur-mer

ABSTRACT: The authors investigated the development of the harpacticoid copepod population in relation to the variations in organic matter and meteorology. Sediment sampling was performed over a 2-year period in the shallow waters (3 m deep) of Banyuls Bay (Western Mediterranean). Each year presents two distinct periods: winter to early spring, and from late spring until fall. During the first period of the annual cycle, the organic carbon and nitrogen cycles are fairly dissociated; the quantity of copepods appears to be dependent upon the climatic and physical conditions. During the second period, the climatic conditions are very similar from year to year, without heavy rains or strong storms, and the values observed both for the organic matter and the copepod population are also similar. The hypothesis is proposed that organic matter can be considered a limiting factor to population increase.

INTRODUCTION

Numerous works describe the seasonal variations in meiofaunal populations of sublittoral soft bottoms (Coull, 1970; Skoolmun & Gerlach, 1971; Warwick & Buchanan, 1971; Dinet, 1972; Nyholm & Olsson, 1973; Bovée & Soyer, 1974; Coull & Vernberg, 1975; Juario, 1975; Nodot, 1978; Coull & Fleeger, 1977; Hicks, 1977; Bell, 1979; Dinet et al., 1982; Boucher, 1983; Coull, 1985; Huys et al., 1986). Correlation analyses between seasonal variations of meiofauna and available trophic resources are scarcer: Bovée (1981), Rudnick et al. (1985) regarding organic matter; Montagna et al. (1983) and Bouvy (1985) regarding primary and bacterial production. Despite the fact that nematodes generally predominate in meiofaunal populations, harpacticoid copepods can be largely responsible for seasonal variations (Witte & Ziljstra, 1984; Rudnick et al., 1985). Recent experimental studies indicate that copepods react more strongly than nematodes to organic enrichment of the sediment (Hockin, 1983; Gee et al., 1985; Moore & Pearson, 1986). The present study succeeds previous works on the harpacticoid copepods of the fine sands of Banyuls Bay (Soyer, 1970; Bodiou & Chardy, 1973; Bodiou, 1975; Bodiou, 1980). The faunistic variations of the harpacticoid population were investigated over 2 years in relation to the main organic variables and the climatic conditions. Interpretation of the field data is supported by a principal components analysis.

MATERIALS AND METHODS

Study area and sampling

The study was performed in Banyuls Bay (Western Mediterranean: 3° 08′ E, 42° 29′ N) (Fig. 1). The sampling area, at a depth of 3 m, is at the upper edge of the well-sorted fine sand area, in a shallower zone than the one studied by Bodiou (1975, 1980), but with similar sediment characteristics. Sampling was performed twice a month, from January 1976 through January 1978. All sampling was made using SCUBA operated corers. Three cores were used for the faunistic studies (8 cm deep and 10 cm^2 in area) and one for the

