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ORIGINAL ARTICLE

Assessing inter-beach differences in semi-terrestrial arthropod assemblages on Maltese pocket sandy beaches (Central Mediterranean)

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Keywords

beta diversity; Malta; non-metric multidimensional scaling; pocket beaches; psammophiles.

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Abstract

The distinctiveness of macrofaunal assemblages on different sandy beaches in the Maltese Islands was previously suggested by different single-season studies. A multi-seasonal sampling programme using pitfall trapping was implemented on four Maltese beaches to test the occurrence of this phenomenon. A total of 29,302 individuals belonging to 191 species were collected over a 2-year period, during which the beaches were sampled once per calendar season. A total of 77 species were recorded from single Maltese beaches only, of which nine were psammophiles. Non-metric multidimensional scaling analyses of pitfall trap species-abundance data resulted in a weak separation pattern, with samples grouping mainly in terms of beach and island rather than in terms of season or year of sampling. No physical variable could conclusively explain these patterns. It is concluded that although operating on Maltese beaches, macrofaunal assemblage distinctiveness is weaker than originally thought and can be attributed to the presence/absence or abundance of just a few psammophilic species. It is postulated that this phenomenon may be related to the 'pocket beach' nature of Maltese beaches, where headlands on either side of the beach to a large extent prevent the occurrence of longshore currents, resulting in semi-isolation of the populations of psammophilic species. A large number of single-beach records reported in this study highlight the high degree of beta diversity and spatial heterogeneity of Maltese beaches, and the conservation importance of the individual beach macrofaunal assemblages.

Introduction

Pocket beaches are amongst the least studied of all beach ecosystems and a symptom of this paucity of studies is the lack of consistency in the literature about the definition of pocket beaches. Whilst Lambie (2005) and Micallef (2003) define pocket beaches as headland-flanked beaches, Defeo & McLachlan (2005) define pocket beaches as beaches with a restricted beach length (*i.e.* short beaches). Maltese beaches satisfy both requirements as they are bound on either side by head-

lands that obstruct and diffract waves and to a large extent prevent the occurrence of longshore currents, and also have a limited length (the longest Maltese beach is only *c.* 1 km long). As a result, Maltese beaches are more or less 'sediment-tight' systems because of the relative lack of sediment exchange between them (Micallef 2003). The lack of attention received by pocket beaches may in part be because of their depauperate macrofaunal assemblages (McLachlan 2001; Defeo & McLachlan 2005).

According to the beach classification system of Wright & Short (1984), Maltese beaches can be described as 'intermediate-reflective', for reasons of their steep con-

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tours, their low water and organic content and coarse sediments.

Maltese beaches are microtidal – the maximum tidal range in the Maltese islands is just 0.20 m (Drago & Xuereb 1993). Community studies on microtidal beaches are few, but include studies on the northern Mediterranean shores (e.g. Dexter 1986, 1989; Fallaci *et al.* 1994, 1997; Colombini *et al.* 2003, 2005; Covazzi Harriague *et al.* 2006; Covazzi Harriague & Albertelli 2007), along the Tunisian coast (e.g. Colombini *et al.* 2002), in the Baltic Sea (e.g. Gheskiere *et al.* 2005), and along the coasts of Uruguay (e.g. Gimenez & Yannicelli 2000) and Brazil (e.g. Veloso & Cardoso 2001).

Researchers working on ocean beaches have tended to overlook the insect component of sandy beach macrofaunal assemblages. In fact, Brown & McLachlan (1990) state that sandy beaches are essentially marine systems with virtually the entire resident fauna being of marine origin, and with insects having in general failed to establish themselves in marine environments. Despite this, insects are an important component of the macrofauna of sandy beaches, especially microtidal ones with wide supralittoral zones such as are generally found in the Mediterranean, and are an integral part of such beach biotic assemblages (Deidun *et al.* 2003).

Previous work on the ecology of Maltese sedimentary beaches has suggested that, despite geographical proximity and the apparent lack of physical obstacles impeding the spread of organisms between beaches, these often harbour distinct faunal assemblages for both the terrestrial and marine components of the beach biota. Deidun *et al.* (2003) first showed that Maltese sandy beaches separated by just a few hundred metres harbour macrofaunal assemblages that are different in species composition; however, these authors' study was limited to sampling beaches during the summer season only. Subsequently, Gauci *et al.* (2005) and Deidun & Schembri (2006) described a similar phenomenon for Maltese shingle beaches and for the upper infralittoral/lower mediolittoral zone of Maltese sandy beaches, respectively, and Saliba (2004) for the macrofaunal assemblages of seagrass wrack deposited on Maltese sandy beaches with similar physical characteristics, including substratum type and wave exposure.

