

Capítulo 5.  
Colonization of prosobranch  
gastropods onto artificial substrates:  
seasonal patterns between habitat  
patches



## 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 collectors 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., *Columbella adansoni* (Menke, 1853), *Gibberula caelata* (Monterosato, 1877), *Mitra* spp., *Rissoa* spp. and *Smaragdia viridis* (Linnaeus, 1758) were observed in artificial collectors deployed in vegetated substrates, highlighting the relevance of vegetation as a matrix habitat for subtidal prosobranch gastropods. *Cerithium rupestre* (Risso, 1986) and *Clavatulula 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; while *Tricolia pullus canarica* (Nordsieck, 1973) showed a peak during winter-early spring. Importantly, the rest of 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.

**Keywords:** colonization, artificial collectors, prosobranch gastropods, habitats, Canary Islands.

Patrones de colonización de organismos bentónicos  
en hábitats litorales de Gran Canaria

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## Capítulo 5

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

## > 5.1 INTRODUCTION

On 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. Russo and Terlizzi, 1998, Chemello *et al.* 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 immigrate 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 –for example– 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 somehow 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 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 collectors) through time, regardless of the mode of dispersion.

## 5.2 MATERIALS AND METHODS

### 5.2.1 Study area

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. 5.1.). 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 *Dyctiota* spp., *Padina pavonica* and *Lobophora variegata*, on rocky substrates. Meadows constituted by *C. 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 (Espino et al., 2008; Medina and Haroun, 1993). All four habitats are found interspersed as a matrix of mosaic patches at ca. 5-10 meters depth.

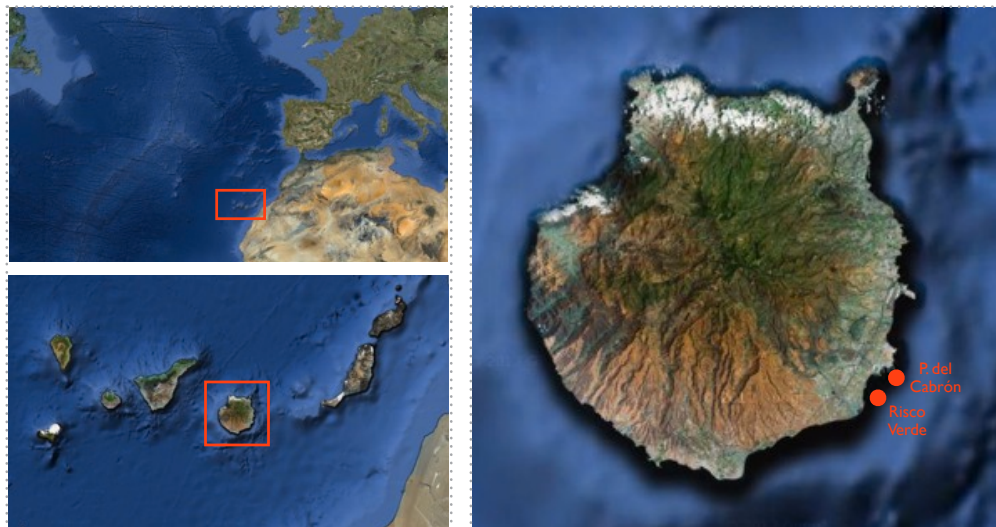


Fig. 5.1 Location of the study area in the eastern Atlantic and study site in Gran Canaria Island.

### 5.2.2 Sampling

We took advantage of artificial collectors so-called 'Cushion-Shaped Leaf Like Units' (CLLU, García-Sanz et al., 2012) to study colonization patterns of gastropods. Collectors consist of a plastic mesh frame (50 cm<sup>2</sup>, 2 cm of diameter of mesh size) folded as a cushion, to which artificial leaves (green plastic raffia, 35 cm long and 10 mm wide) were attached every ca. 4 cm (Fig. 2). Raffia is positively buoyant underwater and so floats upright. A total of 75 cm<sup>2</sup> of concealment gardening mesh ( $\leq 1$  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 100s of m 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.

