

Diel and tidal variations of benthic assemblages in sediments associated with boulder fields

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ABSTRACT: During daytime low tides, assemblages living in sediments below boulders differ from those living in sediments not overlaid by boulders. It is, however, not known whether these differences are consistent under different tidal or diel conditions. In this study, the composition of assemblages living in sediments associated with boulder fields (below and adjacent to boulders) under different diel (day and night) and tidal (high and low) conditions, was investigated. Significant differences between assemblages living in sediments below boulders and those living in sediments without boulders persisted during different combinations of daylight and state of tide. Species responsible for these differences did, however, change in relation to the level of the tide, but not to time of day. The presence of boulders in sediments allows the coexistence of species usually found on rocky substrata with those usually found in sediments. Mechanisms to explain intertidal movements of invertebrates in either hard or soft-bottom benthic assemblages have been very well described in the literature. The patterns of spatial distribution, in relation to diel and tidal fluctuations, of individual taxa found in this study, however, cannot easily be explained by these mechanisms. Consequently, the mechanisms of migrational movements of benthic assemblages associated with boulder fields need development of new conceptual models. A model considering the structural complexity of the boulder fields and the interactions between hard- and soft-bottom habitats is proposed herein.

KEY WORDS: Tidal movements · Diel movements · Intertidal boulder fields · Macrobenthos · Intertidal migration

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INTRODUCTION

The effects of diel and tidal variations on many natural biological and physical processes have been long and widely recognised. More specifically, organisms in coastal areas show strong ecological (e.g. Cabral & Costa 2001, Saigusa 2001), physiological (e.g. Yamaguchi 2001, Gevaert et al. 2003) and/or behavioural (e.g. Kim & Choe 2003) responses to the cycles of the solar day and/or tides. These responses may be controlled by exogenous factors, as reported for the mussel *Mytilus edulis* (Ameyaw-Akumfi & Naylor 1987) and/or endogenous factors, as reported for the crab *Carcinus maenas* (Naylor 1988). One of these responses is migration, which has conspicuous and easily observable consequences to the patterns of spatial distribution of different components of an assemblage

related to the time of the day and the level of the tide. Most studies on the effects of diel and tidal variations on migration have been on individual species, including representatives of almost every major group of organisms, ranging from microphytobenthos (e.g. Blanchard et al. 2002) to dolphins (e.g. Mendes et al. 2002). Very few studies have, however, looked at more than one species simultaneously in the same habitat (e.g. Hicks 1992, Saigusa & Kazushi 2000).

In addition, many studies of invertebrates have been done on rocky platforms, where movements generally occur in a 'horizontal' way, either up and down the shore or in and out of refuges in accordance with the phase of solar day or tide (e.g. Chelazzi et al. 1988). Alternatively, studies have been done on intertidal sand/mud flats, where movements generally have a 'vertical' component (Yannicelli et al. 2001); i.e.

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animals emerge from the sediment into the water column, where they may move 'horizontally' up and down the shore (e.g. Armonies 1992, Takahashi & Kagawuchi 1997), and return to the sediment in accordance with the solar or tidal cycle. On the other hand, the study of intertidal migration has been ignored in complex systems such as boulder fields, which contain hard and soft substrata. Boulders lying on soft sediments create a series of particular micro-environments (the top, the undersurface and the substrata below the boulder) that not only house species unique to this habitat (Cruz-Motta et al. 2003), but also allow the coexistence of species living on rocky substrata and in sediments (Chapman 2002). The particular assemblages living in boulder fields are likely to migrate in response to diel and/or tidal fluctuations, which affect patterns of spatial distribution. Moreover, mechanisms of intertidal migration in boulder fields could comprise combinations of mechanisms already known for either hard or soft substrata.

Assemblages in sediments below boulders are different from assemblages in sediments away from boulders (Cruz-Motta et al. 2003). The results of Cruz-Motta et al. (2003) were variable, but some taxa such as *Bittium granarium* (Gastropoda, Cerithiidae), *Amphipholes* sp. (Echinodermata Ophiuroidea) and *Cirriformia* sp. (Cirratulidae, Polychaeta), among others, were only present below boulders. Given that the study by Cruz-Motta et al. (2003) was done during daytime low tide, it is important to discover whether these differences are consistent under different diel or tidal conditions, since further development of models and associated hypotheses about processes affecting assemblages in these microhabitats will greatly depend on such knowledge.

It is therefore necessary to establish whether (1) assemblages characteristically found below or away from boulders during low tide during the day are specific to these micro-environments, irrespective of diel and tidal conditions (i.e. they comprise a permanent habitat), or (2) animals use the various micro-environments only during certain diel and/or tidal conditions (i.e. they are temporary habitats). In order to evaluate these alternative models, the present study describes patterns of spatial distribution of benthic assemblages living in sediments associated with boulder fields under different combinations of times of the day (day versus night) and tidal levels (high versus low). Under the 'permanent habitat' model, it was predicted that differences between assemblages living in sediments below boulders and those in sediments away from boulders would be consistent under any diel/tidal combination. Consistent means that the magnitude of the average dissimilarities between assemblages below and those away from boulders and that

the species responsible for those differences will not differ among different combinations of diel and tidal conditions. Under the 'temporary habitat' model, at least 1 of the above predictions will not be true. If this second model is supported, it is implicit that differences are due to diel and/or tidal migrations of some or all components of the assemblages living in sediments associated with boulder fields.

Although very specific mechanisms have been proposed for diel and tidal migrations on rocky or in soft substrata, there is no information on diel and tidal migrations of macrobenthonic organisms in boulder fields. Consequently, in addition to testing the above hypotheses, this study describes patterns of spatial distribution of individual taxa in relation to microhabitat (below vs away from boulders) and diel and tidal conditions in order to propose a conceptual model about specific patterns of movements that may be peculiar to boulder fields.