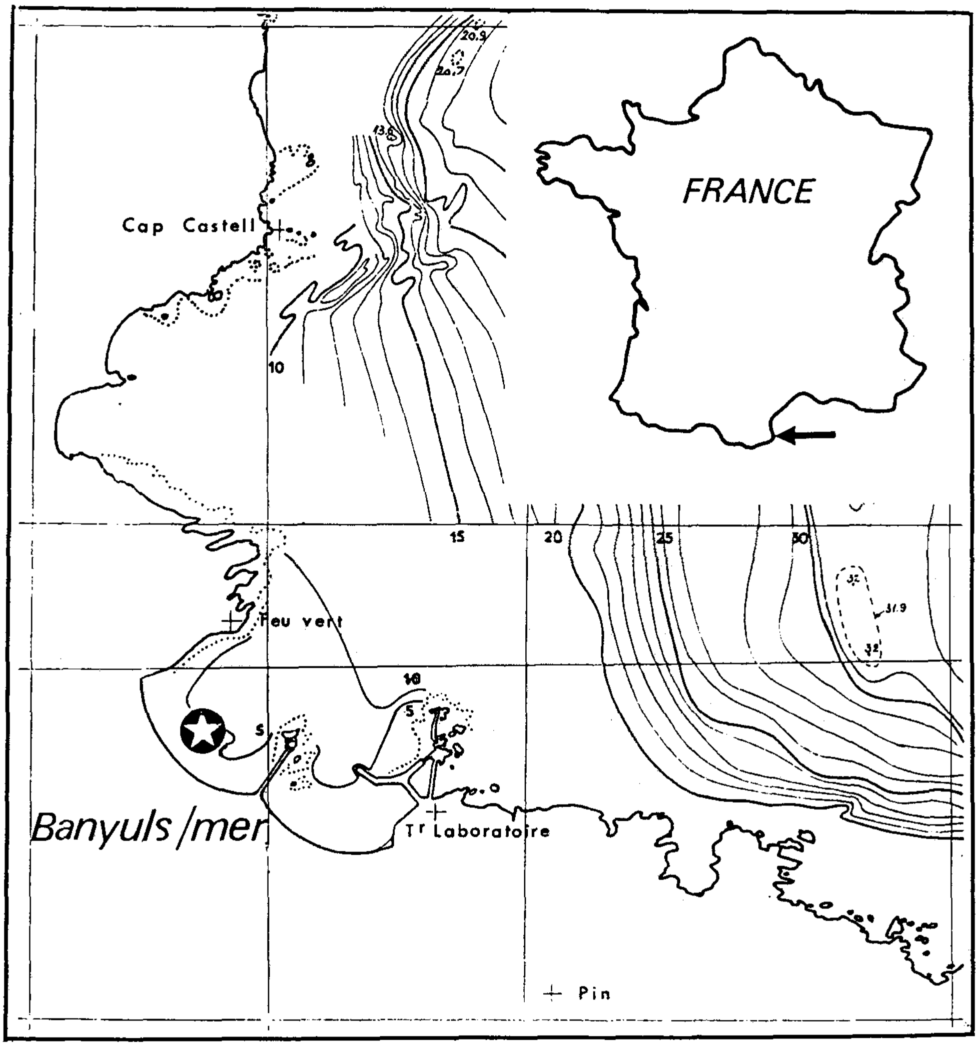

Fig. 1. Location of the sampling area. The zone is at a depth of 3 m, in a sandy part of Banyuls Bay, France, in the western Mediterranean Sea (3° 08′ E, 42° 29′ N)

sediment analyses (8 cm deep and about 20 cm^2 in area). The harpacticoid copepods were sorted under a dissecting microscope after concentration and colouration with Rose Bengale.

Chemical analysis

Carbon was measured according to the LECO technique (IR-212 analyser). The organic carbon content (CORG in the figures) is obtained using a dry sediment sample previously decarbonated by hot orthophosphoric acid (1M). The value given for inorganic carbon (MC) is obtained by calculating the difference between the total carbon measured on raw dry sediment and the organic carbon measured on dry decarbonated sediment.

All nitrogen analyses were performed using the Kjeldahl method. A Buchi apparatus was used for total nitrogen determination. The mineralization and vapour release were carried out in the same container. The distillate was then titrated using N/100 soda. Ammonia value was obtained in the same way, without prior mineralization of the sample. Nitrates and nitrites values were obtained using a colorimetric technique (Technicon apparatus), after extraction by a Normal KCl solution. The organic nitrogen value (NORG) was obtained by calculating the difference between the total nitrogen and the sum of ammonia, nitrates and nitrites.

Principal components analysis

The principal components analysis provides a graphical representation of any set of n heterogeneous variables in mutual correlation (Lebart et al., 1977; Fenelon, 1981). Each sample is defined by the density of benthic copepods and the quantities of organic carbon and organic nitrogen in the sediment.

RESULTS

Meteorological conditions

Winter and spring meteorological conditions in the sampling area were notably different in 1976 and 1977. East to South-East winds (120 to 190°) of more than 5 m/s lasting at least 2 days are shown in Figure 2. Such winds are the cause of a strong littoral swell in the bay (Razouls, 1971). In 1976, from February 1st to May 31st, 10 strong-wind periods were registered; during the same months in 1977 only 4 periods of strong winds were registered. The summer wind conditions were quite similar in 1976 and 1977.

Quantitative evolution of harpacticoid copepods

The quantities of copepods (Fig. 2) varied both in 1976 and 1977 following a cycle of 4 periods: minimum in late May and early June (point 1), maximum in late July and early August (point 2), minimum in late August and early September (point 3) and maximum in late October (point 4).

