

The potential impact of meiofauna on the recruitment of macrobenthos in a subtidal coastal benthic community of the Ligurian Sea (north-western Mediterranean): a field result

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Abstract

The composition and dynamics of meio- and macrofauna in a subtidal location at Zoagli (Ligurian Sea, Italy) were followed for an annual cycle (from January 1991 to January 1992). Polychaete recruitment occurred during spring and late summer–autumn. The increase in density of predatory nematodes (dominated by *Oncholaimellus*, *Viscosia*, *Mesacanthion* and *Chromaspirina*) and turbellarians corresponded to the collapse of macrobenthos recruits. Such alteration was probably due to predation by turbellarians and predator-nematodes during and immediately after the macrofaunal larval settlement. Differences in predator pressure were observed between spring and autumn. Conversely, no significant impact was observed on bivalves. The selective predation operated by predator meiofauna on the dominant polychaete families of the temporary meiofauna (paraonids and spionids) modified the structure of the macrofaunal community. These results suggest that meiofauna may structure macrofaunal communities both altering density and acting selectively on a few families of macrofaunal juveniles.

Keywords: soft sediment community ecology, predation, recruitment, Polychaeta, Bivalvia, Nematoda, Turbellaria, meiofauna, macrofauna.

Introduction

Recent studies have focused on the possible roles of the permanent meiofauna in benthic systems, particularly with regard to the possible interactions with macrofauna (e.g. Watzin 1986). The role of meiofauna in the trophic chain is however not entirely clear. In fact, although competition between meio- and macrofauna has been assessed, Chardy & Dauvin (1992) suggested that meiofauna is an important link between the bacteria-detritus complex and the carnivores, and thus cannot be considered as an independent food web. Other authors have stressed that the importance of competition for space or food might be important, since meio- and macrofauna occupy the same sediment layer (Bell 1979, Coull & Bell 1979) and feed, basically, on the same resources (preferentially on diatoms and bacteria; Fauchald & Jumars 1979, Montagna 1984).

Macrofaunal larvae settling into the benthos are usually defined as 'temporary meiofauna' (*sensu* McIntyre 1964) because they are, only for a certain period of their life, the same size as the meiofauna (< 500 µm, Higgins & Thiel 1988). Another important interaction between the two benthic compartments could be due to the pressure of predation. The 'meiofaunal bottleneck' hypothesis states that permanent meiofauna negatively affect the survivorship of the temporary meiofauna (Neill 1975, Bell & Coull 1980, Zobrist & Coull 1992). In fact, among permanent meiofauna, most turbellarians and some nematodes are voracious predators of macrofaunal juveniles and are able to affect macrofauna both in terms of abundance and community structure (Staarup 1970, Watzin 1983, Watzin 1985). Watzin (1983), by manipulating density of turbellarians and other meiofauna taxa, showed that predation effects on the newly settled macrofaunal juveniles could significantly influence the structure of macrofaunal communities. Predation effects were greater in spring-summer, when the densities of macrofaunal juveniles decreased dramatically. However, Zobrist & Coull (1992) in an experimental study did not detect any significant effect by any meiofaunal taxon on macrofaunal settlement, although they did not consider the pressure of platyhelminthes and predator-nematodes.

The present investigation studied the potential impact of the permanent meiofauna (with special regard to turbellarians and predator-nematodes) on the abundance of juveniles of polychaetes and bivalves (temporary meiofauna) and the potential importance of meiofaunal predators as a structuring factor for the adult macrofaunal community.

Materials and methods

Study site

The study area is located at 10 m depth in the Golfo Marconi, Ligurian Sea (north-western Mediterranean Sea). This area has been intensively investigated over the past ten years for the analysis of the dynamics of the macrofaunal communities and seasonal cycles of phytoplankton composition, production and sedimentation (Cattaneo & Fabiano 1982, Fabiano 1984, Fabiano *et al.* 1984, Albertelli & D'Ambrosio 1986, Albertelli & Fabiano 1990, Bavestrello *et al.* 1991, Albertelli *et al.* 1994a, b).

