

COLONIZATION PATTERNS OF DECAPODS INTO ARTIFICIAL COLLECTORS: SEASONALITY BETWEEN HABITAT PATCHES

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ABSTRACT

Understanding colonization of new habitats by recruits is essential to comprehend local abundance patterns of adult populations. Colonization of benthic habitats by new colonizers is achieved through the influx of larvae from the water column and movements from adjacent habitats. Colonization, i.e., the composition and abundance of new colonizers, into a focal habitat may be affected by surrounding habitats. In this study, we investigated seasonal variation through an annual cycle in postlarval settlement patterns of decapod crustaceans colonizing artificial collectors on different habitats, in particular: *Cymodocea nodosa* seagrass meadows, sandy patches, ‘urchin-grazed’ barrens and macroalgal-dominated beds, which are arranged in patches within seascapes in the eastern Atlantic. Our results showed that: 1) decapods, at least some species, settle preferentially on artificial collectors deployed on vegetated substrates when compared to those deployed on unvegetated substrates; 2) despite most decapods have a planktonic larval phase with wide oceanic dispersal, the presence of crustaceans in particular habitats suggests a great specificity at their early post-larval stages; and 3) although subtropical waters of Gran Canaria have a weak seasonal variation, early postlarval stages of decapod crustaceans showed two distinct settlement periods, i.e., a ‘cold’ and a ‘warm’ season.

KEY WORDS: artificial collectors, Canary Islands, colonization, crustaceans, Decapoda, habitats

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INTRODUCTION

Benthic subtidal habitats are continually colonized by larvae from the plankton, or by dispersal by organisms migrating from adjacent habitats, primarily as juvenile and adults, e.g., via crawling, swimming, rafting on the surface of the water or vegetation, or being transported by currents and waves (Gee and Warwick, 1996; Underwood and Keough, 2001; Chapman, 2002; Cole et al., 2007). Colonization by organisms with planktonic larvae is typically divided in four phases: development (including dispersal as a planktonic form), testing for habitat suitability, settlement, and survival until the organisms might be counted by observers (Underwood, 1979). The number of organisms passing through the fourth phase is termed ‘recruitment,’ while the number passing to the third phase is called ‘settlement’ (Keough and Downes, 1982). Therefore, recruitment is a composite of larval and juvenile stages, while settlement involves only larval stages. These early-stages are frequently major bottlenecks in the life-history of many benthic invertebrates, e.g., sea-urchins (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). A number of settlement cues, including the physical structure of the habitat as well as chemical and acoustic signals, are involved in assisting pelagic larvae of marine crustaceans to locate, settle, and colonize suitable ben-

thic habitats (Butler and Herrnkind, 1991; Eggleston et al., 1999; Forward et al., 2001; Stanley et al., 2011; Gartner et al., 2013). Colonization by new recruits is a major issue to explain shifts in distribution and abundance patterns of benthic dwelling species (Underwood and Keough, 2001).

Habitats with different structural complexity generally offer different resources to associated fauna such as food and shelter (Downes et al., 2000; Gartner et al., 2013; Matias, 2013). Habitat connectivity, i.e., ‘the degree to which the landscape facilitates or impedes movement between patches’ (*sensu* Taylor et al., 1993) depends on the scale and the organisms’ perception of changes across space (Kotliar and Wiens, 1990; Forward et al., 2001), and the spatial configuration of patches (Eggleston et al., 1999; Ricketts, 2001; Debinski, 2006; Roberts and Poore, 2006; Tanner, 2006). Dispersal and resource use by organisms are strongly influenced by the spatial structure of neighboring habitats, which determines the structure and dynamics of natural assemblages (Tilman, 1994; Loreau and Mouquet, 1999; Ricketts, 2001). Several studies on patterns of diversity and distribution of species have shown that the nature of the surrounding habitat affects the composition and abundance of assemblages on a focal habitat (Ricketts, 2001; Tuya et al., 2011). Yet, our understanding of how assemblages of

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species respond to variations in the identity of the habitat surrounding a focal habitat is limited to certain taxa from some locations and environments (Paula et al., 2003; Matias, 2013; Tolley et al., 2013).

Colonization patterns may vary over an annual cycle according to the different life-history traits of organisms, which affects, amongst other processes, their feeding modes, reproduction, development, mobility and dispersal. Settlement of marine benthic organisms can be seasonal (Harms and Anger, 1983; Underwood and Anderson, 1994; Nandakumar, 1996; Rajagopal et al., 1997; Maughan and Barnes, 2000; Watson and Barnes, 2004; Cifuentes et al., 2010), or continuous throughout the year (Reyns and Sponaugle, 1999; Le Vay et al., 2001; Antoniadou et al., 2011). Therefore, patterns of recruitment and growth, which are key structural elements in the marine benthos, can severely influence colonization and subsequent succession processes (Antoniadou et al., 2011). Furthermore, the habitat around a focal habitat may suffer variations through the annual cycle, such as changes in the biomass and frond density of vegetated habitats (Sánchez-Moyano et al., 2001; Tuya et al., 2006; Espino et al., 2008), or their food resources could be affected by processes such as sedimentation, re-suspension, and transport of particulated organic matter (Zajac and Whitlatch, 1982).

Benthic marine organisms include a wide range of life forms. Many of these organisms show a planktonic larval stage, which can last from minutes to months and constitutes the most dispersive period of their life cycle (Sponaugle et al., 2002; Pineda et al., 2007). In the particular case of decapod crustaceans, their life cycle comprises an embryonic, larval (from early developed zoea to settlement decapodid stage) and a postlarval (juvenile-adult) phase. The transition from decapodid to juvenile is driven by a metamorphosis, with dramatic morphological, physiological and behavioral changes (Anger, 2006). Decapod larvae show a wide array of adaptations to the pelagic environment, including modifications in functional morphology, anatomy, the molting cycle, nutrition, growth, chemical composition, metabolism, energy partitioning, ecology, and behavior (Anger, 2001). Therefore, decapod crustaceans are a suitable group for studying the interplay between colonization processes and seasonal habitat selection, due to their complex life history traits.