The years 1976 and 1977 showed similar changes in the population from late May to October (i.e. from point 1 to point 4): 2 peaks of maximum concentration separated by a sharp decline of the populations in August. Apart from this period, there was little similarity between 1976 and 1977. Winter in 1976 showed low concentrations, descending to a minimum in late May (always less than 40 ind./10 cm^2); on the other hand, winter in 1977 showed high concentrations (always more than 40 ind./10 cm^2) from February to late May. The quantity of copepods declined sharply in November 1976 (from 120 to 20 ind./10 cm^2); no such decline was observed in autumn 1977.

Variations in the physical and chemical parameters

The 2 years of sampling provided very similar results. In both 1976 and 1977, 4 maxima of organic carbon (CORG, Fig. 2) were observed (in January, May, September and November). In both 1976 and 1977, a high maximum value of inorganic carbon (MC, Fig. 2) was observed in March and April; two lower maxima were observed in August and September. With the exception of the increased values in autumn, the organic nitrogen content of the sediment (NORG, Fig. 2) was relatively stable during each of the 2 years.

Data from the principal components analysis

The first three factorial axes represent 84.3 % of the total variance of the system (35.3 %, 29.6 % and 19.4 % respectively). The position of each variable and their absolute contribution to the total inertia of each of the first three axes are given in Table 1, and represented in Figure 3 (A, B). Axis I is closely related ($r = 0.95$) to the total concentration of copepods (QTOT). Axis II is in correlation ($r = 0.76$) with organic carbon (CORG) and axis III ($r = 0.84$) with organic nitrogen (NORG).

The analysis distinguishes between the spring samplings of the 2 years. In the spring of 1976, the samples from the period 3 March 1976 till 10 June 1976 (samples 5 to 11) were all gathered in the left zone of the factorial plan of axes I and II (Fig. 3 A). This area corresponds to the samples of low copepod concentration. In the spring of 1977, the samples 31 to 36 (17 March 1977 till 25 May 1977) were spread out along the site of axis I, correlated to QTOT (Fig. 3 A), reflecting the peaks in copepod population observed in this period. Samples 17 to 20 (high population peaks in 1976, from 3 September till 18 October) were in the right part of the factorial plan, correlated with high values of organic matter. From 27 October 1976 till 17 March 1977 (points 21 to 31), alternating positive/negative peaks in copepod population and in organic carbon were apparent in Figure 3 A.

DISCUSSION

Sediment chemistry

The sampling station has an average carbon value of 0.30 % of D.W. Such low values are usual in this kind of sandy sediment (Delille, 1977), and they are higher than the values of carbon observed in the deeper sediments of the same area (0.20 % of D.W. at a depth of 15 m) (Delille, unpubl. data). The values for the organic nitrogen content of the sediment are lower compared with those of the carbon content (0.17 % of D.W.). The C/N values observed are relatively high for a marine sediment (between 15 and 20). These high values are related to the terrestrial influence that differentiates the sampling area

