Capítulo 6.

Colonization patters of decapod crustaceans into artificial collector: seasonality between habitat patches

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 is affected by the surrounding matrix habitat around such focal habitat. In this study, we tested whether colonization of decapod crustaceans into experimental artificial habitats (collectors) were mediated by the identity of the surrounding habitat (seagrasses and sandy patches on soft substrata; 'urchin-grazed' barrens and macroalgal beds on rocky substrata) within a seascape in the eastern Atlantic (Gran Canaria Island). These responses were tested throughout an annual cycle to assess whether seasonality may concurrently affect colonization patterns. Our results showed that (1) colonization into artificial habitats (collectors) by decapods was affected by the type of habitat surrounding collectors; (2) decapods settle preferentially on collectors deployed on vegetated substrates when compared to those deployed on unvegetated substrates; (3) 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 (4) 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.

Keywords: colonization, artificial collectors, crustaceans, decapoda, habitats, Canary Islands.

Índice

Capítulo 6

Colonization patters of decapod crustaceans into artificial collector: seasonality between habitat patches

6.1 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 passively by currents and wave action (Underwood and Keough, 2001; Chapman, 2002). 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 benthic habitats (Butler and Herrnkind, 1991; Eggleston et al., 1999; Forward et al., 2001; Stanley et al., 2011). Habitat colonization by new recruits is a major issue to explain dramatic shifts in distribution and abundance patterns of benthic dwelling species (Underwood and Keough, 2001).

Habitats with different physical structure generally offer different resources to associated fauna, such a food and shelter (Downes *et al.*, 2000; Matias, 2013). Habitat connection (i.e., 'the degree to which the landscape facilitates or impedes movement between patches'; Taylor *et al.*, 1993) depends on the scale and the organisms' perception of changes across space (e.g. Kotliar and Wiens, 1990; Forward *et al.*, 2001), and the spatial configuration of patches (e.g. Roberts and Poore, 2006) and the surrounding matrix (e.g. Eggleston et al., 1999; Ricketts, 2001; Debinski, 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*). Numerous studies on patterns of diversity and distribution of species have shown that the nature of the surrounding matrix of habitats affects the composition and abundance of assemblages on a focal habitat (Ricketts, 2001; Tuya *et al.*, 2011). Investigating the matrix that surrounds each habitat is, therefore, crucial to understand local responses of assemblages of species to habitats (Paula *et al.*, 2003; Matias, 2013; Trolley *et al.*, 2013).

Colonization patterns may vary over an annual cycle according to the different life-history traits of organisms, what affects, between other processes, their feeding modes, reproduction, development, mobility and dispersal (Beesley *et al.*, 1998). 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, these seasonal patterns of recruitment and growth, which are a key structural element in the marine benthos, can severely influence the colonization and subsequent succession processes (Antoiadou *et al.*, 2011). Furthermore, the surrounding matrix around a focal habitat may suffer variations through the annual cycle, such as changes in the biomass and frond density of vegetated habitats (Rueda *et al.*, 2001; Sánchez-Moyano *et al.*, 2001; Rueda and Salas, 2003; Espino *et al.*, 2008), or their food resources could be affected by processes such as sedimentation, re-suspension, and transport of particulate organic matter (Zajac and Whitlatch, 1982).

Benthic marine organisms include a wide range of life forms. Most of these organisms show a common planktonic larval stage, which can last from minutes to months and constitute 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 Substrates (ASs) under a different matrix of surrounding 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 matrix in which a focal habitat, here ASs, are embedded.

6.2 MATERIALS AND METHODS

6.2.1 Study site and sampling

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 sites were selected: Risco Verde (27°51'25.94" N, 15°23'10.26" W, Fig. 1) and Playa del Cabrón (27°52'14.43" N, 15°23'00.31" W, Fig. 1.). These sites 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 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.

Four replicated ASs, cushion-shaped leaf like units according to García-Sanz *et al*., (2012) were deployed monthly on each type of habitat from February 2009 to February 2010. ASs were spread out between multiple habitat patches from month to month, i.e. ASs were interspersed across sites. In all cases, adjacent ASs within a habitat patch were 3-5 m apart; ASs from any two adjacent habitats were 100s of m apart. ASs were anchored using cable ties on hard substrata and by iron rods (ca. 50 cm long) on soft substrata. In all cases, ASs were in contact with the seabed.

Fig. 6.1. Situation of the study area in the eastern Atlantic and study site in Gran Canaria Island.

6.2.2 Data analysis

Statistical analyses focused on the dominant taxa, which accounted for up to 99.84 % of total colonizers and included (in alphabetical order): *Calcinus tubularis* (Linnaeus 1767), *Dardanus calidus* (Risso 1827), *Galathea* spp., Grapsidae spp., Macropodia rostrata (Linnaeus 1761), Majidae spp., *Pagurus anachoretus* (Risso 1827) and *Xantho* spp. Differences in total abundance of postlarvae between 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 sites; site - 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 4 ASs from each habitat as independent replicates. The ANOVA models included the fixed factors: 'Habitat' and 'Season', while 'Month' was a random factor nested within 'Season'. Pairwise comparisons were used to resolve differences between levels of factors, whenever appropriate. For each taxon, we estimated the relative contribution of each factor to explain colonization patterns through calculation of their variance components (Graham, 2001).

