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Source: American Malacological Bulletin, 32(1):94-103. 2014.

Published By: American Malacological Society

DOI: <http://dx.doi.org/10.4003/006.032.0108>

URL: <http://www.bioone.org/doi/full/10.4003/006.032.0108>

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Colonization of prosobranch gastropods onto artificial substrates: Seasonal patterns between habitat patches

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Abstract: We used artificial substrates to investigate the seasonal variation in colonization patterns of subtidal prosobranch gastropods in Gran Canaria (Canary Island, Spain, north-eastern Atlantic), via monthly deployment of artificial substrates throughout an entire annual cycle from February 2009 to January 2010, on each of four habitat patches (seagrasses, sandy patches, ‘urchin-grazed’ barrens and macroalgal-dominated beds) within a coastal landscape. A total of 8,524 prosobranch gastropods, including 12 dominant taxa, were collected as post-larval, juvenile, and adult individuals. In general the amount of variability explained by the type of habitat slightly dominated over seasonal variation, which was outweighed by variation from month to month, to explain colonization patterns. Throughout the study, larger numbers of colonizers of *Bittium* spp. (Leach in Gray, 1847), *Columbella adansonii* (Menke, 1853), *Gibberula caelata* (Monterosato, 1877), *Mitra* spp. (Lamarck, 1798), *Rissoa* spp. (Fremenville in Desmarest, 1814), and *Smaragdia viridis* (Linnaeus, 1758) were observed in artificial substrates deployed in vegetated substrates, highlighting the relevance of vegetation as a matrix habitat for subtidal prosobranch gastropods. *Cerithium rupestre* (Risso, 1986) and *Clavatula mystica* (Reeve, 1843), however, were mainly observed on sandy patches. *Rissoa* spp. showed a peak in the arrival of new colonizers during spring-early summer whereas *Tricolia pullus canarica* (Nordsieck, 1973) showed a peak during winter-early spring. Importantly, the other prosobranch gastropods did not show significant differences in the arrival of colonizers between annual seasons. In summary, these results demonstrate that seasonality is strongly outweighed by small-scale temporal variability (here variation from month to month) and the type of habitat patch as drivers of prosobranch gastropod colonization patterns in coastal landscapes.

Key words: artificial structures, collectors, settlement, subtidal medium, Canary Islands

In coastal environments across the globe, assemblages of gastropods may occupy patches of distinct habitats at varying abundance and diversity (Chapman 2000). Associations between habitat types and the abundances and structure of gastropod assemblages have been identified for a range of geographical regions (e.g., Chemello *et al.* 1998, Russo and Terlizzi 1998, Russo *et al.* 2002, Rueda and Salas 2003, Arroyo *et al.* 2006, Tuya *et al.* 2008).

Early colonization of habitat patches by invertebrates can have important effects on subsequent patterns of succession (Sousa 1979, 1984, Lubchenco 1983, Anderson and Underwood 1997). Yet, dispersal and colonization processes are still poorly known (Cowen and Sponaugle 2009). Colonizers arrive as propagules (*i.e.*, larvae), or emigrate as sub-adults and adults from adjacent habitats via crawling, drifting or rafting through the water-column (Martel and Chia 1991, Chapman 2002). Most marine invertebrates, including gastropods, have a larval dispersal that can last from seconds and minutes to months (Scheltema 1986, Gaines and Bertness 1992). However, even short-lived larvae have the potential to disperse some distance from their parental populations, especially in coastal habitats where water

movement is important (Chapman 2002). In the particular case of gastropods, early larval development is a sensitive period affecting their life cycles (Rumrill 1990, Martel and Chia 1991). Some gastropods undergo direct development and lack a pelagic stage. Others release their eggs into the water column and have pelagic larval stages that are either planktotrophic (*i.e.*, a free-swimming feeding stage capable of spending prolonged periods in the water column) or lecithotrophic (*i.e.*, without a free-swimming feeding stage) (Ávila *et al.* 2012). These distinct modes of reproduction can determine the processes of colonization of new habitats by marine gastropods. Dispersal at the post-larval stage can, for example, provide the opportunity for frequent smaller-scale movements, enhancing exchange of individuals between populations (Norkko *et al.* 2001), but is often highly variable depending on local conditions (Cummings *et al.* 1995, Lundquist *et al.* 2006), including, e.g., the level of hydrodynamics and microhabitat peculiarities (Martel and Diefenbach 1993). Dispersal also depends on species-specific differences in reproductive modes and development, which can play a vital role in local population fluctuations (Thorson 1950, Ólafsson *et al.* 1994).

Many molluscs show a large temporal variability in their abundances, including seasonal patterns (Arroyo *et al.* 2006, Chatzinikolaou and Richardson 2008). For example, peaks in the arrival of gastropods to new habitat patches may coincide with peaks in the biomass and frond density of seagrasses and seaweeds from vegetated bottoms (Rueda *et al.* 2001, Sánchez-Moyano *et al.* 2001, Rueda and Salas 2003). Moreover, recruitment of gastropods into benthic habitats may be not restricted to one single event, but somewhat continuous through time, depending on the sum of all dispersers reaching to a site over time and subsequent survival (Valanko *et al.* 2010).

Artificial substrates may provide shelter for a wide range of meio- and macrofaunal organisms living on intertidal and subtidal habitats (Olabarria and Chapman 2002, Underwood and Chapman 2006, Cole *et al.* 2007, Rule and Smith 2007, Tuya *et al.* 2009). In the eastern Atlantic, for example, a wide range of benthic macrofaunal organisms, including prosobranch gastropods, colonized artificial substrates as recruits and/or as adults (García-Sanz *et al.* 2012). In this study, we took advantage of artificial substrates to investigate the seasonal variation in colonization patterns of subtidal prosobranch gastropods within a matrix of four habitats (seagrass meadows, sandy patches, ‘urchin-grazed’ barrens and macroalgal-dominated beds) arranged in patches within a coastal

landscape in the eastern Atlantic. We expected that colonization of new substrates by gastropods (their identity and abundance) depended on the type of the habitat surrounding a focal habitat (here, artificial substrates) through time, regardless of the mode of dispersion.