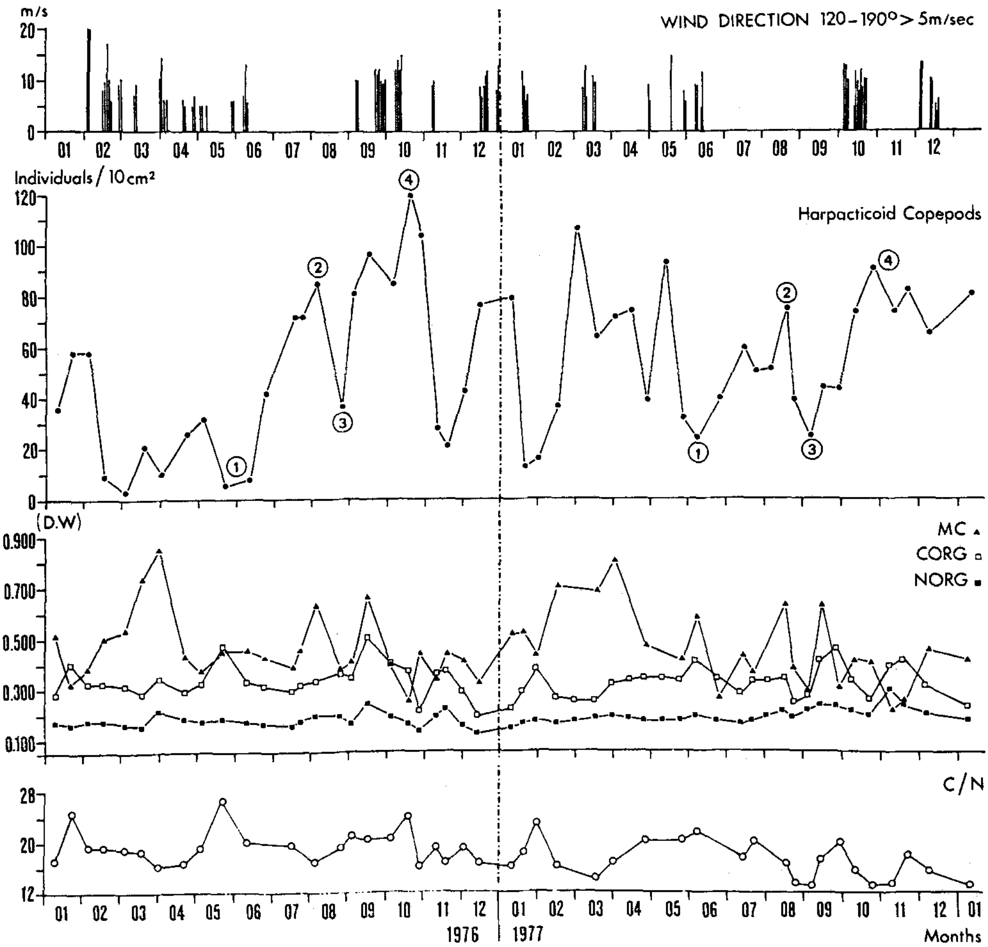

Fig. 2. Seasonal evolution of the harpacticoid copepod population and of the sediment organic content. Abbreviations used: C/N = ratio between organic carbon and nitrogen; CORG = organic carbon content in % of D. W. sediment; MC = mineral carbon content in % of D. W. sediment; NORG = organic nitrogen content in ‰ of D. W. sediment

from deeper zones. At 15 m below sea-level, despite a similar granulometry of the sediment, the C/N values are under 12 and generally close to 8 (Delille, unpubl. data). These lower values are more usual in marine environments (Delille et al., 1979).

Organic nitrogen and carbon values are closely related (Table 1). Seasonal changes of these two parameters are relatively similar. However, some differences can be observed. The C/N ratio depends both upon the origin of the organic matter (predominance of terrestrial or marine deposits), and upon differences in the level of degradation. The differences in C/N ratios in 1976 and 1977 clearly indicate that the composition of the organic matter in the sediment was dissimilar during these two years. The spring situation and its organic nitrogen peak may be related to the increase of the benthic

Table 1. Saturation values of the principal components analysis. – Correlation of paired variables. – Multiple correlation coefficients between the variables and the first three factorial axes (QLT). – Correlation coefficient between each variable and each of the three factorial axes (COR). – Relative contribution of each variable to the inertia of each factorial axis (CTR). All values multiplied by 1000. The critical values for single correlations are t(50.1) = 0.273 (at P = 0.05) and t(50.1) = 0.354 (at P = 0.01). The critical values for multiple correlation coefficients are F (48.3) = 0.386 (at P = 0.05) and F(48.3) = 0.457 (at P = 0.01). N.S. = non significant; * = significant; ** = very significant

	Correlation coefficient of paired variables				
	CORG	NORG	C/N	QTOT	QLT
CORG	*1000*				955**
NORG	604**	*1000*			966**
C/N	634**	−223 NS	*1000*		832**
QTOT	−130 NS	29 NS	−195 NS	*1000*	972**

	1st axis		2nd axis		3rd axis	
	COR	CTR	COR	CTR	COR	CTR
CORG	78 NS	32	760**	367	117 NS	86
NORG	2 NS	1	126 NS	61	838**	618
C/N	97 NS	39	516**	250	219 NS	161
QTOT	955 **	386	13 NS	6	3 NS	2

biomass. Recent works (Delille et al., 1990) indicate the existence of a bacterial bloom in spring in Banyuls Bay. As a result of bacterial mineralization, the organic carbon value decreases as the inorganic form increases. Nitrogen is preferentially used in biosynthesis and shows little variation. Spring is the period of benthic recruitment for most mixobenthic forms (transitory meiofauna), and especially for the bivalve *Spisula subtruncata*. Such organisms may be of some importance in the nitrogen balance. Also, the shells influence the concentration of inorganic carbon.