The sampling station is exposed to wave action and is characterized by relatively high current speed at the water sediment interface ($2.5\text{--}8.0\text{ cm}\cdot\text{sec}^{-1}$). The depth of the RPD (Redox Potential Discontinuity) exceeded 12.0 cm throughout the year. Grain size in the top 4 cm of the sediments (ϕ ranging between 1.7 and 2.2) did not show significant seasonal changes (ANOVA, $F = 0.39$, d.f. = 4). Porosity in the top 2 cm of sediment ranged between 27 and 35%. Salinity ranged between 37.16 psu (May 1991) and 38.35 psu (December 1991) (Danovaro 1993).

Sampling procedure

A series of sediment samples was collected on a monthly basis between January 1991 and January 1992 by scuba divers. For the analyses of the permanent meiofauna, two replicate sediment cores were obtained by inserting PVC tubes (diameter 3.7 cm, 10.7 cm^2 surface area) into the sediments. In this study, only the uppermost 12 cm of sediment were considered. Temporary meiofauna was collected using larger PVC sediment cores (diameter 6.0 cm, 28.5 cm^2 , 12 cm depth, four replicates). Macrofauna was collected using a suction-device (Tunberg 1983) with eight replicates (each replicate sample had an area of 0.1 m^2 , 20 cm deep) using a 1 mm mesh size.

Meiofaunal analyses. Samples were fixed with hot (60°C) 4% formalin in $0.4\text{-}\mu\text{m}$ pre-filtered seawater solution. For permanent meiofauna, sediments were sieved through 1000 and $37\text{ }\mu\text{m}$ mesh sizes. The fraction remaining on the $37\text{-}\mu\text{m}$ sieve was centrifuged three times with Ludox TM (density arranged to $1.18\text{ g}\cdot\text{cm}^{-3}$) in order to separate the lighter organisms from the heavier sediment grains (Heip *et al.* 1985).

For the analysis of the temporary meiofauna, sediments were sieved through 1000 and $80\text{ }\mu\text{m}$ mesh sizes and processed as previously described.

All meiobenthic animals were counted and classified per taxon under a stereo microscope after staining with Rose Bengal ($0.5\text{ g}\cdot\text{l}^{-1}$).

For each replicate core, all or at least 100 nematodes were randomly picked out and determined to genus level (for details see Heip *et al.* 1985). Trophic groups were identified according to Wieser (1953).

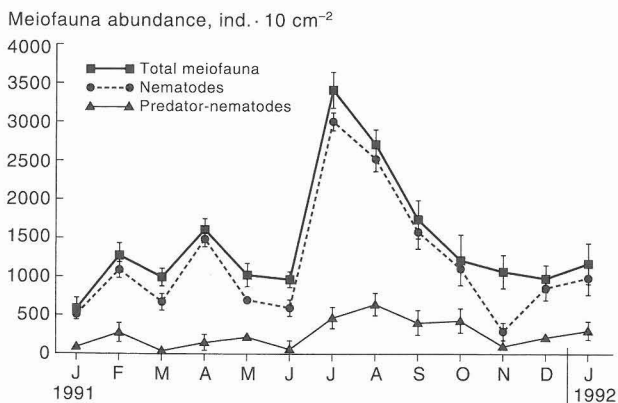
Turbellarians were identified to species level from living material from additional samples. Samples were first treated with MgCl_2 to relax the fauna, which was then extracted by decantation as described by Martens (1984).

Temporary meiofaunal organisms (polychaetes and bivalves) were identified to species level.

Macrofaunal analyses. Each macrofaunal sample was fixed in 10% buffered formalin seawater solution with Rose Bengal. Polychaetes and bivalves were sorted using a stereo microscope and identified to species level.

Statistical analyses. For statistical analyses, the homogeneity of variance was tested using Bartlett's test and one-way analysis of variance (ANOVA) was performed on each group. Regression analysis was carried out on the density of the major groups of meio- and macrofauna and on the dominant polychaete and bivalve families (Draper & Smith 1981).

Figure 1.
Seasonal variations in the abundance of total meiofauna and total and predator-nematodes (bars represent $\pm 1\text{ s.e.}$).