The study started at the beginning of February 2009 and lasted for 1 typical climatically year (January 2010). After 1 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 collector 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. (2010).

### 5.2.3 Data analysis

Differences in the total abundance of the dominant taxa (90.12% of total colonizers), including (in decreasing order of abundance) *Rissoa* spp., *Columbella adansoni* (Menke, 1853), *Bittium* spp., *Tricolia pullus canarica* (Nordsieck, 1973), *Smaragdia viridis* (Linnaeus, 1758), *Alvania* spp., *Clavatula mystica* (Reeve, 1843), *Cerithium rupestre* (Risso, 1986), *Mitra* spp., *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. A certain number of collectors were lost throughout the study at both locations; locality—a random source of variability—was thus 'sacrificed' to maintain a balanced design. We then consider the 4 ASs from each habitat as independent replicates. The ANOVA models included, in all cases, the fixed factors: 'Habitat' and 'Season', while 'Month' (3 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 999 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.

### ➤ 5.3 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), *Clavatulula mystica* (139), *Cerithium rupestre* (130), *Mitra* spp. (129), *Polinices lacteus* (76), *Gibberula caelata* (10) and *Luria 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 5.1) was slightly higher than seasonal variation (main factor 'Season', which accumulated between 0-20%, Table 5.1). Indeed, the amount of variability accounted by months within seasons (between 6-30%, either as main effects or as 'Month (Season) × Habitat', Table 5.1) typically outweighed seasonal variation, and so masked any seasonal differences for most taxa (Table 5.1). Most variation in the number of colonizers of the different taxa onto artificial substrates was accounted by the residual term (between 28-73%, Table 5.1). This supposes a large variation in the number of colonizers at small spatial scales, i.e. from collector to collector deployed at each month and habitat.

Throughout the study, larger numbers of colonizers of *Bittium* spp., *C. adansoni*, *G. caelata*, *Mitra* spp., *Rissoa* spp. and *S. viridis* were mostly observed in collectors deployed on macroalgal beds, relative to the other habitat patches (Figs. 5.2B, 5.2E, 5.2F, 5.2H, 5.2J and 5.2K, respectively, Table 5.1, pairwise tests for 'Habitat'; Table 5.2, pairwise tests for 'Month (Season) × Habitat'). Despite *Alvania* spp. and *P. lacteus* showed inconsistent differences in abundances among habitats from month to month (significant 'Month (Season) × Habitat' interactions), their abundances were larger on barrens (Figs. 5.2A and 5.2I, respectively, Table 5.1; Table 5.2, pairwise tests for 'Month (Season) × Habitat'). *Cerithium rupestre* and *C. mystica* were mainly observed in collectors located on sandy patches (Figs. 5.2C and 5.2D, respectively, Table 5.1, pairwise tests for 'Habitat'; Table 5.2, pairwise tests for 'Month (Season) × Habitat'), though differences depended on the season for both species ('Season × Habitat',  $F=2.8587$ ,  $P=0.0174$ ;  $F=3.8014$ ,  $P=0.003$ , respectively). No differences were observed among habitats for *L. lurida* and *T. pullus canarica*.

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, while *T. pullus canarica* showed

a peak during winter-early spring (Figs. 5.2] and 5.2L, respectively, Table 5.1. 'Season',  $P < 0.05$ ). Importantly, the rest of prosobranch gastropods did not show significant differences between seasons ('Season',  $P > 0.05$ , Table 5.1).