The main aim of this study was to test further the occurrence of the reported distinctiveness of Maltese sandy beaches by providing a wider set of spatial and temporal data on aspects of beta diversity of the beach macrofaunal assemblages. Distinctiveness is here assessed solely on the basis of the number of 'single-site' macrofaunal species recorded from each beach, that is, species only recorded in the present study from a single beach and no other; for any given beach, the more 'single-site'

records that the beach has, the more biotically 'distinct' it is considered to be.

Material and Methods

Study sites

Four Maltese sandy beaches (Golden Bay, White Tower Bay, Ramla l-Hamra and Xatt l-Ahmar) were sampled between 2001 and 2003 in each of eight successive seasons. The length of the four beaches was 220, 120, 500 and 80 m respectively. The geographical location of these beaches is shown in Fig. 1.

Only the 'bare sand' (*i.e.* unvegetated and not covered by any wrack) portion of each beach, taken to extend from the foot of the dunes at the back of the beach to Mean Sea Level (MSL) was considered. Sections of the beach covered by wrack were not sampled directly. According to the Peres & Picard (1964) zonation scheme used widely in the Mediterranean, this zone is equivalent to the supralittoral. Because of its limited width, the 'bare sand' zone at Xatt l-Ahmar was considered as being composed of a wet zone only, as here surf reached almost up to the backing dunes.

Sampling technique and physical parameters characterized

Semi-terrestrial arthropods were targeted through the sampling technique used. These species are considered marginally marine as they can tolerate limited seawater immersion and are found on beaches with a wide supralittoral zone. Nocturnal, surface-active macrofauna were sampled by means of constellations of pitfall traps, each of which consisted of five plastic cups (diame-

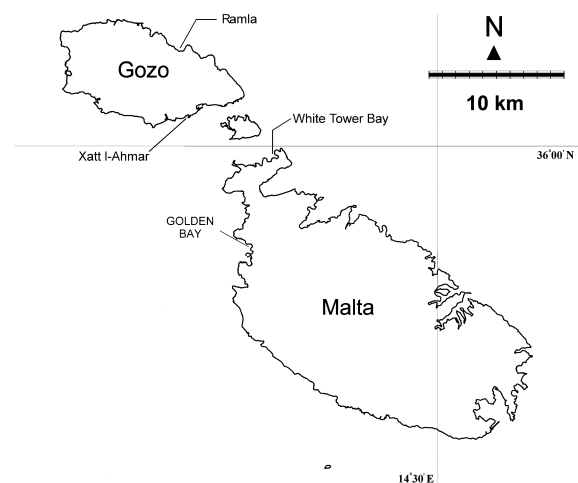
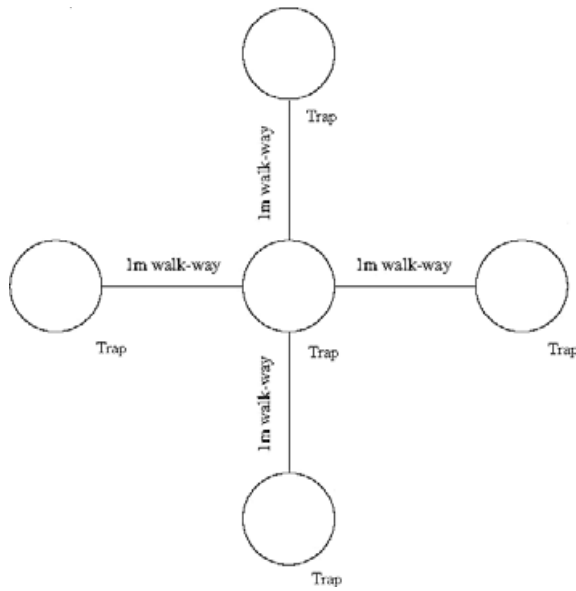


Fig. 1. Map of the Maltese Islands, showing the geographical location of the four beaches sampled.