MATERIALS AND METHODS

Study sites and sampling. Intertidal boulder fields at 3 different locations (Chowder Bay, Hermit Point and Watson's Bay) in Sydney Harbour (New South Wales, Australia) were sampled (Fig. 1). These boulder fields share similar characteristics; they are between 50 to 80 m in length, adjacent to reflective beaches in narrow sheltered bays inside the harbour, and protected from oceanic swells, resulting in little wave-action during most of the year (Short & Trenaman 1992, Short 1993). Boulders at each location are mainly composed of sandstone and the sizes considered in this study ($\approx 1000 \text{ cm}^2$ undersurface area) are minimally disturbed by normal wave-conditions (McGuinness 1984). Boulders typically lie on a layer of sediment, covering a rock platform. The depth of the sediment layer varies between 5 to 12 cm across the 3 locations. Sediments under boulders are typically 'fine sands', with a minimal (<1%) content of fine material (<0.063 mm), with the exception of Watson's Bay that has a coarser sediment ('medium sands').

Each location was sampled under different diel (day and night) and tidal (high and low) conditions on 3 different, randomly selected occasions (i.e. there were 3 replicate times of sampling for each condition; Fig. 2) between October and November 2002. Low or high tides were selected at noon or midnight ($\pm 2.5 \text{ h}$) during spring tides only, to avoid confounding any potential effects of 2 cycles (solar day and tides) with different periods and synodic variations (29 d).

At each combination of location, diel and tidal condition and time, 6 haphazardly chosen boulders of similar size (approximately 1000 cm^2) were totally (low

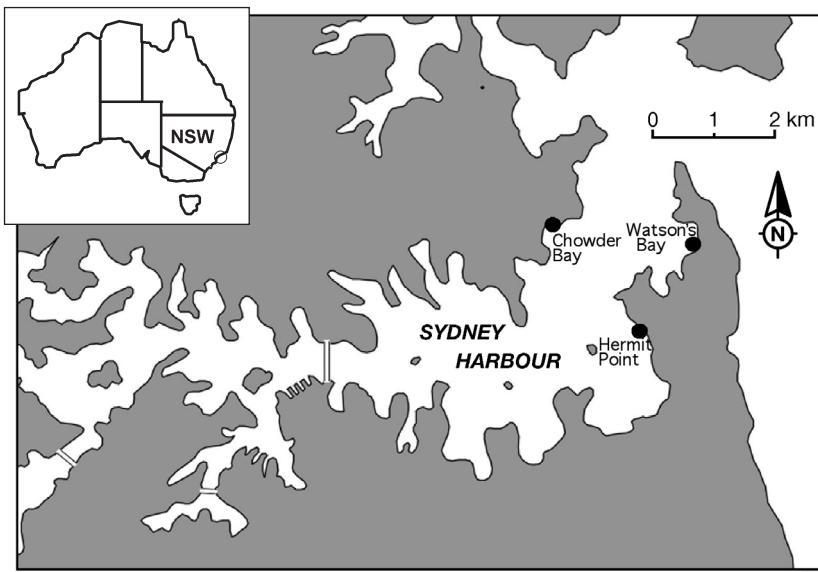


Fig. 1. Study sites in the metropolitan area of Sydney, NSW, Australia

tide) or partially (high tide) overturned and the sediment below sampled using an 18 cm diameter corer, which was pushed down until it made contact with the rock platform. Sediments in the cores were retrieved using an electrically powered suction-sampler. Once sampled, boulders were returned to their original positions. We sampled 6 randomly chosen areas of sediment of equivalent size (1000 cm^2), at least 0.5 m away from each boulder in the same way. The maximum distance between any 2 boulders at these sites ranges between 1 and 1.5 m, so 0.5 m represents a realistic distance away from a boulder.

Samples were taken within a band 1.5 to 2 m up-shore of the lower intertidal edge of the boulder field. Samples were sieved using a 1 mm sieve, stored in a bag, fixed with a buffered 7% solution of formalin in

seawater and stained with neutral red. Samples were later sorted and animals identified to the lowest taxonomic level possible (mainly families and genera). Within each family or genera, animals were distinguished as morpho-species (Oliver & Beattie 1993). Identification to formal species level was difficult to achieve because many of the higher taxa in Australia have not been well-described or have recently been revised. Despite a considerable increase in efforts to describe estuarine invertebrate species in Australia in recent years, a lot of work still needs to be done (Hutchings 1999). Furthermore, some of the animals found in this study would have required dissecting to determine the species, and this was impractical given the number of samples collected.

Analyses of data. Bray-Curtis similarity matrices of samples were constructed from the original biological data matrices. Non-metric multidimensional scaling (nMDS) was used to illustrate patterns in the spatial distribution of the samples. Typically, centroids were plotted; i.e. Bray-Curtis dissimilarity measures were calculated for the averages of the 6 replicates across each one of the treatment combinations. Analyses of similarities (ANOSIM in PRIMER [Plymouth routines in multivariate ecological analysis]; Clarke 1993) tested the null hypothesis of no differences between assemblages in sediments below boulders and assemblages in sediments away from boulders, for each possible combination of locations, diel and tidal conditions and times. When significant differences were found, the taxa making the greatest contribution to these differences were detected using similarity percentages (SIMPER analysis) (PRIMER; Clarke 1993).

To test the null hypothesis of no differences in the magnitude of dissimilarities (between assemblages in sediments below and away from boulders) under different combinations of diel and tidal conditions, 5-factor analyses of variance (ANOVA) tested for differences in this variable among locations (random), tide (fixed and orthogonal), time of day (fixed and orthogonal) and treatment (below and away from boulders, fixed and orthogonal), at 3 different times (random and nested within the first 3 factors). Independent dissimilarity measures were obtained by randomly selecting pairs of samples from the 2 groups of 6 replicate samples (below and away from boulders) per each combination of location, diel and tidal condition and time, in such a way that independent replicate measures of dissimilarity (2) were obtained for (1) dissimilarities within

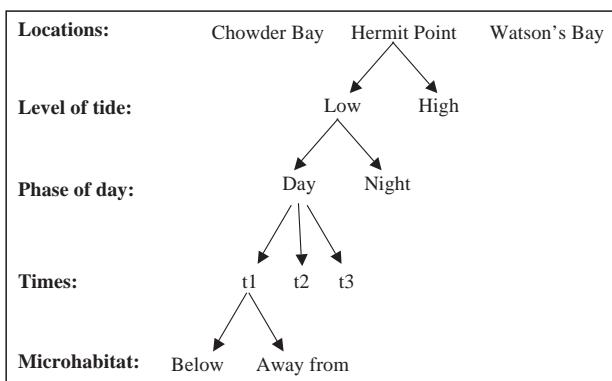


Fig. 2. Experimental design. Below: beneath boulder; Away from: sediment ≥ 0.5 m distant from relevant boulder; further details in 'Materials and methods'

samples taken below boulders, (2) dissimilarities within samples taken away from boulders and (3) dissimilarities between treatment groups (below vs away from boulders). Additionally, similar analyses of variance (5-factor) were done on the abundance of some taxa (those identified in the SIMPER analyses). Heterogeneity of variances were tested using Cochran's C-test, and transformation ($\ln x + 1$) was done when appropriate, following the recommendations of Underwood (1997) and McGuinness (2002).

