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Seasonal dynamics of meiofauna from the oligotrophic continental shelf of Crete (Aegean Sea, eastern Mediterranean)

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ABSTRACT

The response of metazoan meiofauna and nematode communities to the sedimentation of a spring phytoplankton bloom was investigated at four stations of the continental shelf of Crete (south Aegean Sea, eastern Mediterranean). The four stations were located on a transect with depths of 20, 70, 130 and 190 m, and samples were taken monthly from May 1989 to May 1990. After the onset of the spring bloom, a marked increase in sedimentary chlorophyll *α* values was observed (on average 1.6 μg/g). These values remained stable throughout the spring and summer period while during autumn and winter they dropped to very low levels (0.2 μg/g). Nematodes dominated in the meiofauna, ranging from 78% in March to 95% in August and January. Harpacticoid copepods were the second most abundant group, ranging from 2% in August to 18% in April. Total meiofauna biomass was lowest in January (0.03 mg/10 cm^2) and highest during spring and summer after the spring bloom (1.07 mg/10 cm^2). Most meiofaunal taxa displayed significant seasonal changes at the shallower stations (20, 70 and 130 m), with abundances rising during spring and autumn following the productivity of the water column. Conversely, no seasonal variability was evident in terms of abundance or biomass at the deeper station (190 m). Nematode epistrate feeders and selective deposit feeders were more abundant at the two shallower stations, increasing their numbers after the spring bloom. Among the most dominant species, some represented as much as 18% of the total nematode abundance. The nematode community structure displayed a gradual transition, with increasing depth being mostly influenced by the sedimentary characteristics of the environment as well as the overall productivity of the system. The nematode species diversity was found to be significantly lower at the intermediate station (70 m), where physical and biological disturbance were highest.

1. Introduction

At all latitudes, plant and animal populations are known to vary both in space and time. Benthic communities are no exception and their seasonal or spatial fluctuations are generally more pronounced in shallower than in deeper areas (Tyler, 1988; Rex and Etter, 2010). Many different biotic and abiotic factors may be responsible for such fluctuations. In temperate areas, temperature, food availability and predation by organisms of higher trophic levels are among the factors cited to explain spatial or temporal changes in population attributes such as density, biomass or diversity (Tselepides and Eleftheriou, 1992; Danovaro et al., 2007; Danovaro et al., 2010).

Significant seasonal variations have been reported as well for the meiofauna, a group of small benthic invertebrates ranging from 32–1000 μm, which is often neglected in ecological studies. Among the factors mostly used to explain seasonal variation in meiofauna populations, were temperature and food availability (Stripp, 1969; de Bovée and Soyer, 1974; Faubel et al., 1983; Ólafsson and Elmgren, 1997; Nozais et al., 2005). This is not surprising since temperature alone may influence meiofauna either directly, by regulating reproduction and development, or indirectly, by controlling body growth, primary production and, hence, food availability (e.g. see reviews by Hicks and Coull, 1983; Heip et al., 1985). However, there are other meiofaunal studies that have failed to show any pronounced seasonal variation, a result that has been mainly associated with a continuous reproduction throughout the year (Warwick and Buchanan, 1971; Fleeger et al., 1989; Schizas and Shirley, 1996; Sevastou et al., 2011).

Apart from temperature, disturbance has also been suggested to influence population attributes such as diversity and species composition (Huston, 1994). Indeed, meiofaunal studies that have included macrobenthic organisms have clearly shown that processes such as predation, sediment disturbance due to movement and burrowing,

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competition for food and biogenic structures may have a strong effect on a meiofaunal population (Ólafsson, 2003; Nascimento et al., 2011; Passarelli et al., 2012). In most cases (Moens et al., 2013, and references therein), the observed patterns could be explained in terms of the intermediate disturbance hypothesis (IDH) of Connell (1978), although many other studies have not confirmed this hypothesis (Ólafsson and Elmgren, 1991; Ólafsson et al., 1993; Austen and Widdicombe, 1998; Austen and Thrush, 2001).

Studies on temporal changes of meiofauna from the Mediterranean are very few and most of them have been conducted in the western basin. In their study on the coastal terrigenous muds of Banyuls-sur-Mer (western Mediterranean), de Bovée and Soyer (1974) suggested that there is a clear quantitative annual pattern for the main meiofaunal taxa (nematodes, copepods and kinorhynchs) with three distinct maxima, which they attributed mostly to physical disturbance: the first and most important peak occurred at the end of spring, the second during the warmer months of the year (August–September) and the third at the beginning of winter. Guidi-Guilvard and Buscail (1995), in their study of the Têt River outlet in the Gulf of Lion, also reported a strong seasonal fluctuation, which they also attributed mostly to physical disturbance (e.g. mixing, resuspension and erosion), with two peaks, one during autumn and a second one during late spring. This pattern with two or more peaks during one annual cycle is very similar to that reported in most other temporal studies in the western Mediterranean Sea with food availability and fluctuations of the physical parameters being among the factors mostly used to explain the observed patterns (Soyer, 1971; Dinet, 1972; Hulings, 1974; Fava and Volkmann, 1975; Nodot, 1976; Nodot, 1977; Soyer, 1980; de Bovée, 1981; Dinet et al., 1982).