The principal component analysis illustrates the major trends of the organic nitrogen and carbon as described above. Both values are correlated and are well-represented in the reduced factorial space. They induce slightly different behaviour of the samples in the factorial plan of axes II and III (Fig. 3B). The variations are greater along axis II than along axis III, indicating the higher variability of the values of organic carbon than those of organic nitrogen. On the other hand, the spring samples, 5 to 9 in 1976 (3 March till 4 May), and 32 to 36 in 1977 (1 April till 25 May) are spread out along axis III (related to organic nitrogen), and show little variation along axis II (organic carbon). The spring period is well differentiated from the rest of the year with regard to the variations in the organic matter parameters.

Benthic copepod population

In 1976 and 1977, the annual quantitative cycle of the copepod populations were similar in summer and autumn (points 1 to 4 in Fig. 2). During these periods of the year the atmospheric and physical conditions tend to be very stable. The littoral upper mass of water is above the thermocline, is temperate and undergoes few alterations (Jacques,

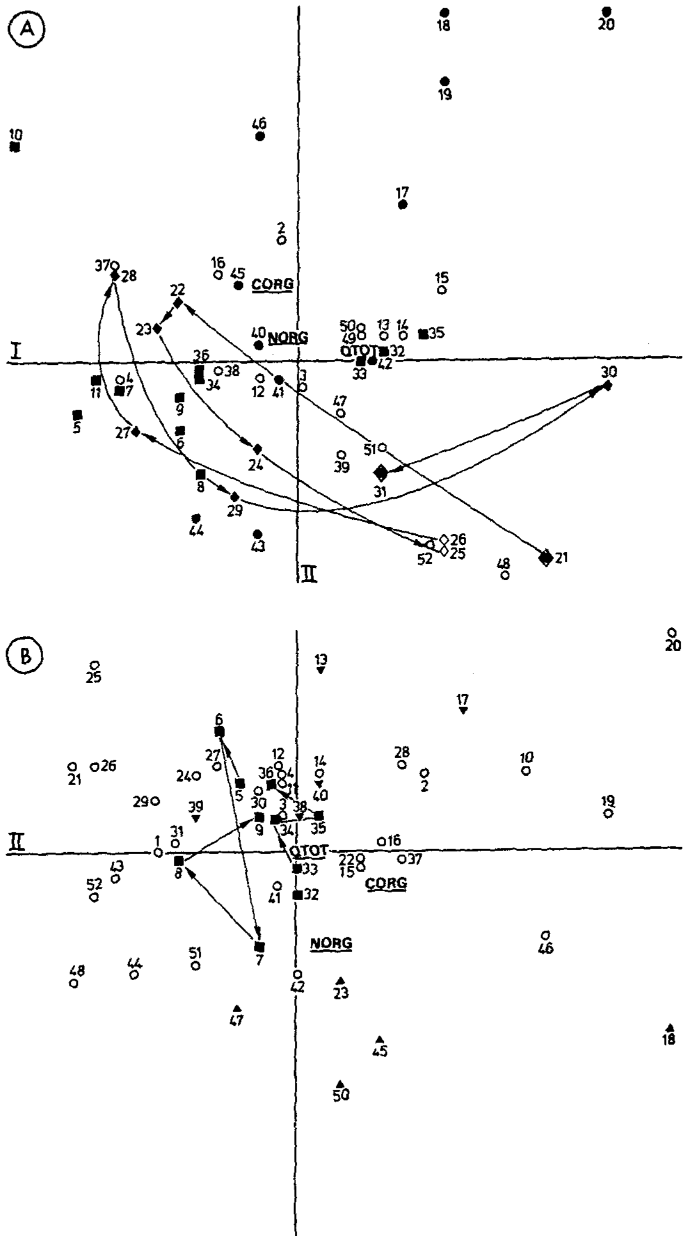

Fig. 3. Principal component analysis. Graphic representation of the variables and of the samples in the factorial space of the first three axes. The samples are numbered from 1 to 52 in chronological order from 08 January 1976 till 11 January 1978. A: Factorial plan of Axis I and II. B: Factorial plan of Axis II and III. ◆ Autumn and winter samples in 1976/1977. ■ Spring samples of both years. ● Summer and early autumn samples of both years. ▲ Samples showing an organic nitrogen maximum preceding the faunistic peaks in autumn and winter in both years. ▼ Samples showing an organic nitrogen minimum preceding the faunistic peaks in summer in both years. QTOT = total number of harpacticoid copepods per sample of 10 cm^2; for other abbrev., see legend of Fig. 2