Table 5.1 Results of 3-way ANOVAs testing for differences in the abundance of *Alvania* spp., *Bittium* spp., *Cerithium rupestre*, *Clavatulula mystica*, *Columbella adansonii*, *Gibberula caelata*, *Luria lurida*, *Mitra* spp., *Polinices lacteus*, *Rissoa* spp., *Smaragdia viridis* and *Tricolia pullus canarica*, between seasons (Winter = Wi, Spring = Sp, Summer = S and Autumn = A), months within seasons and habitats (Barrens = B, Macroalgal Beds = MB, Sandy Patches = SP and Seagrasses = S). 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.

	df	MS	F	P	Variance components (%)	Pairwise comparison
<b><i>Clavatulula mystica</i></b>						
Season	3	0.22	1.78	0.2018	6.51	B vs. MB (0.3572)
Habitat	3	0.48	4.49	0.0124	12.6	B vs. SP (0.0302)
Month (Season)	8	0.12	1.34	0.2228	6.43	B vs. S (0.0342)
Season x habitat	9	0.41	3.80	0.003	22.6	MB vs. SP (0.08)
Month (Season) x Habitat	24	0.11	1.13	0.3052	8.06	MB vs. S (0.4)
Residual	144	9.38E-02			43.8	SP vs. S (0.0908)
<b><i>Columbella adansonii</i></b>						
Season	3	6.55	1.63	0.2352	7.23	B vs. MB (0.1334)
Habitat	3	28.91	10.11	0.0006	23.15	B vs. SP (0.0038)
Month (Season)	8	4.01	2.46	0.013	12.13	B vs. S (0.749)
Season x habitat	9	2.72	0.95	0.4862	0	MB vs. SP (0.002)
Month (Season) x Habitat	24	2.86	1.76	0.0244	17.43	MB vs. S (0.00324)
Residual	144	1.63			40.06	SP vs. S (0.0034)

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	df	MS	F	P	Variance components (%)	Pairwise comparison
<b><i>Alvania</i> spp.</b>						
Season	3	2.24	0.51	0.8376	0	-
Habitat	3	1.98	2.22	0.1034	9.16	-
Month (Season)	8	4.36	9.95	0.0002	30.13	-
Season x habitat	9	0.54	0.604	0.7956	0	-
Month (Season) x Habitat	24	0.89	2.03	0.0054	20.41	-
Residual	144	0.44			40.28	-
<b><i>Bittium</i> spp.</b>						
Season	3	3.42	2.42	0.1650	8.5	B vs. MB (0.0056)
Habitat	3	11.1	8.28	0.001	18.7	B vs. SP (0.0978)
Month (Season)	8	1.41	1.86	0.0754	8.38	B vs. S (0.2276)
Season x habitat	9	2.44	1.82	0.1204	12.54	MB vs. SP (0.0046)
Month (Season) x Habitat	24	1.34	1.77	0.0208	15.85	MB vs. S (0.0086)
Residual	144				36.03	SP vs. S (0.6672)
<b><i>Cerithium rupestre</i></b>						
Season	3	1.43	2.57	0.1214	7.28	B vs. MB (0.2234)
Habitat	3	5.01	5.79	0.0032	15.83	B vs. SP (0.0088)
Month (Season)	8	0.56	1.65	0.1168	6.34	B vs. S (0.0402)
Season x habitat	9	2.47	2.86	0.0174	19.72	MB vs. SP (0.0404)
Month (Season) x Habitat	24	0.86	2.56	0.0004	19.55	MB vs. S (0.0518)
Residual	144	0.33			31.28	SP vs. S (0.0876)
<b><i>Gibberula caelata</i></b>						
Season	3	5.78E-02	0.78	0.6164	0	B vs. MB (0.0218)
Habitat	3	0.11914	2.85	0.0568	12.6	B vs. SP (0.2212)
Month (Season)	8	7.42E-02	1.52	0.1498	12.6	B vs. S (0.3728)
Season x habitat	9	4.55E-02	1.08	0.4142	5.52	MB vs. SP (0.2508)
Month (Season) x Habitat	24	4.18E-02	0.86	0.6566	0	MB vs. S (0.0722)
Residual	144				69.3	SP vs. S (0.4334)
<b><i>Luria lurida</i></b>						
Season	3	5.21E-03	0.17	1	0	-
Habitat	3	6.08E-02	0.92	0.4528	0	-
Month (Season)	8	3.13E-02	0.72	0.6734	0	-
Season x habitat	9	3.30E-02	0.50	0.864	0	-
Month (Season) x Habitat	24	6.60E-02	1.52	0.0652	26.5	-
Residual	144	4.34E-02			73.5	-