We tested the relationship between the multivariate patterns (abundance data) of colonizers into the ASUs per month (by pooling all collectors from all habitats) and the abundance of planktonic larvae collected weekly in the water column off Gran Canaria Island in 2005 and 2006 (Landeira, 2010), using the RELATE routine (PRIMER 6.0). Only taxa presented in both data matrices were included (i.e. *Galathea* spp., *Dardanus calidus*, *Calcinus tubularis*, *Pagurus anachoretus*, Grapsidae spp., *Xantho* spp., Majidae spp.). Rho values were calculated as Spearman rank correlations, and p values using 4999 permutations via the PRIMER 6.0 statistical package. This test assessed whether temporal dissimilarities in the crustacean assemblage structure in water column off Gran Canaria Island were matched by temporal dissimilarities in the assemblage structure of colonizing decapod crustaceans into ASs.

6.3 RESULTS

A total of 3,743 decapod postlarvae were collected. The most abundant taxa were: *Dardanus calidus* (1,667 individuals), Majidae spp. (909 individuals), *Xantho* spp. (522 individuals), Grapsidae spp. (380 individuals), *Galathea* spp. (135 individuals), *Macropodia rostrata* (69 individuals), *Calcinus tubularis* (51 individuals) and *Pagurus anachoretus* (4 individuals). For the majority of these taxa, the amount of variability explained by the main factor 'Season' (between ca. 8-21%, Table 6.1) was similar to variation associated with the type of habitat; main factor 'Habitat', which accumulated between ca. 6-18% (Table 6.1). In most cases, the amount of variability accumulated by months within seasons (between ca. 0-21%, Table 6.1) was lower than seasonal variation. Most variation in the number of colonizers of the different taxa into ASs was accumulated by the residual term (between ca. 26-92%, Table 6.1), i.e. from AS to AS deployed at each month and habitat, highlighting a large variation in the number of colonizers of the distinct taxa at small spatial scales (i.e. between collectors a few meters apart). Overall, there was a connection between temporal dissimilarities in the assemblage structure of colonizing decapod crustaceans and temporal dissimilarities in the crustacean assemblage structure in water column off Gran Canaria Island (Rho = 0.24, P=0.058) (Fig. 6.2).

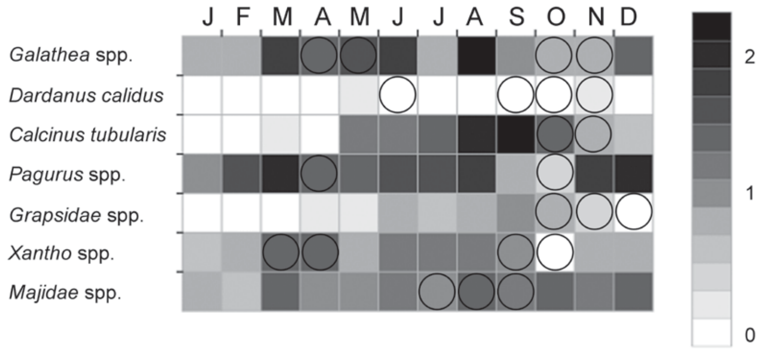

Fig. 6.2. Temporal distribution of planktonic larvae abundance (log (nº larvae m-3 +1)) represented with an intensity color grid. The main settlement peaks of respective postlarvae are superimposed (empty circles) over the grid. .

Table 6.1. Results of 3-way ANOVAs testing for differences in the abundance of *Galathea* spp., Grapsidae spp., *Macropodia rostrata*, Majidae spp., and *Xantho* spp. between seasons (Winter =W, Spring =Sp, Summer =S and Autumn =A), months within seasons and habitats (Barrens =B, Macroalgal Beds =MB, Sandy Patches =SP and Seagrasses =S).

	df	MS	F	P		Variance components (%)	Pairwise comparisons			
							Habitat		Season	
***Galathea* spp.**									A > S > Sp > W	
Season	3	3.0161	8.2638	0.0154		17.24			W *vs.* Sp	0.0938
Habitat	3	2.075	2.2943	0.1054		11.45			W *vs.* S	0.1004
Month (Season)	8	0.36497	0.99272	0.4474		0			W *vs.* A	0.1
Season x Habitat	9	0.65474	0.72393	0.6852		0			Sp *vs.* S	0.19
Month (Season) x Habitat	24	0.90442	2.46	0.001		26.86			Sp *vs.* A	0.19
Residual	144	0.36765				44.45			S *vs.* A	1
Grapsidae spp.									A > W > S > Sp	
Season	3	8.0628	4.416	0.0454		13.69			W *vs.* Sp	0.1008
Habitat	3	4.109	1.5319	0.2182		6.5			W *vs.* S	0.7996
Month (Season)	8	1.8258	2.468	0.0164		9.8			W *vs.* A	0.5932
Season x Habitat	9	3.7506	1.3983	0.2458		11.24			Sp *vs.* S	0.105
Month (Season) x Habitat	24	2.6823	3.6258	0.0002		26.3			Sp *vs.* A	0.1042
Residual	144	0.73978				32.47			S *vs.* A	0.4
Macropodia rostrata							SP > S > MB > B			
Season	3	1.4464	1.3976	0.2982		8.34	B *vs.* MB	0.6706		
Habitat	3	1.2504	3.472	0.0278		12.3	B *vs.* SP	0.0442		
Month (Season)	8	1.0349	4.9996	0.0002		20.55	B *vs.* S	0.0508		
Season x Habitat	9	0.20541	0.57035	0.8072		0	MB *vs.* SP	0.065		
Month (Season) x Habitat	24	0.36015	1.74	0.0266		17.68	MB *vs.* S	0.0632		
Residual	144	0.20699				41.1	SP *vs.* S	0.3692		
Majidae spp.							MB > S > B > SP		A > S > W > Sp	
Season	3	30.432	6.3414	0.0302		20.78	B *vs.* MB	0.001	W *vs.* Sp	0.0984
Habitat	3	23.043	7.7058	0.0014		18.38	B *vs.* SP	0.5042	W *vs.* S	0.2992
Month (Season)	8	4.799	5.86	0.0002		14.18	B *vs.* S	0.0088	W *vs.* A	0.0994
Season x Habitat	9	1.8203	0.60873	0.791		0	MB *vs.* SP	0.018	Sp *vs.* S	0.0978
Month (Season) x Habitat	24	2.9903	3.6515	0.0002		20.9	MB *vs.* S	0.118	Sp *vs.* A	0.1
Residual	144	0.81893				25.76	SP *vs.* S	0.066	S *vs.* A	1
***Xantho* spp.**							MB > S > B > SP		A > Sp > S > W	
Season	3	18.279	6.7462	0.0184		17.5	B *vs.* MB	0.0052	W *vs.* Sp	0.1036
Habitat	3	6.1517	3.3792	0.0356		9.23	B *vs.* SP	0.7292	W *vs.* S	0.086
Month (Season)	8	2.7095	3.1328	0.0034		10.45	B *vs.* S	0.0532	W *vs.* A	0.0998
Season x Habitat	9	6.5174	3.5801	0.0052		19.23	MB *vs.* SP	0.1074	Sp *vs.* S	0.1958
Month (Season) x Habitat	24	1.8204	2.1048	0.0032		15.03	MB *vs.* S	0.828	Sp *vs.* A	0.4958
Residual	144	0.86488				28.56	SP *vs.* S	0.0924	S *vs.* A	0.104

