

Capítulo 3.  
Differences in patterns of  
faunal colonization in seagrass  
meadows between the day- and  
nighttime: consistency through a  
moon cycle



## ABSTRACT

The intensity of colonization of benthic habitats may vary according to varying ambient light intensities, i.e. between the day and the nighttime and through lunar cycles. In this study, we took advantage of artificial seagrass units to test whether the intensity of invertebrate colonization on a seagrass meadow differs between the day and the night through a complete lunar cycle. Artificial collectors were deployed, and subsequently retrieved, during the day and the nighttime at three consecutive days, within each of four successive moon phases. A total of 14,340 organisms were collected, including 5 dominant phyla. Larger abundances of colonizers were collected at the night (78.22% of total individuals) than the day (21.78% of total individuals), particularly for Annelida, Crustacea (particularly amphipods) and Mollusca, yet Echinodermata and Chordata did not show significant differences between the day and the nighttime, as a result of sparse individuals colonizing collectors. These results corroborate previous observations on the different rates of activity of small invertebrates inhabiting seagrass meadows between the day and the night. Significant differences in the number of colonizers among moon phases were additionally observed for Crustacea and Mollusca: larger abundances were detected during the full moon, but not for Annelida, Chordata and Echinodermata.

**Keywords:** colonization, artificial collectors, seagrass, moon phase, day-night, Canary Islands.

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



# Índice

Abstract	107
3.1 Introduction	109
3.2 Materials and methods	112
3.2.1 Study site and Sampling	112
3.2.2 Data analysis	113
3.3 Results	114
3.4 Discussion	120
3.5 References	126



## Capítulo 3

Differences in patterns of faunal colonization in seagrass meadows between the day- and nighttime: consistency through a moon cycle

### > 3.1 INTRODUCTION

Seagrass meadows are one of the most productive marine habitats, providing high-value ecosystem goods and services, which have caused their inclusion within different international conservation legislative frameworks, e.g. EU 92/43/CEE Habitats Directive (Hemminga and Duarte, 2000). Of particular relevance, seagrasses provide a key habitat for the settlement and recruitment of coastal fauna from tropical to temperate latitudes, e.g. macrofaunal invertebrates (Orth and van Montfrans, 1987; Heck *et al.*, 1997; Beck *et al.*, 2001) and fishes (Guidetti and Bussotti, 2000; Ribeiro *et al.*, 2006; Verdiell-Cubedo *et al.*, 2007; Espino *et al.*, 2011). Seagrass meadows provide protection from predators, as well as abundant food resources, both of which are likely to result in more juveniles reaching the adult stage (Heck *et al.*, 2003). In fact, seagrass meadows have been reported as habitats with higher densities of post-larvae and juveniles animals than adjacent unvegetated habitats (Orth and van Montfrans, 1987; Heck *et al.*, 1997; Heck *et al.*, 2003).

The marine phanerogam *Cymodocea nodosa* (Ucria) Ascherson is distributed across the Mediterranean Sea and the adjacent eastern Atlantic, including the archipelagos of Madeira and the Canaries (Tuya *et al.*, 2013). Meadows constituted by *C. nodosa* are the dominant vegetated communities on shallow soft substrates across the Canaries (Barberá *et al.*, 2006), providing food and shelter for diverse invertebrate and fish assemblages (Tuya *et al.*, 2001; Espino *et al.*, 2011).

Colonization of any benthic habitat by the potential pool of colonizers depends on multiple factors, e.g. the physical structure of the habitat (Srinivasan, 2003) and sensory signs (Gardner *et al.*, 2005) related to the presence of benthic organisms, such as conspecifics living in the habitat (Lecchini, 2005; Wright *et al.*, 2005). In turn, the intensity of colonization, in terms of the identity and abundance of new colonizers, of a new habitat may change at a range of spatial and temporal scales. At small temporal scales, differences between the day- and nighttime may affect colonization processes (Blackmon and Eggleston, 2001). Changes in light intensity, typically seen over the course of a day, can affect water column densities and dispersion of many aquatic organisms, as well as previous larval release (Morgan, 1996; Queiroga and Blanton, 2005). For example, active planktonic dispersal of some harpacticoid copepods is typically higher at night than during the day (Walters and Bell, 1986), while crabs megalopae dispersion is less intense during the day than at the night (Olimi, 1994). These strategies aim to minimize the intense predation on the coast (Morgan, 1987), favoring dispersion of organisms during periods of relaxed predation (Morgan and Anastasia, 2008). Mechanistically, light intensity is important since decreases in brightness can lessen capture rate of visual predators, and so many visual predators are not active at nighttime periods (Benfield and Minello, 1996; Clark *et al.*, 2003).

Variation in the magnitude of colonization of any habitat through lunar cycles may also be expected, due to different light intensities associated with each moon phase. For example, lobster post-larvae reach coastal areas within a few days from the new moon each month (Phillips, 1975; Little, 1977; Young, 1991; Acosta *et al.*, 1997), when exposure to predators is lower. In contrast, some amphipods and isopods tend to enter the water column under illumination by the full moon (Alldredge

and King, 1980). Settlement of some crustaceans occurs with a semilunar periodicity during neap tides (around quarter moons) (Paula *et al.*, 2006; Queiroga *et al.*, 2006).

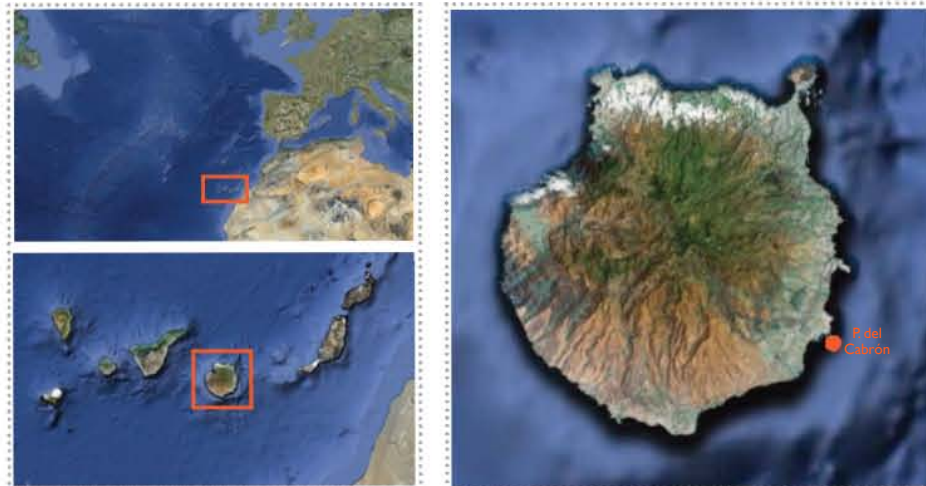
Artificial seagrass units provide a unique habitat to test for specific models of faunal colonization in seagrasses; in this context, the usefulness of these structures to attract most epifaunal elements inhabiting *C. nodosa* seagrass meadows have been demonstrated recently (Gartner *et al.*, 2013). In this study, we used artificial seagrass units to test whether the intensity of marine organism's colonization on a seagrass meadow differs between the day- and nighttime through a lunar cycle.