20 Fig. 2. Schematic diagram of a pitfall trap constellation, as used in the present study. Four peripheral traps were placed symmetrically around a central trap and connected to it by 'walkways' made of thin strips of 'plexiglass'.

ter = 7.5 cm) buried with their mouth flush with the surface of the sand and connected by means of thin 'Plexiglas' walkways resting on the surface of the sand. Such walkways increase greatly the efficiency of the traps as they divert any wandering animals that make contact with the walkways into the traps. Figure 2 illustrates schematically one such pitfall trap constellation. Although pitfall traps are much more efficient at collecting motile animals than other sampling techniques commonly used on sandy beaches, including coring and standardized searching, no information on the absolute population density of the species collected can be inferred from the samples. In addition, as only nocturnal surface active species are targeted, estimates of total species richness for a beach may be skewed, although multiseasonal sampling may mitigate this, at least for species, which are not strictly infaunal

The strandline was taken to demarcate the boundary between the wet and dry zone on the beaches studied, and replicate pitfall trap constellations were deployed within each of these zones. Depending on the length of the beach, two or three constellations were deployed along the beach at a minimum distance of 50 m from each other; the total number of constellations used on a beach every season ranged from 4 (two transects, each with one constellation in the wet zone and one in the dry) to 6 (three transects, as before). Within the wet zone, pitfall trap constellations were deployed at 5 m landwards of MSL, whilst in the dry zone, constellations

were placed at the foot of the dunes or dune remnants backing the beach.

Exposure to wave action was determined using the method described by Thomas (1986), and sediment median grain size and sediment percentage organic content were estimated for all beaches according to the methods of Buchanan (1984); for these determinations, sediment samples were collected systematically at 5-m intervals along shore-normal transects placed at the location of the pitfall trap constellations.

Data analysis

For pitfall trap data, the multivariate classification method of non-metric multidimensional scaling (NMDS) was used, based on the Bray–Curtis measure of the similarity between biotic assemblages. Only psammophilic (sand-specific) species (24 species) were used for these analyses – these are species that are strictly limited to sandy habitats and such species were individuated on the bases of their habitat preferences in Malta as reported in the literature (e.g. Caruso & Lombardo 1982; Mifsud & Scupola 1998; Mifsud 1999; Nardi & Mifsud 2003) or following consultation with relevant taxonomists (see 'Acknowledgements'). Coastal and euryoecious species, although occurring in the samples, are not exclusively found on sandy beaches and were omitted from further the analyses. The collection of non-psammophilic species within traps was considered to be a result of the high sampling efficiency and non-specific nature of the pitfall trapping protocol, and the occurrence of such species was thus not considered as a valid criterion for gauging inter-beach differences.

Psammophilic species, which were collected in <1.5% of all pitfall trap samples (considered arbitrarily as an adequate truncation point to eliminate rare species contributing to data noise), or during one season only, were also excluded from the analyses. Data were log-transformed to downweight the importance of the very abundant species to allow rare species to play some role in determining similarity between samples (Clarke & Warwick 1994).

Two-way ANOSIM was used to test for differences between beaches and between seasons (Clarke & Greene 1988; Clarke 1993). The SIMPER technique was used to identify which species contributed most to the differences between beaches. Seasonal values of the Shannon–Wiener alpha-diversity index (H') were calculated for every beach sampled, whilst the RELATE technique was used to calculate a rank correlation coefficient between all the elements of two (dis)similarity matrices (Warwick & Clarke 1994) for comparing biotic data, abiotic data and generated cyclical model similarity matrices. The latter were

employed to investigate whether the abundance of individual higher taxa (Amphipoda, Isopoda and Coleoptera), and the abundance of the total fauna recorded, exhibited pronounced seasonal patterns.

The non-parametric Chao-Lee II estimator, recommended by Walther & Moore (2005) for its reduced bias and high precision, was computed to gauge the adequacy of the sampling effort. Computations were made using the PRIMER 5 (Clarke & Warwick 1994) and the SPECIES DIVERSITY AND RICHNESS version 3.03 (Henderson & Seaby 2002) program suites and the SPSS version 13 (Norussis 1993) statistical package.