	df	MS	F	P	Variance components (%)	Pairwise comparison
<b><i>Mitra</i> spp.</b>						
Season	3	0.80	1.58	0.2494	4.98	B vs. MB (0.0246)
Habitat	3	6.72	10.35	0.0004	22.5	B vs. SP (0.0978)
Month (Season)	8	0.51	1.51	0.1494	6.62	B vs. S (0.2276)
Season x habitat	9	1.04	1.60	0.1672	11.4	MB vs. SP (0.0046)
Month (Season) x Habitat	24	0.65	1.93	0.0094	17.7	MB vs. S (0.0086)
Residual	144	0.34			36.8	SP vs. S (0.6672)
<b><i>Polinices lacteus</i></b>						
Season	3	0.72	0.79	0.4932	0	-
Habitat	3	0.75	1.32	0.2916	6.19	-
Month (Season)	8	0.91	2.99	0.0014	18.3	-
Season x habitat	9	0.19	0.34	0.9538	0	-
Month (Season) x Habitat	24	0.57	1.85	0.013	24	-
Residual	144	0.31			51.9	-
<b><i>Rissoa</i> spp.</b>						
Season	3	204.72	3.48	0.0592	20.1	B vs. MB (0.0044)
Habitat	3	60.16	3.39	0.0278	10.84	B vs. SP (0.5978)
Month (Season)	8	58.74	9.6117	0.0002	20.9	B vs. S (0.0012)
Season x habitat	9	6.89	0.39	0.9318	0	MB vs. SP (0.1506)
Month (Season) x Habitat	24	17.75	2.90	0.0002	19.66	MB vs. S (0.6334)
Residual	144	6.11			28.5	SP vs. S (0.2122)

	df	MS	F	P	Variance components (%)	Pairwise comparison
<b><i>Smaragdia viridis</i></b>						
Season	3	7.78	2.12	0.127	12.15	-
Habitat	3	3.22	2.17	0.1202	7.9	-
Month (Season)	8	3.66	7.11	0.0002	18.4	-
Season x habitat	9	2.37	1.60	0.164	11.32	-
Month (Season) x Habitat	24	1.49	2.89	0.0004	20.46	-
Residual	144	0.51479			29.77	-
<b><i>Tricolia pullus canarica</i></b>						
Season	3	8.18	4.81	0.0416	15.79	B vs. MB (0.1664)
Habitat	3	5.19	5.18	0.0068	12.7	B vs. SP (0.2962)
Month (Season)	8	1.70	2.46	0.016	10.8	B vs. S (0.2304)
Season x habitat	9	2.10	2.09	0.0688	13.01	MB vs. SP (0.6468)
Month (Season) x Habitat	24	1.01	1.45	0.0926	12	MB vs. S (0.573)
Residual	144	0.69			35.7	SP vs. S (0.9078)



Table 5.2. 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). Barrens = B, Macroalgal Beds = MB, Sandy Patches = SP and Seagrasses = S.

