



Meiobenthic diversity in space and time: The case of harpacticoid copepods in two Mediterranean microtidal sandy beaches

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ABSTRACT

Meiobenthic data from two microtidal sandy beaches of the eastern Mediterranean (Crete, Greece) were used to investigate patterns of both alpha and beta diversity in space and time. Copepod assemblages and environmental variables related to sediment characteristics, morphodynamics and food were studied over a year at four distinct habitats at each beach; the retention, resurgence and saturation zones of Salvat's intertidal scheme (midlittoral zone), and the surf zone of the sublittoral. Alpha diversity analysis indicated similar species richness at both beaches when the whole 13-month data set was considered but was higher at the sheltered site when each sampling period was examined separately. Both beaches supported higher diversity in the sublittoral zone. Species richness increased seawards at the midlittoral zone of the sheltered site whereas, no pattern was evident at the exposed site, where the intense hydrodynamic conditions homogenized the sediments. Beta diversity increased markedly towards the sublittoral, indicating greater differences in alpha diversity between the sublittoral and the midlittoral zone. Species turnover was more variable at the exposed beach and at the most landward stations, where environmental conditions change often between extremes. A proportion of the variation in alpha diversity was explained by food availability at both beaches and additionally by grain size at the sheltered site. However, no environmental variable explained beta diversity patterns. Although the results of our study support the hypothesis of Multicausal Environmental Severity proposed for sandy beach macrofauna, we believe the classic Intermediate Disturbance Hypothesis is a more appropriate framework for the meiofauna communities of the studied sites.

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1. Introduction

During the last decades, widespread concern has emerged on biodiversity loss and its effects on ecosystem processes and functioning due to the accelerating influence human activities have on community structure and diversity. As a result, many scientific articles dealing with biological diversity have been published. However, in spite of all this effort, most of the published scientific work has focused on the terrestrial environment (relevant literature cited in Hooper et al., 2005), while relatively little has been done in the marine systems. In this context, it is necessary that priorities should be directed towards inventories of marine species and how they affect ecosystem services (Snelgrove et al., 1997), the investigation of biodiversity patterns at large spatial and temporal scales, and the identification of key mechanisms (Raffaelli, 2006). In 2000, Clarke and Lidgard (2000) and Gray (2000) pointed out that until that time there had been almost no studies of beta diversity in the sea and

emphasized the extreme importance such studies would have for the description of marine biodiversity. Not surprisingly, many subsequent articles on a variety of marine habitats and organisms have addressed the issue, or at least incorporated measures of beta diversity (e.g., Ellingsen, 2002; Gaertner et al., 2007; Giberto et al., 2007; Koulouri et al., 2006; Perez-Mendoza et al., 2003; Price, 2002), including a few focused on meiofauna (De Troch et al., 2001; Veit-Köhler et al., 2010).

While alpha diversity commonly refers to the diversity of a defined assemblage or habitat (within habitat diversity), beta diversity is primarily applied as a measure of the change in diversity between samples along transects, or across environmental gradients, or even at different spatial configurations or sampling units (Magurran, 2004). Since beta diversity is not a scale of diversity, Gray (2000) suggested instead using the term 'turnover diversity' as used by Clarke and Lidgard (2000). However, the term 'turnover' usually refers to temporal changes of diversity and lies at the heart of MacArthur and Wilson's (1967) theory of island biogeography (Magurran, 2004). Magurran (2004) stresses that the interplay of alpha and beta diversity over ecologically and evolutionary time is a topic that warrants much more consideration. Nevertheless, since the exceptional work of Sepkoski (1988) no marine study has examined species

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turnover rates in terms of both space and time. The present study aims at contributing to this gap by studying diversity patterns of meiobenthic copepods at sandy beaches.

Sandy beaches are extremely dynamic systems that exhibit considerable spatial and temporal habitat variability. Nevertheless, unlike the usually blind sampling of the subtidal (Gray, 2000), the boundaries between habitats in sandy beaches are easier to define. Therefore, this environment is ideal not only for investigating patterns of alpha diversity but also for measuring species turnover in both space and time. Having applied a one year monthly sampling effort at two microtidal Mediterranean beaches of contrasting environmental regimes we aimed at exploring patterns of alpha and beta diversity and species turnover rates. We based this study on one of the usually most abundant metazoan group of sandy beaches, the assemblage of meiobenthic copepods (Brown and McLachlan, 1990). More specifically, we aimed at investigating: (1) whether copepod diversity differs across shore and between beaches, (2) whether meiofauna diversity at the studied sites follows patterns of sandy beach benthos seen elsewhere in the world, (3) whether environmental variables that are likely to affect meiofauna, such as sediment characteristics, food availability, morphodynamics, are possible descriptors of any observed pattern, (4) whether two hypotheses that have been proposed so far for explaining sandy beach macrofauna patterns, namely the Swash Exclusion Hypothesis and the Multicausal Environmental Severity, are suitable explanations for meiofauna patterns.

