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Contrasting recruitment seasonality of sea urchin species in Gran Canaria, Canary Islands (eastern Atlantic)

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Abstract

Although 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. *Paracentrotus lividus* and *A. lixula* had exclusively one main recruitment peak in late winter-spring. *Diadema africanum* recruitment was also seasonal, but recruits appeared in late summer-autumn, particularly on 'urchin-grazed' barrens with large abundances of adult conspecifics. In conclusion, this study has demonstrated non-overlapping seasonal recruitment patterns of the less abundant species (*P. lividus* and *A. lixula*) with the most conspicuous species (*D. africanum*) in the study area.

Keywords: recruitment, artificial collectors, coastal habitats, Canary Islands.

Introduction

Sea-urchins are often considered as strong ecological 'interactors', as changes in their abundances can change community composition and structure on inter- and shallow subtidal substrates (Paine, 1992; Sala & Graham, 2002), including overgrazing events with complete denudation of macrophytes (Valentine & Heck, 1999; Tomás *et al.*, 2004). Factors controlling the structure of sea urchin populations are, however, still poorly understood (Norderhaug & Christie, 2009; Uthicke *et al.*, 2009). Several processes, e.g. predation, settlement, recruitment, migration, disease, etc., may play a crucial role in this sense (e.g. Watanabe & 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: larval 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 defined as recruitment, while the number passing only through the third phase is called settlement (Keough & Downes, 1982). Therefore, recruitment is an interplay of larval and juvenile processes, while settlement involves only larval processes. These early stages are frequently major bottlenecks in the life-history of many benthic invertebrates, including sea-urchins (Gosselin & Qian, 1997; Hunt & 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 & 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 & 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 & Butman, 1991; Goldberg & Foster, 2002). For example, when different habitat patches are interspersed within coastal landscapes, 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, metamorphosis and recruitment might be induced by the presence of particular algae (Benedetti-Cecchi

& Cinelli, 1995; Airoldi, 2000; Bulleri *et al*., 2002; Privitera *et al*., 2011) or conspecifics (Cellario & Fenaux, 1990; Gosselin & 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 & 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 & Pearse (1995), sea-water temperature, rather than food or any other mechanism, best explains development of marine invertebrates, sea-urchins in particular. On the one hand, temperature enhances echinoderm settlement by accelerating larval development and reducing the period during which larvae are exposed to planktonic predators (Hart & Scheibling, 1988; Hoegh-Guldberg & Pearse, 1995). On the other hand, cold nutrient-rich waters may trigger phytoplankton blooms that are thought to be synchronized with sea-urchin 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 increases in abundance with depth (Tuya *et al*., 2007). The locally abundant *D. africanum* occurs in the Eastern Atlantic islands (Rodríguez *et al*., 2013), from Madeira to the Guinean Gulf, including the Salvage Islands, Canary Islands, Cape Verde Islands (Hernández *et al*., 2008), and Sâo 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). On the other hand, *P. lividus* has an Atlanto-Mediterranean distribution (Boudouresque & 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. Finally, *A. lixula* distribution includes the African Atlantic coast from Morocco to Angola, the east Atlantic archipelagos of Cape Verde, the Canaries, Madeira and the 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 three sea urchin species (*D. africanum*, *P. lividus* and *A. lixula*) differed from season to season through an annual cycle between adjacent habitats within a coastal landscape.

Materials and Methods

Study area

This study was carried out at two localities off the east coast of Gran Canaria (Canary Islands, Spain): Playa del Cabrón (27°52'14.43" N, 15°23'00.31" W) and Risco Verde (27°51'25.94" N, 15°23'10.26" W) (Fig. 1). These sites encompass a mosaic of subtidal, neighboring habitats, including seagrass meadows constituted by *Cy-*

