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Demersal amphipod migrations: spatial patterns in marine shallow waters

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Abstract

The nocturnal displacement to the water column of species hiding in the substrate during the day (so-called demersal migration) is a widespread phenomenon in coastal habitats. However, despite the relevance of these migrations to coastal ecosystem functioning, most of their ecological aspects are poorly understood. We aim to characterize spatial distribution patterns of demersal amphipods by comparing samples collected by light traps deployed both at rocky and nearby sandy areas. Dispersal abilities of such species were explored by considering two spatial scales of separation between rocky and sandy substrates: (1) <100 m and (2) >1 km. A total of >45,000 amphipod specimens were collected in the water column during the whole study, belonging to 50 species. The numerically dominant species were *Guernea coalita*, *Bathyporeia* cf. *elegans*, *Perioculodes longimanus* and *Nototropis swammerdamei.* The present study highlights the relevance of substrate type and study location on coastal demersal amphipod migrations. Amphipod assemblages were significantly different in the water column above rocky and sandy bottoms, even at a small spatial scale. Species emerging from rocky bottoms tend to remain in the proximity of this habitat; they showed lower abundances in sandy areas located nearby and almost none of them reached distant sandy areas. In contrast, migrant species commonly found on sediment during the day were collected at higher abundances in light traps deployed above rocky bottoms. Although several factors (e.g. food availability, predation pressure) are proposed to explain these patterns, the purpose of this horizontal migration remains unknown.

Introduction

Marine zooplankton accounts for one of the biggest animal migrations in terms of biomass on the planet (Hays, 2003; Brierley, 2014). Diel vertical migration (DVM) describes the synchronized movement of zooplankton, most commonly descending in the water column before dawn and upwards toward the surface at dusk. This is a common phenomenon both in marine and freshwater pelagic communities worldwide and has profound ecosystem implications in terms of niche partitioning, food chain structure and behavioural adaptations (Hays, 2003; Ringelberg, 2010).

While changes in the vertical distribution of these migrating species have been well described in open waters, the general patterns of such migrations in coastal areas remain poorly understood (Vereshchaka & Anokhina, 2017). In shallow waters, pelagic and benthic communities interact more closely with each other (e.g. stronger pelagic-benthic coupling in food webs) and the expected segregation between both environments becomes blurred (Tranter *et al.*, 1981; Koop *et al.*, 2015). Many small-sized coastal species also show daily vertical movements, hiding at the bottom during the day but emerging in the water column at night. Although there is little consensus about the terms used to designate the organisms living near the bottom, these migrant species are commonly designated as demersal or emergent zooplankton (Alldredge & King, 1977; Jacoby & Greenwood, 1989; Dauvin & Vallet, 2006). These communities are mainly composed of peracarid crustaceans (amphipods, isopods, tanaids, mysids, cumaceans), copepods, ostracods, polychaetes and larval forms, most of them of larger size when compared with open-water plankton (Porter, 1977; Jacoby & Greenwood, 1988).

Coastal zooplankton is a major energy source in tropical and temperate reefs, where demersal zooplankton accounts for up to 80% of plankton biomass at night (Alldredge & King, 2009; Truong *et al.*, 2017; Vereshchaka & Anokhina, 2017). Consequently, demersal zooplankton supports a significant biomass of both sessile and mobile planktivores (from jellyfish and corals to manta rays), especially those who primarily feed at night (e.g. crinoids, cardinal fishes, sea pens) (Pitt *et al.*, 2008; Alldredge & King, 2009; Couturier *et al.*, 2013). Therefore, spatial and temporal dynamics of these migrant organisms will have cascading consequences for the whole ecosystem.

Similarly to holoplankton migrations, light intensity changes constitute the main environmental cue that triggers the migration of demersal zooplankton, and predation avoidance is the main cause of this behaviour (Tranter *et al.*, 1981; Jacoby & Greenwood, 1988; Ringelberg, 2010). Environmental factors such as depth, lunar period, tide, substrate type or season

may influence the abundance of demersal zooplankton, although the relevance of these factors across different habitats and taxa remains unclear (McWilliam *et al.*, 1981; Schlarcher & Wooldridge, 1995; Anokhina, 2006).

Regarding substrate type, most previous works have found a clear relationship between the degree of three-dimensional structure of a certain substrate and the abundance of plankton rising from it (Porter, 1977; Smith *et al.*, 2016; Vereshchaka & Anokhina, 2017), with only few exceptions to this pattern (Melo *et al.*, 2010). In this sense, most taxa emerge in greater numbers from complex substrata (e.g. macroalgae, seagrass meadows or corals) than from open sandy areas that offer less shelter from predators or against hydrodynamism (Alldredge & King, 1977; Jacoby & Greenwood, 1988; Rios-Jara, 2005; Smith *et al.*, 2019). The ability to actively seek for specific refuges when returning to the bottom at dawn determines a spatial segregation of demersal species according to the distribution of different substrates. On the other hand, the decreasing number of specimens collected at farther distance above the substrate (Alldredge & King, 1985; Vereshchaka & Anokhina, 2017) suggests that demersal zooplankton tend to remain close to their place of emergence once they emerge to the water column. Under this scenario, it would be expected that the well-delimited spatial structure observed in the bottom would be reflected, at least broadly, in the pelagic environment. At a small spatial scale, we hypothesized that the lack of dispersal barriers and major environmental differences, together with the effect of water currents, would determine a homogenization of the amphipod assemblage in the water column. However, there are no studies dealing with the horizontal distribution of demersal communities at a low spatial scale nor with the dispersal abilities of these species in coastal habitats.

In the present article, we aim to characterize spatial distribution patterns of demersal zooplankton in the near-shore area by comparing samples collected from the water column above rocky and nearby sandy areas. In contrast to many previous studies, which characterized the whole demersal community using higher taxa (e.g. family, order), we focused on one of the dominant groups in terms of both abundance and biomass (Amphipoda) at the species level. In addition, amphipods can exhibit very specific substrate preferences and their habitat distribution is relatively well-known (e.g. Guerra-García, 2001; Gestoso *et al.*, 2012; Martínez-Laiz *et al.*, 2018). Thus, we expect to reveal complex and specific responses, as well as determining the emergence habitat of species.