6.3.1 Crabs

Throughout the study period, larger numbers of colonizers belonging to Majidae spp. and *Xantho* spp. were observed in ASs deployed in macroalgal beds and seagrasses than on the other habitat patches (Figs., 6.3d and 6.3e respectively; Table 6.1, pairwise tests for 'Habitat'; Table 6.3, pairwise tests for 'Month (Season) × Habitat'). *Macropodia rostrata* showed the largest number of colonizers in ASs deployed on sandy patches and seagrasses (Fig. 6.3c; Table 6.1, pairwise tests for 'Habitat'; Table 6.3, pairwise tests for 'Month (Season) × Habitat'). *Galathea* spp. had larger number of colonizers in ASs deployed in macroalgal beds, but only in some months (March, April, May and July, Fig. 6.3a; Table 6.3, pairwise tests for 'Month (Season) × Habitat'). Grapsidae spp. colonizers were particularly abundant in ASs deployed in seagrasses than in the other habitat patches, but only in some months (November, December and January, Fig. 6.3b; Table 6.3, pairwise tests for 'Month (Season) × Habitat'). For the two latter species, inconsistent patterns between habitat patches through time resulted in lack of significant main effects for 'Habitat' (Table 6.1).

Significant differences in the number of colonizers into ASs were observed between seasons for *Galathea* spp., which showed two mean peaks in the entrance of colonizers during summer and late autumn (Fig. 6.3a, Table 6.1, 'Season', $P<0.05$; marginally significant differences in pairwise tests for 'Season'). *Xantho* spp. also showed two mean peaks of settlement in spring and autumn (Fig. 6.3e, Table 6.1, 'Season', $P<0.05$; marginally significant differences in pairwise tests for 'Season'). Grapsidae spp. showed a single peak during autumn-early winter and Majidae spp. during late summer and autumn (Figs. 6.3b and 6.3d, Table 6.1, 'Season', $P<0.05$; marginally significant differences in pairwise tests for 'Season' in both cases). *Macropodia rostrata* did not show significant differences between seasons ('Season', $P>0.05$, Table 6.1).