1974). In contrast, the atmospheric physical conditions in winter and early spring may be quite different from one year to the next. Sediments are strongly disturbed by the waves induced by easterly storms (Emerson, 1989). Low salinity values related to heavy rains can also affect sediments, even in deeper areas 10 to 20 m deep (Bodiou & Chardy, 1973). Bad weather conditions thus appear to influence the level of copepod concentration. The absence of windy periods in February 1977 can be related to the abundance of copepods observed during this period. In winter 1976, the benthic copepod population was subjected to more turbulent hydrodynamical conditions.

In the summer, the development and peak of copepod population are preceded by high values of C/N ratio which could correspond to the degradation of terrestrial material brought about by the spring rainfalls, and to the microphytal development in the photic zone (Le Bouteiller, 1981). In the autumn, the double peak in copepods corresponds to high values of the C/N ratio in 1976 and to low ones in 1977. Two points are to be emphasized: (1) the C/N ratio increased in early September and mid October in 1976, but not until late September and mid November in 1977. (2) The first easterly storms were registered in September 1976, and not before October in 1977. The level of the C/N ratio appears to be related to the weather conditions, whereas increases in copepod populations can be connected to the presence of fragments of macrophytes in the sampling area. The presence of a large quota of phytophile copepods (e.g. *Porcellidium viride*, Bodiou, unpubl.) supports this hypothesis. Generally, the increase of harpacticoid copepod population is related to a decrease in the organic carbon in the sediment samples, and vice-versa (Fig. 2). More simply, we observe that there are connections between increases in the copepod population and decreases in the organic carbon available. When the available organic matter reaches a threshold value (the residual non-exploitable organic matter), the population decreases. At the same time, the organic carbon content of the sediment increases as the copepod population decreases. Although this study does not allow us to determine whether the relations between copepods and the organic matter are direct or indirect, it is apparent that the harpacticoid copepods are submitted to alternating periods of "abundant food/low or rare food". And it seems likely that these organisms depend more or less directly upon the trophic richness and stability of the sediments, and the presence of specific bacterial populations (McIntyre et al., 1970; Lasker et al., 1970; Marcotte, 1986). The entire copepod population studied here includes, throughout the year, different copepod species (Bodiou, 1980). They could verify the trophic resources hypothesis of Hicks & Coull (1983) that emphasizes the existence of 3 trophic types: trophically adaptable species present throughout the year, abundant in winter in good weather conditions and scarce in bad conditions (e.g. *Halectinosoma herdmani, Pseudobradya beduina, Stenhelia Delavalia normani*). There are two types of trophically specialized species, depending upon food abundant only during certain periods: in this study, the species related to the benthic diatom bloom in late spring and early summer (e.g. *Harpacticus flexus* and *Ameira parvula*) or related to the arrival of macroalgae debris in autumn (e.g. *Porcellidium viride*) (Bodiou, 1980). Similar observations of two peaks and one minimum during the same period are described in muddy sediments by Bovée & Soyer (1974) and Coull (1985). Jonczyk & Radziejewska (1984) also describe 2 maxima peaks in late spring and October on the Baltic Polish coast. Other Mediterranean studies (cf. Dinet, 1972; Nodot, 1978) only describe a single major peak during a 12-month period. The location of our sampling area, in a shallow bay close to a rocky shore covered with algae broken away in summer, induces a diversification of the trophic sources that may complicate the population cycles in autumn.

In conclusion, the abundance of meiofauna, as studied here through the harpacticoid copepods, appears to be controlled by two main factors: (1) meteorological and climatic factors in bad weather conditions, and (2) available organic matter during the rest of the year. The influence of additional factors remains open for debate but nonetheless may be taken into account: predators and their exploitation of the copepod populations (see review in Hicks & Coull, 1983; Morais & Bodiou, 1984; Coull, 1985). All the parameters described in the present paper undergo changes in relation with the dynamics of bacteria in the sediment, and this appears to be a worthwhile direction for further work.

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