## 3.2 MATERIALS AND METHODS

### 3.2.1 Study site and Sampling

This study was carried out at Playa del Cabrón (27°52'14.43" N, 15°23'00.31" W, Fig. 3.1.), located on the east coast of Gran Canaria, Canary Islands, Spain. Four replicated CLLU (cushion-shaped leaf like units, according to García-Sanz *et al.*, 2012) were deployed, and subsequently retrieved, during the day (from ca. 9:00 am to 18:00 pm; i.e. daylight hours) and the nighttime (from 18:00 pm to 9:00 am) at each of 3 consecutive days within each of the 4 moon phases of a complete lunar cycle. Sampling dates were on (March 2013): 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> (first quarter), 9<sup>th</sup>, 10<sup>th</sup> and 11<sup>th</sup> (new moon), 16<sup>th</sup>, 17<sup>th</sup> and 18<sup>th</sup> (third quarter), and 23<sup>rd</sup>, 24<sup>th</sup> and 25<sup>th</sup> (full moon). The artificial structures (ASs) were deployed at 7-9 m depth on a homogenous *Cymodoceanodosa* seagrass meadow. Each collector was ca.5-7 m apart from the adjacent AS. ASs were fixed by iron rods (ca. 50 cm long) and in direct contact with the seabed. During retrieval, each AS was removed 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 cleaned with freshwater, and all organisms retained by a 0.5 mm mesh sieve were preserved in a 70% formalin-seawater solution, and subsequently identified to the lowest possible taxonomic level.



### 3.2.2 Data analysis

Differences in the total abundance of colonizers, including the dominant four phyla (Annelida, Echinodermata, Mollusca, Crustacea and Chordata between the day- and nighttime through the lunar cycle (first quarter; new moon; third quarter; full moon) were tested through 3-way, permutation-based, ANOVAs, based on Euclidian distances calculated from square root-transformed data. Each ANOVA model included the fixed factors 'Moon phase' and 'Day vs. Night', while day was a random factor nested within 'Moon phase'. Pairwise comparisons were used to resolve differences among levels of factors, whenever appropriate. Furthermore, we estimated the relative contribution of each factor to explain colonization patterns through calculation of their variance components.

### 3.3 RESULTS

A total of 14,340 organisms were collected, including 20 taxa belonging to 5 phyla; the abundance by phyla was (in alphabetical order): Annelida (33 individuals), Chordata (6 individuals), Crustacea (13913 individuals), Echinodermata (4 individuals) and Mollusca (384 individuals) (Appendix 3.1). These organisms were identified as post-larval, juvenile and some adult individuals. The amount of variability explained by the main factor 'Day vs. Night' (between 0-38.5%, Table 3.1) usually dominated over variation accumulated by the distinct moon phases (main factor 'Moon Phase', which accumulated between 0-36.96%). In general, larger abundances of colonizers were collected at the night than the day (night: 78.22% of total individuals vs. day: 21.78% of total individuals, Fig. 3.2A). In particular, larger numbers of colonizers of Annelida, Crustacea and Mollusca were collected in ASs deployed at nighttime, relative to ASs deployed during the day (Figs. 3.2.B, E and F, respectively, Table 3.1, pairwise tests for 'Day vs. Night';  $P < 0.01$ ). However, no significant differences were observed between 'Day vs. Night' for Echinodermata and Chordata (Figs. 3.2.C and D, respectively, Table 3.1).

Significant differences in the number of colonizers among moon phases were observed for Crustacea and Mollusca, which showed larger abundances during full moon (Figs. 3.2.E and F, respectively, Table 3.1, pairwise tests for 'Moon Phase'  $P < 0.05$ ). No significant differences were observed for the rest of phyla (Annelida, Chordata and Echinodermata (Figs. 3.2.B, C and D, respectively, Table 3.1, pairwise tests for 'Moon phase'  $P > 0.05$ )).