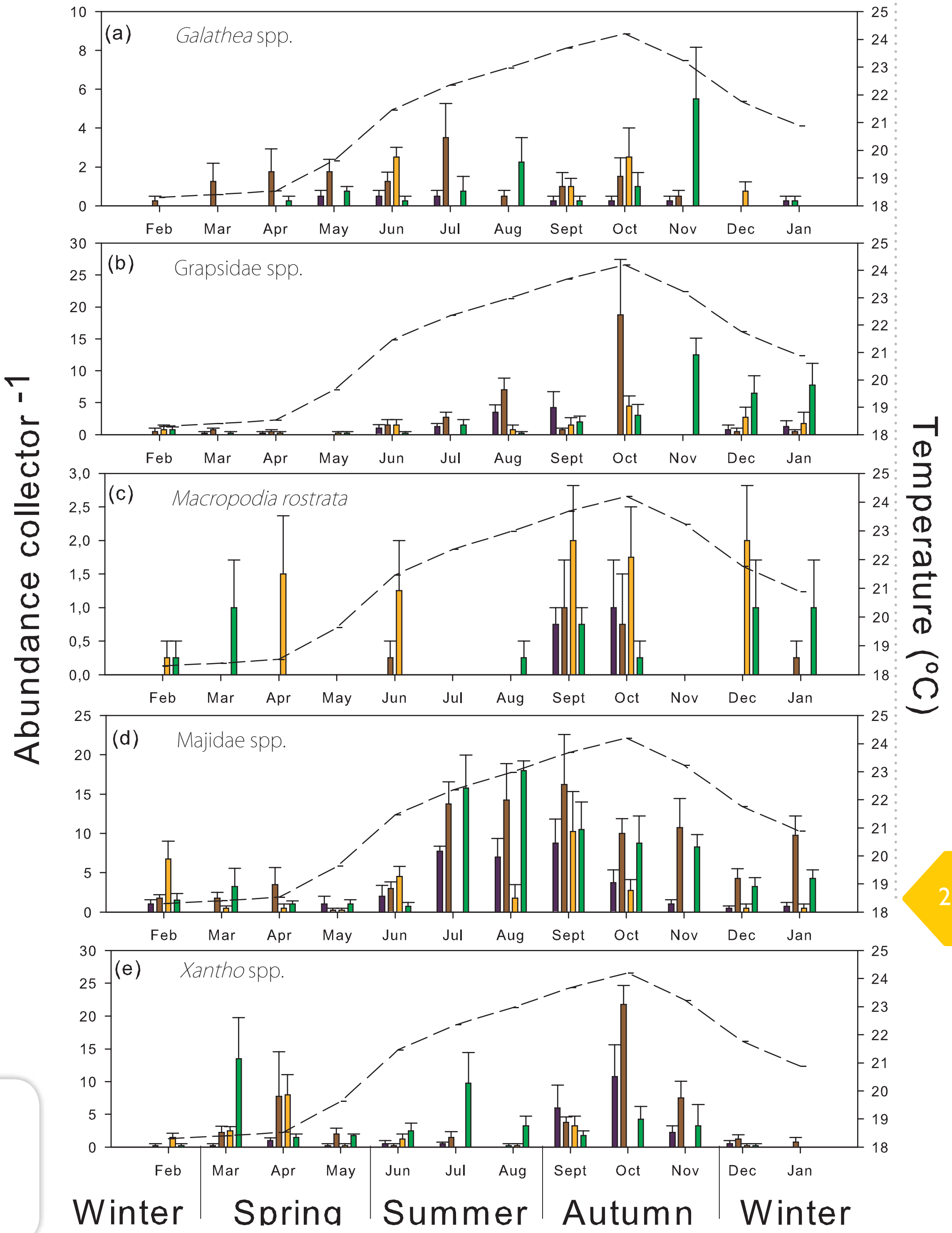

Fig. 6.3. Abundance of (a) *Galathea* spp., (b) Grapsidae spp., (c) *Macropodia rostrata*, (d) Majidae spp., and (e) *Xantho* spp. per month and habitat. The mean sea water surface temperature through an annual cycle is also included. Error bars are + SE of means.

6.3.2 Hermit Crabs

Significant differences in the number of hermit crabs colonizers between habitats were observed only for *Calcinus tubularis* (Fig. 6.4a Table 6.2, 'Habitat', P<0.05); the largest abundances were observed in macroalgal beds (Table 6.2, pairwise tests for 'Habitat'; Table 6.3, pairwise tests for 'Month (Season) x Habitat'). Patterns in the arrival of colonizers of *Dardanus calidus* were irrespective of habitat (Fig. 6.4b, Table 6.2). The few individuals of *Pagurus anachoretus* were collected in ASUs deployed on sandy patches (Fig. 6.4c).

Significant differences in the number of colonizers of *Dardanus calidus* were observed between seasons, showing a single peak during autumn (Fig. 6.4b, Table 6.2, 'Season', P<0.05; marginally significant differences in pairwise tests for 'Season'). The rest of hermit crabs did not show significant differences between seasons ('Season', P>0.05, Table 6.2).