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

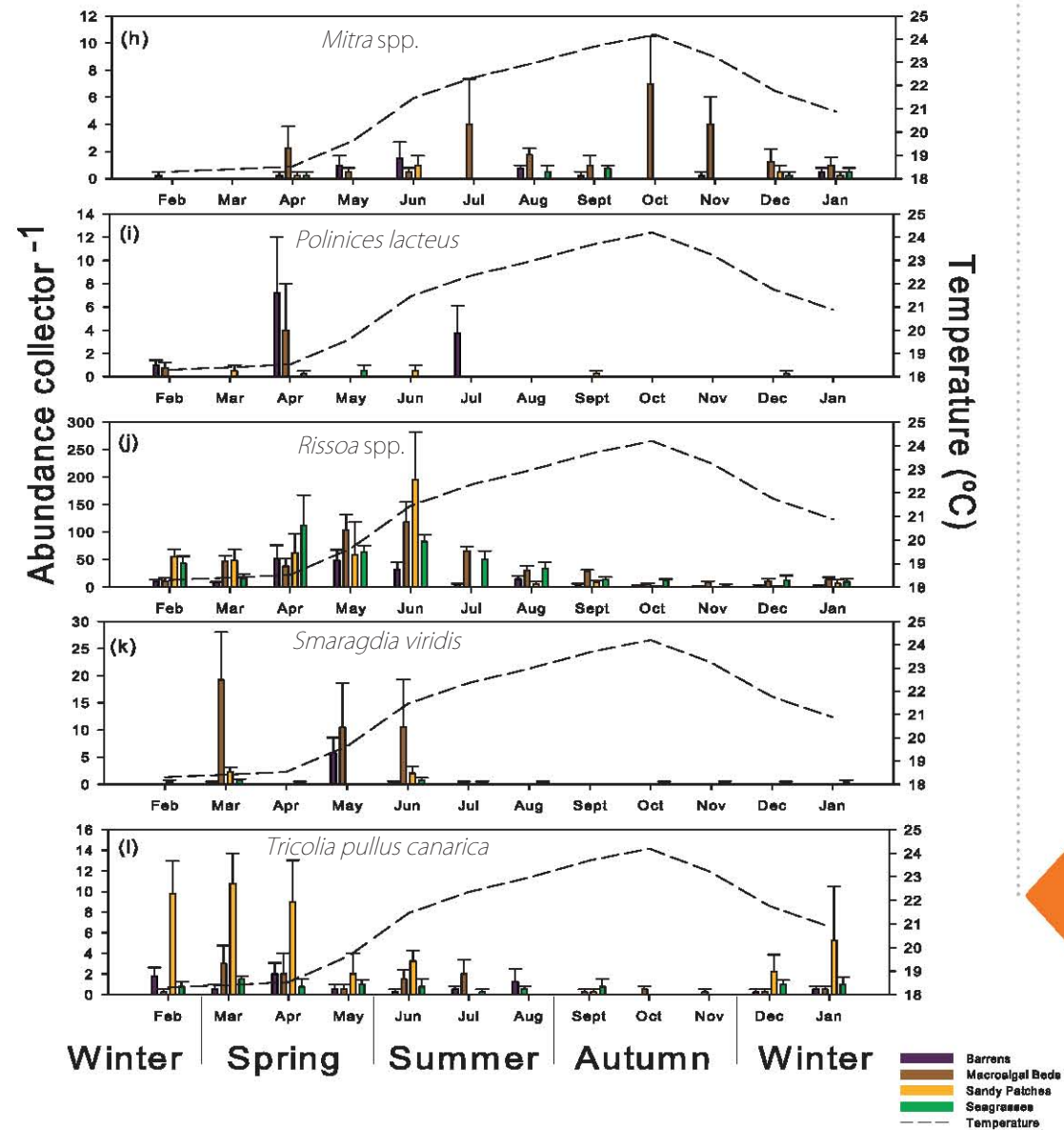
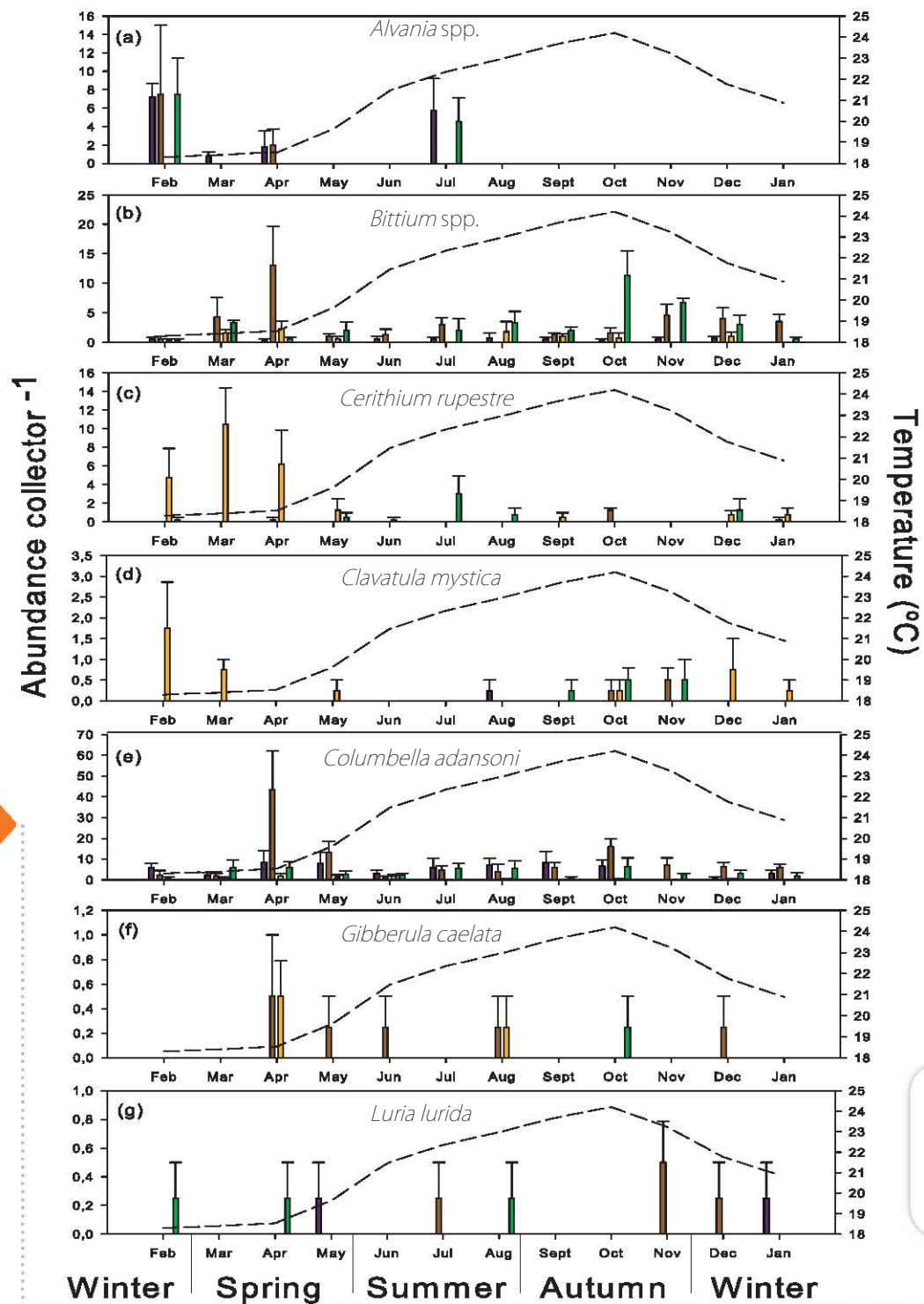


Fig. 5.2. Abundance of (A) *Alvania* spp., (B) *Bittium* spp., (C) *Cerithium rupestre*, (D) *Clavatulula mystica*, (E) *Columbella adansoni*, (F) *Gibberula caelata*, (G) *Luria lurida*, (H) *Mitra* spp., (I) *Polinices lacteus*, (J) *Rissoa* spp., (K) *Smaragdia viridis* and (L) *Tricolia pullus canarica* in ASs per month and habitat. The mean sea water temperature through time is also included. Error bars are standard error of means.

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## 5.4 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 collector 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., *C. adansoni*, *G. caelata*, *L. lurida*, *Mitra* spp., *Rissoa* spp. and *S. 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 larger in habitats occupied by brown seaweeds than in urchin barrens, 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, leafs, etc. (Rawlings, 1999; Przeslawski *et al.*, 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., *C. rupestre*, *Rissoa* spp. (Ávila and Malaquias, 2002), *G. caelata* (Gofas and Zenetos, 2003), *L. 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, *C. adansoni* 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.

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