Sara García Sanz

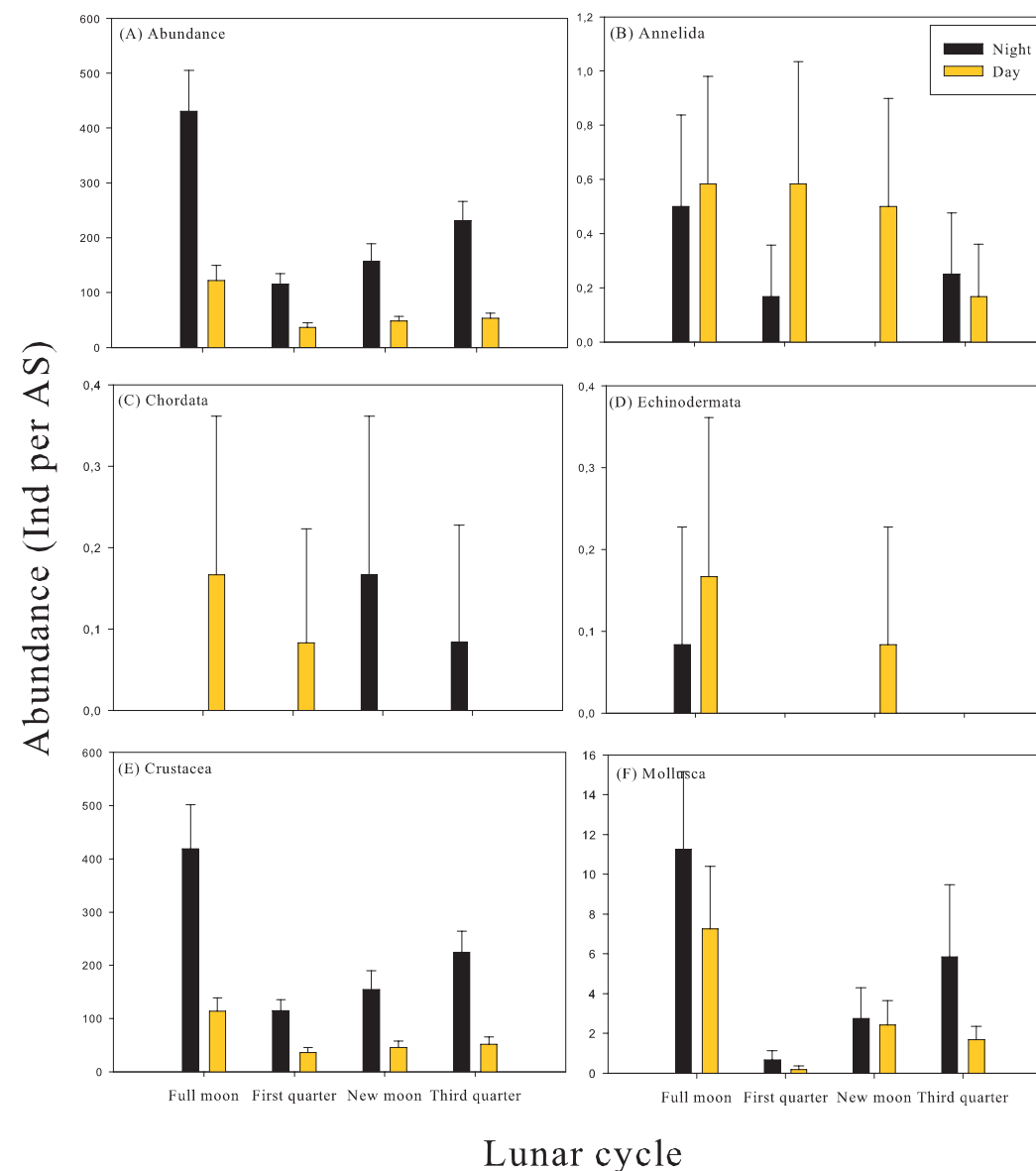


Fig. 3.2. Abundances of (A) total individuals, (B) Annelida, (C) Chordata, (D) Echinodermata, (E) Crustacea and (F) Mollusca per moon phases ('Full Moon', 'First quarter', 'New Moon' and 'Third quarter'), and day vs. night. Error bars are standard error of means.

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



Table 3.1. Results of 3-way ANOVAs testing for differences in abundances of total individuals, Annelida, Chordata, Crustacea, Echinodermata and Mollusca among moon phases ('Lunar cycle': 'First quarter', 'New Moon', 'Third quarter' and 'Full Moon'), days within each moon phase and 'Day vs. Night'. The amount of variation accumulated by each factor is indicated through the variance components (expressed in %). Data transformations, P-values for pairwise comparisons, and Cochran's tests are included for each ANOVA.

	df	MS	F	P	Variance components (%)	Pairwise comparison
<b>Total individuals</b>						
<b>Transform: Sqrt (x+1)</b>						
Moon Phase = Moon	3	245.59	66.278	0.0002	24.55%	First quarter < New Moon 0.0956
Day vs. Night	1	1155.6	89.842	0.0002	37.73%	First quarter < Third quarter 0.1
Days (Moon)	8	3.7055	0.706	0.689	0%	First quarter < Full Moon 0.0952
Moon x Day vs. Night	3	30.348	2.359	0.152	9.34%	New Moon < Third quarter 0.105
Days (Moon) x Day vs. Night	8	12.863	2.451	0.0204	10.67%	New Moon < Full Moon 0.106
Residual	72	5.2481			17.71%	Third quarter < Full Moon 0.0962
Cochran's Test	C= 0.1432 (n.s.)					
<b>Annelida</b>						
<b>Transform: None</b>						
Moon Phase = Moon	3	0.53819	1.9872	0.2132	10.08%	-
Day vs. Night	1	1.2604	6.7222	0.03	14.28%	-
Days (Moon)	8	0.27083	0.65546	0.7326	0%	-
Moon x Day vs. Night	3	0.45486	2.4259	0.1366	14.25%	-
Days (Moon) x Day vs. Night	8	0.1875	0.45378	0.8852	0%	-
Residual	72	0.41319			61.39%	-
Cochran's Test	C= 0.1345 (n.s.)					
<b>Chordata</b>						
<b>Transform: Ln(x+1)</b>						
Moon Phase = Moon	3	6.67E-03	0.19048	1	0.00%	
Day vs. Night	1	3.82E-16	1.09E-14	1	0.00%	
Days (Moon)	8	3.50E-02	1.3125	0.243	11.00%	
Moon x Day vs. Night	3	6.67E-02	1.9048	0.206	17.60%	
Days (Moon) x Day vs. Night	8	3.50E-02	1.3125	0.247	15.60%	
Residual	72	2.67E-02			55.81%	
Cochran's Test	C= 0.25 (P< 0.01)					



	df	MS	F	P	Variance components (%)	Pairwise comparison
<b>Crustacea</b>						
Transform: Sqrt (x+1)						
Moon Phase = Moon	3	229.7	63.808	0.0002	24.00%	First quarter < New Moon 0.1018
Day vs. Night	1	1160.2	96.228	0.0002	38.25%	First quarter < Third quarter 0.0992
Days (Moon)	8	3.5998	0.706	0.6902	0%	First quarter < Full Moon 0.0984
Moon x Day vs. Night	3	30.779	2.553	0.1224	9.77%	New Moon < Third quarter 0.0992
Days (Moon) x Day vs. Night	8	12.057	2.363	0.0262	10.31%	New Moon < Full Moon 0.1004
Residual	72	5.1018			17.66%	Third quarter < Full Moon 0.0978
Cochran's Test	C = 0.1493 (n.s.)					
<b>Echinodermata</b>						
Transform: Ln (x+1)						
Moon Phase = Moon	3	4.00E-02	8	0.073	17.80%	
Day vs. Night	1	2.00E-02	0.8	0.3984	0%	
Days (Moon)	8	5.00E-03	0.25	0.983	0%	
Moon x Day vs. Night	3	6.67E-03	0.26667	0.8532	0%	
Days (Moon) x Day vs. Night	8	2.50E-02	1.25	0.2816	16.40%	
Residual	72	4.17E-02			65.80%	
Cochran's Test	C = 0.25 (P < 0.01)					
<b>Mollusca</b>						
Transform: Ln (x+1)						
Moon Phase = Moon	3	12.485	23.092	0.0002	36.96%	First quarter < New Moon 0.105
Day vs. Night	1	2.888	3.9607	0.0912	11.12%	First quarter < Third quarter 0.1068
Days (Moon)	8	0.54067	1.0236	0.4312	2.07%	First quarter < Full Moon 0.1
Moon x Day vs. Night	3	0.53885	0.739	0.5542	0%	New Moon > Third quarter 0.3044
Days (Moon) x Day vs. Night	8	0.72916	1.3805	0.2178	11.75%	New Moon < Full Moon 0.1008
Residual	72	0.5282			38.10%	Third quarter < Full Moon 0.1006
Cochran's Test	C = 0.1483 (n.s.)					



### 3.4 DISCUSSION

In our study, largest abundances of organisms were caught during the night than the day, particularly the most conspicuous groups (i.e. crustaceans and molluscs), which is consistent with previous studies in seagrass meadows (Heck, 1977; Robertson, 1980; Gray *et al.*, 1998; Guest *et al.*, 2003), with consistent patterns through the different phases of a lunar cycle. The larger abundances during the nighttime suggest an increased activity of this fauna. In addition, and during the night, there is an influx of species and specimens from adjacent sandy bottoms, which are rare or absent during the day, such as several species of crabs or hermit crabs, that look for food resources or shelter (Raso *et al.*, 2006). These diel migrations or movements are frequent in this type of landscapes, where patches of seagrasses and sandy bottoms are usually interspersed on soft bottoms in shallow water (Ledoyer, 1966, 1984). These migrations are also known for other faunal groups such as fishes (Bell and Harmelin-Vivien, 1983; Robertson, 1984; Mattila *et al.*, 1999; Guidetti and Bussotti, 2000). It is worth noting that amphipods, the largely most abundant animal group, moved mainly at night, as some authors has previously observed (Hobson and Chess, 1976; Buschmann, 1990; Taylor, 1998), particularly for amphipods inhabiting *C. nodosa* meadows in the southeastern Mediterranean (Raso *et al.*, 2006). Nocturnal activity of amphipods typically increase at night to feed on suspended matter with antennae outstretched (Taylor, 1998).