Dispersal abilities of such species will also be explored by considering two spatial scales of separation between rocky and sandy substrates (<100 m and >1 km). We hypothesized that: (1) At small scale, demersal amphipods will show a homogeneous distribution in the water column as a result of the mixing of migrating individuals emerging from both rocky bottoms and nearby sediments. (2) Due to the limited dispersal ability of the species, differences in the composition and structure of the amphipod plankton above rocky and sandy areas will become more evident with an increasing distance between each habitat. (3) A higher number of individuals and species will be emerging from rocky bottoms since this habitat provides a better and more heterogeneous diurnal shelter.

Materials and methods

Study area

The study was conducted in the Mediterranean coast of southern Spain (Alborán Sea). The study area encompasses a stretch of ~30 km of shoreline and comprises a heterogeneous coast with a mixture of long sandy beaches (>1 km long) and small coves delimited among rocky cliffs (mostly limestone). The north side of the Alborán Sea constitutes one of the Mediterranean regions for which a good knowledge of shallow water amphipod fauna is available, with ~240 species cited in more than 30 studies (Navarro-Barranco, 2015). Ruffo (1982–1998) and Navarro Barranco (2015) compiled the available information regarding the habitat (e.g. coarse sand, muddy bottoms, sessile invertebrate, macroalgae, seagrass) of many amphipod species reported by previous studies conducted in the Mediterranean and the Alboran Sea, respectively. However, with the exception of a few reports of certain species collected by light traps at night, no studies have been conducted in the Mediterranean dealing with the vertical migration of demersal amphipods (Ruffo, 1982–1998; Michel, 2011; Fernández-González *et al.*, 2014).

Eight sampling locations were selected within this area; in four of them it was possible to collect samples over sandy bottoms separated by more than 1 km from the nearest rocky substrate (hereafter 'Long beaches', LB), while separation between sandy and rocky bottoms was less than 100 m at the other four locations (hereafter 'Short beaches', SB). The four LB considered were *El Morche* (36°44′17″N 3°59′38″W), *Nerja* (36°44′36″N 3° 57′51″W), *La Herradura* (36°44′16″N 3°45′00″W) and *Almuñecar* (36°44′24″N 3°39′59″W), while the four SB were *El Peñoncillo* (36°43′38″N 3°57′13″W), *Caleta de Maro* (36° 45′12″N 3°50′38″W), *El Cañuelo* (36°44′36″N 3°47′16″W) and *Marina del Este* (36°43′23″N 3°43′39″W). Both LB and SB were evenly distributed along the study shoreline in order to avoid correlation of the patterns obtained with unanticipated environmental gradients (Figure 1). A biocoenosis of photophilic algae (dominated mainly by *Halopteris scoparia* (Linnaeus) Sauvageau, 1904 accompanied by *Cystoseira* sp., *Ulva* sp. and *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders, 2013) was present at all rocky substrates, while medium-fine sand characterized all sediments (with the exception of a high dominance of gravel at *Almuñecar*).

Sampling design and data collection

All samples were collected between 8–25 August 2017 during new moon, crescent moon or time intervals of no moon, avoiding periods of high moonlight intensity or poor water visibility. Since light is the major stimulus driving this migrating behaviour (acting as the 'releasing stimulus' that triggers the migration and the 'directional stimulus' that guides animals' movement), light traps have been proposed as a suitable sampling method when studying demersal zooplankton (e.g. Sale *et al.*, 1978; Smith *et al.*, 1979; Tranter *et al.*, 1981; McLeod & Costello, 2017). Other sampling devices commonly used to collect demersal zooplankton include the use of emergence traps, but this methodology was discarded since they collect those organisms coming from the immediate bottom substrate but they are unsuitable for exploring the dispersal abilities of species migrating from other areas (e.g. McWilliam *et al.*, 1981; Yahel *et al.*, 2005*a*; Melo *et al.*, 2010). Among the limitations of the use of light traps are their inability to provide density values and to assess variability among samples due to abiotic conditions (turbidity, currents, etc.), as well as resulting in a minor bias in the abundance of certain groups (e.g. the dominance of pelagic species seems to be overestimated, probably due to their stronger attraction to light) (Sale *et al.*, 1978; Fernández-González *et al.*, 2014; McLeod & Costello, 2017).

Light traps were deployed after sunset (21:00 h) in shallow waters (depth: 2–4 m) and retrieved 3 h later. Three replicates were collected in each habitat within each location. We used a combined design of the two light trap models described in Michel (2011) (Figure 2). Collection efficiency of several low-cost light traps made of plastic bottles has been previously tested

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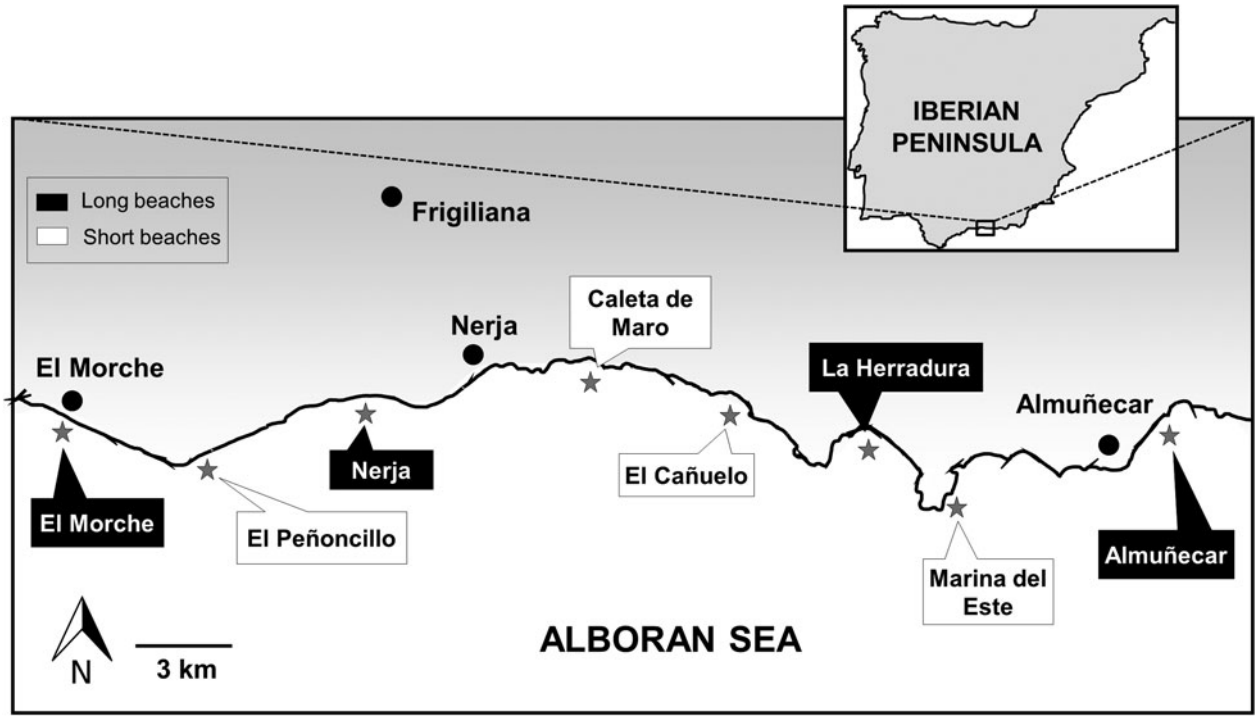