In this study, we investigated seasonal variation through an annual cycle in postlarval settlement patterns of decapod crustaceans colonizing artificial collectors located on different habitats, in particular: seagrass meadows, sandy patches, 'urchin-grazed' barrens, and macroalgal-dominated beds, which are arranged in patches within seascapes in the eastern Atlantic. Specifically, we tested the hypothesis that seasonal colonization of decapod assemblages would vary according to the habitat in which a focal habitat, here collectors, are embedded. In particular, we expected differences in the structure and composition of crustacean assemblages between vegetated (seagrass meadows and macroalgal-dominated beds) and unvegetated habitats ('urchin-grazed' barrens and sandy patches) that may vary through time as a result of seasonal patterns in both the ar-

rival of propagules from the water column and the vitality of vegetated habitats.

MATERIALS AND METHODS

Study Site

This study was carried out in the east coast of Gran Canaria (Canary Islands, Spain), where the predominant Canary Current and the trade winds are enhanced by the 'island mass' effect (Barton et al., 2000). Two coastal localities were selected: Risco Verde (RV, 27°51'25.94"N, 15°23'10.26"W; Fig. 1) and Playa del Cabrón (PC, 27°52'14.43"N, 15°23'00.31"W; Fig. 1). These localities encompass a mosaic of subtidal, neighboring, habitats, including seagrass meadows constituted by the seagrass *Cymodocea nodosa* (Ucria) Ascherson, 1870 and sandy patches on soft substrata, as well as 'urchin-grazed' barrens mainly generated by large densities of the sea urchin *Diadema africanum*, Rodríguez, Hernández, Clemente and Coppard, 2013 and macroalgal-dominated beds, primarily constituted by the frondose *Cystoseira abies-marina* (S. G. Gmelin) C. Agardh, 1820 and *Sargassum* spp., as well as *Dictyota* spp., *Padina pavonica* (Linnaeus) Thivy, 1960 and *Lobophora variegata* (J. V. Lamouroux) Womersley ex E. C. Oliveira, 1977 on rocky substrates (García-Sanz et al., 2012). All four habitats are found interspersed as mosaic patches at ca. 4-8 meters depth with similar orientation and exposure to waves.

Sampling

Four replicated artificial collectors, cushion-shaped leaf-like units (CLLU) according to García-Sanz et al. (2012) (Fig. 2) were deployed monthly on each habitat and locality (4 collectors per habitat = 16 collectors per locality every month; 384 collectors for the overall study) from February 2009 to February 2010. Collectors consisted of a plastic mesh frame (50 cm², 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 approximately every 4 cm. Raffia is positively buoyant underwater and so floats upright. A total of 75 cm² of concealment gardening mesh (\leq 1 mm diameter) was included inside, creating small holes and shelters (García-Sanz et al., 2012). In all cases, adjacent collectors within a habitat patch were 3-5 m apart; collectors from any two adjacent habitats were 100 s of m apart. Collectors were anchored using cable ties on hard substrata and through iron rods (\approx 50 cm long) on soft substrata. In all cases, collectors were in contact with the seabed (Fig. 2). After 1 month underwater, collectors were retrieved; this typically occurred between 5 to 7 days after new moon. We decided to be consistent in this issue, since settlement patterns of many crustaceans have been linked with the lunar phases (Roessler and Rehner, 1971; Phillips, 1972; Little, 1977; Victor, 1986), often taking place during the darkest phase of the moon, when predation is expected to be minimal. Each collector was removed by SCUBA divers by carefully enclosing each unit in a cloth bag (García-Sanz et al., 2012). The bags were immediately transported to the laboratory, where each collector was cleaned with freshwater. The samples were quickly preserved in 80% ethanol for further taxonomic identification. Most of the organisms caught were postlarvae. In the present study, the term 'postlarva' refers to early juvenile stages of crabs and hermit crabs (Anger, 2006).

Data Analysis

Differences in the total abundance of postlarvae of *Dardanus calidus* (Risso, 1827), *Majidae* spp., *Xantho* spp., *Grapsidae* spp., *Galathea* spp., *Macropodia rostrata* (Linnaeus, 1761), *Calcinus tubularis* (Linnaeus, 1767) and *Pagurus anachoretus* Risso, 1827 between habitats, seasons and localities were tested through 3-way permutation-based ANOVAs (www.stat.auckland.ac.nz/~mja/Programs.htm), based on Euclidean distances calculated from square root-transformed data. A high number of collectors (144 from a total of 384) were lost throughout the study at both localities as a result of swells or sabotages (Playa del Cabrón; Winter 6, 4, 8 and 3; Spring 4, 0, 6, and 1; Summer 3, 6, 7 and 3; and Autumn 4, 6, 8 and 5; Risco Verde: Winter 5, 5, 7 and 5; Spring 5, 3, 8, and 4; Summer 2, 2, 8 and 2; and Autumn 5, 4, 7 and 5 for barrens, macroalgal beds, sandy patches and seagrasses, respectively, from a total of 12 collectors per season and habitat). Month – a random source of variability – was thus 'sacrificed' to maintain a balanced design (i.e., equal sample sizes per treatment combination of Habitat and Season). When the sample sizes are not the same, the calculated *F*-ratios may be dominated by the sample variances from the larger samples (Underwood, 1997). We then considered the 4 collectors from each season (winter, spring, summer and autumn) as independent replicates. The