Results

Mean values of percentage sediment organic content and median grain size are given in Table 1. Values of the former ranged from 0.03% (Ramla I-Hamra, summer 2003) to 0.25% (Xatt I-Ahmar, winter 2003). Four different sediment categories (on the Wentworth Scale) from very fine sand to coarse sand were recorded from the different beaches. The four beaches exhibited low wave exposure values, with Thomas Index values ranging from 2.21 to 8.72 (in contrast, the most exposed site on the Islands has a wave exposure value of 27.58 – Mallia 1993). Beach slope ranged from 1.5° (Xatt I-Ahmar, winter 2002) to 8.0° (Golden Bay, spring 2002). Table 1 gives the values of the different physical variables recorded for the beaches studied.

The sampling effort is considered adequate as values obtained for Chao’s non-parametric estimator for species richness coincided very closely with the recorded values of species richness, with the exception of the White Tower Bay dry zone values. The reason for this anomaly could be the proximity of sizeable dune remnants to the ‘bare sand’ zone sampled and to the presence of large amounts of seagrass wrack on the beach, two biocoenoses, which were not considered in this study, but from which species could be ‘spilling over’ to the bare sand zone.

The pitfall trap samples resulted in 15,566 individuals comprising 141 species and 13,736 individuals comprising 129 species during the first and second years of sampling, respectively. In total, 191 species were recorded from all the traps. Of these, 77 species (40.3% of all species collected) were found on a single beach only (Table 2). The number of macrofaunal species recorded during one season from a single beach zone ranged from 3 (recorded on different beaches, zones and seasons) to 21 (Ramla, dry zone, spring 2003). Not considering the pitfall trap samples in which no macrofauna were collected, the catch per unit effort (CPUE) ranged from 0.14 individuals trap⁻¹ h⁻¹ (Golden Bay, wet zone, autumn 2002) to 229.75 individuals trap⁻¹ h⁻¹ (Ramla, wet zone, spring

Table 1. Mean values of sediment organic content (oc) and median grain size (gs) and of catch per unit effort (CPUE) and the Shannon–Wiener diversity index (H'), as well as the total species richness (S), total number of 'single-site' ('s-s') species (i.e. species recorded on just one beach in the present study) and the total number and identity of psammophilic 'single-site' species (p. 's-s'), for the beaches sampled (C = Coleoptera; H = Hymenoptera; I = Isopoda, Ps = Pseudoscorpiones). The total number of 'single-site' species is expressed as a per cent of the species richness recorded for that beach

Beach	Length (m)	Beach width (m)	Sediment oc (% ±SD)		Sediment gs (μ, mean ± SD)		Mean CPUE (ind trap ⁻¹ h ⁻¹ ; ±SD)	No of species (S)	H' (±SD)	Total number of 's-s' species (%)	Number and identity of p. 's-s' species (no truncation)	Number and identity of p. 's-s' species (truncation) (%)
			Wet	Dry	Wet	Dry						
White Tower Bay	120	40	0.07 ± 0.02	0.07 ± 0.02	0.15 ± 0.02	0.14 ± 0.02	5.05 ± 8.77	56	0.95 ± 0.32	17 (30.3)	1 (1.8%) <i>Monomorium subopacum</i> (H)	0
Golden Bay	220	90	0.07 ± 0.01	0.07 ± 0.02	0.32 ± 0.01	0.32 ± 0.02	3.29 ± 4.49	52	1.74 ± 0.86	16 (30.8)	2 (3.9%) <i>Styphloides exsculptus</i> , <i>Cryptophonus fulvus</i> (both C)	0
Ramla I-Hamra	500	80	0.05 ± 0.01	0.04 ± 0.01	0.24 ± 0.07	0.22 ± 0.01	35.4 ± 50.4	55	1.10 ± 0.21	23 (41.8)	3 (5.4%) <i>Tylos europaeus</i> (I) <i>Anthicus fenestratus</i> , <i>Cryptophonus tenebrosus</i> (both C)	2 (3.63)
Xatt I-Ahmar	80	20	0.14 ± 0.07		0.41 ± 0.02		30.2 ± 43.5	36	1.30 ± 0.42	20 (55.6)	3 (8.3%) <i>Erodium siculus melitensis</i> , <i>Cyclodinus minutus minutus</i> (both C) <i>Olpium pallipes</i> (Ps)	0
All sites										77 (40.3)	9 (4.7%)	2 (1.05)

Table 2. Results of the two-way ANOSIM analysis without replication for faunal data from the Maltese beaches sampled

	Contrasts between different beaches		Contrasts between different seasons	
	Rho value	Significance value	Rho value	Significance value
1st year wet zones	0.838	0.004	0.505	0.013
1st year dry zones	0.419	0.127	0.429	0.070
2nd year wet zones	0.857	0.001	-0.038	0.564
2nd year dry zones	0.250	0.265	-0.143	0.650

Values in bold are significantly different at $P = 0.05$.