MATERIALS AND METHODS

Study site

This study was carried out at two locations off the east coast of Gran Canaria (Canary Islands, Spain): Risco Verde (27°51'25.94"N, 15°23'10.26"W) and Playa del Cabrón (27°52'14.43"N, 15°23'00.31"W) (Fig. 1). These locations encompass a mosaic of subtidal neighboring habitats, including seagrass meadows constituted by the seagrass *Cymodocea nodosa* and sandy patches on soft substrata, as well as ‘urchin-grazed’ barrens mainly generated by large densities of the sea urchin *Diadema africanum* and macroalgal-dominated beds, primarily constituted by brown seaweeds of the genera *Cystoseira* and *Sargassum*, as well as *Dictyota* spp., *Padina pavonica*, and *Lobophora variegata*, on rocky substrates. Meadows constituted by *Cymodocea nodosa* are the dominant vegetated communities on shallow soft substrates across the Canaries (Barberá *et al.* 2006). Vegetated habitats show maximum vitality during spring and summer (Medina and Haroun 1993, Espino *et al.* 2008). All four habitats are found interspersed as a matrix of mosaic patches at ca. 5–10 meters depth.

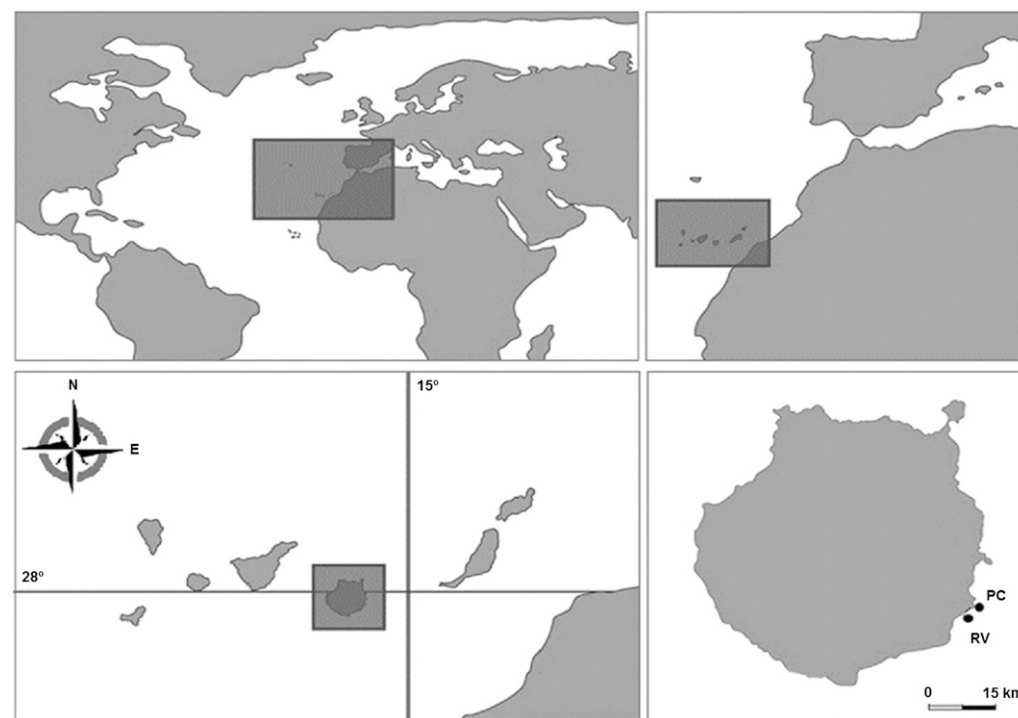


Figure 1. Position of the study area in the north-eastern Atlantic, and study locations at Gran Canaria Island. Abbreviations: PC, Playa del Cabrón and RV, Risco Verde.

Sampling

We took advantage of artificial substrates so-called ‘Cushion-Shaped Leaf-Like Units’ (CLLU, García-Sanz *et al.* 2012) to study colonization patterns of gastropods. Artificial substrates consist of a plastic mesh frame (50 cm², 2 cm diameter mesh size) folded as a cushion, to which artificial leaves (green plastic raffia, 35 cm long and 1 cm wide) were attached every ca. 4 cm (Fig. 2). Raffia is positively buoyant underwater and so floats upright. A total of 75 cm² of concealment



Figure 2. Artificial substrate, a cushion-shaped leaf-like unit (CLLU), on a sandy patch. [Figure in color only in electronic version].

gardening mesh (≤ 1 mm diameter) was included inside, creating small holes and shelters (García-Sanz *et al.* 2012). Four replicated artificial substrates were deployed, on each habitat type, at each locality on a monthly basis. Adjacent artificial substrates within each type of habitat were, in all cases, 3–5 m apart to guarantee independence. Artificial substrates from any two adjacent habitats were hundreds of meters apart. Artificial substrates were fixed through cable ties on hard substrata and by iron rods (ca. 50 cm long) on soft substrata. In all cases, artificial substrates were in contact with the seabed (Fig 2).