RESULTS

In a total of 432 samples, there were 157 taxa, of which between 10 and 21 taxa comprised 75 % of all animals at each location (Table 1). Of these abundant taxa, only *Erithonius* sp. (Gammarida), *Amphipholes* sp. (Ophiuroidea) and *Birubius* sp. (Gammarida) were common to all 3 locations.

As previously observed during daytime low tides, assemblages from below boulders were clearly different from those away from boulders in any diel/tidal combination (Fig. 3). These patterns were mostly confirmed by analyses of dissimilarities within and between treatments (i.e. below and away from boulders; Table 2). Despite the significant third-order interaction

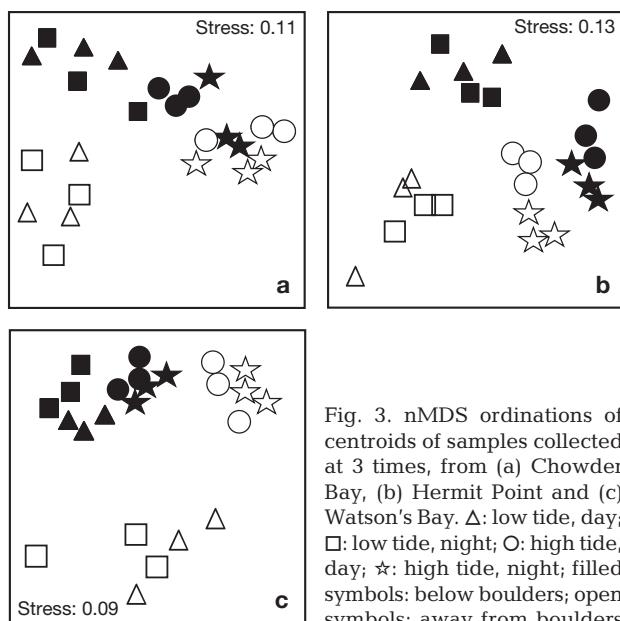


Fig. 3. nMDS ordinations of centroids of samples collected at 3 times, from (a) Chowder Bay, (b) Hermit Point and (c) Watson's Bay. Δ : low tide, day; \square : low tide, night; O : high tide, day; \star : high tide, night; filled symbols: below boulders; open symbols: away from boulders

among location, tide and treatment, *a posteriori* comparisons (Student-Newman-Keuls tests) showed that dissimilarities between assemblages below and those away from boulders were larger than dissimilarities among replicates in samples taken below boulders (in 5 of 6 possible combinations) and among replicates in samples taken away from boulders (always) (Table 2, Fig. 4). As there was no significant variability among 'times' in analyses of dissimilarities (Table 3), times were averaged (Fig. 4).

In addition, Fig. 3 shows that assemblages sampled during low tide were clearly separated from assemblages sampled during high tide; this was particularly conspicuous at Hermit Point (Fig. 3b). Similarly, the magnitude of the average dissimilarity between assemblages found below boulders and those away from boulders was significantly different in relation to tide across all 3 locations (Table 2, Fig. 4). These results support the temporary habitat model that assemblages use different micro-environments in sediments associated with boulder fields only during certain diel and tidal conditions. More specifically, it would appear that only tidal variations are important. No significant effect of day/night was found in the structure of assemblages (Table 3, Fig. 3).

Table 1. Most abundant taxa (totalling 75 % of total abundance) in assemblages sampled at 3 locations, Sydney, Australia. N: no. of taxa; n: no. of individuals

Class	Chowder Bay (N = 120; n = 8421)	Hermit Point (N = 114; n = 4161)	Watson's Bay (N = 114; n = 4680)
Cnidaria			<i>Actinia tenebrosa</i>
Crustacea	<i>Anthuridae</i> sp. B <i>Dexaminidae</i> sp. A <i>Erithonius</i> sp. <i>Hyale</i> sp. <i>Melita</i> sp. <i>Mysidacea</i> sp. A <i>Birubius</i> sp. <i>Podoceridae</i> sp. A <i>Tannaidacea</i> sp. B	<i>Anthuridae</i> sp. B <i>Dexaminidae</i> sp. C <i>Erithonius</i> sp. <i>Paraphoxus</i> sp. <i>Gammaridae</i> sp. D <i>Hyale</i> sp. <i>Leucothoidae</i> sp. A <i>Melita</i> sp. <i>Birubius</i> sp. <i>Sphaeromatidae</i> sp. A	<i>Aora</i> sp. <i>Erithonius</i> sp. <i>Isaeidae</i> sp. A <i>Pagurus</i> sp. <i>Birubius</i> sp.
Gastropoda		<i>Bittium granarium</i>	<i>Bittium granarium</i>
Nemertini			<i>Nemertean</i> sp. A
Oligochaeta		<i>Oligochaete</i> sp. A	
Polychaeta		<i>Capitella</i> sp. <i>Mediomastus</i> sp. <i>Cirriformia</i> sp. <i>Nereididae</i> sp. B <i>Orbiniidae</i> sp. A <i>Syllidae</i> sp. A	<i>Capitella</i> sp. <i>Cirriformia</i> sp. <i>Eunice</i> sp. p. B <i>Nereididae</i> sp. B <i>Orbiniidae</i> A <i>Syllidae</i> sp. A
Sipunculida		<i>Golfingiidae</i> sp. A <i>Phascolosoma</i> sp.	<i>Golfingiidae</i> sp. A <i>Phascolosoma</i> sp.
Holothuria	<i>Amphipholes</i> sp.	<i>Amphipoles</i> sp.	<i>Amphipoles</i> sp. <i>Chiridota</i> cf. <i>gigas</i>