Fig. 1. Study area showing all sampling locations.

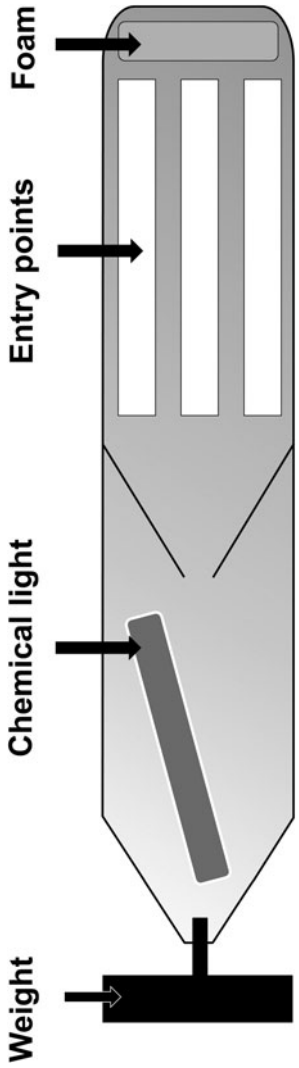


Fig. 2. Diagram of the light traps. See text for a detailed description of design.

(Watson *et al.*, 2002; Michel *et al.*, 2010; Chan *et al.*, 2016). The used design was made of two nested 1.5 l transparent plastic bottles placed in reversed position. The top bottle presented vertical rectangular slits (1.5 cm wide × 15 cm long) and was inserted in the bottom one, which contains a chemoluminescent yellow light (Cyalume® Lightstick). The trap was anchored to the bottom by a weight, while the top bottle contained foam to ensure the vertical position of the trap, which remained ~50 cm above the sea floor. Phototactic zooplankton entered the trap through the slits and were attracted to the bottom of the trap. The bottle neck separating the 'light chamber' (i.e. bottom bottle) from the 'entrance chamber' (top bottle) limits the potential escape of animals. In order to reduce any potential loss of individuals and hydrodynamic influences, samples were collected during very calm periods. Once retrieved from the water, the bottom bottle cap was opened and the specimens gathered around the lightstick were transferred to a plastic container and preserved in 70% ethanol. In the laboratory, samples were sieved through a 0.5-mm mesh and all amphipods were identified to the species level and counted.

Data analyses

Many species found in the light traps showed very low abundances and frequency of occurrence (they were often present as singletons and/or in one replicate). Thus, they were not considered as truly demersal migrants and these accidental catches were removed from the statistical analyses (only those species with an abundance of at least 20 individuals in the whole study were included). Spatial patterns in the abundance and number of amphipod species were explored using analysis of variance (ANOVA) with three factors: Substrate (Su), Distance (Di) and Location (Lo). Substrate was a fixed factor with two levels: Hard and Soft. Distance was also a fixed factor, orthogonal with substrate, with two levels: Long and Short. Finally, Location was a random factor, orthogonal with Substrate but nested in Distance, with three levels (four different LB and four SB) (N = 3). Prior to ANOVA, homogeneity of variances was tested using

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Table 1. Abundance (mean number of individuals per replicate ± SE) of the dominant amphipod species (Total abundance >20 individuals) collected by the light traps deployed at each habitat

	Mean abundance (±SE)		
Amphipod species	Hard bottoms	Soft bottoms (SB)	Soft bottoms (LB)
Species emerging from hard bottoms			
Apherusa sp.	7.1 ± 1.7	19.4 ± 7.5	–
Dexamine spiniventris (Costa, 1853)	9 ± 3.1	0.6 ± 0.3	0.1 ± 0.1
Dexamine spinosa (Montagu, 1813)	2.1 ± 1.2	2.2 ± 1.3	–
Echinogammarus planicrurus (Reid, 1940)	151.1 ± 92.3	115.3 ± 61.9	2.3 ± 1.6
Gammaropsis palmata (Stebbing & Robertson, 1891)	2.8 ± 1.4	–	–
Hyale sp.	2.8 ± 1.6	0.2 ± 0.2	–
Jassa ocia (Spence Bate, 1862)	6.2 ± 1.7	2.5 ± 0.8	–
Jassa slatteryi Conlan, 1990	1.9 ± 0.8	–	–
Lysianassa costae (H. Milne Edwards, 1830)	3.1 ± 1.1	0.6 ± 0.4	–
Microdeutopus chelifer (Spence Bate, 1862)	1.4 ± 0.8	0.3 ± 0.2	–
Microdeutopus obtusatus Myers, 1973	9.5 ± 5.3	1.3 ± 0.8	
Pleonexes helleri (Karaman, 1975)	2.7 ± 2	0.5 ± 0.3	–
Stenothoe monoculoides (Montagu, 1813)	8.8 ± 2	1.7 ± 1.2	–
Species emerging from soft bottoms			
Bathyporeia cf. *elegans* Watkin, 1938	284.6 ± 125.7	176.7 ± 87.2	19.2 ± 6.8
Guernea coalita (Norman, 1868)	414 ± 207.1	122.3 ± 51.8	2.3 ± 0.9
Hippomedon sp.	0.2 ± 0.1	1.5 ± 0.4	1.1 ± 1.1
Megaluropus massiliensis Ledoyer, 1976	12.7 ± 4.1	44.8 ± 17.8	6.3 ± 2.1
Megaluropus monasteriensis Ledoyer, 1976	8.9 ± 2.9	0.3 ± 0.1	–
Nototropis swammerdamei (H. Milne Edwards, 1830)	223.8 ± 101.1	84.6 ± 32.1	2.2 ± 0.6
Perioculodes longimanus (Spence Bate & Westwood, 1868)	231 ± 65	211.4 ± 84.3	40.6 ± 21.8
Pontocrates arenarius (Spence Bate, 1858)	50.8 ± 13.1	47.3 ± 11.7	32.6 ± 14.4
Synchelidium longidigitatum Ruffo, 1947	1.2 ± 0.7	0.2 ± 0.2	–

SB, Short beaches; LB, Long beaches.
Division between SB and LB has not been applied to Hard bottoms since there are no differences in the degree of isolation of rocky areas (see text).