The study started at the beginning of February 2009 and lasted for one typical climatic year (January 2010). After one month underwater, artificial substrates were retrieved by SCUBA divers by carefully enclosing each unit within a cloth bag (García-Sanz *et al.* 2012). The bags were carried to the laboratory, where each artificial substrate was carefully cleaned with freshwater. All prosobranch gastropods retained by a 0.5 mm mesh sieve were preserved in an ethanol-seawater solution, until identification to the lowest possible taxonomic level. The main key for gastropod identification was provided by Rolán *et al.* (2011).

Data analysis

Differences in the total abundance of the dominant taxa (90.12% of total colonizers), including (in decreasing order of abundance) *Rissoa* spp. (Fremenville in Desmarest, 1814),

Columbella adansoni (Menke, 1853), *Bittium* spp., (Leach in Gray, 1847), *Tricolia pullus canarica* (Nordsieck, 1973), *Smaragdia viridis* (Linnaeus, 1758), *Alvania* spp. (Risso, 1826), *Clavatula mystica* (Reeve, 1843), *Cerithium rupestre* (Risso, 1986), *Mitra* spp. (Lamarck, 1798), *Polinices lacteus* (Guilding, 1834), *Gibberula caelata* (Monterosato, 1877), and *Luria lurida* (Linnaeus, 1758) among habitats, seasons and months within seasons were tested through 3-way, permutation-based, ANOVAs, based on Euclidian distances calculated from square root-transformed data. High numbers of artificial substrates were lost throughout the study at both sites during the different months of the study and equally in the different habitats and at both locations; locality--a random source of variability--was thus 'sacrificed' to maintain a balanced design (*i.e.*, equal sample sizes per treatment). If the sample sizes are not the same,

then the calculated *F*-ratios may be dominated by the sample variances for the larger samples (Underwood 1997). We then consider the four artificial substrates from each habitat as independent replicates. The ANOVA models included, in all cases, the fixed factors: 'Habitat' and 'Season', while 'Month' (three months per season; winter: December, January and February, spring: March, April and May, summer: June, July and August and autumn: September, October and November) was a random factor nested within 'Season'. Pairwise comparisons (via 4999 permutations) were used to resolve differences among levels of factors, whenever appropriate. The significance level of pairwise comparisons were established at the 0.01 level (instead of the conventional 0.05) to avoid increasing a type I error rate. For each taxon, we estimated the relative contribution of each factor to explain differences in the intensity of colonization (abundance) patterns through calculation of their variance components.

RESULTS

A total of 8,640 prosobranch gastropods were collected during the study, including *Rissoa* spp. (6,265 individuals), *Columbella adansoni* (890), *Bittium* spp. (334), *Tricolia pullus canarica* (277), *Smaragdia viridis* (220), *Alvania* spp. (149), *Clavatula mystica* (139), *Cerithium rupestre* (130), *Mitra* spp. (129), *Polinices lacteus* (76), *Gibberula caelata* (10), and *Luria*

Table 1. Results of 3-way ANOVAs testing for differences in the abundance of *Alvania* spp., *Bittium* spp., *Cerithium rupestre*, *Clavatula mystica*, *Columbella adansoni*, *Gibberula caelata*, *Luria lurida*, *Mitra* spp., *Rissoa* spp., *Smaragdia viridis*, *Tricolia pullus canarica* and *Polinices lacteus* between seasons (**A**, Autumn, **S**, Summer, **Sp**, Spring, and **Wi**, Winter), months within seasons and habitats (**B**, Barrens, **MB**, Macroalgal Beds, **S**, Seagrasses, and **SP**, Sandy Patches). The amount of variation accumulated by each factor is indicated through the variance components (expressed in %). *P*-values for pairwise comparisons are included in parenthesis.

	<i>df</i>	MS	<i>F</i>	<i>P</i>	Variance components (%)	Pairwise comparisons
<i>Alvania</i> spp.						
Season	3	2.241	0.513	0.837	0	-
Habitat	3	1.976	2.225	0.103	9.16	-
Month (Season)	8	4.361	9.955	0.001	30.13	-
Season x Habitat	9	0.537	0.604	0.795	0	-
Month (Season) x Habitat	24	0.888	2.027	0.005	20.41	-
Residual	144	0.438			40.28	-
<i>Bittium</i> spp.						
Season	3	3.421	2.426	0.165	8.5	B vs. MB (0.005)
Habitat	3	11.10	8.28	0.001	18.7	B vs. SP (0.097)
Month (Season)	8	1.409	1.866	0.075	8.38	B vs. S (0.227)
Season x Habitat	9	2.439	1.819	0.120	12.54	MB vs. SP (0.004)
Month (Season) x Habitat	24	1.340	1.774	0.020	15.85	MB vs. S (0.008)
Residual	144	0.755			36.03	SP vs. S (0.667)
<i>Cerithium rupestre</i>						
Season	3	1.435	2.568	0.121	7.28	B vs. MB (0.223)
Habitat	3	5.003	5.791	0.003	15.83	B vs. SP (0.008)
Month (Season)	8	0.558	1.657	0.116	6.34	B vs. S (0.041)
Season x Habitat	9	2.471	2.858	0.017	19.72	MB vs. SP (0.041)
Month (Season) x Habitat	24	0.864	2.562	0.001	19.55	MB vs. S (0.051)
Residual	144	0.337			31.28	SP vs. S (0.087)
<i>Clavatula mystica</i>						
Season	3	0.225	1.788	0.201	6.51	B vs. MB (0.357)
Habitat	3	0.478	4.488	0.012	12.6	B vs. SP (0.031)
Month (Season)	8	0.126	1.344	0.222	6.43	B vs. S (0.034)
Season x Habitat	9	0.404	3.801	0.003	22.6	MB vs. SP (0.08)
Month (Season) x Habitat	24	0.106	1.135	0.305	8.06	MB vs. S (0.4)
Residual	144	9.38E-02			43.8	SP vs. S (0.091)
<i>Columbella adansoni</i>						
Season	3	6.548	1.632	0.235	7.23	B vs. MB (0.133)
Habitat	3	28.909	10.108	0.001	23.15	B vs. SP (0.003)
Month (Season)	8	4.012	2.466	0.013	12.13	B vs. S (0.749)
Season x Habitat	9	2.723	0.952	0.486	0	MB vs. SP (0.002)
Month (Season) x Habitat	24	2.86	1.757	0.024	17.43	MB vs. S (0.003)
Residual	144	1.627			40.06	SP vs. S (0.003)
<i>Gibberula caelata</i>						
Season	3	0.050	0.779	0.616	0	B vs. MB (0.021)
Habitat	3	0.119	2.847	0.056	12.6	B vs. SP (0.221)
Month (Season)	8	0.07	1.526	0.149	12.6	B vs. S (0.372)
Season x Habitat	9	0.04	1.088	0.414	5.52	MB vs. SP (0.251)
Month (Season) x Habitat	24	0.04	0.861	0.656	0	MB vs. S (0.072)
Residual	144				69.3	SP vs. S (0.433)