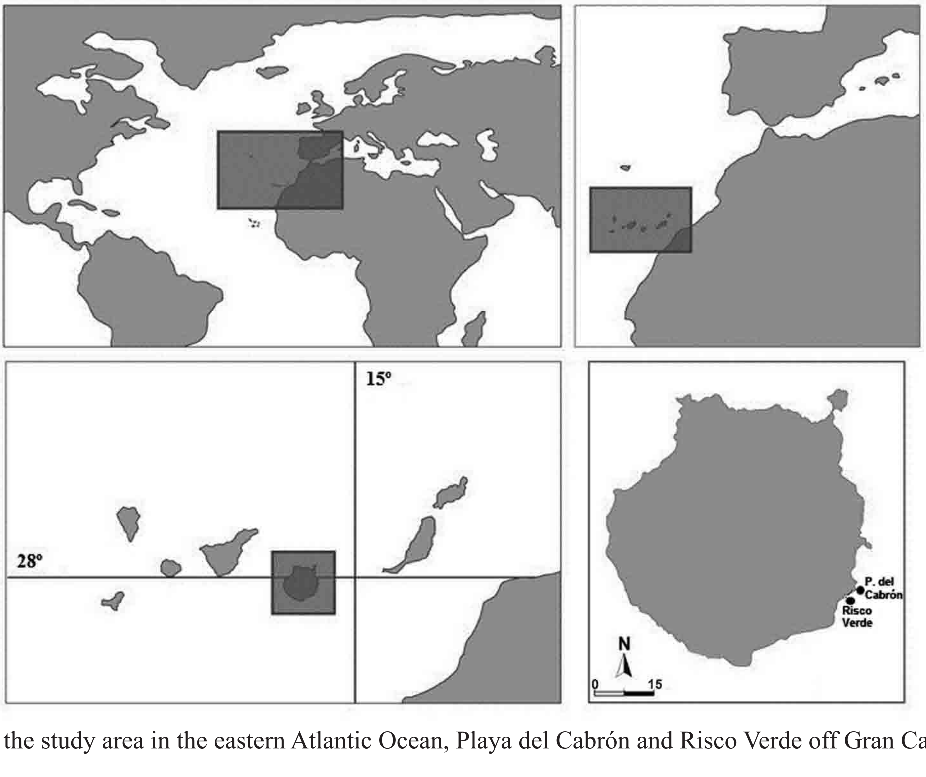

Fig. 1: Location of the study area in the eastern Atlantic Ocean, Playa del Cabrón and Risco Verde off Gran Canaria Island.

modocea nodosa and sandy patches on soft substrata, as well as 'urchin-grazed' barrens mainly generated by large densities of the sea urchin *D. 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 substrates. All four habitats are found interspersed as a matrix of mosaic patches at 5-10 meters depth with similar orientation and exposure to waves.

Collector deployment

Recruitment of *D. africanum*, *P. lividus* and *A. lixula* was assessed through artificial collectors (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^2, 2 cm 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 under water and consequently tends to float upright. A total of 75 cm^2 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, at each locality. 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 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 fresh water, and all sea-urchins retained by a 0.5 mm mesh sieve subsequently identified and counted.

Data analysis

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.

Differences in the total abundance of *D. africanum*, *P. lividus* and *A. 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 Euclidean 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.

Results

A total of 291 sea urchin recruits (larvae and juveniles) were collected during the study (226 *P. lividus*, 38 *D. africanum* and 27 *A. lixula*). Although no significant differences were found for season (Table 1), *P. lividus* had a main recruitment peak in late winter-spring, while only a few colonizers were observed during late summer and early autumn (Fig. 2a). During the recruitment peak, significant differences in the abundance of *P. lividus* recruits were found between habitats ('Habitat', F= 3.028, P= 0.001, Table 1); soft-substrate habitats (sandy patches and seagrasses) showed larger abundances than hard-substrate habitats ('urchin-grazed' barrens and macroalgal beds) (Fig. 2a, pairwise tests, Table 1), but not in the other seasons.

Recruitment of *D. africanum* was also seasonal, with recruits, however, appearing in autumn-winter (Fig. 2; Table 1, 'Season', F=3.314, P=0.016), showing differences between months in season (Fig. 2; Table 1, 'Month (Season)', F=2.311, P=0.018). The abundance of *D. africanum* recruits was larger in 'urchin-grazed' barrens and sandy patches than in the other 2 habitats (Fig. 2.b, 'Habitat' F=10.112, P=0.001, pairwise comparisons, Table 1). Seasonal differences in the abundance of *D. africanum* recruits were inconsistent between habitats ('Season x Habitat', F=4.681, P=0.001, Table 1).

Arbacia lixula showed a main recruitment peak in late winter-spring (Fig. 2c) that resulted in marginally significant differences between seasons (Table 1, 'Season', F=3.057, P=0.063); that may be due to significant differences observed for month in season (Table 1, 'Month (Season)', F=3.661, P=0.001). This seasonal pattern was irrespective of the type of habitat ('Season x Habitat', F=0.581, P=0.812, Table 1).

Discussion

Our study has shown that *D. africanum* has a clear unimodal recruitment pattern, with a main peak occurring in autumn (September, October and November); this has been previously reported for Tenerife Island (Canary Islands, Hernández *et al*., 2010), which typically occurs 2 months after the maximum spawning period in the study area, 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

Table 1. Results of 3-way, permutation-based, ANOVA testing for differences in the abundance of *Diadema africanum*, *Paracentrotus lividus* and *Arbacia lixula* recruits 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). Pairwise comparisons for significant 'Habitat', 'Season' and 'Season x Habitat' interactions are included.