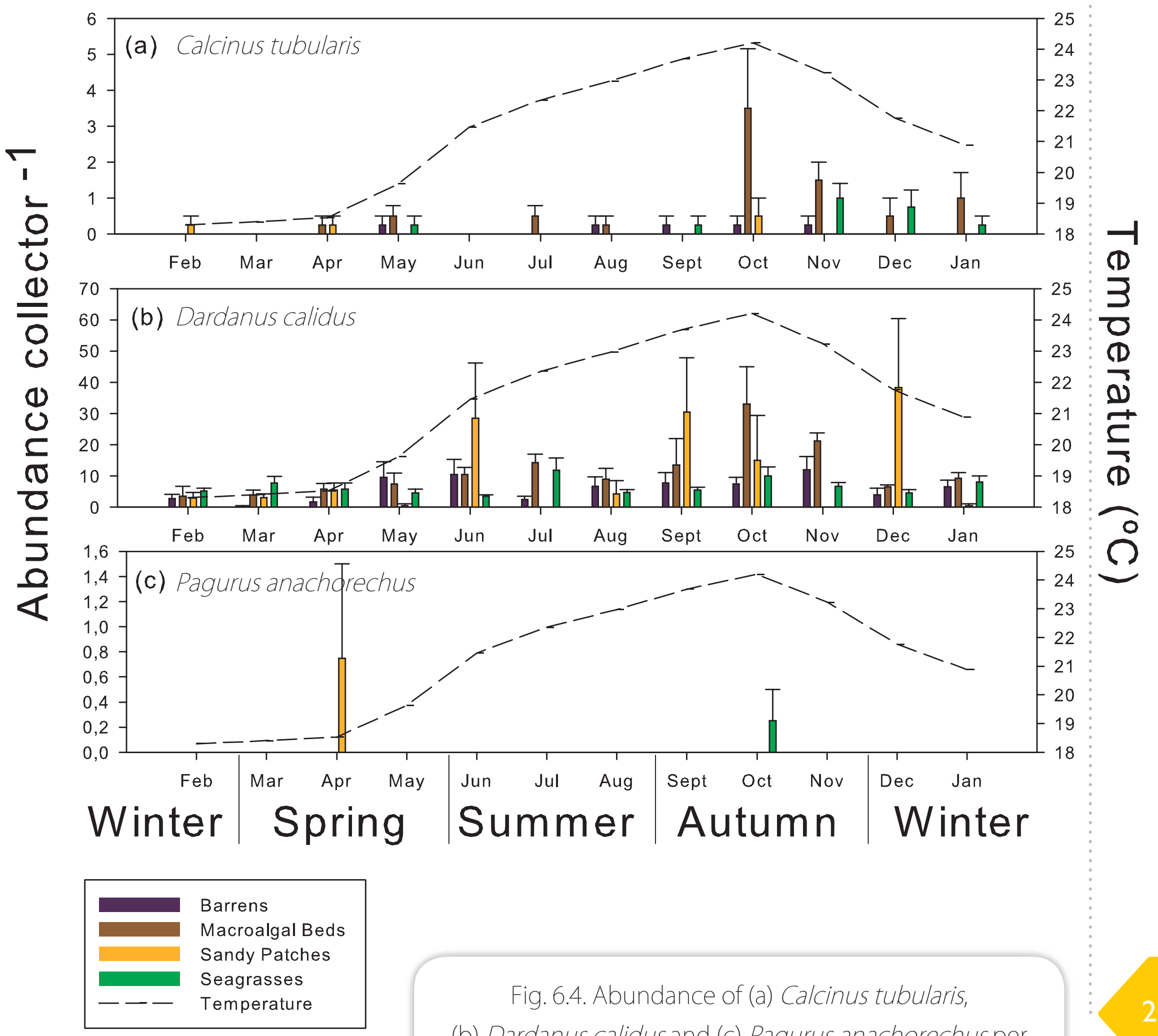

Fig. 6.4. Abundance of (a) *Calcinus tubularis*, (b) *Dardanus calidus* and (c) *Pagurus anachorechus* per month and habitat. The mean sea water temperature through an annual cycle is also included. Error bars are + SE of means.

Table 6.2. Results of 3-way ANOVAs testing for differences in the abundance of *Calcinus tubularis, Dardanus calidus* and *Pagurus anachorechus* between seasons (Winter = W, Spring =Sp, Summer = S and Autumn = A), months within seasons and habitats (Barrens = B, Macroalgal Beds = MB, Sandy Patches = SP and Seagrasses = S).

	df	**MS**	**F**	**P**		**Variance components (%)**	**Pairwise comparisons**			
							Habitat		**Season**	
Calcinus tubularis							MB > S > B > SP			
Season	3	1.1231	2.8559	0.0952		12.25	B *vs.* MB	0.0464		
Habitat	3	1.4341	4.123	0.019		14.95	B *vs.* SP	0.5612		
Month (Season)	8	0.39325	2.6329	0.0088		12.26	B *vs.* S	0.346		
Season x Habitat	9	0.26946	0.77467	0.6532		0	MB *vs.* SP	0.0264		
Month (Season) x Habitat	24	0.34784	2.3289	0.0016		22.14	MB *vs.* S	0.1308		
Residual	144	0.14936				38.4	SP *vs.* S	0.3486		
Dardanus calidus									A > W > S > Sp	
Season	3	13.284	3.9972	0.0592		12.7			W *vs.* Sp	0.4992
Habitat	3	13.294	2.2001	0.1186		10.83			W *vs.* S	0.6986
Month (Season)	8	3.3233	1.3835	0.214		6.68			W *vs.* A	0.2084
Season x Habitat	9	2.5543	0.42273	0.9136		0			Sp *vs.* S	0.0958
Month (Season) x Habitat	24	6.0425	2.5154	0.0004		26.58			Sp *vs.* A	0.1086
Residual	144	2.4022				43.21			S *vs.* A	0.2026
Pagurus anachoretus										
Season	3	1.48E-02	0.71132	1						
Habitat	3	1.48E-02	0.71132	0.5812						
Month (Season)	8	2.08E-02	1	0.461						
Season x Habitat	9	2.28E-02	1.0962	0.3958						
Month (Season) x Habitat	24	2.08E-02	1	0.5084						
Residual	144	2.08E-02								

Table 6.3. Summary of results of pairwise tests for differences between 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 6.1). Barrens = B, Macroalgal Beds = MB, Sandy Patches = SP and Seagrasses = S.

	B>MB	B>SP	B>S	MB>B	MB>SP	MB>S		SP>B	SP>MB	SP>S	S>B	SP>MB	SP>S
***Galathea* spp.**	-	-	-	7	4	4		4	-	2	4	2	2
Grapsidae spp.	1	2	1	1	2	2		-	-	-	3	3	3
Macropodia rostrata	-	-	-	-	-	-		4	4	4	3	3	3
Majidae spp.	-	2	1	6	7	3		1	1	2	5	-	7
***Xantho* spp.**	-	-	-	4	3	3		-	-	1	6	3	5
Calcinus tubularis	-	-	-	5	5	5		-	-	-	1	-	1
Dardanus calidus	-	3	-	2	4	1		4	2	3	1	-	3

6.4 DISCUSSION

Colonization patterns of decapod crustaceans have been successfully studied using artificial collectors in previous 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 substrata that mimic natural habitats (Phillips, 1972; Edgar, 1991; Flores *et al*., 2002; García-Sanz *et al*., 2012). In the present study, experimental substrates (ASs) 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 ASs). Our findings have demonstrated that colonization of decapods into a focal habitat (here, our ASs) were dependent on the surrounding habitat, even though several species did not show any particular response to different matrices. In this sense, decapod postlarvae settled, preferentially, on collectors deployed on vegetated substrates when compared to those deployed on unvegetated substrates (i.e. 6 of the 8 tested taxa and 2332 organisms of the 3737 analyzed in this study, = 62.4% of total organisms).

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 stratified settlement patterns in relation with specific habitats within a mangrove swamp, where their adult populations occurred. Other studies also found that Callinectes sapidus (Rathbun 1896) megalopae (Olmi *et al*., 1990) and Palaemonid shrimps (Eggleston *et al*., 1999) settled preferentially on collectors deployed in seagrass meadows, whereas Cancer 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), what can (i) induce settlement of recruits from the water column and/or (ii) provide a source of new colonizers from adjacent vegetated habitats. Probably, both mechanisms may help out to explain the observed patterns. Despite at the moment, it remains untested which of both processes prevails as determinants of our results, our results suggested that temporal variability in the arrival of crustaceans into artificial collectors was, at some extent, predicted by their abundances in the offshore waters of Gran Canaria (Landeira, 2010). Of course, data from both datasets come from different years, what 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 ASUs is, at least partially, performed by planktonic larvae from the water column.