Patterns in faunal colonization of the most conspicuous groups between the day and the night were consistent among moon phases. Importantly, however, our results have demonstrated that there were lunar influences on the abundance of organisms colonizing ASs. Several studies have shown the relationship between lunar phases and the settlement/arrival of invertebrates into the benthic system; most of them have concluded that less lighting facilitates the arrival of new settlers due to decreased predation (e.g. Little, 1977; Olafsson *et al.*, 1994; Acosta *et al.*, 1997; Blackmon and Eggleston, 2001; Butler *et al.*, 2005). This phenomenon has also been observed for oceanic larvae of different invertebrates (Kinsey and Hopkins, 1994; Hernández-León *et al.*, 2004; Moyano, 2009; Landeira, 2010). Nevertheless, the largest abundances of Crustaceans, dominated mainly by Amphipods (Appendix 3.1), were

detected during full moon. These results agree with those observed by Alldredge and King (1980). Molluscs, dominated mainly by *Rissoa* spp. (Appendix 3.1), also showed larger abundances during the nighttime during full moon, in contrast with results observed by Taylor (1998). These results could indicate that colonization processes of benthic organisms, as well as related to differences in the light intensity between the day and the night and the moon phases, may also be influenced by tides, which are unambiguously connected with the moon phases (McDowall, 1969). Therefore, colonization processes can be intensified by extreme tides (coinciding with the full moon).

In conclusion, colonization of invertebrate fauna in a shallow-water seagrass meadow was larger during the nighttime than during the day, consistently through an entire moon cycle. The magnitude of colonization was particularly intense during the full moon





Appendix 3.1. Maximum, minimum, total and mean abundance (+ SE of means) of organisms colonizing ASs at each moon phase (Full Moon, First quarter, New Moon and Third quarter), and day vs. night.

Specie	Full moon											First quarter									
	Day					Nighth						Day					Nighth				
	Min	Max	Total	Mean	Error	Min	Max	Total	Mean	Error		Min	Max	Total	Mean	Error	Min	Max	Total	Mean	Error
<b>Annelida</b>	0	2	6	0.5	0.34	0	2	7	0.58	0.4		0	1	2	0.17	0.19	0	2	7	0.58	0.45
<b>Echinodermata</b>																					
<i>Paracentrotus lividus</i>	0	1	2	0.17	0.19	0	1	1	0.08	0.14		0	0	0	0	0	0	0	0	0	0
<b>Crustacea</b>																					
<b>Amphipoda</b>	45	174	1366	113.8	24.5	242	816	5017	418.08	82.41		17	78	431	35.92	8.99	70	210	1357	113.08	20.35
<i>Dardanus calidus</i>	0	1	2	0.17	0.19	0	2	6	0.5	0.4		0	0	0	0	0	0	1	1	0.08	0.14
<i>Galathea</i> spp.	0	0	0	0	0	0	1	1	0.08	0.14		0	0	0	0	0	0	1	1	0.08	0.14
<i>Macropodia rostrata</i>	0	0	0	0	0	0	0	0	0	0		0	1	1	0.083	0.14	0	0	0	0	0
Majidae	0	0	0	0	0	0	1	1	0.08	0.14		0	0	0	0	0	0	0	0	0	0
<i>Pagurus anachoretus</i>	0	0	0	0	0	0	1	1	0.08	0.14		0	2	3	0.25	0.31	0	5	14	1.17	0.76
<b>Chordata</b>																					
<i>Canthigaster capistrata</i>	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
<i>Gobius</i> spp.	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
<i>L. candolle</i>	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
<i>L. lepadogaster</i>	0	1	2	0.17	0.19	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
<i>Sparisoma cretense</i>	0	0	0	0	0	0	0	0	0	0		0	1	1	0.083	0.14	0	0	0	0	0
<b>Mollusca</b>																					
<i>Aplysia</i> spp.	0	1	3	0.25	0.23	0	1	2	0.17	0.19		0	0	0	0	0	0	0	0	0	0
<i>Bittium</i> spp.	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	1	1	0.08	0.14
<i>Cerithium</i> spp.	0	0	0	0	0	0	1	1	0.08	0.14		0	0	0	0	0	0	0	0	0	0
<i>Mitra</i> spp.	0	0	0	0	0	0	1	4	0.33	0.25		0	0	0	0	0	0	0	0	0	0
<i>Rissoa</i> spp.	0	18	84	7	3	0	24	126	10.5	3.83		0	1	2	0.17	0.19	0	3	7	0.58	0.45
<i>Smagardia viridis</i>	0	0	0	0	0	0	1	0	0	0		0	0	0	0	0	0	0	0	0	0
<i>T. pullus canarica</i>	0	0	0	0	0	0	1	2	0.17	0.19		0	0	0	0	0	0	0	0	0	0



Specie	New moon										Third quarter														
	Day					Night					Day					Nigth									
	Min	Max	Total	Mean	Error	Min	Max	Total	Mean	Error	Min	Max	Total	Mean	Error	Min	Max	Total	Mean	Error					
<b>Annelida</b>																									
	0	0	0	0	0	0	2	6	0.5	0.39						0	1	3	0.25	0.23	0	1	2	0.17	0.19
<b>Echinodermata</b>																									
<i>Paracentrotus lividus</i>	0	1	1	0.08	0.14	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<b>Crustacea</b>																									
<b>Amphipoda</b>	18	99	543	45.25	11.7	85	340	1846	153.8	35.7						21	100	620	51.7	13.23	117	411	2692	224.3	39.42
<i>Dardanus calidus</i>	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Galathea</i> spp.	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Macropodia rostrata</i>	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
Majidae	0	2	2	0.17	0.23	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Pagurus anachoretus</i>	0	0	0	0	0	0	1	3	0.25	0.23						0	0	0	0	0	0	2	5	0.42	0.39
<b>Chordata</b>																									
<i>Canthigaster capistrata</i>	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	1	1	0.08	0.14
<i>Gobius</i> spp.	0	0	0	0	0	0	1	1	0.08	0.14						0	0	0	0	0	0	0	0	0	0
<i>L. candolle</i>	0	0	0	0	0	0	1	1	0.08	0.14						0	0	0	0	0	0	0	0	0	0
<i>L. lepadogaster</i>	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Sparisoma cretense</i>	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<b>Mollusca</b>																									
<i>Aplysia</i> spp.	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	1	1	0.08	0.14
<i>Bittium</i> spp.	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Cerithium</i> spp.	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Mitra</i> spp.	0	0	0	0	0	0	0	0	0	0						0	0	0	0	0	0	0	0	0	0
<i>Rissoa</i> spp.	0	8	29	2.42	1.23	0	9	31	2.58	1.54						0	3	20	1.67	0.68	0	26	67	5.58	3.53
<i>Smargadia viridis</i>	0	0	0	0	0	0	1	1	0.08	0.14						0	0	0	0	0	0	1	2	0.17	0.19
<i>T. pullus canarica</i>	0	0	0	0	0	0	1	1	0.08	0.14						0	0	0	0	0	0	0	0	0	0