Table 1. (Continued)

	<i>df</i>	MS	<i>F</i>	<i>P</i>	Variance components (%)	Pairwise comparisons
<i>Luria lurida</i>						
Season	3	0.005	0.166	1.000	0	-
Habitat	3	0.06	0.921	0.452	0	-
Month (Season)	8	0.03	0.720	0.673	0	-
Season x Habitat	9	0.03	0.500	0.864	0	-
Month (Season) x Habitat	24	0.06	1.520	0.065	26.5	-
Residual	144	0.04			73.5	-
<i>Mitra</i> spp.						
Season	3	0.803	1.577	0.249	4.98	B vs. MB (0.024)
Habitat	3	6.721	10.353	0.001	22.5	B vs. SP (0.097)
Month (Season)	8	0.509	1.511	0.149	6.62	B vs. S (0.227)
Season x Habitat	9	1.039	1.601	0.167	11.4	MB vs. SP (0.004)
Month (Season) x Habitat	24	0.649	1.926	0.009	17.7	MB vs. S (0.008)
Residual	144	0.336			36.8	SP vs. S (0.667)
<i>Rissoa</i> spp.						
Season	3	204.72	3.485	0.059	20.1	B vs. MB (0.004)
Habitat	3	60.165	3.388	0.027	10.84	B vs. SP (0.597)
Month (Season)	8	58.743	9.611	0.001	20.9	B vs. S (0.001)
Season x Habitat	9	6.890	0.388	0.931	0	MB vs. SP (0.150)
Month (Season) x Habitat	24	17.755	2.905	0.001	19.66	MB vs. S (0.633)
Residual	144	6.111			28.5	SP vs. S (0.212)
<i>Smaragdia viridis</i>						
Season	3	7.778	2.123	0.127	12.15	-
Habitat	3	3.227	2.169	0.121	7.9	-
Month (Season)	8	3.662	7.113	0.001	18.4	-
Season x Habitat	9	2.379	1.599	0.164	11.32	-
Month (Season) x Habitat	24	1.487	2.890	0.001	20.46	-
Residual	144	0.514			29.77	-
<i>Tricolia pullus canarica</i>						
Season	3	8.183	4.808	0.041	15.79	B vs. MB (0.166)
Habitat	3	5.196	5.181	0.006	12.7	B vs. SP (0.296)
Month (Season)	8	1.702	2.465	0.016	10.8	B vs. S (0.230)
Season x Habitat	9	2.103	2.097	0.068	13.01	MB vs. SP (0.646)
Month (Season) x Habitat	24	1.002	1.452	0.092	12	MB vs. S (0.573)
Residual	144	0.691			35.7	SP vs. S (0.907)
<i>Polinices lacteus</i>						
Season	3	0.722	0.788	0.493	0	-
Habitat	3	0.753	1.322	0.291	6.19	-
Month (Season)	8	0.916	2.989	0.001	18.3	-
Season x Habitat	9	0.195	0.343	0.953	0	-
Month (Season) x Habitat	24	0.569	1.859	0.013	24	-
Residual	144	0.306			51.9	-

lurida (9). These organisms were identified as post-larval, juvenile and adult individuals. For all taxa, the amount of variability explained by the factor 'Habitat' (between 6–23%, Table 1) was slightly higher than seasonal variation (main factor 'Season', which accumulated between 0–20%, Table 1).

Indeed, the amount of variability accounted by months within seasons (between 6–30%, either as main effects or as a 'Month (Season) x Habitat' interaction, Table 1) typically outweighed seasonal variation, and so masked any seasonal differences for most taxa (Table 1). Most variation in the