Table 2. *A posteriori* comparisons (Student-Newman-Keuls tests) among combinations of treatments of the significant third-order interaction (location \times tide \times treatment; see Table 3). BE: within samples from sediments below boulders; OUT: within samples from sediments away from boulders; BET: between samples collected in these environments. $>$ and $<$ indicate significant differences at $p < 0.05$

Source		Chowder Bay	Hermit Point	Watson's Bay
Within and between samples	Low tide	BET = BE $>$ OUT	BET $>$ BE = OUT	BET $>$ BE = OUT
	High tide	BET $>$ BE = OUT	BET $>$ BE $>$ OUT	BET $>$ BE = OUT
Tidal comparison	BE	Low $>$ High	Low $>$ High	Low = High
	OUT	Low $>$ High	Low = High	Low $>$ High
	BET	Low $>$ High	Low $>$ High	Low $>$ High

Moreover, the taxa responsible for 70 % of the total differences between assemblages in sediments below boulders and those away from boulders mainly varied with tidal condition and between locations (Table 4). During the day or night, only between 6 and 21 % of taxa (depending on the location), were found at low and high tide. Conversely, during low or high tide, between 25 and 60 % of taxa responsible for differences between assemblages below and those outside boulders, were found during the day and night.

Analyses of individual taxa revealed the existence of 11 different patterns of spatial distribution in relation to the microhabitat (below vs away from boulders), diel and tidal condition (Table 5, Fig. 5): (1) taxa found below boulders almost exclusively during low tide (e.g. Fig. 5a); (2) taxa found in sediments away from boul-

Table 3. Analysis of variance of 3 types of dissimilarity (treatments [Tr]: BE, OUT and BET; see Table 2) at 3 random locations (L), 2 fixed tidal (H) levels (low and high) and 2 fixed diel (D) conditions (day and night) during 3 random times (Ti; nested in Location \times Tide \times Diel). Significance: * $p < 0.05$; ** $p < 0.01$; ns = not significant

Source	df	MS	F	p
Location (L)	2	1625.34	7.55	**
Tide (H)	1	12459.45	115.17	**
Diel (D)	1	157.59	0.89	ns
Treatment (Tr)	2	7136.08	50.54	**
Time (L \times H \times D)	24	215.25	1.5	ns
L \times H	2	108.18	0.5	ns
L \times D	2	178.06	0.83	ns
L \times Tr	4	141.18	0.99	ns
H \times D	1	4.89	0.02	ns
H \times Tr	2	309.11	0.78	ns
D \times Tr	2	207.78	5.87	ns
Tr \times Ti (L \times T \times D) ^a	48	123.51		
L \times H \times D	2	288.02	1.34	ns
L \times H \times Tr	4	397.36	2.78	*
L \times D \times Tr	4	35.39	0.25	ns
H \times D \times Tr	2	266.55	3.01	ns
L \times D \times H \times Tr	4	88.54	0.62	ns
Residual ^a	108	151.83		
Total pooled ^a	156	143.12		
Total	215			

^aPost-hoc pooling ($p > 0.25$)

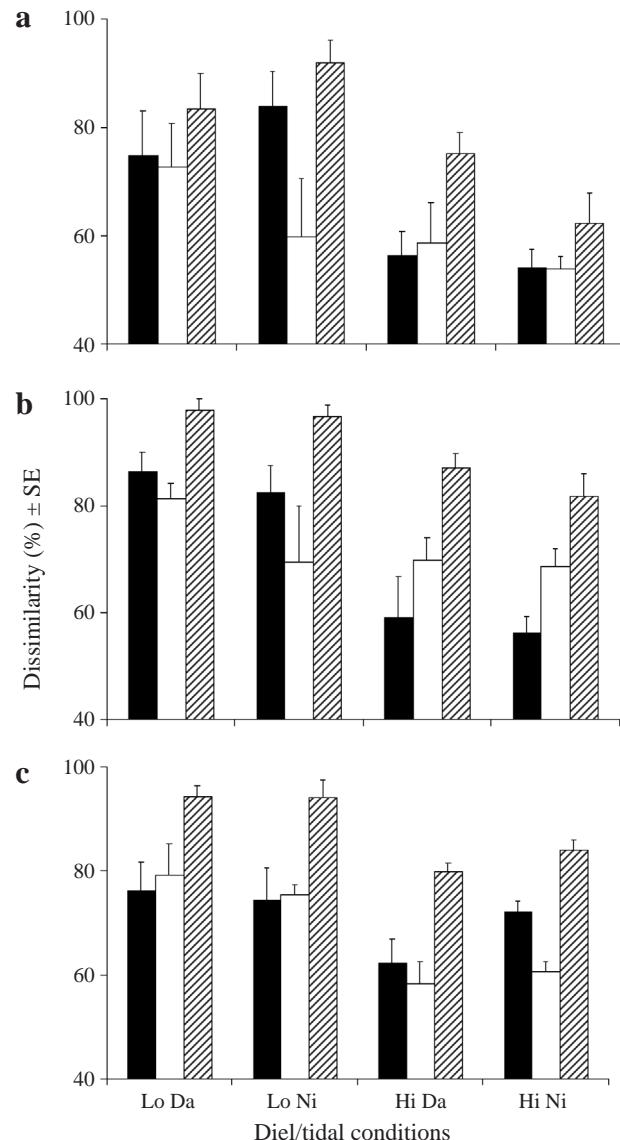


Fig. 4. Bray-Curtis dissimilarity values for 4 different diel/tidal combinations—low day (Lo Da), low night (Lo Ni), high day (Hi Da) and high night (Hi Ni)—at 3 locations—(a) Chowder Bay, (b) Hermit Point and (c) Watson's Bay. ■: dissimilarities within samples collected in sediments below boulders; □: dissimilarities within samples collected in sediments away from boulders; ▨: dissimilarities between the 2 groups of samples (below and away from boulders)