Results

Permanent meiofauna. Meiofaunal dynamics showed a well-defined pattern characterized by highest abundances in summer and low densities in winter. Total meiofaunal abundance (number of individuals per $10\text{ cm}^2 \pm 1\text{ s.e.}$) ranged between 595 ± 36 and 3463 ± 247 (in January 1991 and July, respectively; Figure 1). Nematodes were, with the exception of November only, the numerically dominant taxon and represented on average 75% of the total density (ranging between 504 ± 22 and $3006 \pm 90\text{ ind.} \cdot 10\text{ cm}^{-2}$). Seasonal changes in density of total and predator-nematodes are shown in Figure 1. All predator-nematode genera (2B, Wieser 1953) found at Zoagli are listed in Table 1. Densities of predator-nematodes accounted for, on average, 39.6%

<i>Belbolla</i>	<i>Oncholaimellus</i>
<i>Chromaspirina</i>	<i>Onyx</i>
<i>Choniolaimus</i>	<i>Oxyonchus</i>
<i>Ditlevsenella</i>	<i>Paramesacanthion</i>
<i>Enoploides</i>	<i>Paramonohystera</i>
<i>Enoplolaimus</i>	<i>Pomponema</i>
<i>Eurystomina</i>	<i>Sigmophoranema</i>
<i>Filoncholaimus</i>	<i>Siphonolaimus</i>
<i>Halichoanlaimus</i>	<i>Symplocostoma</i>
<i>Latronema</i>	<i>Synonchiella</i>
<i>Mesacanthion</i>	<i>Thoracostomopsis</i>
<i>Metachromadora</i>	<i>Valvaelaimus</i>
<i>Metoncholaimus</i>	<i>Viscosia</i>

Table 1.
Predator-nematode genera encountered at Zoagli Station.

of total nematode density (ranging between 10.6% in March and 58.6% in November). Dominant genera were *Chromaspirina*, *Viscosia*, *Oncholaimellus*, and *Mesacanthion* which together represented about 90% of total predator-nematodes. The dynamics of the most important genera (Figure 2) showed that *Chromaspirina* and *Viscosia* are mainly responsible for the observed trend. Harpacticoid copepods were the second most abundant taxon ranging from 22 ± 4 to 583 ± 258 ind. $\cdot 10$ cm $^{-2}$ (in January 1991 and November, respectively) and comprised from 2 to 16% of the total density (Figure 3). Turbellarians were the third most abundant taxon, ranging from 21 ± 5 to 169 ± 42 ind. $\cdot 10$ cm $^{-2}$ (January and November, respectively) (Figure 3). Turbellarian density accounted on average for 5.6% of total meiofaunal density (ranging between 2.0% in July and 16.4% in November). Data relative to the species, average size and ecological habits of turbellarians encountered at Zoagli are

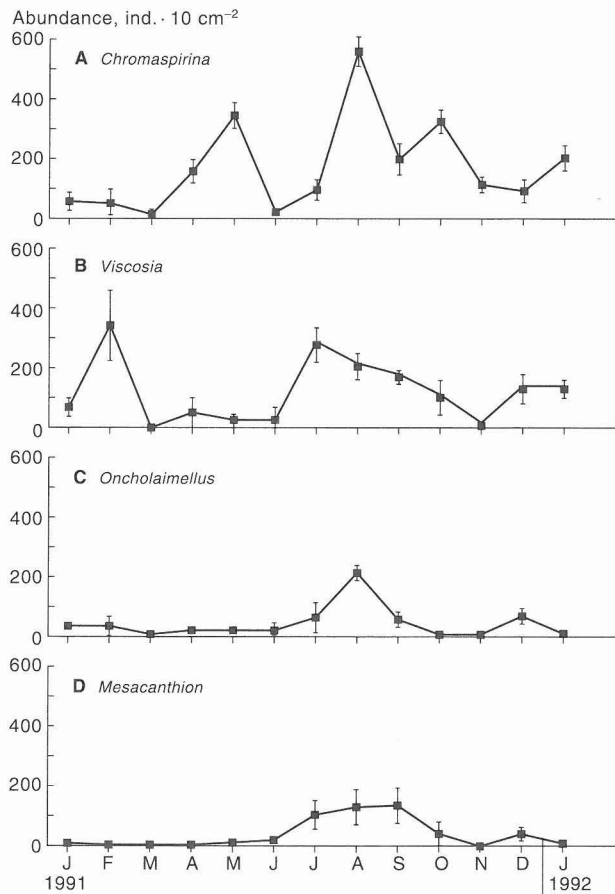


Figure 2.
Seasonal dynamics of the four most abundant genera of predator-nematodes (bars represent ± 1 s.e.).