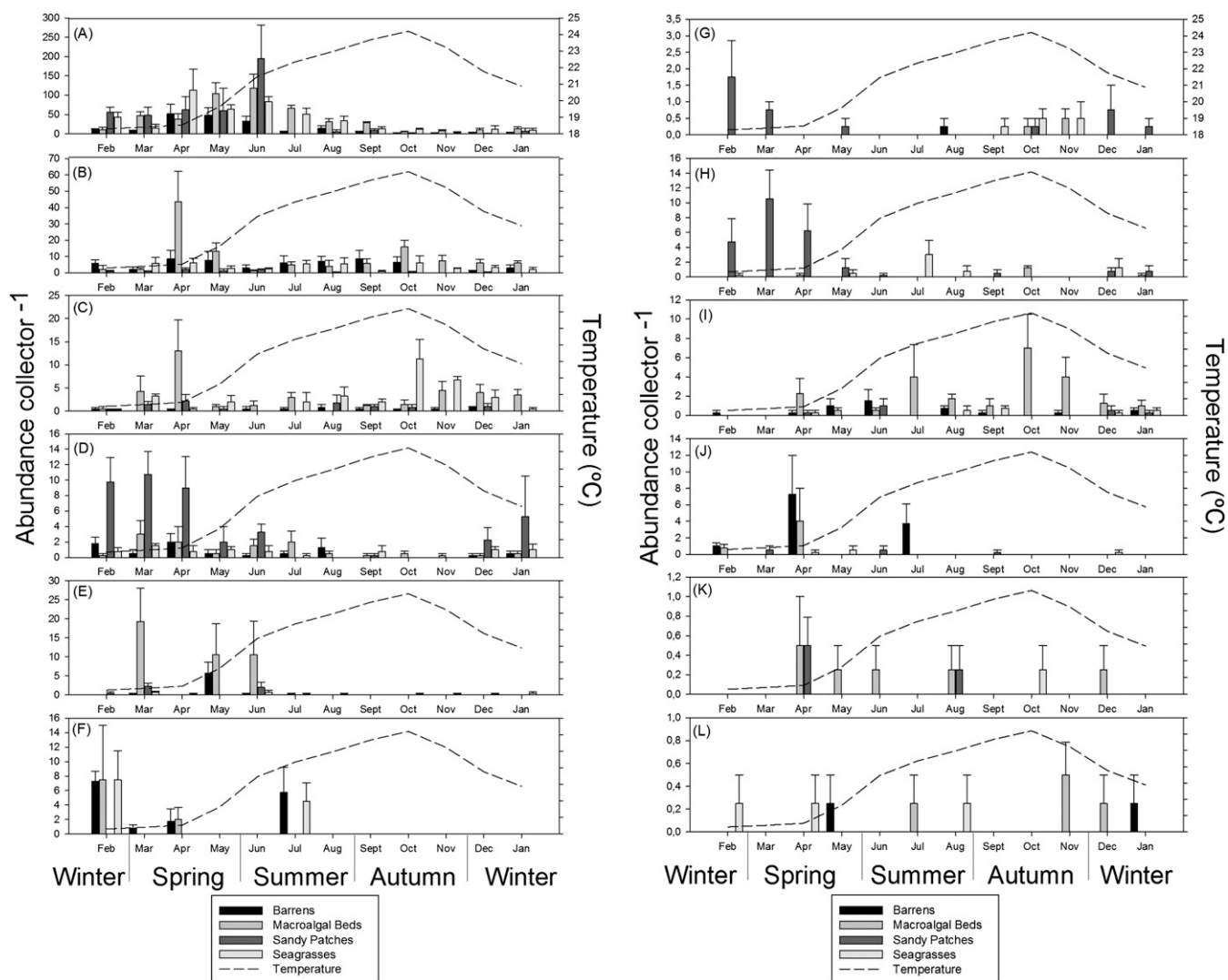


Figure 3. Abundance of: **A**, *Rissoa* spp., **B**, *Columbella adansoni*, **C**, *Bittium* spp., **D**, *Tricolia pullus canarica*, **E**, *Smaragdia viridis*, **F**, *Alvania* spp., **G**, *Clavatulula mystica*, **H**, *Cerithium rupestre*, **I**, *Mitra* spp., **J**, *Polinices lacteus*, **K**, *Gibberula caelata* and **L**, *Luria lurida* in artificial substrates per month and habitat. The mean seawater surface temperature through time is also included. Error bars are standard error of means.

arrival of colonizers of the different taxa onto artificial substrates was accounted by the residual term (between 28–73%, Table 1). This supposes a large variation in the number of colonizers at small spatial scales, *i.e.*, from artificial substrate to artificial substrate deployed at each month and habitat.

Throughout the study, the colonizers *Bittium* spp., *Columbella adansoni*, *Gibberula caelata*, *Mitra* spp., *Rissoa* spp., and *Smaragdia viridis* were mostly observed in artificial substrates deployed on macroalgal beds, relative to the other habitat patches (Figs. 3C, 3B, 3K, 3I, 3A and 3E, respectively, Table 1, pairwise tests for ‘Habitat’; Table 2, pairwise tests for ‘Month (Season) x Habitat’). Despite *Alvania* spp., *Cerithium*

rupestre, *Clavatulula mystica*, and *Polinices lacteus* showed inconsistent differences in abundances among habitats from month to month (significant ‘Month (Season) x Habitat’ interactions; Figs. 3F, 3H, 3G, and 3J, respectively), differences between habitats depended on certain months (Table 1, ‘Season x Habitat’). No differences were observed among habitats for *Luria lurida* and *Tricolia pullus canarica* (Figs. 3L and 3D, respectively).

Significant differences in the number of colonizers onto artificial substrates were observed between seasons for *Rissoa* spp., which showed a peak in the arrival of colonizers during spring-early summer whereas *Tricolia pullus canarica* showed

Table 2. Summary of results of pairwise tests for differences among habitats from month to month within each season. The number of incidences (from a total of 12 months) of a significant difference between each pair of habitats is outlined for each species with a significant 'Month (Season) x Habitat' interaction (see Table 1). **B**, Barrrens, **MB**, Macroalgal Beds, **S**, Seagrasses, and **SP**, Sandy Patches.