2002). Mean values for CPUE, species richness and H' for each beach are given in Table 1.

The macrofauna collected belonged to 17 major faunal groups, however, in terms of individual abundance, only six of these contributed more than 1% each to the total individuals collected over the 2-year sampling period, with Isopoda (46.1%) and Coleoptera (39.5%) being the most represented. In terms of species richness, 10 principal faunal groups contributed more than 1% each to the total number of species collected over the 2-year sampling period, with Coleoptera (100 species – 50.5% of the total number of species collected) and Diptera (22 species – 11.1% of total number of species collected) being the most represented.

The total number of non-psammophilic species collected from just a single beach was 69. Of these, 34 were Coleoptera, 10 were Diptera, seven were Isopoda, five were Hymenoptera (Formicoidea), six were Aranea and two were Collembola, and Pseudoscorpiones, Hymenoptera (other than Formicoidea), Opiliones, Orthoptera and Zygentoma were represented by one species each.

Similar numbers of species were collected over the entire 2-year sampling period from the four beaches studied – 56 from White Tower Bay (37 from the wet zone; 40 from the dry zone), 52 from Golden Bay (35 wet zone; 31 dry zone), 55 from Ramla l-Hamra (30 wet zone; 43 dry zone) and 36 from Xatt l-Ahmar (this beach was considered to only have a wet zone because of its restricted width).

A total of nine psammophilic (*i.e.* sand-specific) species were collected only from single beaches (Table 2), of which six were beetles (*Anthicus fenestratus*, *Cryptophonus fulvus*, *Cryptophonus tenebrosus*, *Styphloderes exsculptus*, *Erodium siculus melitensis* and *Cyclodinus minutus minutus*), one was an isopod (*Tylos europaeus*), one was an ant (*Monomorium subopacum*) and one was a pseudoscorpion (*Olpium pallipes*).

On the other hand, if those species which were collected in <1.5% of all pitfall trap samples or during one season only are excluded, the number of psammophilic

species restricted to a single beach would decrease to two (*T. europaeus* and *A. fenestratus*).

The results of the SIMPER analysis showed that a very small number of species (maximum of 4) explain the observed clustering patterns. Between them, the isopod *T. europaeus* (mainly in terms of its presence/absence), and the tenebrionid beetles *Phaleria* spp. (*P. acuminata* and *P. bimaculata*) and the amphipods *Orchestia stephensi* and *Talitrus saltator* (in terms of individual abundance) in different combinations explained over 90% of the dissimilarity between samples.

The RELATE analysis indicated interannual variation in faunal samples as first and second year biotic data was significantly different. The wet and dry zone samples collected during the first year of sampling also differed significantly. The only significant difference between seasonal biotic and abiotic data similarity matrices was found for winter 2003. Most of the selected faunal taxa did follow a cyclical pattern of variation over the two sampling years, with the only samples to differ significantly from the generated cyclic pattern being the 'total fauna' sample collected from the dry zone of Golden Bay and the 'Coleoptera' sample collected from the dry zone of the same beach.

In the NMDS analyses, samples from different beaches separated out from each other (Fig. 3A), with the most distinct being the spring samples from the wet zone of Ramla l-Hamra and the autumn and winter Golden Bay samples. The degree of biotic separation between samples collected from different Maltese islands (Fig. 3B) was more pronounced. Samples did not separate out in terms of season or year of collection. Table 2 gives the results of the two-way ANOSIM analysis, as *rho* values and as significance levels at $P = 0.05$.