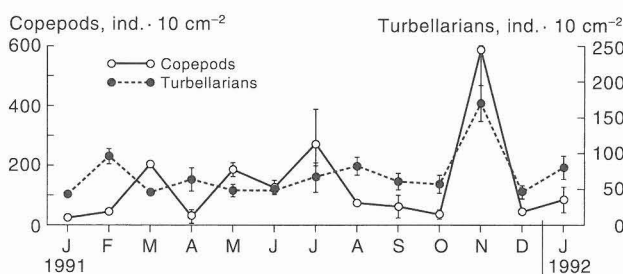


Figure 3.
Seasonal variations of the copepod and turbellarian abundances (bars represent ± 1 s.e.).

Order	Species	Dimension	Ecological notes
Kalyptorhynchia	<i>Cystiplex axi</i>	< 2 mm	Predators
	<i>Gnathorhynchus</i> sp.		
Proseriata	<i>Coelogyphora gynocotyla</i>	2-15 mm	Predators or scavengers, Feed on polychaetes, nematodes and crustaceans
	<i>Pratoplana</i> sp.		
	<i>Monostichoplana philum</i>		
	<i>Monotoplana</i> sp.		
Acoela	<i>Convoluta</i> sp.	< 2 mm	Predators of turbellarians and nematodes
	<i>Acoela</i> ind.		
Dalyellida	Provorticidae ind.	5-10 mm	Large predators
Typhoplana	Trigonostominae spp.	1.5-3 mm	Small predators
	Paramesostominae sp.		

Table 2.
Species of turbellarians encountered at Zoagli.

Higher taxa / Genus and species	Trophic group
Polychaeta	
Capitellidae	
Capitellidae ind.	Limivorous
<i>Capitomastus minimus</i>	Limivorous
<i>Notomastus formianus</i>	Limivorous
<i>Peresiella clymenoides</i>	Limivorous
Cirratulidae	
<i>Cauleriella alata</i>	Deposit feeder
<i>Cauleriella binocolata</i>	Deposit feeder
<i>Cirratulus cirratus</i>	Deposit feeder
Dorvilleidae	
<i>Protodorvillea kefersteini</i>	Deposit feeder
<i>Schistomeringos neglecta</i>	
Glyceridae	
<i>Glycera celtica</i>	Deposit feeder/predator
<i>Glycera</i> cf. <i>lapidum</i>	Predator
<i>Glycera alba convoluta</i>	Predator
Hesionidae	
<i>Microphthalmus</i> cf. <i>similis</i>	Micro predator
Lumbrineridae	
<i>Lumbrineris</i> sp.	Predator
Nephtyidae	
<i>Nephtys cirrosa</i>	Deposit feeder/predator
<i>Nephtys</i> sp.	Deposit feeder
Orbiniidae	
<i>Nerimides tridentata</i>	Deposit feeder
<i>Schroderella laubieri</i>	Deposit feeder
<i>Scoloplos armiger</i>	Deposit feeder
Paraonidae	
<i>Aricidea capensis bansei</i>	Limivorous
<i>Aricidea catherinae</i>	Limivorous
<i>Aricidea quadrilobata</i>	Limivorous
<i>Paradoneis armata</i>	Limivorous
<i>Paradoneis ilvana</i>	Limivorous
<i>Paraonis fulgens</i>	Limivorous
Phyllodocidae	
<i>Phyllodoce mucosa</i>	Predator
Sabellidae	
<i>Chone filicaudata</i>	Suspension feeder
Syllidae	
<i>Sphaerosyllis thomasi</i>	Micro predator
<i>Streptosyllis websteri</i>	Micro predator
Spionidae	
<i>Prionospio caspersi</i>	Deposit feeder
<i>Prionospio malmgreni</i>	Deposit feeder
<i>Spio decoratus</i>	Deposit feeder
Bivalvia	
<i>Abra alba</i>	Suspension feeder
<i>Lucinella divaricata</i>	Suspension feeder
<i>Parvicardium</i> sp.	Suspension feeder
<i>Spisula subtruncata</i>	Suspension feeder
Tellinidae	Deposit feeder/suspension feeder
<i>Thracia papyracea</i>	Suspension feeder