	df	MS	F	P	Pairwise comparisons	
Paracentrotus lividus						
Season	3	8.286	1.575	0.261		
Habitat	3	2.505	3.028	**0.044**	Sp > S = B = MB	
Month (Season)	8	5.258	8.161	**0.001**		
Season x Habitat	9	0.793	0.958	0.505		
Month (Season) x Habitat	24	0.827	1.284	0.159		
Residual	144	0.644				
Diadema africanum						
Season	3	1.284	3.314	**0.016**	A > W > S = Sp	Season x Habitat
Habitat	3	0.491	10.112	**0.001**	B > SP > M > S	W: B > SP > MB = S
Month (Season)	8	0.387	2.311	**0.018**		Sp: B = SP = MB = S
Season x Habitat	9	0.227	4.681	**0.001**		S: B = SP = MB = S
Month (Season) x Habitat	24	0.048	0.29	0.999		A: B > SP > MB > S
Residual	144	0.167				
Arbacia lixula						
Season	3	1.004	3.057	**0.063**		
Habitat	3	0.188	0.967	0.433	S = SP > B > M	
Month (Season)	8	0.328	3.661	**0.001**		
Season x Habitat	9	0.113	0.581	0.812		
Month (Season) x Habitat	24	0.195	2.175	**0.004**		
Residual	144	0.089				

well-adapted to the oligotrophic waters around the Canaries (Hernández *et al*., 2006).

This study has also 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 (< 20ºC) 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 & Willsie, 1987; Lozano *et al*., 1995; Sala & 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; 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); however, the arrival of new recruits associated with the summer peak has not been recorded (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 in Tenerife, as a result of the oceanographic east-to-west gradient 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. In the particular case of *A. lixula*, our results (optimal recruitment at 18ºC) clearly contrast with the temperature (22ºC) identified in the Mediterranean at which larvae optimize survivorship through metamorphosis (Privitera et al. 2011). This discrepancy points towards potential differences at which recruits reach optimum competence across the species' distribution range.

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 & Fenaux, 1990; Gosselin & Jangoux, 1996). Such a pattern has been observed here 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

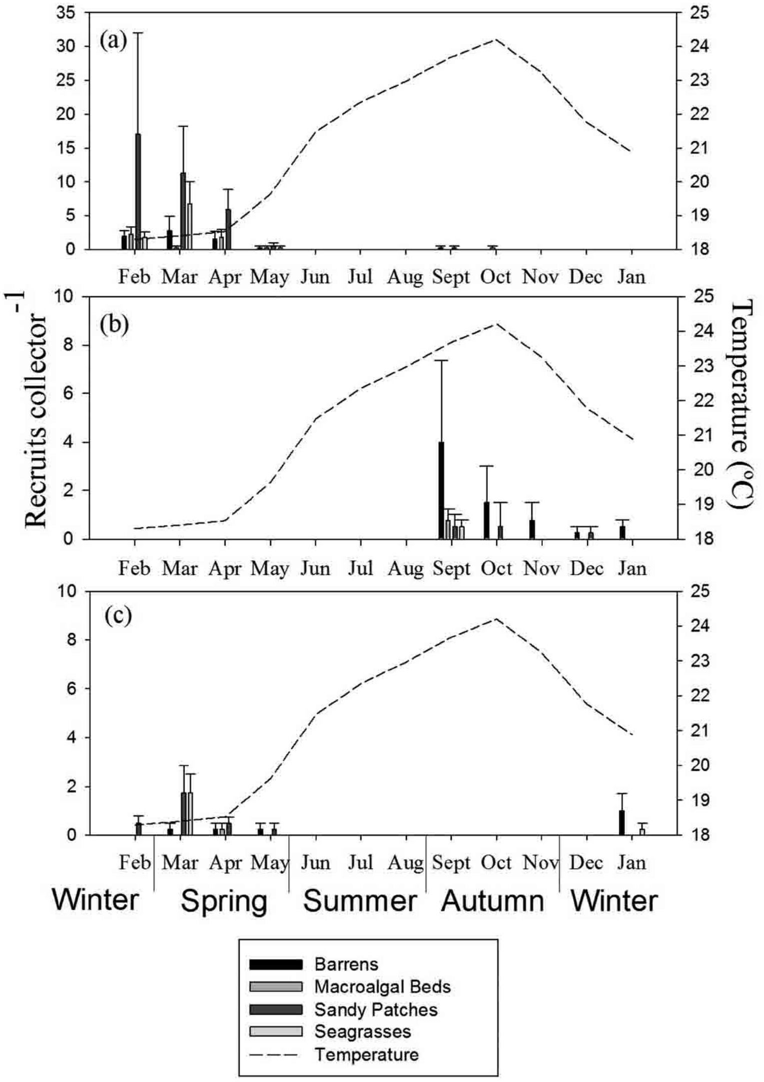

Fig. 2: Abundance of (a) *Paracentrotus lividus*, (b) *Diadema africanum* and (c) *Arbacia lixula* recruits in artificial collectors per month and habitat. The mean sea water temperature is also included. Error bars are + SE of means.

survivorship by releasing predation, which notoriously can affect *Diadema* recruits in the study area (Clemente *et al*., 2007). Although such a 'canopy' effect has also been described for some short-spined sea-urchins (Tegner & 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 'grazed urchin' 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 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* recruits 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 any 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), which could guarantee further arrival of individuals to favorable rocky substrates covered by macroalgae (Tuya *et al*., 2007). In conclusion, this study has demonstrated non-overlapping seasonal recruitment patterns of the less abundant species (*P. lividus* and *A. lixula*) with the most conspicuous species (*D. africanum*) of the study area.

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