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. The most abundant decapods in ASs 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. poressa (Olivi 1792) and X. sexdentatus (Miers 1881), inhabit rocky shores of the inter- and shallow subtidal zone, mostly occurring under stones (González, 1995; 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; Udekem D’Acoz, 1999). Thus, settling of these species seem to follow adult populations distribution, as also was observed by Paula *et al*., (2003) for mangrove crabs, as well as for *Uca pugilator* (O’Connor, 1991) and for two *Petrolisthes* species (Jensen, 1989). Without a doubt, settling into habitats adjacent to adult population ensures that larvae arrive to a suitable substrate.

Surprisingly, the greatest abundance of *Macropodia rostrata* was found 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 those of Portunidae family were never collected in the ASs deployed in sandy substrates.

To increase larval survivorship is of special importance in oceanic islands, i.e. Gran Canaria, where local populations have to be mainly shelf-maintained, due to the 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, e.g. 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, t 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 during autumn and early spring. Likewise, a single peak was observed for Grapsidae spp. during autumn-early winter, while Majidae spp. showed a settlement peak during late summer-early autumn. *Dardanus calidus* had a peak during autumn. This illustrates the existence of a ‘cold’ season in early spring and a ‘warm’ season that encompasses from summer to autumn. 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 south Iberian Peninsula, Xanthid larvae is 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 to those observed in 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; Trolley *et al*., 2013). In general, settlement patterns of decapod crustaceans in tropical regions are in consonance with the seasonal trends observed in 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 months, and a subsequent increase in autumn (Reyns and Sponaugle, 1999; Le Vay *et al*., 2001; Trolley *et al*., 2013).

In conclusion, early postlarvae of decapods tend to show a higher degree of preference for substrates located within vegetated habitats, which most likely provide shelter and food for new settlers coming from either the water column or from adjacent vegetated habitats. In the future, further research with these assemblages should investigate whether the chemoreception of new settlers determines the selection of new habitats and whether the cues vary along the time as seasonal changes occur in the habitat.

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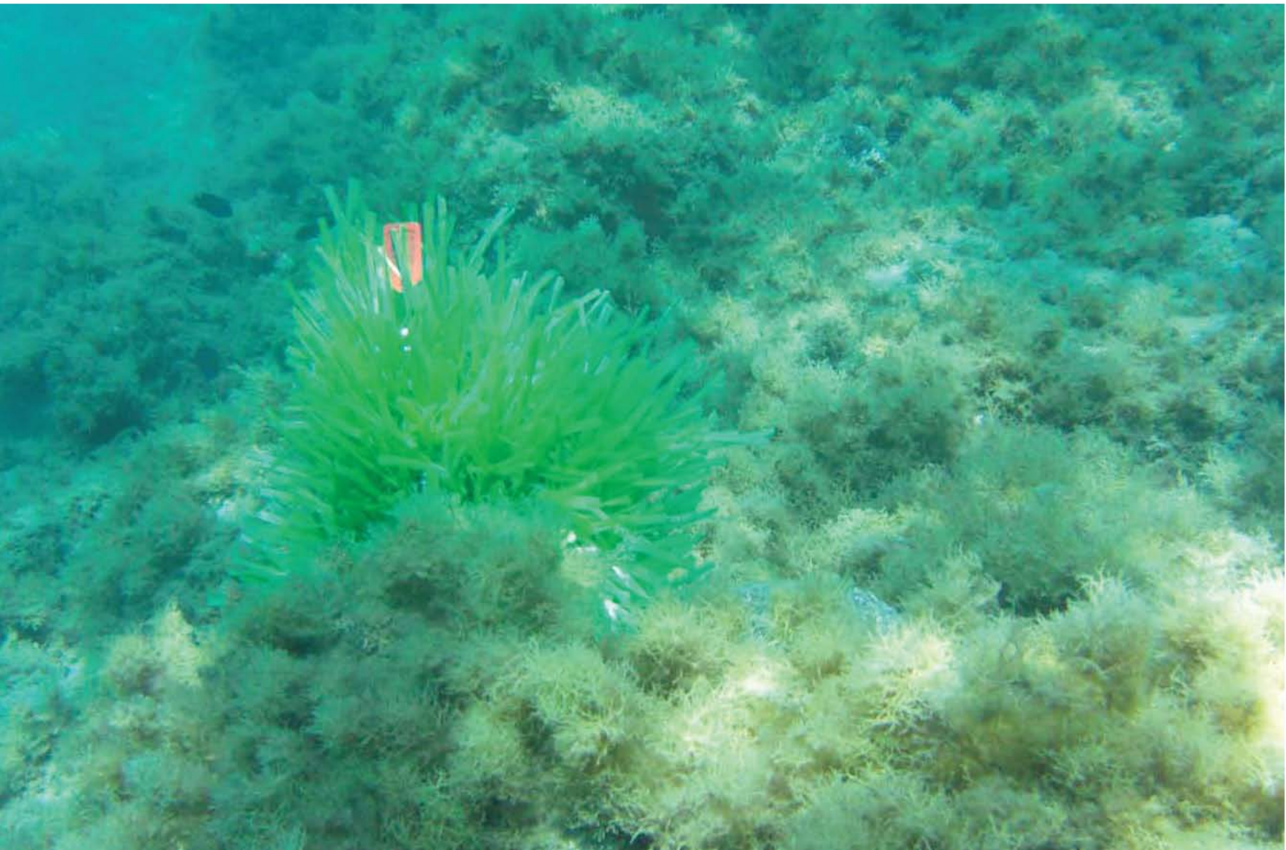
Capítulo 7.