Table 4. Taxa responsible for 70% of total dissimilarity (SIMPER) between assemblages sampled in sediments below boulders and sediments away from boulders at 3 locations and 4 diel/tidal combinations. Percentages of taxa common to the 3 locations under each of the diel/tidal combinations are also indicated

Condition	Chowder Bay	Hermit Point	Watson's Bay	% common
Low tide, day	<i>Hyale</i> sp. <i>Mediomastus</i> sp. <i>Phoxocephalidae</i> sp. A <i>Amphiphiles</i> sp. <i>Melita</i> sp. <i>Cirriformia</i> sp.	<i>Hyale</i> sp. <i>Cirolanidae</i> sp. A <i>Golfingiidae</i> sp. A <i>Oligochaeta</i> sp. A <i>Mediomastus</i> sp. <i>Syllidae</i> sp. A	<i>Nemertean</i> sp. A <i>Syllidae</i> sp. A <i>Birubius</i> sp. <i>Actinia tenebrosa</i> <i>Cirriformia</i> sp. <i>Bittium granarium</i> <i>Erithonius</i> sp.	0
Low tide, night	<i>Hyale</i> sp. <i>Birubius</i> sp. <i>Mediomastus</i> sp. <i>Erithonius</i> sp.	<i>Hyale</i> sp. <i>Cirolanidae</i> sp. A <i>Cirriformia</i> sp. <i>Paraphoxus</i> sp. <i>Erithonius</i> sp. <i>Patiriella exigua</i> <i>Anthuridae</i> sp. B <i>Mediomastus</i> sp. <i>Birubius</i> sp.	<i>Nemertean</i> sp. A <i>Sphaeromatidae</i> sp. A <i>Birubius</i> sp. <i>Bittium granarium</i> <i>Amphiphiles</i> sp. <i>Mediomastus</i> sp. <i>Syllidae</i> sp. A <i>Cirriformia</i> sp. <i>Paraphoxus</i> sp.	10
High tide, day	<i>Melita</i> sp. <i>Anthuridae</i> sp. B <i>Erithonius</i> sp. <i>Aora</i> sp.	<i>Bittium granarium</i> <i>Paraphoxus</i> sp. <i>Birubius</i> sp. <i>Melita</i> sp. <i>Amphiphiles</i> sp. <i>Capitella</i> sp. <i>Orbiniidae</i> sp. A <i>Syllidae</i> sp. A	<i>Syllidae</i> sp. A <i>Isaeidae</i> sp. A <i>Erithonius</i> sp. <i>Aora</i> sp. <i>Pagurus</i> sp. <i>Amphiphiles</i> sp. <i>Chiridota cf. gigas</i> <i>Birubius</i> sp. <i>Orbiniidae</i> sp. A	7
High tide, night	<i>Dexaminidae</i> sp. A <i>Anthuridae</i> sp. B <i>Tannaidacea</i> sp. B <i>Erithonius</i> sp.	<i>Bittium granarium</i> <i>Erithonius</i> sp. <i>Dexaminidae</i> sp. C <i>Leucothoidae</i> sp. A <i>Birubius</i> sp. <i>Melita</i> sp. <i>Capitella</i> sp.	<i>Isaeidae</i> sp. A <i>Erithonius</i> sp. <i>Actinia tenebrosa</i> <i>Capitella</i> sp. <i>Aora</i> sp. <i>Syllidae</i> sp. A <i>Chiridota cf. gigas</i> <i>Nereididae</i> sp. B <i>Pagurus</i> sp.	6

ders almost exclusively during low tide (e.g. Fig. 5b); (3) taxa found in sediments below boulders almost exclusively during high tide (e.g. Fig. 5c); (4) taxa found in sediments away from boulders almost exclusively during high tide (e.g. Fig. 5d); (5) taxa that were more abundant during high than low tide, but in similar numbers in sediments below or away from boulders (e.g. Fig. 5e); (6) taxa found in sediments below boulders almost exclusively during low tide but which, during high tide, were more abundant in sediments away from than below boulders (e.g. Fig. 5f); (7) taxa found almost exclusively below boulders, but in larger numbers during the day than the night (e.g. Fig. 5g); (8) taxa found only during high tides at night in similar numbers in sediments below or away from boulders (e.g. Fig. 5h); (9) taxa found almost exclusively in sediments below boulders under any diel and tidal combination (e.g. Fig. 5i); (10) taxa found almost exclusively in sediments away from boulders under any diel/tidal conditions (e.g. Fig. 5j) and (11) taxa showing no clear

pattern of spatial distribution, in most cases due to great temporal variability (Table 5).

As for the entire assemblage, most of these individual taxa showed patterns of spatial distribution that could be explained by the temporary habitat model (Patterns 1 to 8; Table 5, Fig. 5a–h); i.e. they were found in a particular microhabitat associated with the boulder field only during certain diel and tidal combinations. Nevertheless, a few taxa showed patterns of spatial distribution that could be explained by the permanent habitat model. They were always found in the same microhabitat, either below (Pattern 9; Table 5, Fig. 5i) or away from (Pattern 10; Table 5, Fig. 5j) boulders, during any diel and/or tidal condition.

Most taxa with patterns of spatial distribution that could be explained by the temporary habitat model, showed a strong pattern associated with tidal fluctuations (Patterns 1 to 6; Table 5, Fig. 5a–f) and only a few showed a pattern associated with diel or tidal and diel changes (Patterns 7 and 8; Table 5, Fig. 5g,h).