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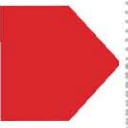
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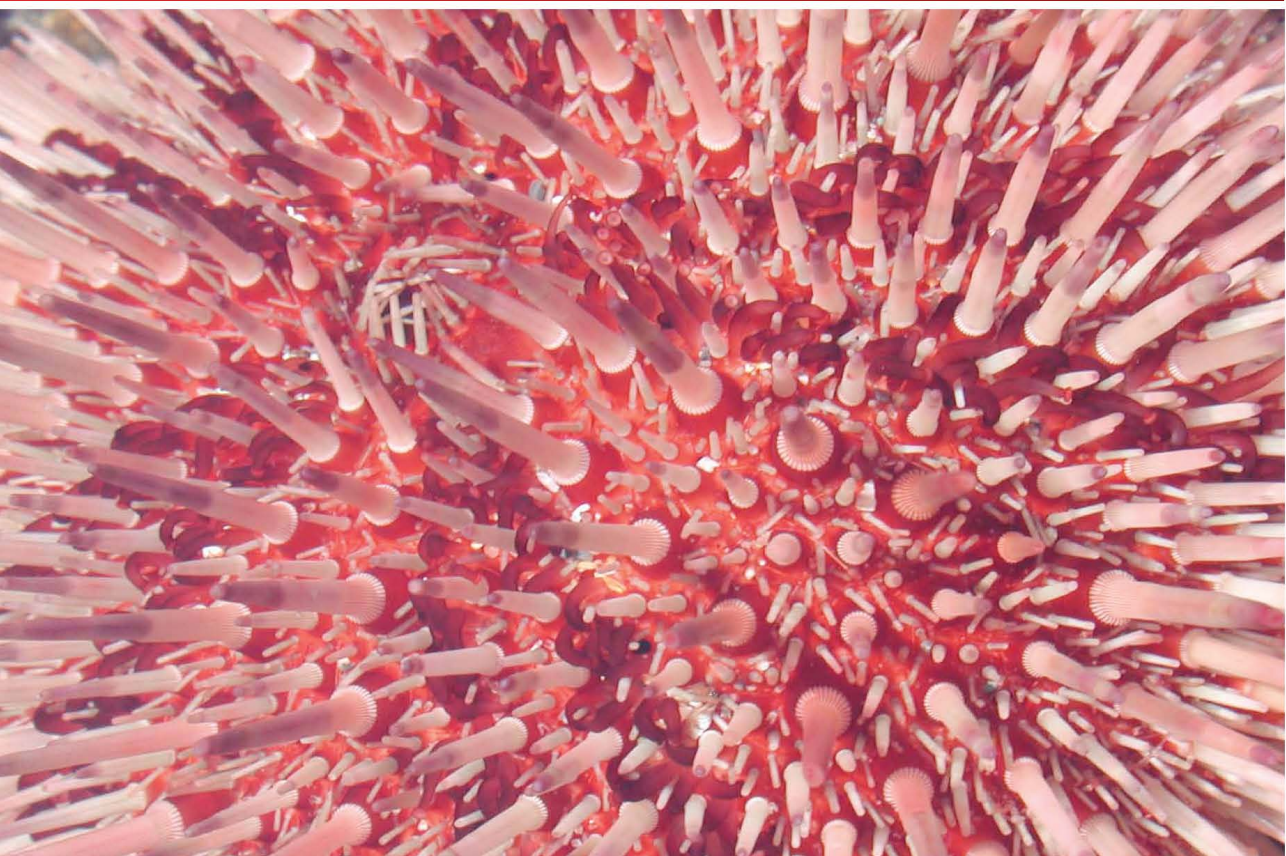
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Capítulo 4.  
Contrasting recruitment  
seasonality of sea urchin species  
at an oceanic island: a way to  
facilitate coexistence?



## ABSTRACT

Despite sea-urchins can play an important role affecting the community structure of subtidal bottoms, factors controlling the dynamics of sea-urchin populations are still poorly understood. We assessed the seasonal variation in recruitment of three sea-urchin species (*Diadema africanum*, *Paracentrotus lividus* and *Arbacia lixula*) at Gran Canaria Island (eastern Atlantic) via monthly deployment of artificial collectors throughout an entire annual cycle on each of four adjacent habitat patches (seagrasses, sandy patches, 'urchin-grazed' barrens and macroalgal-dominated beds) within a shallow coastal landscape. *P. lividus* and *A. lixula* had exclusively one main recruitment peak in late winter-spring. *D. africanum* recruitment was also seasonal, but recruits appeared in late summer-autumn, particularly on 'urchin-grazed' barrens with large abundances of adult conspecifics. Since *D. africanum* is locally the most abundant herbivore (~1 order of magnitude relative to *P. lividus* and *A. lixula*), it is plausible that the coexistence of these 3 sea urchin species is facilitated by the non-overlapping seasonal recruitment patterns of the less abundant species with the most conspicuous species.

**Keywords:** recruitment, artificial collectors, sea urchin, coastal habitats, Canary Islands.

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





# Índice

Abstract	137
4.1 Introduction	139
4.2 Materials and methods	142
4.2.1 Study area	142
4.2.2 Collector deployment	142
4.2.3 Data analysis	143
4.3 Results	144
4.4 Discussion	147
4.5 References	150

## > Capítulo 4

### Contrasting recruitment seasonality of sea urchin species at an oceanic island: a way to facilitate coexistence?

#### > 4.1 INTRODUCTION

Sea urchins are often considered as strong ecological 'interactors', as changes in their abundance can change community composition and structure on inter- and shallow subtidal substrates (Paine, 1992; Sala and Graham, 2002), including overgrazing events with complete denudation of macrophytes (Valentine and Heck, 1999; Tomás *et al.*, 2004). Factors controlling the structure of sea urchin populations are, however, still poorly understood (Norderhaug and Christie, 2009; Uthicke *et al.*, 2009). Several processes, e.g. predation, settlement, recruitment, migration, disease, etc., may exert a crucial role in this sense (e.g. Watanabe and Harrold, 1991; Hagen, 1995; McClanahan, 1998; Scheibling *et al.*, 1999; Tomás *et al.*, 2004). Colonization of new habitats by organisms with planktonic larvae, e.g. sea urchins, is typically divided in four phases: development (including dispersal as a planktonic form), testing of a habitat for 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, including sea urchins (Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Tomás *et al.*, 2004).