2. Materials and methods

2.1. Study sites

The coastline of Crete (Greece, Eastern Mediterranean) exceeds 800 km and has wide variability in beach morphology and types, all of which are almost atidal; therefore, wave action, currents and winds are particularly important for determining beach systems. The study was carried out at two sandy beaches of Crete (Fig. 1), which vary in exposure according to the rating system of McLachlan (1980) (Table 1). Elafonisi Beach (35.2692N–23.5325E), part of the NATURA 2000 Network, is a sheltered environment located at the southwestern coast of the island that experiences high tourism use during an extended summer period (May–October). A small islet a few metres offshore at the westernmost part of the beach protects the specific part of the beach, where all samplings took place, from wind and wave action. The islet protection also results in very shallow waters (<1.5 m) between the beach and the islet. The beach supports a very well-developed dune system along its entire length. In contrast, Pahia Ammos (35.1333N–25.8000E) is an exposed beach, classified as intermediate according to the beach morphodynamic scale of Short and Wright (1983), and is located at the northeast coast of Crete, at the centre of the Gulf of

Table 1

Main characteristics and environmental variables of the main zones of the studied beaches. The exposure rate was calculated after McLachlan (1980). BDI: beach deposit index; BI: beach index; Mz: mean sand particle size; σ_i : sorting coefficient; Sk_i : skewness coefficient; T: temperature; S: salinity; Eh: redox potential; TOC: total organic carbon; chl-*a*: chlorophyll *a*; phaeo: phaeopigments; CPE: chlorophyll pigment equivalent.

	Elafonisi		Pahia Ammos	
	Midlittoral	Sublittoral	Midlittoral	Sublittoral
Exposure	Sheltered (7.5/20)		Exposed (11/20)	
Length (m)	ca. 1300		ca. 1200	
Width (m)	30–100		50–70	
Slope	1/18–1/5		1/14–1/4	
BDI	18.81–67.73		9.84–49.02	
BI (log phi-m)	0.85–1.41		0.64–1.29	
Mz (mm)	0.20–0.29	0.29–0.50	0.29–0.45	0.19–0.34
σ_i (phi)	0.50–0.97	0.56–1.06	0.49–0.76	0.42–0.84
Sk_i (phi)	–0.39 to –0.09	–0.20 to –0.05	–0.28 to –0.04	–0.42 to –0.02
T (°C)	13.5–27.8	15.0–27.0	16.7–32.0	15.0–29.5
S (‰)	35.7–46.3	35.5–40.5	32.5–40.0	35.0–40.0
Eh (mV)	311.7–379.2	31.0–370.0	387.2–415.7	156.0–398.0
TOC (mg/g)	1.37–1.87	1.60–2.45	0.65–0.96	0.73–1.11
chl- <i>a</i> (µg/g)	0.03–0.10	0.08–0.39	0.02–0.15	0.03–0.24
Phaeo (µg/g)	0.03–0.13	0.07–0.84	0.01–0.07	0.03–0.20
CPE (µg/g)	0.06–0.21	0.21–1.04	0.03–0.20	0.09–0.34

Mirabello, where north-northwestern winds prevail. The main characteristics of the two study sites are summarized in Table 1.

2.2. Sampling design

Thirteen sampling surveys were carried out monthly between May 2001 and June 2002 at the two study sites. Each month we sampled four stations along a transect oriented perpendicular to the shoreline with acrylic tube corers (inner diameter, 4.4 cm). At Elafonisi Beach the transect was fixed throughout the study at the most protected, westernmost part of the beach, whereas at Pahia Ammos the transect was fixed at the mid-eastern part of the beach, thereby avoiding small settlements and tourists. Stations 1, 2 and 3 were located at the midlittoral zone and corresponded to the retention, resurgence and saturation zones respectively of Salvat's intertidal scheme (Salvat, 1964). Station 4, which corresponded to the surf zone, was located at the sublittoral, at approximately 1 m water depth. From each station, we collected triplicate cores for meiofaunal analysis at 1-m intervals along the shore, while two additional cores were collected to measure sediment temperature, organic carbon, chloroplastic pigment concentrations and particle size analysis (PSA). Each sediment core was subdivided in fractions in order to determine the vertical distribution of faunal and environmental parameters; however, for the purposes of

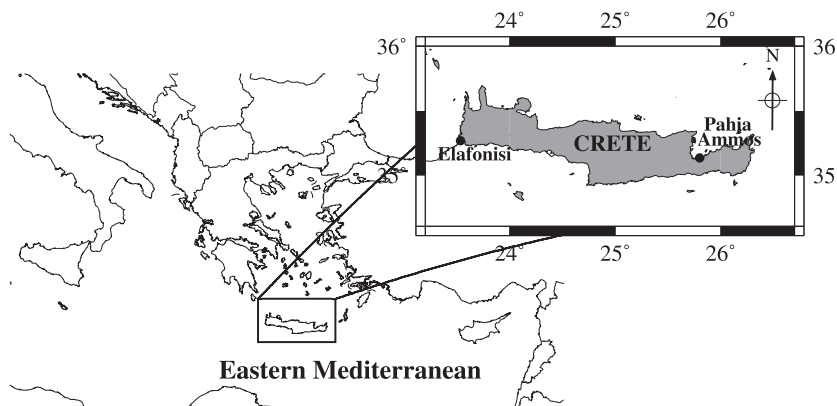


Fig. 1. Location of the two studied beaches, Elafonisi (sheltered beach) and Pahia Ammos (exposed beach), in the Eastern Mediterranean.

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