Table 5. Patterns of spatial distribution of most important taxa. Low: low tide; high: high tide; below: sediments below boulders; away from: sediments away from boulders; day: during day; night: during night; always: under any combination of diel and tidal condition

Pattern	Description	Chowder Bay	Hermit Point	Watson's Bay
1	Low > high Below > away from	<i>Mediomastus</i> sp.	<i>Patiriella exigua</i>	<i>Paraphoxus</i> sp.
2	Low > high Away from > below	<i>Hyale</i> sp.	<i>Cirolanidae</i> B <i>Hyale</i> sp.	<i>Sphaeromatidae</i> sp. A
3	High > low Below > away from	<i>Bittium granarium</i> <i>Orbiniidae</i> sp. A <i>Amphipholes</i> sp. ^a	<i>Bittium granarium</i> <i>Paraphoxus</i> sp. <i>Birubius</i> sp. <i>Amphipholes</i> sp. <i>Orbiniidae</i> sp. A	<i>Pagurus</i> sp. <i>Golfingiidae</i> sp. A <i>Idoteidae</i> sp. A <i>Orbinnidae</i> sp. A ^b
4	High > low Away from > below	<i>Anthuridae</i> sp. B <i>Erichtonius</i> sp. <i>Tannaaidacea</i> sp. B <i>Aora</i> sp. <i>Anthuridae</i> sp. A	<i>Pyramidellidae</i> A <i>Ciliindrobelerididae</i> sp. A <i>Soletellina</i> sp.	<i>Capitella</i> sp. <i>Aora</i> sp. <i>Eunice</i> sp. <i>Isaeidae</i> sp. A <i>Erichtonius</i> sp.
5	High > low Below = away from	<i>Podoceridae</i> sp. A <i>Hymenosomoatidae</i> sp. A	<i>Capitella</i> sp. <i>Melita</i> sp.	<i>Nereididae</i> sp. B
6	At high tide: away from > below At low tide: below > away from	<i>Hemichordata</i> sp. A	<i>Oligochaeta</i> sp. A	<i>Actinia tenebrosa</i> <i>Nematoneis</i> sp.
7	Day > night Below > away from	<i>Pilumnidae</i> sp. A <i>Alphidae</i> sp. A	<i>Syllidae</i> sp. A	<i>Syllidae</i> sp. A
8	Only during high tide at night Below = away from	<i>Mysidacea</i> sp. A	<i>Dexaminiidae</i> sp. C <i>Erichtonius</i> sp. <i>Leucothoidae</i> sp. A	
9	Below > away from Always	<i>Phascolosoma</i> sp. <i>Polyonidae</i> sp. A	<i>Cirriformia</i> sp. <i>Golfingiidae</i> sp. A <i>Phascolosoma</i> sp.	<i>Bittium granarium</i> <i>Cirriformia</i> sp. <i>Birubius</i> sp. <i>Phascolosoma</i> sp.
10	Away from > below Always	<i>Emerita</i> sp.	<i>Hemichordata</i> sp. A	
No	No pattern, high temporal variability	<i>Birubius</i> sp. <i>Melita</i> sp. <i>Cirriformia</i> sp.	<i>Anthuridae</i> sp. B <i>Mediomastus</i> sp. <i>Nereididae</i> sp. B	<i>Amphipholes</i> sp. <i>Nemertean</i> sp. A <i>Mediomastus</i> sp.

^aDiel component significant, high > low only during day; ^bdiel component significant, below > outside only during day

DISCUSSION

At each location and each time sampled, assemblages living in sediments below boulders were different from assemblages living in sediments away from boulders under any diel and tidal combination. Never-

theless, the species responsible for these differences varied markedly with level of the tide, but not with time of day (Table 6). These results support the temporary habitat model, implying that different microhabitats associated with sediments in boulder fields (below and away from boulders) are used by most invertebrate species during different phases of the tide. There was a clear temporal separation of the use of the resources provided by boulders (e.g. refuge, shelter, food, mating ground, etc.), associated with level of the tide.

Although these patterns were similar for different locations, species composition differed between locations, indicating that different species were subjected to similar ecological processes at different locations. In contrast, in some cases, the same taxon showed different patterns of spatial distribution in relation to time of day and level of tide in different locations. For example, *Bittium granarium* at Watson's Bay was always more

Table 6. Percentage of taxa in Table 5, shared between day and night under each tidal condition and between low and high tides at each diel condition at the 3 locations studied

Condition		Chowder Bay	Hermit Point	Watson's Bay
Day vs	Low	43	25	46
Night	High	60	38	46
Low vs	Day	13	8	21
High	Night	14	20	6