Patterns of distribution and abundance of adult benthic invertebrates can often be determined by recruitment into specific habitats (Underwood and Fairweather, 1989; Roughgarden *et al.*, 1994), although post-recruitment processes, such as competition (Dayton, 1975), predation (Menge, 1976), or physical stress (Garrity, 1984), can modify initial patterns. Variability in recruitment patterns at large spatial scales can result from variations in larval supply, e.g. currents delivering larvae to some locations, but not to others (Minchinton and Scheibling, 1991; Tomás *et al.*, 2004). At smaller scales, active larval choice and preferential recruitment onto the substratum are important in determining the distribution and abundance of benthic organisms, with physical factors such as surface texture, shear stress and patterns of water flow influencing patterns of recruitment (Mullineaux and Butman, 1991; Goldberg and Foster, 2002). For example, when different habitat patches are interspersed within a coastal landscape, the abundance and assemblage structure of new colonizers is affected by the identity of habitat patches (García-Sanz *et al.*, 2012). In the particular case of sea urchins, processes such as settlement, larval metamorphosis and recruitment might be induced by the presence of particular algae (Benedetti-Cecchi and Cinelli, 1995; Airoidi, 2000; Bulleri *et al.*, 2002) or conspecifics (Cellario and Fenaux, 1990; Gosselin and Jangoux, 1996).

Thorson's (1950) hypothesis points out that temperature causes variation among and within species in larval development and duration. A strong temporal variability is a general feature in sea urchin settlement and recruitment in both temperate (e.g. Ebert *et al.*, 1994; Balch and Scheibling, 2000; Hereu *et al.*, 2004; Hereu *et al.*, 2012) and subtropical and tropical seas (e.g. Keesing *et al.*, 1993; Hernández *et al.*, 2006), including seasonal patterns in recruitment every year following specific thermal patterns. According to Hoegh-Guldberg and Pearse (1995), seawater temperature, rather than food or any other mechanism, best explains development of marine invertebrates, sea urchins in particular. On the one hand, temperature enhances echinoderms settlement by accelerating

larval development and reducing the period that larvae are exposed to planktonic predators (Hart and Scheibling, 1988; Hoegh-Guldberg and Pearse, 1995). On the other hand, cold nutrient-rich waters may trigger phytoplankton blooms that are thought to be synchronized with sea urchins spawning, thereby improving their reproductive success (Starr *et al.*, 1990) and subsequent settlement and recruitment of certain species (Ebert, 1983).

In the Canary Islands (eastern Atlantic), three sea urchin species co-occur in the rocky subtidal from 0 to 30 m depth: *Diadema africanum*, *Paracentrotus lividus* and *Arbacia lixula*. Both *P. lividus* and *A. lixula* are well adapted to the turbulent waters of the first few meters of the subtidal, while *D. africanum* commonly increase in abundance with depth (Tuya *et al.*, 2007). *D. africanum* occurs in the Eastern Atlantic islands (Rodríguez *et al.*, 2013), from Madeira Islands to the Guinean Gulf, including Salvage Islands, Canary Islands, Cape Verde Islands (Hernández *et al.*, 2008), and São Tome Island (Lessios *et al.*, 2001). It has also been recorded in continental areas of Ghana (John *et al.*, 1977, 1992) and in Ngor Island, Senegal (P. Wirtz, pers. com). *P. lividus* has an Atlanto-Mediterranean distribution (Boudouresque and Verlaque, 2001), including panmixia within the Atlantic and Mediterranean basins (Durán *et al.*, 2004; Calderón *et al.*, 2008). In the Atlantic, this sea urchin is distributed from Ireland to the Canary Islands (southern range edge), therefore showing an affinity for temperate and warm-temperate waters. *A. lixula* distribution includes the African Atlantic coast from Morocco to Angola, the east Atlantic archipelagos of Cape Verde, Canaries, Madeira and Azores, and the whole Mediterranean basin, excluding the Black Sea (Wangensteen *et al.*, 2012).

In this study, we aimed to assess whether recruitment patterns of these three sea urchin species (*D. africanum*, *P. lividus* and *A. lixula*) differed between seasons through an annual cycle between adjacent habitats within a coastal landscape.

## ➤ 4.2 MATERIALS AND METHODS

### 4.2.1 Study area

This study was carried out at two localities 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). These localities encompass a mosaic of subtidal neighboring habitats, including seagrass meadows of the species *Cymodocea nodosa* and sandy patches on soft substrata, as well as 'urchin-grazed' barrens generated by large densities of the sea urchin *Diadema africanum* and macroalgal-dominated beds (primarily constituted by the frondose genera *Cystoseira* and *Sargassum*, as well as *Dyctiota* spp., *Padina pavonica* and *Lobophora variegata*) on rocky substrata. All four habitats are found interspersed as mosaic patches at ca. 5-10 meters depth with similar orientation and exposure to waves.

### 4.2.2 Collector deployment

Recruitment of *Diadema africanum*, *Paracentrotus lividus* and *Arbacia lixula* was assessed through artificial collector (a cushion-shaped leaf-like unit), which has been previously shown to attract postlarvae and newly metamorphosed juveniles of sea urchins in the study area (García-Sanz et al., 2012). This collector consists of a plastic mesh frame (50 cm<sup>2</sup>, 2 cm of diameter of mesh size) to which artificial leaves (green plastic raffia, 35 cm long and 10 mm wide) are attached every ca. 4 cm, and folded as a cushion. Raffia is positively buoyant underwater and so float 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 (for an image of the collector, see García-Sanz et al., 2012). Four artificial substrates (ASs) were deployed, on a monthly basis through one year (from February 2009 to February 2010), on each of the four habitats. Adjacent ASs within each type of habitat were 5 m apart; ASs from any two adjacent habitats were 100s of m apart. ASs were fixed through cable ties on hard substrates and by iron rod (ca. 50 cm long) on soft substrates. ASs were in contact with the seabed. Collectors were retrieved, in all cases, after a period of approximately 4 weeks. Each AS was removed by SCUBA-divers by carefully enclosing each unit within

a cloth bag. The bags were carried to the laboratory, where each collector was cleaned with freshwater, and all sea urchins retained by a 0.5 mm mesh sieve subsequently identified and counted.

### 4.2.3 Data analysis

Differences in the total abundance of *Diadema africanum*, *Paracentrotus lividus* and *Arbacia lixula* recruits between seasons (winter, spring, summer and autumn), months within seasons and habitats were separately tested through a 3-way, permutation-based, (via 4999 random permutations), ANOVA based on Euclidian distances calculated from square-root transformed data. The model included the fixed factors: 'Season' and 'Habitat', while 'Month' was a random factor nested within 'Season'. Pairwise comparisons (through 4999 random permutations) were used to resolve differences among levels of factors, whenever appropriate, particularly when a significant 'Season x Habitat' was detected. A large number of ASs was lost and/or stolen during the study. As a result, locality (a random source of variability) was 'sacrificed' to maintain a balanced design by pooling AS from each month and habitat from both localities; the 4 replicates of each AS from each month and habitat are considered as independent replicates.