Table 3.
List of the species of macrofaunal juveniles encountered at Zoagli.

shown in Table 2. Among them, the suborder of Proseriata was the most abundant. Polychaetes of the permanent meiofauna were represented by *Streptosyllis websteri* (ranging from 0.4 to 4.6 ind. · 10 cm⁻², in February and September, respectively), *Schroederella laubieri* (ranging from 0.2 to 2.0 ind. · 10 cm⁻², in August and December, respectively) and *Microphthalmus similis* (ranging from 0.2 to 5.7 ind. · 10 cm⁻², in November and June, respectively).

Temporary meiofauna. All juveniles of macrofaunal species encountered at Zoagli are listed in Table 3. Temporary meiofaunal density accounted for, on average, 1% of total meiofauna. Polychaetes were generally dominant over bivalves, with the exception of February (Figure 4). Paraonids and spionids were the most abundant polychaete families, followed by orbinids and capitellids (Figure 5). The most abundant species of polychaete juveniles were: *Spio decoratus*, *Prionospio caspersi*, *Paradoxeis armata*, *Scoloplos armiger*. Bivalves were strongly dominated by *Spisula subtruncata* throughout the year (ranging from 0.4 to 5.3 ind. · 10 cm⁻² in April and February, respectively).

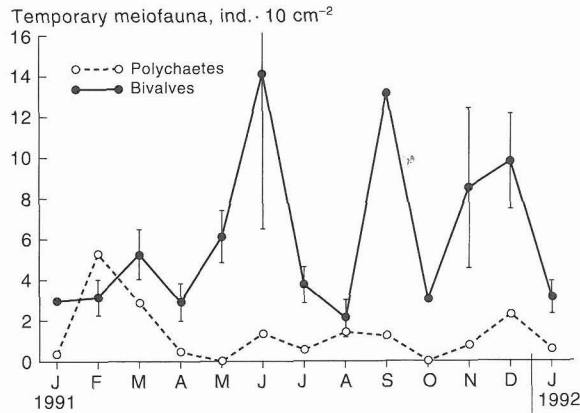


Figure 4. Temporary meiofauna: seasonal variations of total juvenile polychaetes and bivalves (bars represent ± 1 s.e.).