Species	B vs. MB	B vs. SP	B vs. S	MB vs. B	MB vs. SP	MB vs. S	SP vs. B	SP vs. MB	SP vs. S	SP vs. MB	SP vs. S	S vs. B
<i>Rissoa</i> spp.	-	-	-	8	4	2	3	1	2	2	4	4
<i>C. adansoni</i>	-	7	1	4	10	4	-	-	-	-	5	-
<i>Bittium</i> spp.	-	-	-	7	7	3	-	1	-	3	6	6
<i>S. viridis</i>	-	-	-	4	3	3	-	-	-	-	-	-
<i>Alvania</i> spp.	2	4	2	-	-	-	-	-	-	-	-	-
<i>C. rupestre</i>	-	-	-	2	1	2	7	6	6	1	1	1
<i>Mitra</i> spp.	-	3	2	6	8	7	-	-	1	-	2	-
<i>P. lacteus</i>	1	3	3	-	2	2	-	-	-	-	-	-

a peak during winter-early spring (Figs. 3J and 3L, respectively, Table 1. 'Season', $P < 0.05$). Importantly, the rest of the prosobranch gastropods did not show significant differences between seasons ('Season', $P > 0.05$, Table 1).

DISCUSSION

This study has demonstrated that the habitat where artificial substrates were deployed has a relevant influence on the arrival of prosobranch gastropods. The season of artificial substrates deployment was less relevant, as a result of large variation from month to month within each season. This result is in accordance with previous observations pointing towards small-scale temporal variability as a more relevant source of variation than seasonal variation (Crowe 1999).

The type of habitat where artificial substrates are deployed is strongly related to the proximity (sources) of new colonizers. Indeed, a previous study showed that numbers of colonizers onto artificial substrates correlated positively with the abundance of prosobranch gastropods inhabiting habitats surrounding artificial substrates (Tuya *et al.* 2009). In our study, the number of colonizers of *Bittium* spp., *Columbella adansoni*, *Gibberula caelata*, *Luria lurida*, *Mitra* spp., *Rissoa* spp., and *Smaragdia viridis* were larger in vegetated than unvegetated habitats, particularly in macroalgal beds. Vegetated habitats supply food for prosobranch gastropods, including algal epiphytes, bacteria, etc. (Bell *et al.* 1993, Arroyo *et al.* 2006, Tuya *et al.* 2008, Gartner *et al.* 2013), as well as provide refuges from predation, as branched-habitats give better protection from visual predators (Jacobi and Langevin 1996). In turn, juvenile and adult gastropods can actively migrate between different algae within macroalgal beds (Crowe and Underwood 1998). Furthermore, epifaunal productivity is higher in habitats occupied by brown seaweeds than in urchin barrrens, which directly influence the abundance of mobile invertebrates such as gastropods (Taylor 1998). Coastal habitats are routinely exposed to waves, tides and currents. When organisms are not permanently attached to their substrate, *e.g.*, prosobranch gastropods, transport of post-larvae in the bedload is an especially important process (Valanko *et al.* 2010). The presence of vegetation may provide a range of suitable microhabitats during dispersal and so prevent large numbers of individuals from drifting away and getting lost (Rogers 1994).

Rates of dispersal of marine invertebrates do not have a simple linear or monotonic relationship with water movement, *e.g.*, species behavioral responses (Valanko *et al.* 2010), and species-specific differences in reproductive modes and development can play a crucial role in local population

fluctuations (Thorson 1950, Ólafsson *et al.* 1994). Colonization success, and the ability to reach new habitats, could be limited by the capacity to swim during the early life stages of their development. In this sense, the type of reproduction of prosobranch gastropods also affects their colonization of new substrates. It is well known that some prosobranch gastropods enclose their eggs within benthic egg masses that are deposited on surfaces, *e.g.*, rocks, leaves, etc. (Rawlings 1999, Przeslawski and Benkendorff 2004), while other prosobranch gastropods release their eggs into the water column. The majority of taxa observed in this study have a planktotrophic development, including *Alvania* spp., *Bittium* spp., *Cerithium rupestre*, *Rissoa* spp. (Ávila and Malaquias 2002), *Gibberula caelata* (Gofas and Zenetos 2003), *Luria lurida* (Wilson 1985), *Mitra* spp. (Solsona *et al.* 2000), *Polinices lacteus* (Kingsley-Smith *et al.* 2005), and *Smaragdia viridis* (Barroso and Matthews-Cascon 2009); the survival of their larvae in the water column is a fundamental process to guarantee replenishment of adult populations. Nevertheless, *Columbella adansonii* has a non-planktotrophic development (Oliveiro 1995), and, coincidentally, this was the most abundant species throughout this study. It is plausible, therefore, that a non-planktotrophic development reduces the chances of larvae drifting away into the open ocean and successfully colonize distant habitats (Bhaud and Duchêne 1996), favoring, therefore, colonization of adjacent habitats.

In this study, only two species showed significant differences between seasons. *Tricolia pullus canarica* showed a peak in the arrival of colonizers during winter-early spring, while *Rissoa* spp. had a peak during spring-early summer. These abundance maxima onto artificial substrates coincide with maxima in the 'vitality' of subtidal vegetation in the study area, *e.g.*, seagrass canopy height and shoot density (Tuya *et al.* 2006, Espino *et al.* 2008) and the biomass of frondose seaweeds (Medina and Haroun 1993). In turn, connections between increases in the abundance of macroinvertebrates and the availability of food and habitat provided by vegetation have been described (Arroyo *et al.* 2006). This outcome, in conjunction with the larger number of individuals colonizing artificial substrates in vegetated substrates, reinforces the notion of the relevance of vegetation affecting patterns of associated fauna, prosobranch gastropods in particular.

ACKNOWLEDGMENTS

We thank J. Suárez for providing help in the laboratory and Puertos del Estado, who kindly provided seawater temperature data. This study was financed by a postgraduate fellow grant provided by the Cabildo de Gran Canaria. Two anonymous reviewers provided valuable comments that significantly improved a previous draft of this paper.