Cochran's test and appropriate transformations were applied to the data when necessary (Underwood, 1997). When ANOVA indicated a significant difference for a given factor (at $\alpha = 0.05$) the source of difference was identified using the Student–Newman–Keuls (SNK) tests. ANOVA were conducted with GMAV5 software (Underwood *et al.*, 2002).

The permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in the amphipod assemblage according to the same experimental design as explained above. Analysis was based on both square-root and presence/absence transformed data; the former approach allows us to explore differences in the assemblage structure but dampening the effects of dominant species while all abundance effects are removed by presence/absence transformation (therefore revealing patterns on species composition). Similarity matrix was generated using Bray–Curtis similarity index. Terms found to be significant in the analysis were examined individually using appropriate pairwise comparisons. Monte Carlo *P*-values was used for those terms where the number of permutations was low (Anderson, 2005). Finally, Non-metric Multidimensional Scaling (nMDS) was also carried out to explore differences in the amphipod assemblage between hard and soft substrates, using the Bray–Curtis similarity matrix based on square-root transformed data. Multivariate analyses were carried out using the PRIMER V.6 + PERMANOVA package (Clarke & Gorley, 2001).

Results

In total, 45,890 amphipod specimens belonging to 50 species were found in samples (Supplementary Table 1). Among them, 22 taxa were collected in such numbers to be considered as demersal migrant species (Table 1), while the remaining 28 species comprised less than 0.5% of total abundance. The numerically dominant species was *Guernea coalita* (Norman, 1868), which comprised 24% of total abundance (TA) and was present in 77% of the light traps deployed (frequency of occurrence, FO), followed by *Bathyporeia* cf. *elegans* Watkin, 1938 (20% TA; 88% FO), *Perioculodes longimanus* (Spence Bate & Westwood, 1868) (18.7% TA; 98% FO), *Nototropis swammerdamei* (H. Milne Edwards, 1830) (14% TA; 83% FO) and *Echinogammarus planicrurus* (Reid, 1940) (11% TA; 38% FO). All demersal amphipods were collected in the light traps deployed both on hard and soft bottoms, the only exceptions being *Jassa slatteryi* Conlan, 1990 and *Gammaropsis palmata* (Stebbing & Robertson, 1891) that were only found in rocky areas. Species commonly associated with rocky shores showed higher abundance above this habitat and were also collected (although with very low abundances)

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above sandy bottoms located in SB. Among these 'rocky species' only a few individuals of *Dexamine spiniventris* (Costa, 1853) and *E. planicrurus* were able to reach sandy areas far away from rocky bottoms. On the other hand, nine species were commonly associated with sandy areas, although most of them showed higher abundances in the water column above rocky areas.

According to ANOVA, there were significant differences in the number of species collected by light traps deployed above hard and soft bottoms, although this pattern only applied to long beaches (Table 2). When hard and soft bottom areas were separated by a longer distance, the number of species was significantly higher on hard substrates. Analysis of the interaction 'Su × Di' showed significant differences for LB but not for SB and, similarly, separate comparisons for each location (Interaction 'Su × Lo(Di)') pointed out significant differences between substrates at each one of LB considered but only at one SB (Table 2, Figure 3). Regarding abundance, there were no clear patterns; hard substrates showed higher abundance at *El Morche* and *Almuñecar* (both LB) and the opposite pattern was found at *El Cañuelo* (SB), while no significant differences between substrates were found at *Peñoncillo*, *Nerja*, *Caleta de Maro*, *La Herradura* and *Marina del Este* (Table 2, Figure 3).

PERMANOVA using presence/absence data showed similar results to those obtained for number of species: while significant differences between substrates were found for LB, hard and soft bottoms located nearby showed similar species composition. Results obtained using square-root transformed data indicated a significant influence of factors Substrate and Location, as well as for the interaction between them, while Distance did not show significant results. Further examination of the interaction 'Su × Lo' showed significant differences between substrates at all locations, the exception being *Marina del Este*. nMDS ordinations reflected the same pattern: there was no overall segregation among substrates but hard and soft bottom replicates were clearly separated within each location (Figure 4).

Discussion

Habitat of emergence and migrating behaviour

None of the pelagic amphipod species (most of them included within the suborder Hyperiidea) reported either for the Alborán Sea or the Mediterranean Sea was collected in the present study (Madin, 1991; Christodoulou *et al.*, 2013). Therefore, the possibility of 'contamination' of the samples by holoplanktonic species can be discarded. The phototactic behaviour of hyperiid species is well known (Land *et al.*, 1995; Fernández-González *et al.*, 2014) so the lack of holoplanktonic amphipods could be due to their absence in very shallow waters.