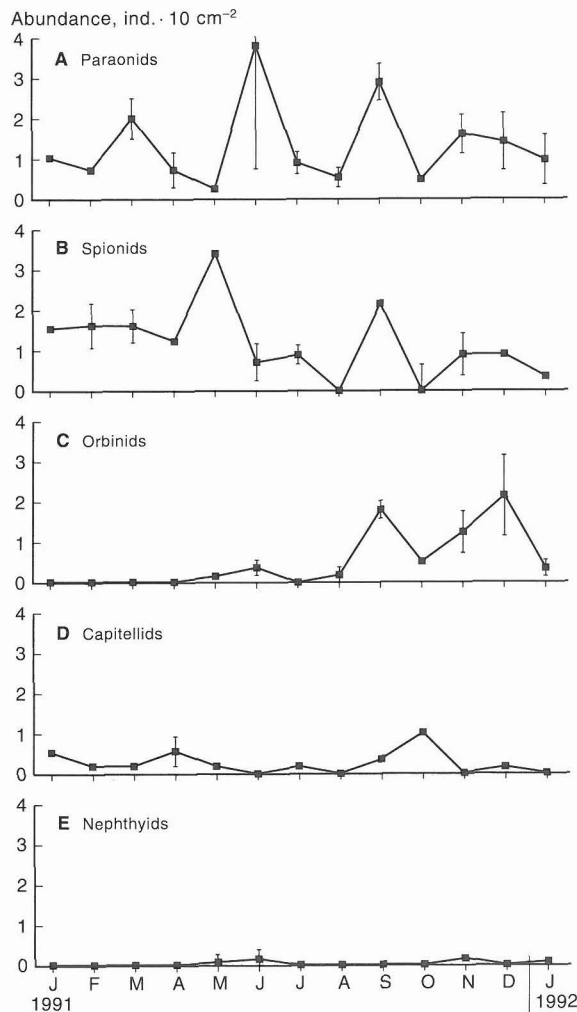


Figure 5. Seasonal dynamics of the four most abundant families of juvenile polychaetes (bars represent ± 1 s.e.). Illustrated from A to E in order of importance.

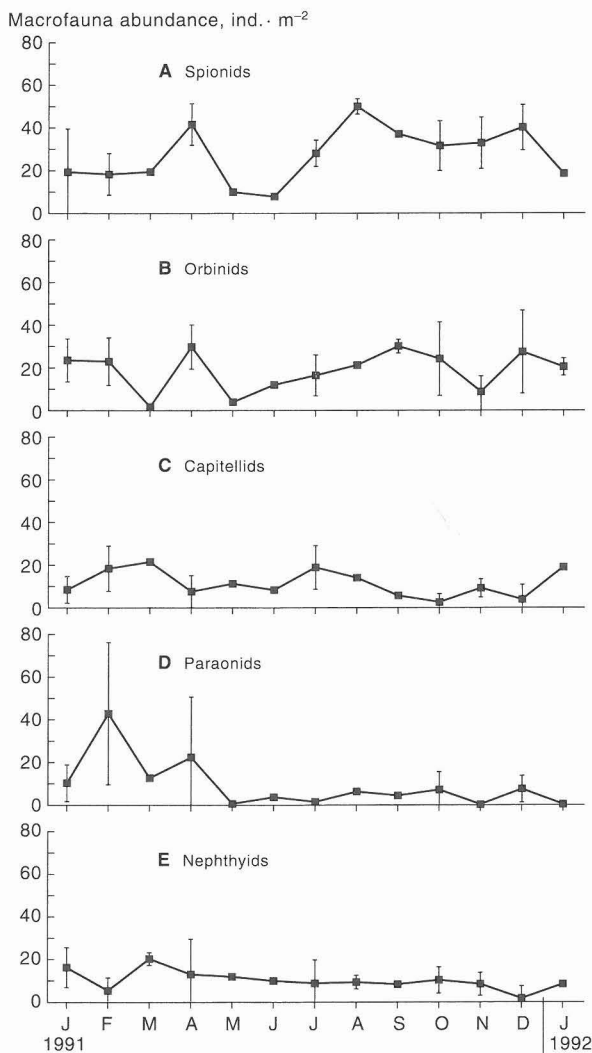
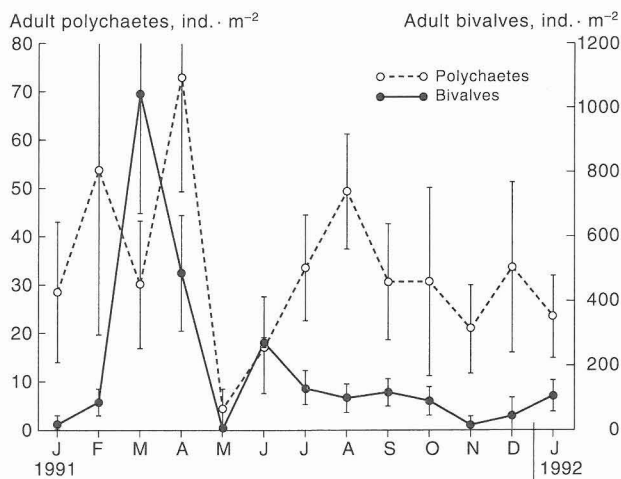


Figure 6. (upper) Dynamics of the adult polychaete and bivalve communities (bars represent ± 1 s.e.).