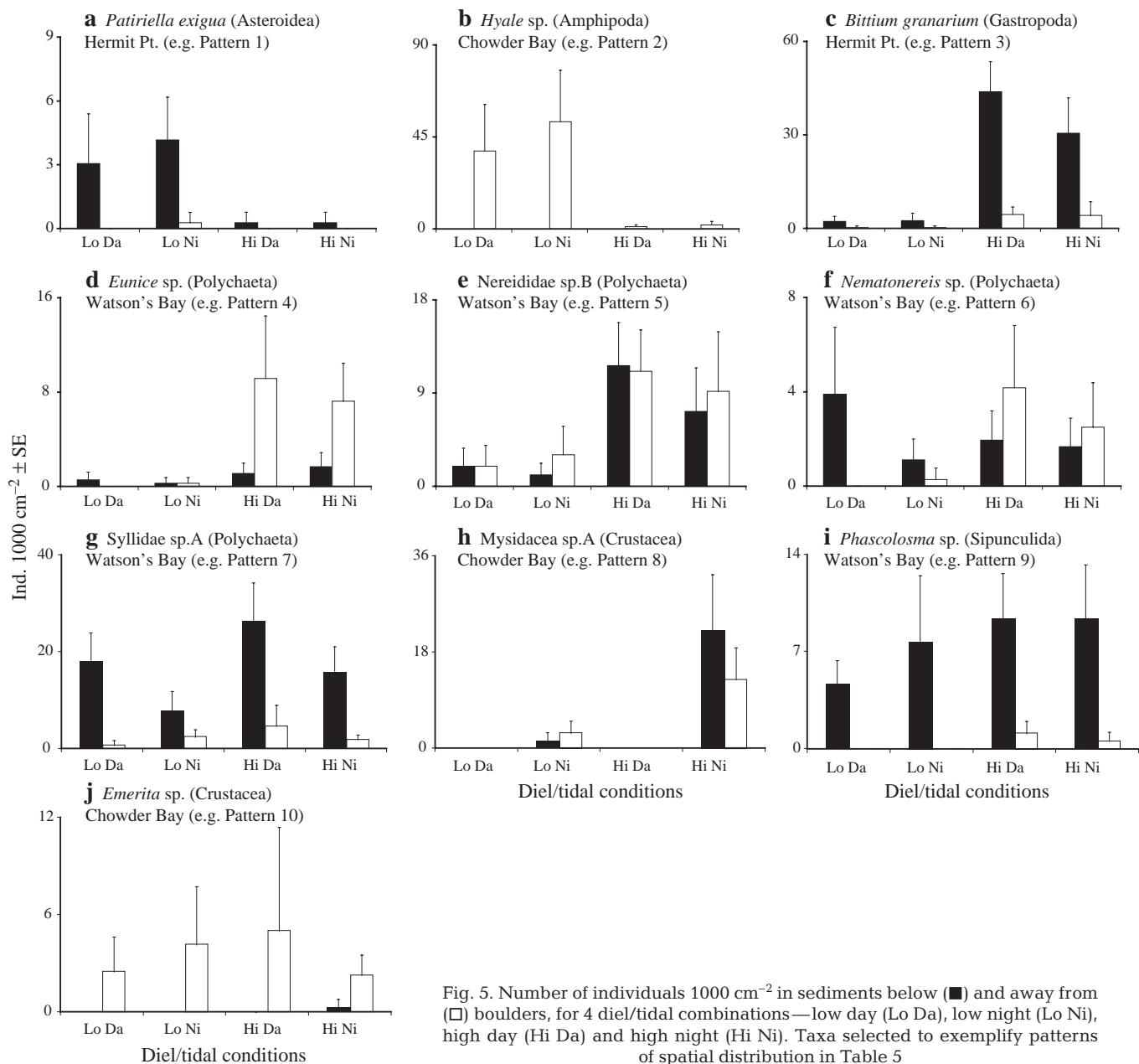


Fig. 5. Number of individuals 1000 cm^{-2} in sediments below (■) and away from (□) boulders, for 4 diel/tidal combinations—low day (Lo Da), low night (Lo Ni), high day (Hi Da) and high night (Hi Ni). Taxa selected to exemplify patterns of spatial distribution in Table 5

abundant in sediment below boulders than in sediments away from boulders in any diel and tidal combination, whereas at Hermit Point and Chowder Bay it was also more abundant in sediments below boulders than in sediments away from boulders, but only during high tide. This species was almost absent from samples taken during low tide. More conspicuously, the unidentified Gammaridae sp. A, was always found below boulders at Watson's bay during low tide, while at Hermit Point it was below boulders during high tide.

Other studies have reported a site-specific behaviour. For example, the coastal European sea urchin *Paracentrotus lividus* migrates up and down the shore only dur-

ing the day in some areas of the Mediterranean, in contrast to other studies in other areas where this sea urchin only migrates up and down shore during the night (Barnes & Crook 2001). These differences between locations in patterns shown by individuals of the same species may be due to differences in physical and/or chemical conditions, such as the composition and/or structure of the sediment (Saigusa 2001), or to differences in population structure at different locations. For example, it has been reported that juveniles of the crab *Carcinus maenas*, the isopod *Eurydice pulchra* and the amphipod *Orchestoidea tuberculata* behave differently from the adults (Naylor & Kennedy 2003).

As found for the entire assemblage, univariate analyses demonstrated significant differences in relative abundances of most of the taxa in relation to diel and/or tidal fluctuations, supporting the temporary habitat model. Of all the taxa reported by Cruz-Motta et al. (2003) to be found in sediments below boulders during daytime low tides, only the cirratulid (Polychaeta) *Cirriformia* sp. and the sipunculid *Phascolosoma* sp. used the microhabitat below the boulder (Pattern 9; Table 5) consistently at any diel or tidal phase across all locations where they were observed (permanent habitat model).

Most of the temporal changes in individual taxa responded exclusively to the level of the tide (Patterns 1 to 6; Table 5, Fig. 5a-f). Few taxa, however, showed significant differences in relation to time of day (Pattern 7; Table 5, Fig. 5g) or due to interactions between time of day and level of tide (Pattern 8 and exceptions in Pattern 3; Table 5, Fig. 5h). These results strongly suggest a very dynamic migrational movement in response to the movement of the tides and, in a minor degree, to time of day. This has similarly been the case in studies of internal clocks determining the rhythms of intertidal organisms. The majority of these organisms respond exclusively to tides, and not to phase of the solar day (Palmer 1995, 2000). Some exceptions to this generalisation are the crabs *Carcinus maenas* (Warman et al. 1993) and *Sesarma reticulatum* (Palmer 1990) and the amphipod *Orchestoidea tuberculata* (Naylor & Kennedy 2003).

The existence of several patterns of spatial distribution in relation to level of tides and, to a lesser degree, to the phase of the solar day, implies the existence of different mechanisms of migration. Migrational movements are considered to be different in different habitats. For example, it has been proposed that organisms living on rocky shores would tend to have 2 types of 'horizontal' movement: in and out of refuges as the phase of the day and/or tide changes ('isospacial' strategy) or up- and downshore with the phase of the tide ('isophasic' strategy; e.g. Chelazzi et al. 1988). On the other hand, organisms living in sediments tend to show 'vertical' movement, emerging from the sediment into the water and moving back into the sediment according to the day and/or phase of tide (e.g. Warman et al. 1991, Takahashi & Kawaguchi 1997). Note that the words 'horizontal' and 'vertical' have been stressed because they represent the main difference between the movements found in soft sediments versus hard substrata.

Boulder fields may comprise one of the few habitats in which there could be a combination of these strategies. In the present study, taxa such as the gammarid (Amphipoda) *Hyale* sp. and 2 unidentified isopods of the families Cirolanidae and Sphaeromatidae had patterns of spatial distribution (found in sediments away

from boulders almost exclusively during low tide) that would be easily explained by the process of emergence typically seen in soft-bottom benthic organisms (e.g. De Ruyck et al. 1991, Yanicelli et al. 2001). Conversely, taxa like the anemone *Actinia tenebrosa*, which is typically found on hard substrata, had a pattern of spatial distribution that would be more easily explained by isospacial behaviour.

The patterns of spatial distribution of individual taxa described in this paper suggest, however, that there may be more mechanisms of migrational movements in intertidal boulder fields than those previously described for exclusively soft or hard substrata. For example, Patterns 1 and 2 (Table 5) may be the result of movements of organisms up and down the shore with the phase of the tide (isophasic), but this movement may result in taxa leaving or entering sediments below boulders, a potential refuge (Pattern 1; Table 5), while other taxa (Pattern 2; Table 5) do not.