Discussion

The patterns emerging from the NMDS analyses (Fig. 3) suggest some degree of separation of the beach assemblages sampled. In fact, within the same analysis, interseasonal samples from the same beach consistently clustered together, with the exception of spring Ramla l-Hamra wet zone and autumn and winter White Tower Bay dry zone samples; this suggests that site-specific factors are more important than seasonal ones, even if the observed separation between the different beach assemblages could be attributed to the presence of just a few species. For example, the distinctiveness of the Ramla l-Hamra wet zone macrofaunal assemblages can be mainly attributed to the presence of large numbers of *T. europaeus*, whose abundance ranged from 46.6 to 282.1 individuals trap⁻¹ h⁻¹ in these samples, whilst the uniqueness of the White Tower Bay assemblages can be attributed to the large numbers of

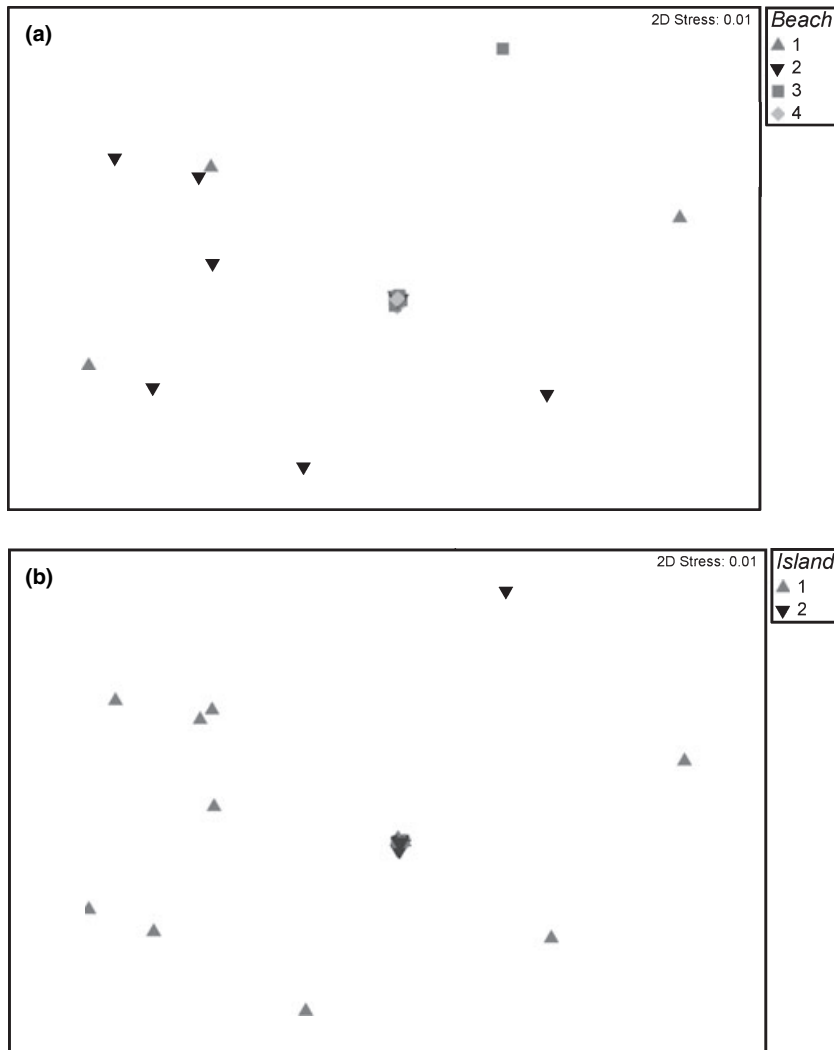


Fig. 3. NMDS ordination plots for the pitfall trap data for all samples from both years of the study, based on the Bray–Curtis resemblance measure, labelled in terms of beach (a) and island (b). Legend for plot a: Beach 1 = White Tower Bay; 2 = Golden Bay; 3 = Ramla; 4 = Xatt L-Ahmar. Legend for plot b: Island 1 = Malta; Island 2 = Gozo.

arachnids (mainly spiders and opilionids) in these samples.

Some authors (e.g. Gheskiere *et al.* 2005), report a complete lack of insect species from the upper zone of tourist beaches in Poland, possibly because of the destruction of backbeach dune areas, the removal of marine debris and the presence of coastal constructions and bathing facilities which interfere with the fetch of winds used by insects to disperse through anemochory. The beaches of Ramla l-Hamra and Xatt l-Ahmar had the largest number of single-beach psammophiles; these two beaches are also the least affected by touristic development and Ramla l-Hamra has the best preserved sand dune remnants in the Maltese Islands (Cassar & Stevens 2002).