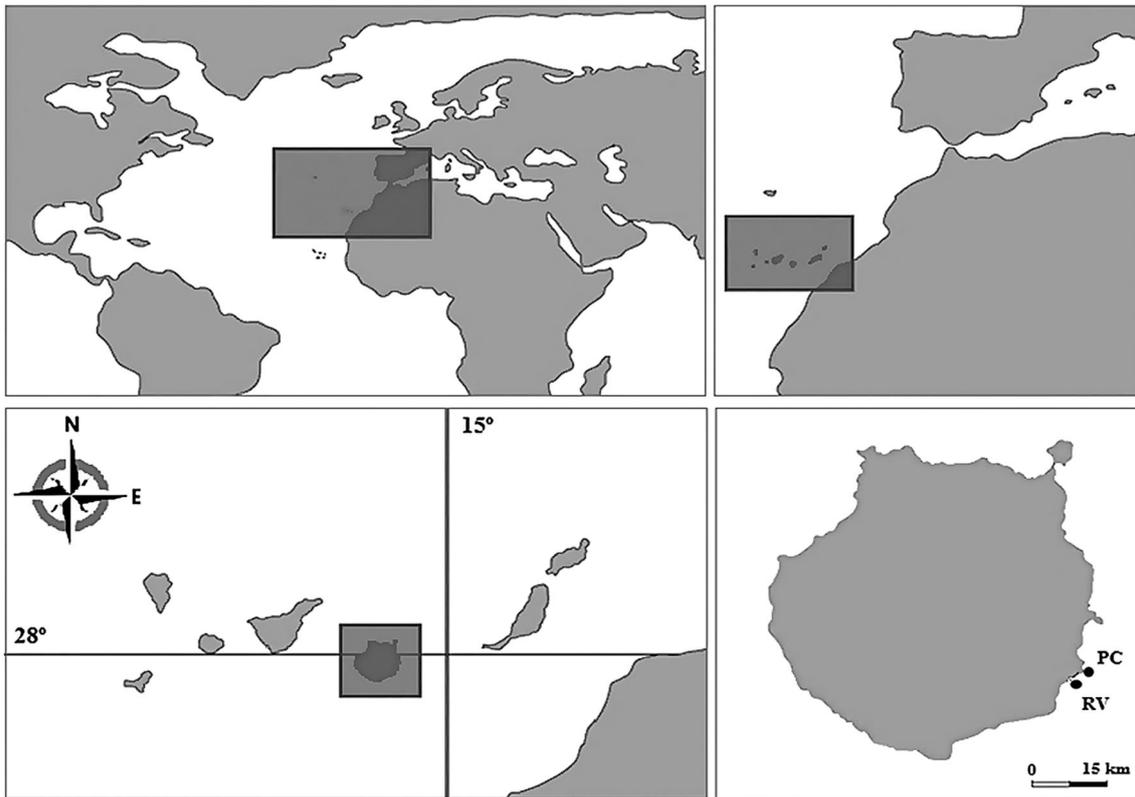


Fig. 1. Situation of the study area in the eastern Atlantic and study localities in the eastern coast of Gran Canaria Island (PC: Playa del Cabrón and RV: Risco Verde).

ANOVA models included the fixed factors Habitat and Season, while Locality was considered as a random factor. Pairwise comparisons were used to resolve differences between factors, whenever appropriate via 999 permutations of the raw data. Data was initially square-root transformed to achieve homogeneous variances.

To visualize differences in the assemblage structure of crustaceans between habitats and seasons for both localities, non-metric Multi-Dimensional Scaling (MDS) ordination plots were obtained, while a permutational multivariate ANOVA (PERMANOVA) tested the significance of dif-

ferences in crustacean assemblage structure between seasons, habitats and localities by using the same model outlined above for univariate ANOVAs. Ordination plots and the PERMANOVA were obtained via calculation of Euclidean distances from squared-root transformed data.

RESULTS

A total of 3092 decapod postlarvae were collected throughout the entire study. The most abundant taxa were: *D. calidus*

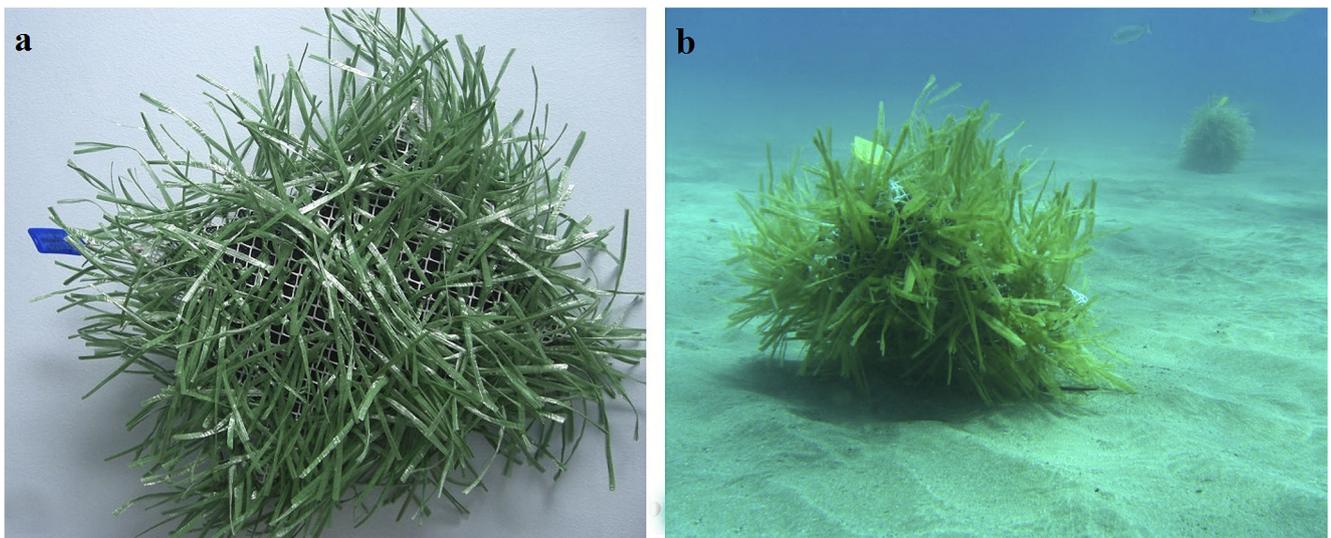


Fig. 2. Artificial collector, a cushion-shaped leaf-like unit (CLLU). a, out the water; b, placed on a sandy patch. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