The extensive number of studies dealing with shallow-water amphipods conducted in the study area allows us to determine the diurnal habitat of each one of the species collected (Ruffo, 1982–1998; Navarro Barranco, 2015 and references therein). Most of the species found at very low abundances (e.g. *Coxischyrocerus inexpectatus* (Ruffo, 1959), *Monocorophium sextonae* (Crawford, 1937), *Caprella acanthifera* '*sensu lato*' Leach, 1814, *Stenothoe tergestina* (Nebeski, 1881)) were collected only by light traps deployed in rocky areas. These species are commonly associated with macroalgae, hydroids or sponges inhabiting hard substrates and their presence in our samples could be related to accidental catches due to sporadic movements of the organisms or disturbance of the surrounding habitat when deploying the light traps. A nocturnal migrant behaviour has been reported for some of these species (e.g. *Urothoe elegans* Spence Bate, 1857, *Metaphoxus fultoni* (Scott, 1890)) but, unlike most demersal species, their emergence can be delayed until late

Table 2. Results of the three way ANOVA for species richness (number of species per replicate) and abundance (number of individuals per replicate)

		Number of species								Abundance								
Source of variation	df	MS					F		P	MS					F		P	
Substrate = Su	1	147.00					17.79		0.006**	11024667.00					2.96		0.136	
Distance = Di	1	52.08					6.14		0.480	593630.08					0.12		0.737	
Location(Di) = Lo(Di)	6	8.49					4.74		0.002**	4796196.04					8.80		<0.001***	
Su × Di	1	90.75					10.98		0.016*	10824300.75					2.91		0.139	
Su × Lo(Di)	6	8.26					4.61		0.002**	3722243.71					6.83		<0.001***	
Residuals	32	1.70								544948.67								
SNK test (Exploring differences between pairs of levels of factor 'substrate' for each significant interaction)																		
		LB					SB											
	Su × Di	**					n.s.			LB					SB			
		EM	NE	LH	AL	EP	CM	CA	ME	EM	NE	LH	AL	EP	CM	CA	ME	
	Su × Lo(Di)	**	**	**	**	n.s.	**	n.s.	n.s.	Su × Lo(Di)	**	n.s.	n.s.	***	n.s.	n.s.	**	**

LB, Long beaches; SB, Short beaches; EM, *El Morche*; NE, *Nerja*; LH, *La Herradura*; AL, *Almuñecar*; EP, *El Peñoncillo*; CM, *Caleta de Maro*; CA, *Cañuelo*; ME, *Marina del Este*.
Significant at: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
Abundance data were Ln(x) transformed while no transformation were necessary for species richness.

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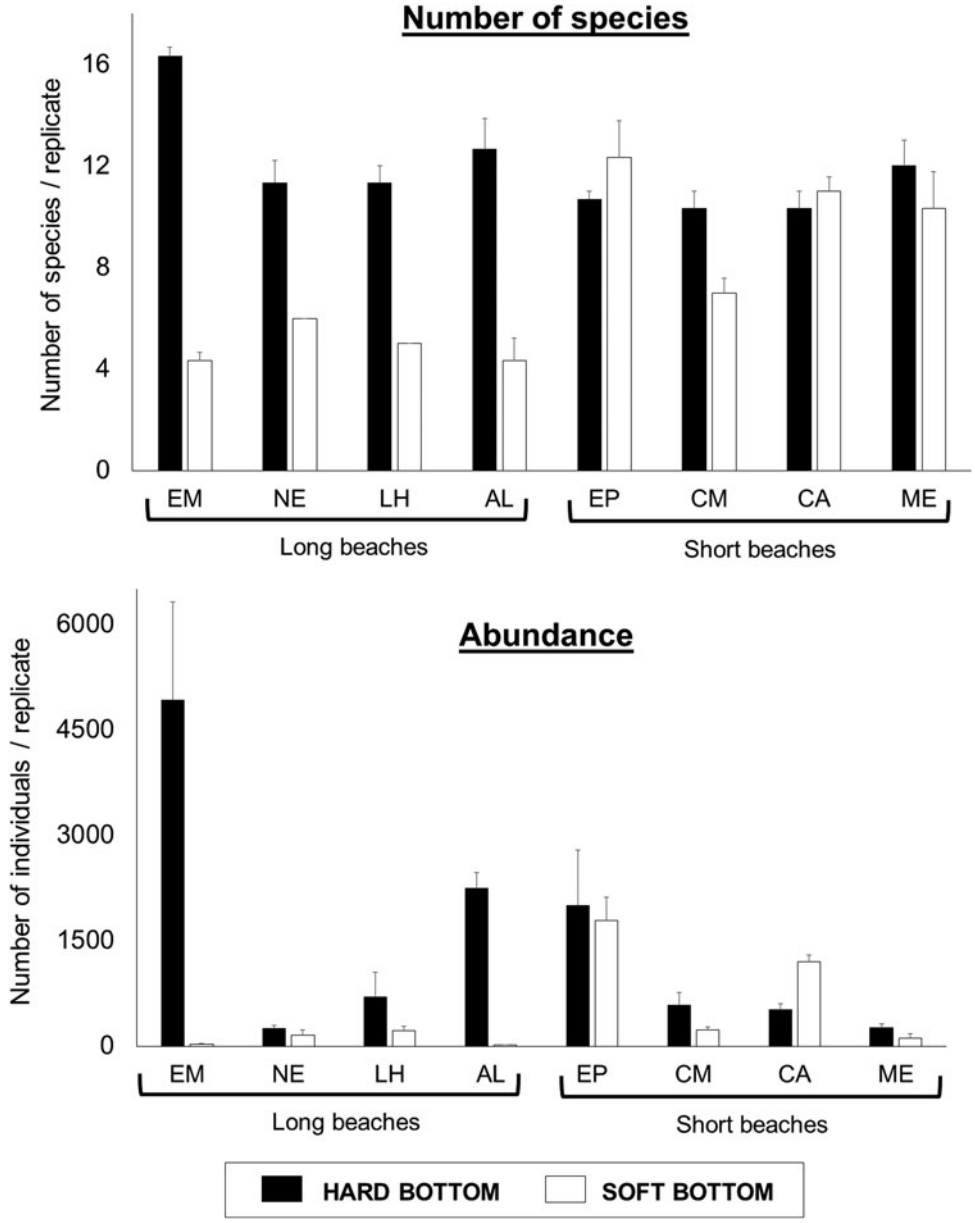


Fig. 3. Mean values (± SE) of number of amphipod species and abundance at each sampling location per habitat (Hard, Soft). EM, *El Morche*; NE, *Nerja*; LH, *La Herradura*; AL, *Almuñecar*; EP, *El Peñoncillo*; CM, *Caleta de Maro*; CA, *Cañuelo*; ME, *Marina del Este*.

at night (Macquart-Moulin, 1984). Thus, their abundance in our study area could be underestimated by our sampling timing (focused in the first hours after sunset).