Conclusiones



Índice

Capítulo 7.

Conclusiones

CAPÍTULO 2. POST LARVAL, SHORT-TERM, COLONIZATION PATTERNS: THE EFFECT OF SUBSTRATE COMPLEXITY ACROSS SUBTIDAL, ADJACENT, HABITATS

1. Los colectores artificiales se muestran como herramientas eficaces para estudiar los procesos de colonización (asentamiento y reclutamiento) en los cuatro hábitats que principalmente componen los mosaicos del paisaje costero de Gran Canaria: praderas de algas y 'blanquizales' sobre fondos rocosos, y parches de arena y 'sebadales' en fondos arenosos.

2. La variación en los patrones de colonización de macrofauna en colectores artificiales, a corto plazo, está principalmente afectada por la variación asociada a los tipos de hábitats sobre los que estos se colocan, más que por diferencias en la complejidad estructural de los distintos tipos de colectores.

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CAPÍTULO 3. DIFFERENCES IN PATTERNS OF FAUNAL COLONIZATION IN A SEAGRASS MEADOW BETWEEN THE DAY- AND NIGHTTIME: CONSISTENCY THROUGH A MOON CYCLE

3. La colonización de nuevos hábitats por organismos bentónicos difiere entre el día y la noche, observándose mayor intensidad (i.e. abundancia) durante la fase nocturna, cuando existe una mayor actividad para alimentarse como consecuencia de la disminución de la depredación.

4. Las diferentes fases lunares que comprenden un ciclo lunar afectan a la colonización de organismos bentónicos, siendo la luna llena la fase lunar con mayor intensidad (i.e. abundancia).

CAPÍTULO 4. CONTRASTING RECRUITMENT SEASONALITY OF SEA URCHIN SPECIES AT AN OCEANIC ISLAND: A WAY TO FACILITATE COEXISTENCE?

5. *Paracentrotus lividus* y *Arbacia lixula* muestran un único máximo de reclutamiento durante finales de invierno y primavera.

6. El reclutamiento de *Diadema africanum* fue estacional; los reclutas aparecieron durante finales de verano y otoño, especialmente en blanquizales.

7. Debido a que *D. africanum* es localmente el herbívoro más abundante (~1 orden de magnitud con respecto a *P. lividus* y *A. lixula*), es plausible que la coexistencia de estas 3 especies de erizo de mar se vea favorecida a que los patrones de reclutamiento no se solapan entre las especies menos abundantes con la más abundante.

CAPÍTULO 5. COLONIZATION OF PROSOBRANCH GASTROPODS ONTO ARTIFICIAL SUBSTRATES: SEASONAL PATTERNS BETWEEN HABITAT PATCHES

8. El hábitat es un factor más influyente en la colonización de gasterópodos prosobranquios que la estación del año, siendo los sustratos provistos de vegetación los que mayor abundancia muestran.

9. *Tricolia pullus canarica* y *Rissoa* spp. mostraron un patrón de colonización unimodal con un máximo de mayor abundancia durante invierno e inicio de primavera y durante primavera e inicio de verano, respectivamente, coincidiendo con el máximo de vitalidad de los hábitats vegetados.

CAPÍTULO 6. COLONIZATION PATTERS OF DECAPOD CRUSTACEANS INTO ARTIFICIAL COLLECTOR: SEASONALITY BETWEEN HABITAT PATCHES

10. La colonización de hábitats artificiales por crustáceos decápodos está afectada por el hábitat, siendo esta preferentemente sobre sustratos provistos de vegetación en comparación con sustratos desprovistos de vegetación.

11. A pesar de que la mayoría de los decápodos tienen una fase larvaria planctónica con amplia dispersión oceánica, la presencia de crustáceos en hábitats determinados demuestra una gran especificidad durante sus etapas larvales, post-larvales y juveniles.