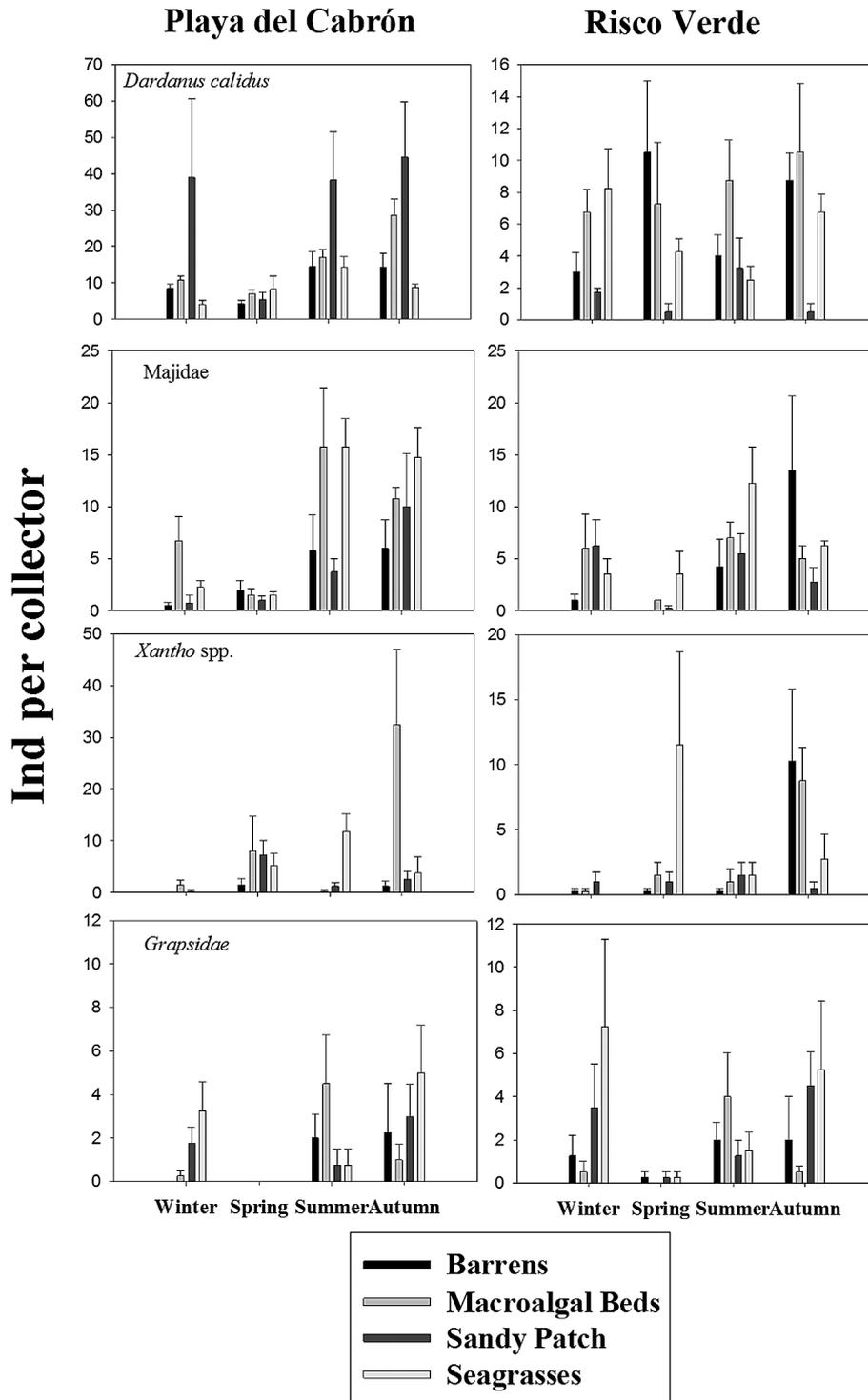


Fig. 3. Abundance of *Dardanus calidus*, *Majidae* spp., *Xantho* spp., *Grapsidae* spp., *Galathea* spp., *Macropodia rostrata*, *Calcinus tubularis* and *Pagurus anachoretus* per habitat and season at each locality. Error bars are +SE of means. The scale bars used for each graph are not necessarily the same.

(1418 individuals), *Majidae* spp. (707 individuals), *Xantho* spp. (477 individuals), *Grapsidae* spp. (235 individuals), *Galathea* spp. (117 individuals), *M. rostrata* (67 individuals), *C. tubularis* (54 individuals), and *Pagurus anachoretus* (17 individuals).