Regarding dominant migrant species, nine of them were associated with sandy and/or muddy bottoms while the other 13 were associated with rocky bottoms (either living on algal biotopes, sessile invertebrates or under stones). Previous studies conducted in the same localities highlighted the high abundance of some of the amphipod species collected within the photophilic macroalgal epifauna (e.g. *Dexamine spiniventris*, *Dexamine spinosa* Montagu, 1813, *Gammaropsis palmata* (Stebbing & Robertson, 1891), *Hyale* sp., *Microdeutopus chelifer* (Spence Bate, 1862), *Apherusa* sp., *Stenothoe monoculoides* (Montagu, 1813)) or shallow sandy bottoms (e.g. *Hippomedon massiliensis* Bellan-Santini, 1965, *Perioculodes longimanus*, *Megaluropus massiliensis* Ledoyer, 1976, *Pontocrates arenarius* (Spence Bate, 1858)) (Izquierdo & Guerra-García, 2011; Soler & Guerra-García, 2011; Navarro-Barranco *et al.*, 2014, 2018). However, these studies provide an extensive list of benthic amphipod species (most of them not found in the present study) and, in contrast, some of the most abundant species in the light traps (e.g. *Guernea coalita*, *Nototropis swamerdamei*) were less numerically dominant in the benthic environment. This suggests that diel vertical displacement is not a widespread behaviour within Amphipoda and, consequently, amphipod assemblages in the water column are not merely a reflection of the assemblage structure in their habitats of emergence. An accurate comparison of our results with those obtained by previous studies in different areas or habitats is not feasible due to the heterogeneity of methodologies and sampling efforts and lack of studies conducted at the species level of identification. Despite this, many of the dominant taxa (such as the genera *Dexamine*, *Jassa*, *Guernea*, *Apherusa*, *Perioculodes*, *Bathyporeia*, *Megaluropus*, *Hippomedon* or *Stenothoe*) have already been collected by light traps and/or nocturnal plankton hauls from Mediterranean coasts (Ruffo, 1982–1998; Macquart-Moulin, 1984; Bellan-Santini & Vader, 1988; Michel, 2011; Fernández-González *et al.*, 2014). It also becomes evident that the ability to conduct nocturnal migrations and a phototactic response is a common behaviour within several amphipod families such as Dexaminidae, Megaluropidae, Atylidae, Calliopidae,

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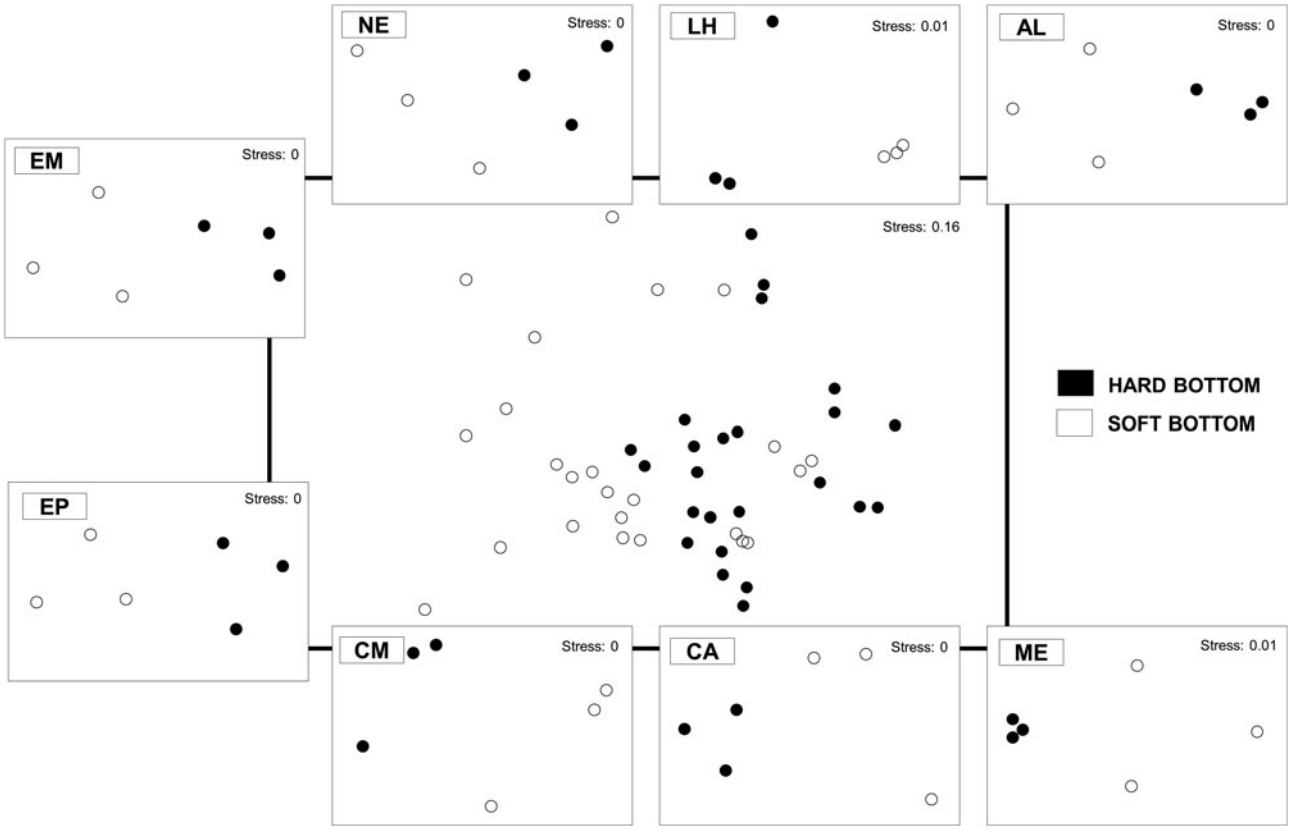


Fig. 4. nMDS plots of replicates comparing the amphipod assemblage collected at each habitat (Hard vs Soft bottom) for the whole study (centre) and each sampling location separately. EM, *El Morche*; NE, *Nerja*; LH, *La Herradura*; AL, *Almuñecar*; EP, *El Peñoncillo*; CM, *Caleta de Maro*; CA, *Cañuelo*; ME, *Marina del Este*. nMDS were based on Bray–Curtis similarity matrix generated using square-root transformed abundance data.

Phoxocephalidae or Oedicerotidae (Macquart-Moulin, 1984; Anokhina, 2006; Michel, 2011; Navarro-Barranco & Hughes, 2015).