The ANOSIM II results indicated that differences between collections made across different beaches within one season were more pronounced than collections made within the same beach across different seasons. In

addition, a relatively large fraction of macrofaunal species (ranged: 30.8–55.6% for the four beaches) were collected from one beach only; most of these were Coleoptera (51 species – 53.7% of total, of which 23.5% were Tenebrionidae, 21.6% Staphylinidae and 17.6% Curculionidae), followed by Diptera (13 species – 13.5% of total), Araneae (eight species – 15.7% of total) and Hymenoptera (six species, 6.3% of total, of which five species were Formicoidea). The preponderance of insect species with limited or no flying ability (Tenebrionidae, Staphylinidae, Curculionidae) amongst the ‘single-beach’ psammophiles is to be expected in view of the lack of dispersal abilities of these species. Many studies highlight the high degree of endemism observed in the Tenebrionidae (e.g. Fattorini & LEO 2000). The high number of ‘single-beach’ Diptera with good powers of flight can be attributed to site-specific characteristics, such as the presence of beached seagrass

debris, which is a habitat the larvae of many wrack flies (Rebello 1987).

Of the 24 psammophilic species considered in the ordination analyses, only 13 were present in at least 1.5% of all the samples, whilst of these, only two (the anthicid beetle *A. fenestratus* and the oniscoidean isopod *T. europaeus*) were not collected in just one sampling season. *Anthicus fenestratus* was collected consistently over both spring seasons, whilst *T. europaeus* was collected throughout all eight sampling seasons; both species were collected from the beach at Ramla l-Hamra only. However, whilst one and two individuals of *A. fenestratus* were collected during spring 2002 and spring 2003 respectively, a maximum of 9978 individuals of *T. europaeus* were collected during one sampling season (autumn 2001). The fact that both species were collected from Ramla l-Hamra underscores the importance of this beach, which is backed by the best preserved sand dune remnants in the Maltese Islands, in relation to biodiversity (Cassar & Stevens 2002). The uniqueness of the Ramla l-Hamra wet zone bare sand assemblages is further confirmed by the results of the multivariate analyses. The other beach sampled that is backed by significant dune remnants is White Tower Bay, whose dry zone samples also exhibited a high degree of uniqueness in the multivariate analyses.

It is only when considering the total suite of species recorded from a single beach, and not just the psammophiles, that the importance of some of the local beaches sampled, in relation to biodiversity, becomes evident. For example, the endemic *Stenosis schembrii* and the sub-endemic *Clitobius ovatus* are two non-psammophilic ten-ebrionids recorded only from the beach at Xatt l-Ahmar in the present study. The relatively low number of species (36) collected from this beach over the 2 years of sampling is probably because of the lower number of pitfall trap constellations used (for the reason of its small size). The high percentage of single-beach records (*i.e.* psammophiles and non-psammophiles together – 55.6%) reported from Xatt L-Ahmar could be related to the relative isolation of the beach and its inaccessibility.

Interbeach differences in the physical parameters monitored (beach slope, median grain size, sediment organic content and beach length) (Table 1), cannot fully explain the observed biotic separation patterns. Physical parameters, which were not monitored in this study but which are considered to regulate the zonation of at least some of the sandy beach macrofauna, include air and sand temperatures, sand water content (especially important for burrowing isopods), the relative humidity of the air and the sea-land direction of the wind (Colombini, *et al.*, 1996; Fallaci *et al.* 1996). A difficulty in identifying the most important community-shaping physical parameters was experienced by Riccardi & Bourget (1999) who report

that linear combinations of physical variables explained just 44% of the variance in total biomass on sedimentary shores, with grain size being the best single predictor. There is general agreement that no unique key factor structures beach macrofaunal communities but rather, a number of environmental parameters, including such biotic factors as food sources, recruitment, predation and competition, operate together (Brazeiro 2001; Veloso & Cardoso 2001; Rodil & Lastra 2004).

For the beaches sampled, the dry zone faunal assemblages were more beach-specific than those of the wet zone, which exhibited a greater degree of homogeneity between the different beaches. The largest differences in the H' values of the different beaches were recorded in winter. This might be related to the appearance of phytophagous species in the rainy season on beaches where sizeable dune remnants occur, such as at Ramla l-Hamra and White Tower Bay.