Differences in the abundance of *D. calidus* between seasons and habitats were inconsistent between the two study localities (Fig. 3, Table 1, ANOVA: Locality \times Season and Locality \times Habitat, $P < 0.05$). At PC, the abundance of *D. calidus* was larger in autumn and summer than in winter

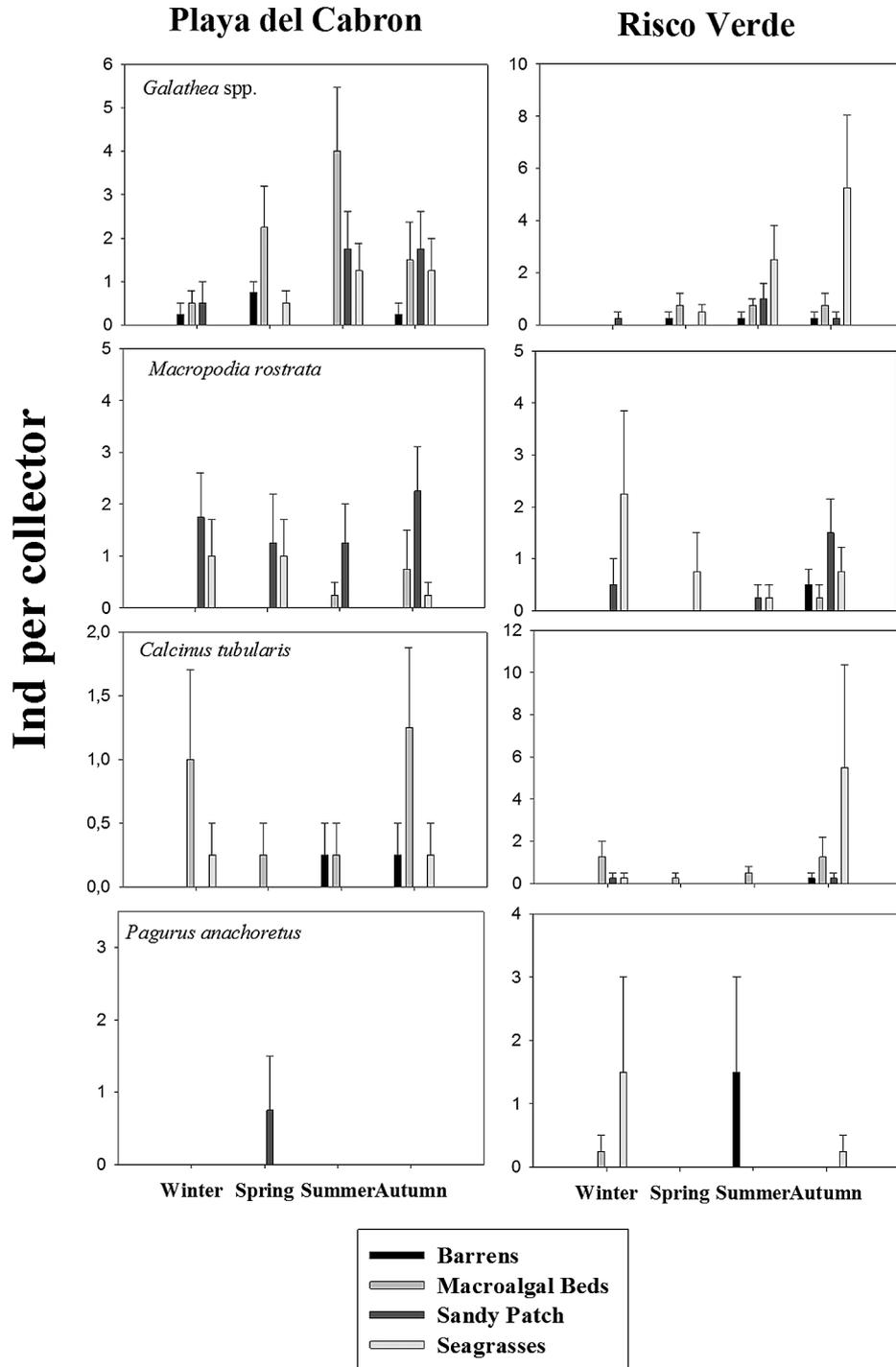


Fig. 3. (Continued.)

and spring; at RV, the abundance of *D. calidus* did not significantly differ between seasons (Fig. 3, Table 1, ANOVA: pairwise tests for Locality \times Season). At PC, the abundance of *D. calidus* was larger in collectors deployed on sandy patches than in the other habitats, whereas this pattern was reversed at RV (Fig. 3, Table 1, ANOVA: pairwise tests for Locality \times Habitat). The abundance of Majidae spp. was larger during summer and autumn at both study localities

(Fig. 3, Table 1, ANOVA: Season, $P = 0.05$, pairwise tests for Season). The abundance of *Xantho* spp. also differed between seasons (Fig. 3, Table 1, ANOVA: Season, $P < 0.05$); abundances were larger in autumn and spring than in summer and winter (pairwise tests for Season, Table 1). The abundance of Grapsidae was larger in spring than in the other seasons; however, the effect of seasons was marginally significant (Fig. 3, Table 1, ANOVA: Season, $P > 0.05$).

Table 1. Results of 3-way ANOVAs testing for differences in the abundance of *Dardanus calidus*, Majidae spp., *Xantho* spp., Grapsidae spp., *Galathea* spp., *Macropodia rostrata*, *Calcinus tubularis* and *Pagurus anachoretus* between seasons (W = winter, Sp = spring, S = summer and A = autumn), months within seasons, habitats (B = barrens, MB = macroalgal beds, SP = sandy patches and S = seagrasses) and localities (PC = Playa del Cabrón and RV = Risco Verde).