> 4.3 RESULTS

A total of 291 sea urchin recruits (larvae and juveniles) were collected during the study (226 *Paracentrotus lividus*, 38 *Diadema africanum* and 27 *Arbacia lixula*). *Paracentrotus lividus* had exclusively one recruitment peak in late winter-spring (Fig. 4.1a). Differences in the abundance of *P. lividus* recruits through seasons were inconsistent between habitats ('Season x Habitat',  $F= 3.02$ ,  $P= 0.0166$ , Table 4.1). During the recruitment peak, larger abundances of *P. lividus* recruits were observed on sandy patches relative to the other 3 habitat patches (Fig. 4.1a, Table 4.1, pairwise tests), but not in the other seasons. Recruitment of *D. africanum* was also clearly seasonal, with recruits, however, appearing in late summer-autumn (Fig. 4.1b). Seasonal differences in the abundance of *D. africanum* recruits were inconsistent between habitats ('Season x Habitat',  $F=4.68$ ,  $P=0.0008$ , Table 4.1). The abundance of *D. africanum* recruits was larger on barrens than on the other 3 habitat patches in summer and autumn, but not in early winter (Fig. 4.1b, pairwise tests, Table 4.1). *Arbacia lixula* showed a recruitment peak in late winter-spring (Fig. 4.1c) that resulted in marginally significant differences between seasons ( $F=3.05$ ,  $P=0.0636$ , Table 4.1). This seasonal pattern was irrespective of the type of habitat (Table 4.1).

Sara García Sanz

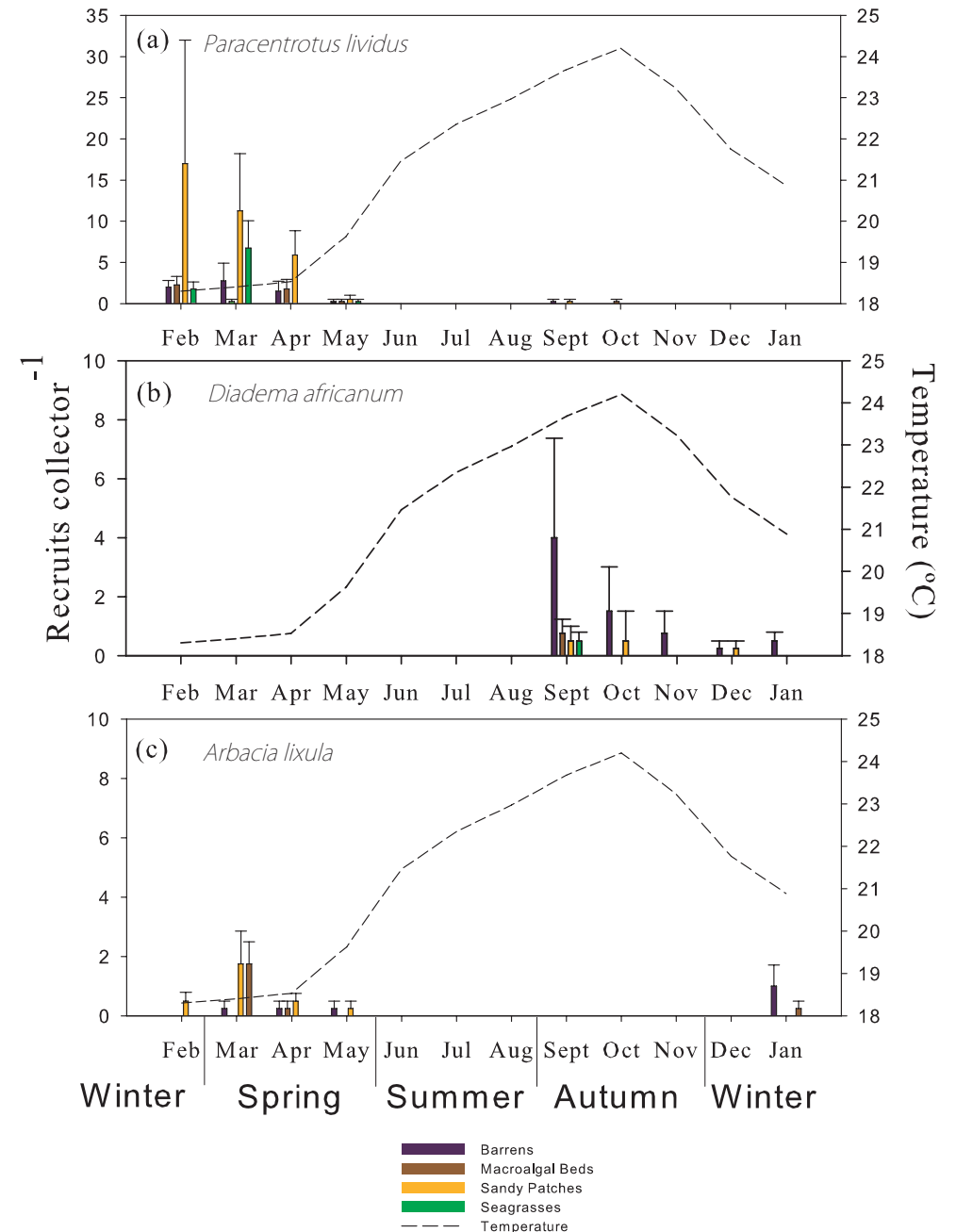


Fig. 4.1 Abundance of (a) *Paracentrotus lividus*, (b) *Diadema africanum* and (c) *Arbacia lixula* colonizers in artificial collectors per month and habitat. The mean seawater temperature is also included. Error bars are standard error of means.