Spatial patterns, dispersal ability and migration directions

Contrary to our expectations, demersal amphipod assemblages above rocky and nearby sandy areas were significantly different even at a small spatial scale, highlighting the short-range movements of most demersal amphipods. The absence of physical barriers in the water column and its apparent environmental homogeneity, together with dispersal facilitation by water currents, seems to promote the exchange of individuals among assemblages. However, dispersal capabilities and connectivity of marine populations is often lower than predicted (Marshall *et al*., 2009; Srivastava & Kratina, 2013). An increasing number of small-scale studies in the water column (supported by technical advances and new approaches such as bioacoustics) have highlighted how subtle differences in nutrient resources, temperature, shade or turbulence can determine fine-scale distribution patterns of both low and highly motile pelagic species, especially in nearshore areas (Holliday *et al*., 2003; McManus & Woodson, 2012; Abe *et al*., 2013). Our results support this assumption, highlighting that migrating amphipods in nearshore areas can exhibit well-defined distribution patterns in the water column even at a small spatial scale.

Although differences in assemblage structure were found both at SB and LB, our results pointed out an obvious and noticeable pattern: assemblages collected by light traps were more different the greater the distance between them. When abundance was not considered (analyses conducted using presence/absence transformed data or number of species), there were no significant differences between rocky and sandy areas at SB. On the other hand, differences between habitats at LB were significant when considering several assemblage descriptors: species composition (presence/absence data), assemblage structure (square-root transformed data) and number of species (lower in sandy areas). Physical habitat attributes constitute one of the main factors affecting nearshore motile species and, in this sense, higher number of both large (e.g. fishes) and small (e.g. crustaceans, gastropods) species are commonly found inhabiting rocky bottoms or seagrass meadows than unvegetated sands (Sánchez-Jerez *et al*., 1999; Guidetti, 2000). Shallow rocky bottoms dominated by macroalgae (such as those considered in the present study) provide an enhanced quality habitat compared with sandy bottoms in terms of niche heterogeneity, predation refuge or reduction of abiotic stress (Guidetti, 2000; Benedetti-Cecchi *et al*., 2001; Ólafsson, 2016). Thus, the greater species diversity collected by light traps on rocky shores could be a consequence of the higher number of species that seek shelter in this habitat during the day and/or a nocturnal migration towards rocky areas by species from nearby habitats.

A further evaluation of the species distribution together with their habitat of emergence shed some light on the possible causes of the patterns obtained (Figure 5). All amphipod species that presumably hide on rocky bottoms during the day tend to remain above this habitat during the night: they showed higher abundances in light traps deployed above rocky bottoms and barely a few individuals of only two species reached sandy areas far away from rocky bottoms. Presence of most 'rocky species' (although at very low abundance) above sandy bottoms located nearby explained the lack of significant differences in number of species and species composition between habitats at SB. Previous works studying the effects of rocky reefs (both natural

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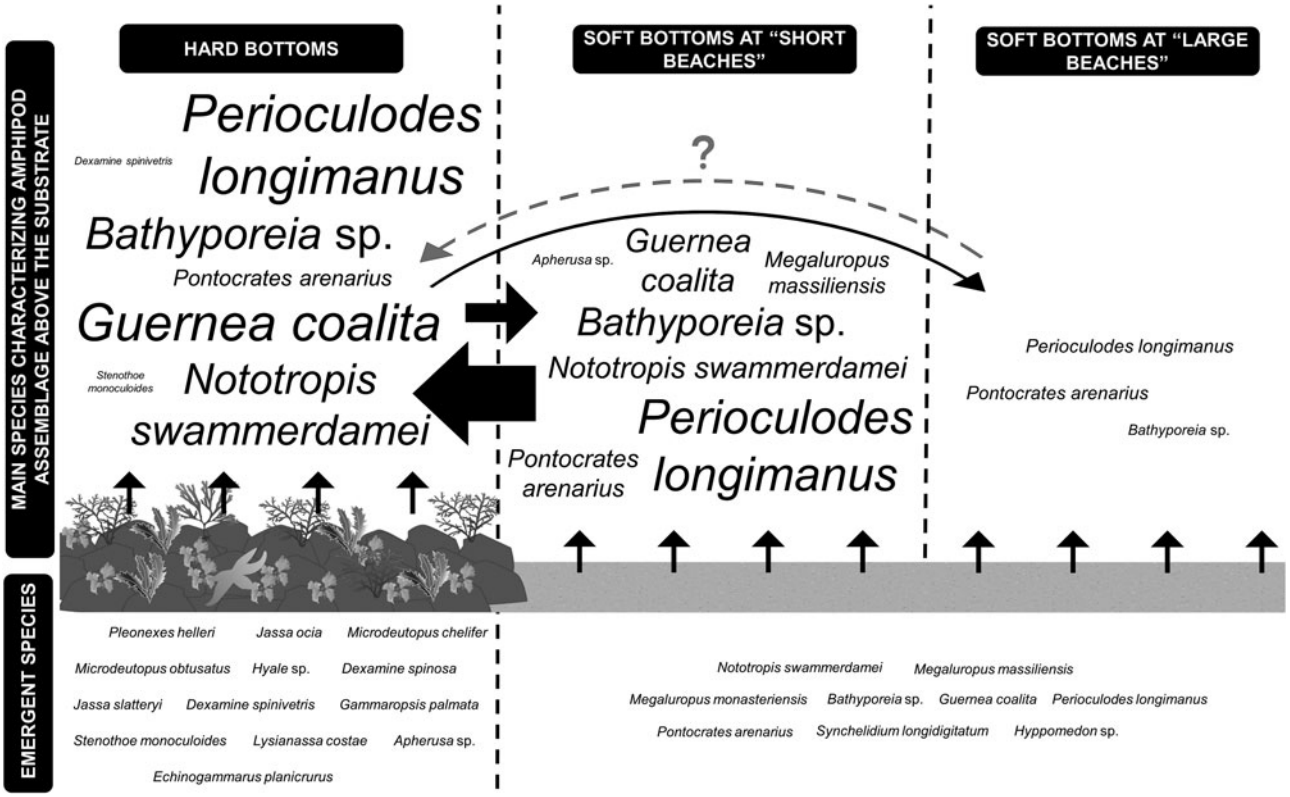