In addition, due to the 3-dimensionality added by boulders, isophasic movements in relation to the phase of the tide by some organisms may be in 2 different dimensions, with some organisms moving up and down the shore horizontally, and others moving up and down the boulders vertically. An example of the latter is the sea-urchin *Helicon pruinosa*, which migrates from the bottom to the top of boulders as the tide rises (Henniger & Hodgson 2001). The presence of boulders may be important in determining and/or modulating the mechanisms of intertidal migration and the consequent patterns of spatial distribution for 2 reasons: (1) the added 3-dimensionality created by the boulders, and (2) because the boulders are potential refuges and, as proposed by some authors (e.g. Lawrie et al. 1999), migration of some taxa may depend on the availability of refuges. For example, some species may be intrinsically isospacial, but a shortage of refuges may force them to move isophasically.

The idea of refuge itself has to be considered cautiously. Some investigators have the intuitive idea that the micro-environment below a boulder is a refuge, whereas sediments next to it or the areas on the top of boulders are not (e.g. Rao & Sarma 1979, Rocha 1995). It may be, however, that the top of a boulder constitutes a refuge for taxa whose predators arrive in sediments below boulders during high tide (e.g. the taxa in Patterns 3 & 5 in Table 5). A similar process has been reported for the snail *Littorina irrata* that moves up and down stalks of seagrass with the tide, and stays in a spatial refuge out of the reach of predators (e.g. Vaughn & Fisher 1988). In these circumstances, the concept of isospaciality would have to be reconsidered.

The above are only a few of many possible types of movement that could exist and which could explain the patterns observed in this study. Fig. 6 presents

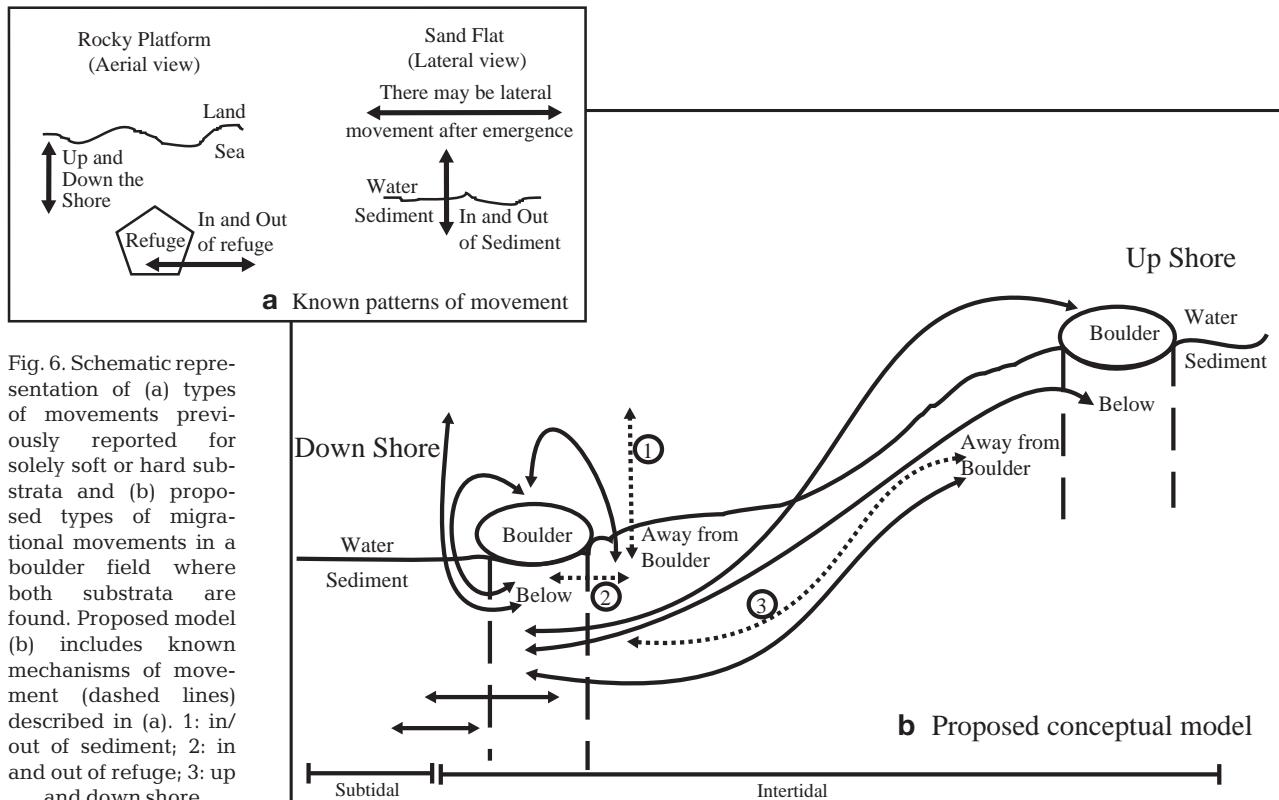


Fig. 6. Schematic representation of (a) types of movements previously reported for solely soft or hard substrata and (b) proposed types of migrational movements in a boulder field where both substrata are found. Proposed model (b) includes known mechanisms of movement (dashed lines) described in (a). 1: in/out of sediment; 2: in and out of refuge; 3: up and down shore

a schematic representation of the possible types of migrational movements that might be found in intertidal boulder fields, and compares them with the main mechanisms previously reported for intertidal sand-flats and rocky shores. The situation would be more complicated if other possible pathways for assemblages living in other micro-environments associated with boulder fields (e.g. those on top of boulders), but not considered in this study, were included.

CONCLUSIONS

This study has shown that assemblages in sediments associated with boulder fields respond strongly to tidal and, to a lesser degree, diel fluctuations. Very few organisms used a specific micro-environment (sediments either below or away from boulders) as a permanent habitat. This study has also shown that more mechanisms could potentially explain migrational movements of organisms in boulder fields than those predicted by models proposed for either hard or soft substrata. Consequently, a new conceptual model on the possible migrational mechanisms is suggested. To evaluate this model, further studies are needed to test hypotheses on the different patterns of movements proposed herein.

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