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



Table 4.1 Results of 3-way ANOVAs testing for differences in the abundance of *Diadema africanum*, *Paracentrotus lividus* and *Arbacia lixula* recruits 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).

	df	MS	F	P	Pairwise comparison
<b><i>Diadema africanum</i></b>					
Season	3	1.2848	3.3145	0.016	B: A > Wi = Sp = S
Habitat	3	0.49175	10.112	0.0004	MB: A > Wi = Sp = S
Month (Season)	8	0.38763	2.3116	0.018	SP: A = Wi > Sp = S
Season x habitat	9	0.22767	4.6815	0.0008	S: A > Wi = Sp = S
Month (Season) x Habitat	24	0.048632	0.29001	0.9992	
Residual	144	0.16769			
<b><i>Paracentrotus lividus</i></b>					
Season	3	4.5543	6.5	0.0168	B: Wi = Sp = S = A
Habitat	3	0.1505	0.25	0.8636	MB: Wi = Sp = S = A
Month (Season)	8	0.7011	2.61	0.0094	SP: Wi = Sp > S = A
Season x habitat	9	1.8528	3.02	0.0166	S: Wi = Sp = S = A
Month (Season) x Habitat	24	0.613	2.28	0.0016	
Residual	144	0.2685			
<b><i>Arbacia lixula</i></b>					
Season	3	1.004	3.0572	0.0636	
Habitat	3	0.1887	0.9671	0.4332	
Month (Season)	8	0.3284	3.6616	0.001	
Season x habitat	9	0.1134	0.5812	0.8122	
Month (Season) x Habitat	24	0.1951	2.1756	0.004	
Residual	144	0.089693			

## > 4.4 DISCUSSION

Our study has shown that *Diadema africanum* has a clear unimodal recruitment pattern, with a main peak occurring in autumn (September, October and November); this has been reported for Tenerife Island (Canary Islands, Hernández *et al.*, 2010), which typically occurs 2 months after the maximum spawning period, i.e. April–June (Hernández *et al.*, 2006). The recruitment of *D. africanum* is therefore negatively related to food availability in the water column, i.e. phytoplankton availability in the 2 months preceding settlement, which indicates that *D. africanum* larvae are able to reach competence when limited food is available (Hernández *et al.*, 2010). Indeed, *Diadema* species are able to survive and develop in low-food environments (McAlister, 2008), and our results reinforce the notion that *D. africanum* is well adapted to the oligotrophic waters around the Canaries (Hernández *et al.*, 2006).

This study has shown one main recruitment peak in late winter-early spring (February, March and April) for both *P. lividus* and *A. lixula* in Gran Canaria Island. This recruitment peak coincides with the lower temperatures observed during the year (< 20°C) and the period of maximum primary production in the study area (Hernández *et al.*, 2006). *A priori*, this suggests that pelagic larvae of *P. lividus* and *A. lixula* require cold, nutrient-rich, waters for their development, metamorphosis and subsequent recruitment into the bottom. This outcome coincides with the main recruitment peak observed for *P. lividus* during spring and early-summer in Mediterranean areas with similar temperature regimes (Azzolina and Willsie, 1987; Lozano *et al.*, 1995; Sala and Zabala, 1996; Hereu *et al.*, 2004; Tomás *et al.*, 2004). We also observed a secondary recruitment peak in early autumn (September–October), which coincides with similar observations from the Mediterranean Sea (Verlaque, 1984; Lopez *et al.*, 1998; Guettaf *et al.*, 2000). At Tenerife Island (Canary Islands), two peaks of gonadal maturation have been observed for this echinoid during winter (December) and early-summer (June–July), respectively (Girard *et al.*, 2006); the arrival of new recruits associated with the summer peak has not been recorded nevertheless (Girard *et al.*, 2006). At Gran Canaria Island, a few recruits were observed corresponding with the second, early-summer, peak. This could be explained since offshore waters around Gran Canaria are typically colder and richer in primary productivity than Tenerife, as a result of the oceanographic gradient along an east to west direction crossing the Canarian Archipelago (Barton *et al.*, 1998). Most likely, this guarantees competence and survivorship of *P. lividus* larvae in the water column during summer.

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

Coexistence of species is facilitated through different mechanisms (Gause, 1934; MacArthur, 1958). Species can adjust their temporal reproductive and recruitment patterns to the most favorable times of the year; for example, offsetting the breeding period and thus giving relief to competition, what facilitates the presence of other species, e.g. a competitor (Álvarez-Lajonchere, 1976; Ibáñez-Aguirre, 1993). In the Canary Islands, *D. africanum* is, by far, the most abundant herbivore on subtidal rocky reefs (~1 order of magnitude relative to *P. lividus* and *A. lixula*, Tuya *et al.*, 2007), determining the community structure of subtidal reefs (Tuya *et al.*, 2004). Therefore, it is plausible that the coexistence of these 3 sea-urchin species is facilitated by the non-overlapping seasonal recruitment patterns of the less abundant species with the most conspicuous sea-urchin species.

It is widely known that processes such as settlement, larval metamorphosis and recruitment of sea urchins are often induced and/or facilitated by the occurrence of adult conspecifics (Cellario and Fenaux, 1990; Gosselin and Jangoux, 1996). Such a pattern has been here observed for *D. africanum* recruits, which reached larger abundances in 'urchin-grazed' barrens than in the other habitat patches. In contrast, the abundance of both *P. lividus* and *A. lixula* recruits was not higher in those habitat patches where adults have been typically found in the study area, i.e. rocky substrates at shallow water dominated by macroalgal beds (Tuya *et al.*, 2007). Most likely, *Diadema* recruits have a tendency to look for protection under the long-spined 'canopy' provided by adult conspecifics (Atkinson *et al.*, 1973), and so increase their survivorship by releasing predation, which notoriously can affect *Diadema* recruits (Clemente *et al.*, 2007). Despite such a 'canopy' effect has also been described for some short-spined sea urchins (Tegner and Dayton, 1981), this mechanism seems irrelevant for both *P. lividus* and *A. lixula*, i.e. two short-spined sea urchin species. Across the Canary Islands, these two sea urchins have overall adult abundances considerably lower than *D. africanum* (Tuya *et al.*, 2007), which is the species that majorly generates 'urchin-grazed' barrens (Tuya *et al.*, 2004, Clemente *et al.*, 2007). The low abundances of both *P. lividus* and *A. lixula* do not seem to promote a 'canopy' effect on small-sized individuals as a way to provide shelter to the new recruits. Hence, this might help to explain the lack of recruits of both *P. lividus* and *A. lixula* in collectors deployed on rocky substrates.

Contrary to our expectations, *P. lividus* had larger abundances on sandy patches relative to the other habitats. This result may be an artifact caused by the presence of collectors on bottoms that lack provision of shelter; i.e. an 'oasis' effect: attraction of new individuals to the only available substrate (García-Sanz *et al.*, 2012). Indeed, individuals of *P. lividus* can easily move among adjacent habitat patches (Ceccherelli *et al.*, 2009), what could guarantee further arrival of individuals to favorable rocky substrates covered by macroalgae (Tuya *et al.*, 2007).

Post-recruitment processes determine sea urchin adult abundances. Although the largest abundance of new recruits was observed for *P. lividus*, *D. africanum* is the most conspicuous sea urchin in the region (Tuya *et al.*, 2007). Therefore, it is possible that few organisms of *P. lividus* are able to survive to adulthood relative to *D. africanum*. This latter species forms aggregations at high densities (Atkinson *et al.*, 1973; Tuya *et al.*, 2004) that, as previously indicated, likely enhance the 'canopy' effect, and so protection, over small-sized individuals. Such an effect has not been described for both *P. lividus* and *A. lixula*, and so might suppose a larger exposure to predation, confirming that post-recruitment processes such as predation (Menge, 1976) may notoriously affect the abundance of sea urchin recruits.

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