	df	MS	F	P	Pairwise comparisons	
<i>Dardanus calidus</i>						
Season	3	8.787	1.147	0.483	Season × Locality	
Locality	1	81.317	42.216	0.001	PC	A = S > W > SP
Habitat	3	3.594	0.184	0.888	RV	A = SP = W = S
Season × Locality	3	7.654	3.974	0.009		
Season × Habitat	9	1.905	1.158	0.421	Locality × Habitat	
Locality × Habitat	3	19.489	10.118	0.001	PC	SP > M > B = S
Sex × Locality × Habitat	9	1.645	0.854	0.562	RV	M = B = S > SP
Residual	96	1.926				
Majidae spp.						
Season	3	23.738	10.356	0.054		
Locality	1	2.289	1.92	0.164		
Habitat	3	9.431	15.076	0.078		
Season × Locality	3	2.292	1.922	0.126		
Season × Habitat	9	1.264	0.771	0.647		
Locality × Habitat	3	0.625	0.524	0.669		
Sex × Locality × Habitat	9	1.638	1.374	0.206		
Residual	96	1.192				
<i>Xantho</i> spp.						
Season	3	16.167	21.765	0.019	Season A = Sp > S = W	
Locality	1	4.796	3.506	0.063		
Habitat	3	6.711	2.392	0.232		
Season × Locality	3	0.742	0.543	0.647		
Season × Habitat	9	7.412	2.372	0.107		
Locality × Habitat	3	2.804	2.051	0.109		
Sex × Locality × Habitat	9	3.125	2.284	0.022		
Residual	96	1.367				
Grapsidae spp.						
Season	3	8.066	37.838	0.079	Season × Habitat	
Locality	1	1.257	1.404	0.239	Winter	S > SP > B = M
Habitat	3	2.121	6.571	0.109	Spring	M = B = S = SP
Season × Locality	3	0.213	0.238	0.878	Summer	M > S = SP = B
Season × Habitat	9	2.829	25.203	0.001	Autumn	S = SP > B = M
Locality × Habitat	3	0.322	0.361	0.782		
Sex × Locality × Habitat	9	0.112	0.125	0.999		
Residual	96	0.895				
<i>Galathea</i> spp.						
Season	3	3.069	29.516	0.021	Season A > S > W > Sp	
Locality	1	1.346	3.193	0.076	Locality × Habitat	
Habitat	3	2.268	1.449	0.312	PC	M > SP > S > B
Season × Locality	3	0.103	0.246	0.869	RV	S > M > SP > B
Season × Habitat	9	0.972	2.657	0.075		
Locality × Habitat	3	1.564	3.712	0.014		
Sex × Locality × Habitat	9	0.365	0.867	0.555		
Residual	96	0.421				
<i>Macropodia rostrata</i>						
Season	3	0.858	4.869	0.122	Season × Habitat	
Locality	1	0.241	0.731	0.387	Winter	Locality × Habitat
Habitat	3	3.004	3.067	0.221	Spring	S > SP > M = B PC S > SP > M = B RV
Season × Locality	3	0.176	0.534	0.659	Summer	SP > S = M > B
Season × Habitat	9	0.429	4.325	0.021	Autumn	SP > S = M > B
Locality × Habitat	3	0.979	2.971	0.036		
Sex × Locality × Habitat	9	0.099	0.301	0.977		
Residual	96	0.329				
<i>Calcinus tubularis</i>						
Season	3	1.322	7.141	0.065		
Locality	1	0.337	1.026	0.328		
Habitat	3	1.605	8.303	0.077		

Table 1. (Continued.)

	df	MS	F	P	Pairwise comparisons
Season × Locality	3	1.185	0.564	0.656	
Season × Habitat	9	0.264	1.132	0.425	
Locality × Habitat	3	0.193	0.588	0.631	
Sex × Locality × Habitat	9	0.233	0.711	0.719	
Residual	96	0.328			
<i>Pagurus anachoretus</i>					
Season	3	0.034	0.215	0.862	
Locality	1	0.208	1.571	0.226	
Habitat	3	0.034	0.215	0.866	
Season × Locality	3	0.158	1.194	0.329	
Season × Habitat	9	0.148	1.387	0.305	
Locality × Habitat	3	0.158	1.194	0.326	
Sex × Locality × Habitat	9	0.107	0.807	0.642	
Residual	96	0.132			

Differences in the abundance of Grapsidae between habitats were inconsistent with seasons (Fig. 3, Table 1, ANOVA: Season × Habitat, $P < 0.05$); pairwise tests indicated, however, that at all seasons the abundance of Grapsidae was at a maximum in a vegetated habitat (seagrasses in winter and autumn; macroalgal beds in spring and summer). The abundance of *Galathea* spp. differed between seasons (Fig. 3, Table 1, ANOVA: Season, $P < 0.05$); pairwise tests indicated larger abundances in autumn and summer than in winter and spring. Differences in the abundance of *Galathea* spp. between habitats were inconsistent between localities (Fig. 3, Table 1, ANOVA: Locality × Habitat, $P < 0.05$); the abundance of *Galathea* spp. was, however, larger in vegetated than in non-vegetated habitats (macroalgal beds for PC and seagrasses for RV, pairwise tests for Locality × Habitat, Table 1). The abundance of *M. rostrata* differed between habitats inconsistently through seasons (Fig. 3, Table 1, ANOVA: Season × Habitat, $P < 0.05$); at all seasons, however, abundances were larger in collectors deployed either on seagrasses or sandy patches relative to barrens and macroalgal beds (pairwise tests for Season × Habitat). *Macropodia rostrata* showed inconsistent differences in the abundance between localities (Fig. 3, Table 1, ANOVA: Locality × Habitat, $P < 0.05$); however, pairwise tests indicated, again, that abundances of *M. rostrata* were larger in collectors deployed either on seagrasses or sandy patches relative to barrens and macroalgal beds. The abundance of *C. tubularis* was, in general, larger in vegetated habitats (seagrasses and macroalgal beds) than in unvegetated habitats; however, the effect of habitat was marginally significant (Fig. 3, Table 1, ANOVA: Habitat, $P > 0.05$). Finally, the abundance of *P. anachoretus* did not show any difference between seasons and habitats (Fig. 3, Table 1, ANOVA: all terms $P > 0.05$).