LITERATURE CITED

- Anderson, M. J. and A. J. Underwood. 1997. Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: A multivariate and univariate approach. *Oecologia* **109**: 442–453.
- Arroyo, M. C., C. Salas, J. L. Rueda, and S. Gofas. 2006. Temporal changes of mollusc populations from a *Zostera marina* bed in southern Spain (Alboran Sea), with biogeographic considerations. *Marine Ecology* **27**: 417–430.
- Ávila, S. P., J. Goud, and A. M. de Frias Martins. 2012. Patterns of diversity of the Rissoidea (Mollusca: Gastropoda) in the Atlantic and the Mediterranean region. *Scientific World Journal* doi: 10.1100/2012/164890.
- Ávila, S. P. and M. A. Malaquias. 2002. Biogeographical relationships of the molluscan fauna of the Ormonde Seamount (Gorringe Bank, Northeast Atlantic Ocean). *Journal of Molluscan Studies* **69**: 145–150.
- Barberá, C., F. Tuya, A. Boyra, P. Sánchez-Jerez, I. Blanch, and R. J. Haroun. 2006. Spatial variation in the structural parameters of *Cymodocea nodosa* seagrass meadows in the Canary Islands: A multiscaled approach. *Botanica Marina* **48**: 122–126.
- Barroso, C. X. and H. Matthews-Cascon. 2009. Spawning and intra-capsular development of *Neritina zebra* (Bruguère, 1792) (Mollusca: Gastropoda: Neritidae) under laboratory conditions. *Invertebrate Reproduction & Development* **53**: 137–143.
- Bell, S. S., M. J. Lechowicz, A. Appenzeller, M. Chandler, E. Deblois, L. Jackson, B. Mackenzie, R. Preziosi, M. Schallenberg, and N. Tinker. 1993. The spatial structure of the physical environment. *Oecologia* **96**: 114–121.
- Bhaud, M. and J. C. Duchêne. 1996. Change from planktonic to benthic development: Is life cycle evolution an adaptive answer to the constraints of dispersal? *Oceanologica Acta* **19**: 335–346.
- Chapman, M. G. 2000. A comparative study of differences among species and patches of habitat on movements of three species of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* **244**: 181–201.
- Chapman, M. G. 2002. Early colonization of shallow subtidal boulders in two habitats. *Journal of Experimental Marine Biology and Ecology* **275**: 95–116.
- Chatzinikolaou, E. and C. A. Richardson. 2008. Population dynamics and growth of *Nassarius reticulatus* (Gastropoda: Nassariidae) in Rhosneigr (Anglesey, UK). *Marine Biology* **153**: 605–619.
- Chemello, R., G. Scotti, and S. Riggio. 1998. The molluscan assemblage of the leaf stratum in a *Cymodocea nodosa* bed of a marine coastal lagoon. *Bollettino Malacologico* **33**, 69–76.
- Cole, V. J., M. G. Chapman, and A. J. Underwood. 2007. Landscapes and life-histories influence colonization of polychaetes to intertidal biogenic habitats. *Journal of Experimental Marine Biology and Ecology* **348**: 191–199.
- Cowen, R. K. and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Sciences* **1**: 443–466.
- Crowe, T. P. 1999. Limits to generality: Seasonal and temporal variation in dispersal of an intertidal gastropod. *Journal of Experimental Marine Biology and Ecology* **232**: 177–196.