Fig. 5. Summary of the amphipod assemblage in each habitat considered and the assumed direction of their migration. Size of each species is related with their abundance in each habitat and size of arrows represents intensity of displacement. Species emerging either from hard or soft bottoms are listed below.

and artificial) on surrounding soft-bottom amphipod assemblages also reported decreasing diversity values as the distance from the reef increases, due to the lower number of species associated with rocky reefs (Fabi *et al.*, 2002; Barros, 2005). Despite lacking a larval dispersal stage, the high dispersal rates of some of these nocturnal migrants (e.g. the genera *Jassa*, *Apherusa*, *Dexamine*) have been previously highlighted (Myers, 1993; Jørgensen & Christie, 2003; Havermans *et al.*, 2007). However, long-distance dispersal abilities of amphipod species are density dependent, limited to certain life-stages or periods of the year and often related to drifting by currents or rafting (Grant, 1980; Franz & Mohamed, 1989; Thiel & Gutow, 2005; Munguia *et al.*, 2007). The influence of these factors (e.g. fewer numbers of juveniles potentially or strong currents in our study area/period) could explain the limited dispersal abilities showed by 'rocky species' as found here.

On the other hand, our study design does not allow us to explore the dispersal ability of 'sandy species' since the degree of isolation of rocky areas cannot be properly ascertained (there are no rocky bottoms without sediments located nearby). Thus, it is not surprising that all demersal amphipods arising from soft bottoms were dominant above rocky areas, taking into account that sandy bottoms constitute the more extensive environment in the whole study area. However, the higher abundance of these species above rocky than sandy areas is noticeable. This suggests a directional migration from their habitat of emergence towards rocky areas at night and a return trip at dawn to take shelter in sandy bottoms. Many amphipod species have clear habitat preferences and show active host selection when dispersing (Poore *et al.*, 2000; Poore, 2005; Mártinez-Laiz *et al.*, 2018). Migrant amphipods from adjacent sandy biotopes have also been collected above meadows of *Posidonia oceanica* (Linnaeus) Delile, 1813 (Michel, 2011); light traps deployed on this habitat provide exclusive species (e.g. *Synchelidium* sp., *Hippomedon* spp.) not collected by any other sampling methodologies on the foliar stratum, rhizome or seagrass litter. Nocturnal migrations of pelagic species to coral-reef areas have also been suggested by several authors (Yahel *et al.*, 2005*b*; Nakajima *et al.*, 2009). Reasons explaining this migration of demersal amphipods to rocky reefs remain obscure. Predation pressure has often been advocated to explain spatial distribution of demersal species in the water column; near-bottom depletion of zooplankton over coral reefs has been related to the high abundance of benthic predators (both fishes and invertebrates), while the opposite pattern over soft bottoms (higher concentration of demersal zooplankton within 1 m from the bottom at night) is related to the scarcity of sessile zooplanktivorous species (Alldredge & King, 1985; Holzman *et al.*, 2005). Although fish assemblages associated with rocky reefs are more diverse than those from sandy habitats (Guidetti, 2000; Pihl & Wennhage, 2002), abundance and number of predators significantly decrease at night in the former (Azzurro *et al.*, 2007). Pihl & Wennhage (2002) found higher fish abundances at night at shallow soft bottoms, while this significant increase was less pronounced on rocky bottoms. Thus, higher predator abundance and/or predator exposure could explain this horizontal migration pattern. Some herbivorous species (such as *Nototropis swammerdamei*) may migrate to feed on macroalgal beds, but this explanation seems less feasible for detritivorous (e.g. *Bathyporeia* cf. *elegans*, *Megaluropus* sp., *Hippomedon* sp.) or carnivorous species (e.g. *Pontocrates arenarius*, *Perioculodes longimanus*, *Synchelidium longidigitatum* Ruffo, 1947) (Guerra-García *et al.*, 2014). However, it has been proposed that emergence to the water column may be related with mating or ecdysis in some species (Alldredge & King, 1980). A better knowledge of demersal migration purposes would be necessary in order to understand spatial and temporal dynamics of demersal zooplankton.

The highlighted migration patterns may have relevant consequences for coastal ecological processes, such as habitat

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Table 3. Results of the PERMANOVA analysis conducted for the amphipod assemblage, based on Bray–Curtis similarities of square-root transformed data

		Square-root transformed data								Presence/Absence		
Source of variation	df	MS				Pseudo-*F*			*P*(perm.)	MS	Pseudo-*F*	*P*(perm.)
Substrate = Su	1	9911.5				3.826			0.023* (9897)	8962.2	21.181	0.002** (9908)
Distance = Di	1	8132.5				1.011			0.521 (MC) (35)	5223.2	2.023	0.168 (MC) (35)
Location(Di) = Lo(Di)	6	48,247				18.221			<0.001** (9875)	2582.3	12.896	<0.001*** (9915)
Su × Di		6615				2.553			0.073 (9908)	2313.7	5.468	0.046* (9923)
Su × Lo(Di)	6	15,545				5.871			<0.001** (9886)	423.13	2.113	0.069 (9938)
Residuals	32	14,122								200.24		
SNK test (Exploring differences between pairs of levels of factor 'substrate' for each significant interaction)												
										LB	SB	
		LB				SB				Su × Di	**	n.s.
		EM	NE	LH	AL	EM	NE	LH	AL			
	Su × Lo(Di)	**	*	*	**	**	*	*	n.s.			

LB, Long beaches; SB, Short beaches; EM, *El Morche*; NE, *Nerja*; LH, *La Herradura*; AL, *Almuñecar*; EP, *El Peñoncillo*; CM, *Caleta de Maro*; CA, *Cañuelo*; ME, *Marina del Este*; MC, Monte Carlo.
Number of permutations are provided in parentheses.
Significant at: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

connectivity and resource availability (e.g. nutrient flows between rocky and sedimentary habitats caused by the daily horizontal migration of hundreds of thousands of individuals). Fine-scale differences in community structure also raise interesting questions regarding the behavioural adaptations and coevolutionary processes between emergent zooplankton and its predators. Finally, these results (i.e. the high heterogeneity and complexity of apparently homogeneous habitats, as well as the low mobility of these migrant species) also have conservation implications; communities differ even at short distances (i.e. <1 km) and, thus, conservation and management strategies on these habitats should be addressed locally.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S002531542000003X

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