The structure of crustacean assemblages differed between seasons (Fig. 4a, PERMANOVA: Pseudo- $F = 6.15$, $P < 0.05$); assemblages that colonized the collectors in summer and autumn differed, in terms of their assemblage structure, relative to those that recruited in winter and spring (pairwise tests, $P < 0.01$). However, the structure of crustacean assemblages did not differ between habitats (Fig. 4b, PERMANOVA: Pseudo- $F = 0.87$, $P > 0.05$).

DISCUSSION

Colonization patterns of decapods crustaceans have been successfully studied using artificial collectors in previous

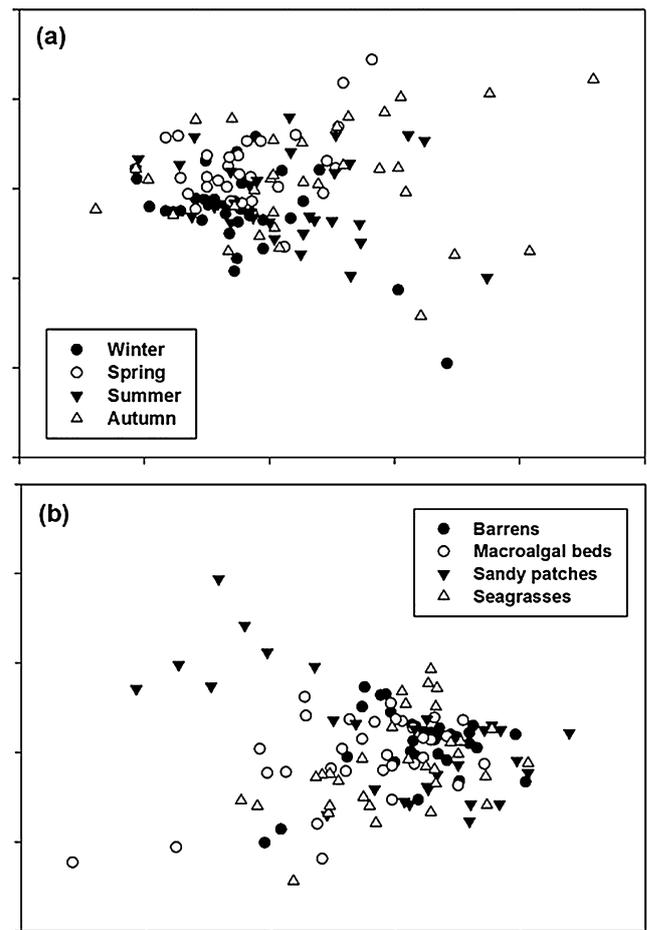


Fig. 4. MDS ordination plots showing similarities in crustacean assemblage structure between (a) seasons (stress = 0.17) and (b) habitats (stress = 0.17).

studies, e.g., to determine the relationship between the structure of the habitat and the diversity and abundance of new settlers (Eggleston et al., 1999; Paula et al., 2003; Paula et al., 2006; Christie et al., 2007). Most studies are based on artificial collectors that mimic natural habitats (Phillips, 1972; Edgar, 1991; Flores et al., 2002; Cole et al., 2007; García-Sanz et al., 2012; Gartner et al., 2013). In the present study, artificial collectors had the same structure and period of colonization across the different habitat patches, which removed potential differences in the structure of the focal habitat, i.e., the collectors. Our findings have demonstrated that colonization of decapods into a focal habitat (here, our collectors) were dependent on the surrounding habitat exclusively for some species; in particular, Grapsidae, *Galathea* spp. and *M. rostrata*. For these taxa, postlarvae settled, preferentially, on collectors deployed on vegetated substrates when compared to those deployed on unvegetated substrates. For the overall study, 2332 organisms (62.4%) of the 3737 that colonized the artificial collectors come from collectors deployed on vegetated habitats.

Active selection for structurally complex habitats at settlement appears to be a common behavior for decapod postlarvae (Moksnes, 2002). Paula et al. (2003) observed that brachyuran megalopae species displayed distinct settlement patterns in relation to specific habitats within a mangrove swamp, where their adult populations occurred. Other studies also found that *Callinectes sapidus*, Rathbun, 1896 megalopae (Olm et al., 1990) and palaemonid carideans (Eggleston et al., 1999) settled preferentially on collectors deployed in seagrass meadows, whereas *Metacarcinus magister* Dana, 1852 megalopae selected habitat plots containing oyster shells relative to muddy habitats (Eggleston and Armstrong, 1995). These results apparently agree with the fact that vegetated habitats provide shelter and food for the new settlers (Shaffer et al., 1995; Eggleston et al., 1999; Moksnes, 2002) that can: 1) induce settlement of recruits from the water column, and/or 2) provide a source of new colonizers from adjacent vegetated habitats. Probably, both mechanisms may help to explain the observed patterns. At the moment, however, it remains untested which of both processes prevails as determinants of our results.

Macroalgal beds and seagrasses share many species, because they both provide protection and food for faunal assemblages (Shaffer et al., 1995; Moksnes, 2002); this has caused the consideration of macroalgae and seagrasses as biogenic 'foundation' species across coastal landscapes. In this study, the most abundant decapods in collectors deployed in macroalgal beds were *Calcinus tubularis*, *Galathea* spp., Majidae spp., and *Xantho* spp. In the Canary Islands, *C. tubularis* is one of the most abundant crustaceans in *Cymodocea nodosa* seagrass meadows (González, 1995; Espino et al., 2008). In this habitat, *Galathea* spp., Majidae spp., and *Xantho* spp. are also present, but at lower abundances (González, 1995; Espino et al., 2008). Xanthid crabs, represented in the archipelago by at least four species: *X. hydrophilus* (Herbst, 1790), *X. pilipes* A. Milne-Edwards, 1867, *X. porressa* (Olivi, 1792) and *X. sexdentatus* (Miers, 1881), inhabit rocky shores of the inter- and shallow subtidal zone, mostly occurring under stones (González, 1995; d'Udekem d'Acoz, 1999). Likewise, Majidae spp.