- Crowe, T. P. and A. J. Underwood. 1998. Testing behavioral 'preference' for suitable microhabitat. *Journal of Experimental Marine Biology and Ecology* **225**: 1–11.
- Cummings, V. J., R. D. Pridmore, S. F. Thrush, and J. E. Hewitt. 1995. Post-settlement movement by intertidal benthic macroinvertebrates: Do common New Zealand species drift in the water column? *New Zealand Journal of Marine and Freshwater Research* **29**: 59–67.
- Espino, F., F. Tuya, I. Blanch, and R. J. Haroun. 2008. Los sebadales en Canarias. Oasis de vida en los fondos arenosos. BIOGES, Centro de Biodiversidad y Gestión Ambiental, Universidad de Las Palmas de Gran Canaria. [In Spanish].
- Gaines, S. D. and M. D. Bertness. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**: 579–580.
- García-Sanz, S., F. Tuya, P. G. Navarro, C. Angulo-Preckler, and R. J. Haroun. 2012. Post larval, short-term, colonization patterns: The effect of substratum complexity across subtidal, adjacent, habitats. *Estuarine Coastal and Shelf Science*, **112**: 183–191.
- Gartner, A., F. Tuya, P. S. Lavery, and K. McMahon. 2013. Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *Journal of Experimental Marine Biology and Ecology* **439**: 143–151.
- Gofas, S. and A. Zenetos. 2003. Exotic molluscs in the Mediterranean basin: Current status and perspectives. *Oceanography and Marine Biology* **41**: 237–277.
- Jacobi, C. M. and R. Langevin. 1996. Habitat geometry of benthic substrata: Effects on arrival and settlement of mobile epifauna. *Journal of Experimental Marine Biology and Ecology* **206**: 39–54.
- Kingsley-Smith, P. R., C. A. Richardson, and R. Seed. 2005. Growth and development of the veliger larvae and juvenile of *Polinices lacteus* (Gastropoda: Naticidae). *Journal of the Marine Biological Association of the United Kingdom* **85**: 171–174.
- Lubchenco, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* **64**: 1116–1123.
- Lundquist, C. J., S. F. Thrush, J. E. Hewitt, J. Halliday, I. Macdonald, and V. Cummings. 2006. Spatial variability in recolonisation potential: Influence of organism behavior and hydrodynamics on the distribution of macrofaunal colonists. *Marine Ecology Progress Series* **324**: 67–81.
- Martel, A. and F. S. Chia. 1991. Foot-raising behavior and active participation during the initial phase of post-metamorphic drifting in the gastropod *Lacuna* spp. *Marine Ecology Progress Series* **72**: 247–254.
- Martel, A. and T. Diefenbach. 1993. Effects of body size, water current and microhabitat on mucous-thread drifting in post-metamorphic gastropods *Lacuna* spp. *Marine Ecology Progress Series* **99**: 215–220.
- Medina, M. and R. J. Haroun. 1993. Preliminary study on the dynamics of *Cystoseira abies-marina* populations on Tenerife (Canary Islands). *Courier Forschungsinstitut Senckenberg* **159**: 109–112.
- Norkko, A., V. J. Cummings, S. F. Thrush, J. E. Hewitt, and T. Hume. 2001. Local dispersal of juvenile bivalves: Implications for sand-flat ecology. *Marine Ecology Progress Series* **212**: 131–144.
- Olabarria, C. and M. G. Chapman. 2002. Inconsistency in short-term temporal variability of microgastropods within and between two different intertidal habitats. *Journal of Experimental Marine Biology and Ecology* **269**: 85–100.
- Ólafsson, E. B., C. H. Peterson, and W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology Annual Review* **32**: 65–109.
- Oliveiro, M. 1995. Larval development and allozyme variation in the East Atlantic *Columbella* (Gastropoda: Prosobranchia: Columbellidae). *Scientia marina* **59**: 77–86.
- Przeslawski, R. and K. Benkendorff. 2004. The role of surface fouling in the development of encapsulated gastropod embryos. *Journal of Molluscan Studies* **71**: 75–83.
- Rawlings, T. 1999. Adaptations to physical stresses in the intertidal zone: The egg capsules of neogastropod molluscs. *American Zoologist* **39**: 230–243.
- Rolán, E., J. M. Hernández, F. Swinnen, R. Gómez, and J. M. Pérez. 2011. *Moluscos y Conchas Marinas de Canarias*. ConchBooks, Hackenheim, Germany. [In Spanish].
- Rogers, A. D. 1994. The biology of seamounts. *Advances in Marine Biology* **30**: 305–350.
- Rueda J. L., M. Fernandez-Casado, C. Salas, and S. Gofas. 2001. Seasonality in a taxocoenosis of molluscs from soft bottoms in the Bay of Cadiz (southern Spain). *Journal of Marine Biological Association United Kingdom* **81**: 903–912.
- Rueda, J. L. and C. Salas. 2003. Seasonal variation of a molluscan assemblage living in a *Caulerpa prolifera* meadow within the inner Bay of Cádiz (SW Spain). *Estuarine, Coastal and Shelf Science* **57**: 909–918.
- Rule, M. J. and S. D. A. Smith. 2007. Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs. *Journal of Experimental Marine Biology and Ecology* **345**: 38–51.
- Rumrill, S. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* **32**: 163–198.
- Russo, G. F., S. Fraschetti, and A. Terlizzi. 2002. Population ecology and production of *Bittium latreillii* (Gastropoda, Cerithidae) in a *Posidonia oceanica* seagrass bed. *Italian Journal of Zoology* **69**: 215–222.
- Russo, G. F. and A. Terlizzi. 1998. Structural patterns in the mollusk assemblages of *Posidonia oceanica* beds: Methodological, edaphic or biogeographical product? *Bollettino Malacologico* **33**: 89–94.
- Sánchez-Moyano, J. E., F. J. Estacio, E. M. García-Adiego, and J. C. García Gomez. 2001. Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal variation of invertebrate macrofauna. *Aquatic Botany* **70**: 163–174.
- Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. *Bulletin of Marine Science* **39**: 290–322.
- Solsona, M., C. Gili, and J. Martinell. 2000. Patterns of change in the biogeographic distribution of Atlanto-Mediterranean Aporrhaidae (Gastropoda) from the Neogene to the Present. *Palaeogeography, Palaeoclimatology, Palaeoecology* **158**: 83–97.

- Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* **49**: 227–254.
- Sousa, W. P. 1984. Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. *Ecology* **65**: 1918–1935.
- Taylor, R. B. 1998. Density, biomass and productivity of animals in four subtidal rocky reef habitats: The importance of small mobile invertebrates. *Marine Ecology Progress Series* **172**: 37–51.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society* **25**: 1–45.
- Tuya, F., J. A. Martín, and A. Luque. 2006. Seasonal cycle of a *Cymodocea nodosa* seagrass meadow and associated ichthyofauna at Playa Dorada (Lanzarote, Canary Islands, eastern Atlantic). *Ciencias Marinas* **32**: 695–704.
- Tuya, F., T. Wernberg, and M. S. Thomsen. 2008. The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats. *Estuarine, Coastal and Shelf Science* **78**: 774–782.
- Tuya, F., T. Wernberg, and M. S. Thomsen. 2009. Colonization of gastropods on subtidal reefs depends on density in adjacent habitats, not disturbance regime or latitude. *Journal of Molluscan Studies* **75**: 27–33.
- Underwood, A. J. and M. G. Chapman. 2006. Early development of subtidal macrofaunal assemblages: Relationships to period and timing of colonization. *Journal of Experimental Marine Biology and Ecology* **330**: 221–233.
- Valanko, S., A. Norkko, and J. Norkko. 2010. Rates of post-larval bedload dispersal in a non-tidal soft-sediment system. *Marine Ecology Progress Series* **426**: 145–163.
- Wilson, B. R. 1985. Direct development in Southern Australian cowries (Gastropoda: Cypraeidae). *Australian Journal of Marine and Freshwater Research* **36**: 267–280.

Submitted: 19 April 2013; **accepted:** 19 December 2013;
final revisions received: 3 January 2014