The degree of macrofaunal assemblage distinctiveness of upper infralittoral assemblages reported by Deidun & Schembri (2006), who worked on the same beaches, is more pronounced than that for the mediolittoral and supralittoral assemblages sampled in the present study. This is surprising, especially in view of the fact that fewer obstacles to dispersal occur in the marine environment than in the terrestrial one, especially for fauna with planktonic larvae. In fact, in the same study, the highest number of 'single-site' species was recorded for decapods and polychaetes, followed by amphipods and fish. Whilst high levels of patchiness in individual species distributions are expected for benthic recruiters, like amphipods and isopods, the low degree of homogeneity for pelagic recruiters like polychaetes and decapods is unexpected, indicating that site-specific characteristics and other factors are important in determining species distributions. Deidun & Schembri (2006) attribute their results to the surf zone circulation cells acting within small bays, which restrict dispersal of the propagules of surf fauna out of the embayment. It would seem that the terrestrial component of the beach biota find dispersal to other beaches easier than the aquatic component, albeit still problematic.

Results from the present study seem to suggest that macrofaunal assemblage distinctiveness may operate over small distances under certain circumstances; while the two most distant beaches sampled in this study (Golden Bay and Ramla l-Hamra; Fig. 1) are separated by a maximum distance of 15 km, even adjacent beaches may be ecologically isolated because of their 'pocket-beach' nature, which debar the occurrence of longshore currents, and because of long stretches of non-sandy coastline between them. Pocket beaches may give rise to independent 'sediment cells' as a result of wave diffraction by the

associated headlands. For Maltese beaches, Turi *et al.* (1990) exclude the possibility of beach sediments being supplied from the marine environment outside the individual embayments at the head of which such pocket beaches occur.

Another factor contributing to the observed distinctiveness of beach macrofaunal assemblages might be the dearth of sediment shores in the Maltese Islands where just 2.4% of the coastline is sandy (Mallia *et al.* 2002); hence, sandy beaches can be considered as isolated refuges for psammophiles amidst the vastly more abundant rocky coast habitats. Pockets of sandy coastline are a few and may be separated by large expanses of presumably hostile environments associated with rocky coastlines, which limit dispersal of psammophilic macrofauna from one beach to another. In such circumstances, 'waif dispersal' events, for example via rafting on floating wrack, may be the only way in which fauna from one beach may disperse to another. Although this mechanism of macrofaunal dispersal may appear to be equally feasible for infralittoral species, the results of Deidun & Schembri (2006) indicate otherwise. Differences in community composition were more pronounced between Malta and Gozo than were those between different beaches on the same island, suggesting that the interisland obstacles to macrofaunal recruitment and dispersal are more important than the interbeach one.

Many authors have suggested the use of fauna as indicators of beach state. Indicators which have been suggested include species which cycle a high proportion of the energy flow on a beach, such as *T. saltator* (Weslawski *et al.* 2000; Scapini, 1998; DeMatthaeis *et al.*, 2000; Kettmaier *et al.* 2003), and species which form the bulk of the beach faunal biomass, such as isopods and coleopterans in general (Colombini *et al.* 2003). We propose that the number of 'single-site' species may be used as generic indicators of the degree of human disturbance of beach macrofaunal assemblages. Deidun & Schembri (2004) report that the number of psammophiles decreases whilst that of euryecious species (*e.g.* Formicoidea) concomitantly increases with increasing levels of human disturbance. In agreement with this, the largest numbers of psammophiles and of 'single-site' species recorded in the present study were for Ramla l-Hamra and Xatt l-Ahmar, the two least disturbed beaches sampled, whilst the lowest counts of such species were for the most popular bathing beach (Golden Bay). Site-specific factors, such as the presence of dune remnants (as at Ramla l-Hamra), might also be important, however.

In conclusion, the macrofaunal assemblage distinctiveness of Maltese bare sand assemblages, previously hinted at by single-season studies, has been confirmed by the current, multi-seasonal study, although the phenomenon

appears to be weaker than originally thought and mainly limited to differences between beach assemblages on different Maltese islands. This distinctiveness in turn points to a high degree of beta diversity and spatial heterogeneity of Maltese beaches, which is mainly attributable to their relative ecological isolation, rather than to site-specific factors. The assemblage distinctiveness of Maltese beach macrofaunal communities, however weak, leads to the conclusion that no local beach biotic assemblage is expendable and this is especially important in a country where anthropogenic pressures (*e.g.* tourism and tourism infrastructure) on sandy beach environments are intense (Cassar & Stevens 2002).

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