(mainly represented by species of *Maja*, *Herbstia*, *Acanthonix*, and *Inachus*) is also present on rocky shores, particularly in macroalgal beds (González, 1995; d'Udekem d'Acoz, 1999). Thus, the settling of these species seem to follow adult populations distribution, as observed by Paula et al. (2003) for mangrove crabs, as well as for *Uca pugi-lator* (Bosc, 1802) (O'Connor, 1991) and for two species of *Petrolisthes* (Jensen, 1989). Without a doubt, settling into habitats adjacent to adult population ensures that larvae arrive to a suitable substrate.

Surprisingly, we found large numbers of *M. rostrata* on sandy patches, where adults are not present and predation-induced mortality rates are often very high, reaching more than ca. 80% in 2 days (Moksnes et al., 1998). This outcome is likely an artifact caused by the presence of collectors on bottoms that lack provision of any shelter, i.e., an 'oasis' effect: attraction of new individuals to the only available substrate (García-Sanz et al., 2012). On the other hand, typical sand dwelling species, such as *Cryptosoma cristatum* Brullé, 1837 and Portunidae, were never collected in the collectors deployed in sandy substrates.

Increasing larval survivorship is of special importance in oceanic islands, i.e., at Gran Canaria Island, where local populations have to be mainly shelf-maintained, due to distant external larval sources (Landeira et al., 2010). After release, planktonic larvae can be flushed out to the narrow Gran Canaria shelf by ebbing currents. This transport can export larval pools to the open ocean, far from their natal origin without the possibility to return (Landeira et al., 2009). However, islands normally have larval retention areas in the coast through fronts, eddies and internal waves, as a result of the interaction of currents with the coastal topography, e.g., capes, headlands, banks, and bays (Sponaugle et al., 2002). Retention near parental population is also determined by intrinsic larval behavior, as larvae of many species perform daily or tidal vertical migration by active swimming to avoid predation and/or offshore currents (Queiroga and Blanton, 2005).

Landeira (2010) showed that decapod larvae occurred in the plankton during all year round in the shelf edge off Gran Canaria Island. The highest proportion of crab and hermit crab larvae were in their early zoeal stages of development, while megalopae stages were very scarce. This indicates that the planktonic phase of hermit crabs takes place over the shelf; after this phase, the megalopae should tend to migrate back to the coast accomplished by selective tidal stream transport, as has been observed in other regions (Queiroga and Blanton, 2005).

Our study has shown settlement of postlarvae at varying periods. The temporal distribution of *Galathea* spp., for example, included two main settlement peaks during late autumn-winter and summer, whereas *Xantho* spp. settled preferentially during autumn and early spring. Likewise, a single peak was observed for Grapsidae spp. during autumn-early winter, and *D. calidus* and Majidae spp. showed a settlement peak during summer and autumn. This somehow illustrates the existence of a 'cold' season in early spring and a 'warm' season that encompasses from summer to autumn, in which most of the analyzed crustaceans tend to settle. Broadly, the settlement pattern seems to correlate with the

annual cycle of decapod larvae in the plankton at the island scale (Landeira, 2010), although studies with higher temporal resolution are required to verify this. The subtropical conditions of the Canary Islands (Barton et al., 1998) induce a less marked larval seasonality than in temperate regions of the Northeast Atlantic (Lindley, 1998). As an example, xanthid larvae and postlarvae are found in the water column all year round offshore the Canary Islands with settlement peaks in spring and autumn (Landeira et al., 2010), whereas in estuaries of the southern Iberian Peninsula, Xanthid larvae are only present in the plankton during spring (González-Gordillo and Rodríguez, 2003), or from April to September (Paula, 1987), while the settlement period is restricted to July-October (Flores et al., 2002). In tropical regions, similar patterns have been reported relative to the present study. Minimal annual temperature fluctuations in the tropics favor continuous reproduction that leads to the permanent presence of decapod larvae in the plankton throughout the year (Reyns and Sponaugle, 1999; Le Vay et al., 2001; Tolley et al., 2013). In general, settlement patterns of decapod crustaceans in tropical regions are in consonance with the seasonal trends observed for the Canary Islands. For example, the settlement of postlarval brachyurans is year round and characterized by a large spring pulse, followed by a drop in abundance during summer, and a subsequent increase in autumn (Reyns and Sponaugle, 1999; Le Vay et al., 2001; Tolley et al., 2013). As a result, the outcomes of this study suggest that temporal variability in the arrival of crustaceans into artificial collectors was, to some extent, predicted by their abundances in the offshore waters of Gran Canaria Island (Landeira, 2010), and habitat selection due to the response of a complex set of biotic and abiotic cues (Chapman and Underwood, 2008). Of course, data from both datasets come from different years, which add an unknown source of random variability to our data and preclude solid conclusions. In any case, this outcome points out that the arrival of colonizing crustaceans onto collectors is, at least partially, performed by planktonic larvae from the water column.

In summary, this study has indicated that early postlarvae of decapods, at least for some taxa, tend to show a higher degree of preference for substrates located within vegetated habitats; early postlarval stages of decapod crustaceans showed two distinct settlement periods, i.e. a 'cold' and a 'warm' season.

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