Figure 7. (lower) Temporal patterns of the most abundant families of the adult polychaete community (bars represent ± 1 s.e.). Illustrated from A to E in order of importance.

meiofauna on polychaetes, indicated that during the second period, despite the higher nematode and turbellarian densities, the apparent predation pressure was reduced (Figure 9). Watzin (1986) explained the seasonal difference of predatory pressure with a decrease in the temperature and consequently of the invertebrate predatory activity. Conversely, this is not the case in this study since reduced predation was observed during the warmest months. The most likely explanation is that during this period a larger fraction of juvenile predator-nematodes was observed (Danovaro 1993), which could have a lower predatory efficiency on the settled juveniles and/or could be feeding on other resources. It has been shown that juvenile predator-nematodes live as deposit feeders (Heip *et al.* 1985).

Adult macrofaunal community. Adult macrofaunal community structure was dominated by polychaetes and bivalves (Figure 6) which, during recruitment, accounted for more than 80% of the entire community. The dynamics of the adult polychaete community showed a well-defined pattern characterized by highest density in April ($186 \text{ ind.} \cdot 10 \text{ cm}^{-2}$) followed by a decrease in May ($48 \text{ ind.} \cdot 10 \text{ cm}^{-2}$). Temporal patterns of the most abundant families are presented in Figure 7. The most important family was the spionids, dominated by *P. caspersi*. Orbinids were the second most abundant polychaete family with *S. armiger* as the most abundant orbinid species. Nephtyds and paraonids were also well represented with *Nephtys cirrosa* and *P. armata*, respectively. As to bivalves, *S. subtruncata* was the most important species, reaching a density of $992 \text{ ind.} \cdot 10 \text{ cm}^{-2}$ (March) immediately after the recruitment period and with a mean annual density of $150.6 \text{ ind.} \cdot 10 \text{ cm}^{-2}$.

Discussion

The success of recruitment can have a great influence in determining the relative abundance of adult populations (Dauvin 1990, Fogarty *et al.* 1991, Zobrist & Coull 1992). The present study has shown that the annual dynamics of juvenile polychaetes showed two periods of recruitment (spring and autumn). After recruitment, a high mortality was observed (the difference between the peak density of juveniles and the density of the following peak of adults was on average more than 98%). During recruitment periods, a significant increase in the density of the most important meiofaunal predators was also observed. It appears evident that the density of juvenile polychaetes was significantly affected by the increase in the density of meiofaunal predators (ANOVA, $p < 0.05$ and $p < 0.05$ for nematodes and turbellarians, respectively; Figure 8). Even more clearly, the abundance of different polychaete families (i.e. paraonids and spionids with dominant species, *P. caspersi*) was significantly affected when increased the number of predators (Figure 8C, for paraonids and *P. caspersi*, respectively). Such patterns are probably due to predation by Turbellaria and predator-nematodes during and immediately after settlement. Direct microscopic observation revealed that specimens of *Monotoplana* sp. contained parts of different polychaetes. Although the field findings support the hypothesis (i.e. that turbellarians and nematodes had a significant impact on polychaete survivorship in the early stages of the recruits), the data do not allow estimation of mortality due either to predation or to other interactions.

Other polychaete families were, however, able to avoid predators. Nephtyds and glycerids were not significantly affected by increasing predator densities. In agreement with Watzin (1986), the more likely explanation for this is that these groups are predators and consequently are active, mobile and capable of defending themselves against preying meiofauna.

The comparison between the two recruitment periods (spring and autumn) of the presumed impact of

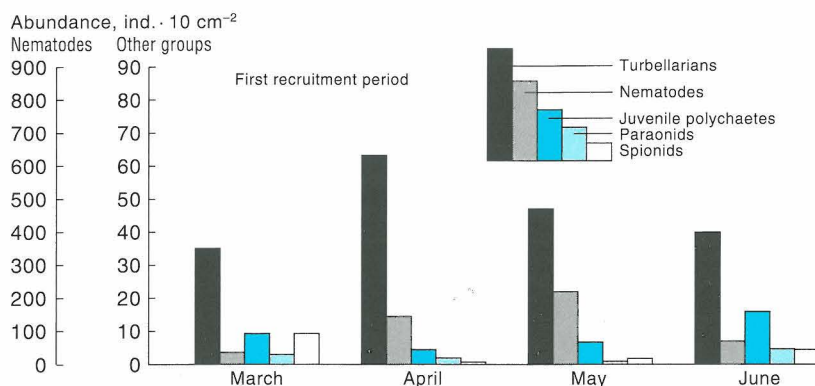


Figure 8. Predator-nematode and turbellarian densities versus total juvenile polychaete density, paraonid density and *Prionospio caspersi* density during the first recruitment period (spring).