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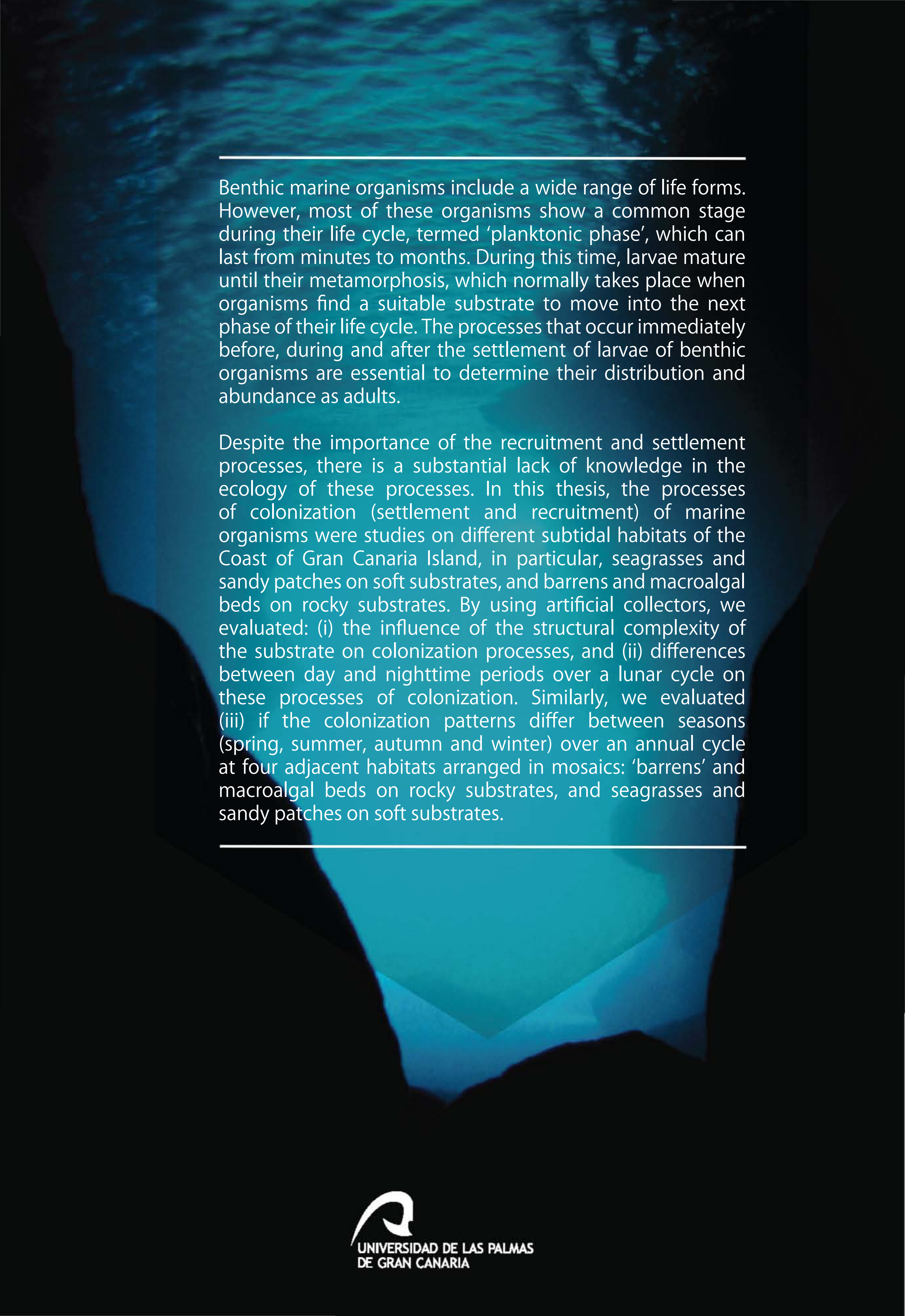
Sara García Sanz

Sara García Sanz (Gran Canaria, 1981) licenciada en Ciencias del Mar y master en gestión costera en la universidad de Las Palmas de Gran Canaria. durante su formación ha trabajado en proyectos destinados a estudios de impactos medioambientales, conservación y ecología marina en países como Cabo Verde, Portugal, México, Costa Rica y Ecuador, donde trabajó en el Parque Nacional Galápagos y posteriormente en la Fundación Charles Darwin.

En los últimos años, su interés investigador se ha centrado en los procesos de asentamiento y reclutamiento de invertebrados marinos.



Benthic marine organisms include a wide range of life forms. However, most of these organisms show a common stage during their life cycle, termed 'planktonic phase', which can last from minutes to months. During this time, larvae mature until their metamorphosis, which normally takes place when organisms find a suitable substrate to move into the next phase of their life cycle. The processes that occur immediately before, during and after the settlement of larvae of benthic organisms are essential to determine their distribution and abundance as adults.

Despite the importance of the recruitment and settlement processes, there is a substantial lack of knowledge in the ecology of these processes. In this thesis, the processes of colonization (settlement and recruitment) of marine organisms were studies on different subtidal habitats of the Coast of Gran Canaria Island, in particular, seagrasses and sandy patches on soft substrates, and barrens and macroalgal beds on rocky substrates. By using artificial collectors, we evaluated: (i) the influence of the structural complexity of the substrate on colonization processes, and (ii) differences between day and nighttime periods over a lunar cycle on these processes of colonization. Similarly, we evaluated (iii) if the colonization patterns differ between seasons (spring, summer, autumn and winter) over an annual cycle at four adjacent habitats arranged in mosaics: 'barrens' and macroalgal beds on rocky substrates, and seagrasses and sandy patches on soft substrates.

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Los organismos bentónicos marinos abarcan una gran variedad de formas de vida. Sin embargo, la mayoría muestran una etapa común durante su ciclo de vida, denominada 'fase planctónica', que puede durar desde minutos a meses. Durante este tiempo, las larvas maduran hasta sufrir la metamorfosis, que normalmente tiene lugar cuando encuentran un sustrato adecuado para pasar a la siguiente fase de su ciclo de vida. Los procesos que suceden inmediatamente antes, durante y después del asentamiento de las larvas de organismos bentónicos son fundamentales para determinar su distribución y abundancia como adultos.

A pesar de la importancia de los procesos de asentamiento y reclutamiento, aún existe un notable vacío de conocimiento en la ecología de estos procesos. En la presente tesis, se estudiaron los procesos de colonización (asentamiento y reclutamiento) de organismos marinos en diferentes hábitats submareales de la costa de la isla de Gran Canaria; en particular, 'sebadales' y arenales en sustrato blando, y 'blanquizales' y bosques de macroalgas en sustratos rocosos. Mediante el uso de colectores artificiales, evaluamos: (i) la influencia de la complejidad estructural del sustrato sobre los procesos de colonización, así como (ii) las diferencias entre periodos diurnos y nocturnos a lo largo de un ciclo lunar sobre dichos procesos de colonización. De igual modo, evaluamos (iii) si los patrones de colonización difieren entre estaciones (primavera, verano, otoño e invierno) a lo largo de un ciclo anual y entre cuatro hábitats submareales.

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