In the present study, the spatial and temporal patterns of meiofaunal communities, focusing particularly on nematodes, is discussed. The study was carried out in the eastern Mediterranean, one of the most oligotrophic areas of the worlds' oceans (Ignatiades, 1998; Psarra et al., 2000). The data presented here are part of a multidisciplinary investigation of the benthic ecosystem of the Cretan continental shelf. Some results of the physical and chemical parameters of the sediments, as well as of the macrofaunal communities, have previously been reported by Eleftheriou and Smith (1993). Specifically, the aims of the present study were as follows: (1) to investigate spatial and seasonal trends in the composition, abundance and biomass of meiofaunal communities in a highly oligotrophic environment; (2) to test whether the spring phytoplankton bloom has an effect on meiofaunal major taxa and nematode species composition; (3) to investigate whether nematode species or functional diversity differ across a depth transect and between months; and (4) to identify which of the investigated environmental parameters are good descriptors for the observed patterns.

2. Materials and methods

2.1. Field location and sampling

The study area is situated on the continental shelf of the north coast of Crete (Fig. 1), offshore from the city of Heraklion on a northerly transect into the Cretan Sea. Four stations with depths ranging from 20 to 190 m (20, 70, 130 and 190 m, respectively) were sampled monthly from May 1989 to May 1990, with the exception of February 1990, when no sampling was carried out, due to ship maintenance. Samples for biological and physicochemical analyses were obtained with the R/V PHILIA by means of a Craib corer, with a penetration of 20 to 30 cm into the sediment. The sampling surface area of each corer was 26.4 cm^2. At each station, six replicate cores were taken, three for faunal analyses, one for chlorophyll and pigment determination, one for organic carbon content and one for sediment grain size analysis. Samples for faunal analysis were initially relaxed for 10 min with $MgCl_2$ and then fixed in 5% formalin. The overlying water in the cores was filtered through a sieve of 45 μm mesh, and material retained on the sieve was backwashed into the respective sample containers. Samples for environmental parameters were frozen at −20 °C on board until transferred to the laboratory for further analysis. All samples were sectioned into three layers: 0–2, 2–4 and 4–7 depth, with the exception of samples for grain size analysis of which only the top 5 cm was taken.

2.2. Sample processing

Samples for meiofauna were sieved through 500 and 45 μm mesh, and the fauna from the fraction retained on the 45 μm mesh was suspended in a colloidal silica solution (Ludox TM) with a specific gravity of 1.15 g cm^{-3}. After settling for 1 h, the supernatant was decanted through a 45 μm mesh and the sediment was resuspended in Ludox, a process repeated five times. This flotation method, a modification of the method proposed by de Jonge and Bouwman (1977), gave an average extraction efficiency of 96% for nematodes, 97% for copepods, and on average, 99% for the other metazoan organisms. Samples from the 20 m station consisted predominantly of fine sand; therefore, these samples were decanted five times, as recommended for sandy sediments (Pfannkuche and Thiel, 1988), prior to applying the above extraction method with Ludox. Following extraction, all metazoans were stained with Rose Bengal (0.5 g l^{-1}), counted and identified to higher taxa under a stereomicroscope.

For nematode identification, approximately 250 specimens were selected randomly from each station and each sampling month as follows: 100 specimens from each of the first two layers (0–2 and 2–4 cm) and 50 specimens from the 4–7 cm layer. As enough individuals were not always present in each core, replicate samples were pooled in order to reach the desired number of 250 individuals. After selection, specimens were slowly evaporated in anhydrous glycerol, evenly spread on microscope slides and identified to species level.

For the nematode biomass determination, body volume was estimated using Andrassy's formula (Andrassy, 1956) with the adaptation of Feller and Warwick (1988)

$$V = L \times W^2 \div 16 \times 10^5$$

where V is the volume in nanolitres, L is the length (μm) excluding the filiform tail, if present, and W is maximal width (μm). Body volume was converted to biomass assuming a specific gravity of 1.13 and a dry/wet weight ratio of 0.25 (Wieser, 1960). Biomass determination of the other taxa was carried out as described in Feller and Warwick (1988) using a different conversion factor for each taxon as well as for each different copepod body form.

Particle size analyses of the top 5 cm layer of the sediments were carried out as described by Buchanan (1984). The median diameter (MD), graphic sorting coefficient (σ_I) and skewness Sk_I of the sediments were calculated after Folk (1966). In particular, the scale used for sorting, is based on the logarithmic scale of Folk and Ward (1957) with the following division points: under 0.35, very well sorted; 0.35–0.50, well sorted; 0.50–0.70, moderately well sorted; 0.70–1.00, moderately sorted; 1.00–2.00, poorly sorted; 2.00–4.00, very poorly sorted; over 4.00 extremely poorly sorted (Blott and Pye, 2001). Total organic carbon (TOC) was analysed by wet oxidation (Walkey and Black, 1934). Algal pigments were extracted from the sediments with 90% acetone, and concentrations of chlorophyll *α* and phaeopigments were determined by using a TURNER 112 fluorometer (Yentsch and Menzel, 1963; Lorenzen and Jeffrey, 1980). The sum of chlorophyll *α* and phaeopigment is referred to as the chloroplastic pigment equivalents (CPE).

For the 190 m station, samples for nematode species determination were available only for July, November 1989 and March, May 1990, while data for particle size analysis as well as data for TOC were not available and consequently this station was excluded from the canonical correspondence analysis (CCA) and Spearman's correlation analyses.