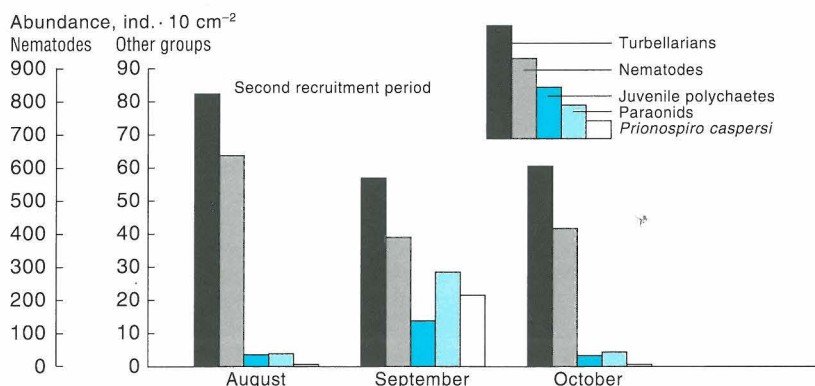


Figure 9. Predator-nematode and turbellarian densities versus total juvenile polychaete density, paraonid density and spionid density during the second recruitment period (late summer-early autumn).

Bivalve recruitment occurred in February-March and mortality rate seems to be independent of predator density (about 20% of the settling *S. subtruncata* larvae became adults). In fact, the highest density of *S. subtruncata* coincided with the highest density of turbellarians and nematodes of the genus *Viscosia*. Whether turbellarians and nematodes prey significantly on bivalves is still not clear (Heip *et al.* 1985, Martens & Schockaert 1986). The results presented here might indicate that predators are not determinant in the success of bivalve recruitment, at least when bivalve densities are high. These results are consistent with those reported by Watzin (1983) who, experimentally, did not detect any significant difference in bivalve density under different treatments with increasing turbellarian abundance. Other factors, such as migration or sediment instability, may be responsible for the observed dynamics (Bachelet *et al.* 1991, Muus 1973, Albertelli *et al.* 1994b).

An interesting result of the impact of turbellarian and predatory nematodes on the most important families of juvenile polychaetes, is that adult community structure is clearly different from that which could be deduced on the basis of the abundance and community structure of the juveniles. The predation pressure appears to be selective since paraonids, dominant in the juvenile polychaete community, were drastically reduced in importance in the macrofaunal community (0.7% average survivorship). A similar pattern was observed for *Spio decoratus* (0.3% average survivorship) among spionids. In the macrofaunal compartment, the still high spionid density was due to the strong dominance of *S. filicornis* which was not found in juvenile form. Moreover, the macrofaunal dominance of polychaete families which were characterized by low density when belonging to meiofaunal sizes (i.e. orbinids, *S. armiger*; capitellids, *Notomastus formignus*; and nephtyids, *N. cirrosa*) gives further confirmation of the ability of these families to avoid a significant predation impact.

This study represents a first attempt in the Mediterranean to clarify the role of meiofauna in regulating macrofaunal community structure. Other studies are, however, needed to quantify the juvenile mortality fraction actually attributable to predation and to identify the mechanisms responsible for the selective predation.

Conclusions

The results presented here clearly indicate that the period of the recruitment is of crucial importance for the characteristics of the macrofaunal community. Turbellarians and predator-nematodes could have, particularly in spring, a significant impact on the density of the juvenile polychaetes, though not, apparently for bivalves. The selective predation operated by predator meiofauna on the dominant polychaete families of the temporary meiofauna (paraonids and spionids) results in a modification of the structure of the macrofaunal community. Such results suggest that meiofauna may structure macrofaunal communities both altering density and acting selectively on a few families of macrofaunal juveniles.

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