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# Herbivore control in connected seascapes: habitat determines when population regulation occurs in the life history of a key herbivore

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## **Abstract**

Herbivore outbreaks often trigger catastrophic overgrazing events in marine macrophyte ecosystems. The sea urchin *Paracentrotus lividus*, the dominant herbivore of shallow Mediterranean seascapes, is capable of precipitating shifts to barrens when its populations explode. *P. lividus* is found ubiquitously in rocky macroalgal communities and in sandy seagrass meadows of *Posidonia oceanica*, two of the most important subtidal habitats in the Mediterranean. We explored if habitat-specific regulation across the principal stages of the urchin life cycle could help explain the persistence of these populations in connected mosaics. We measured each of three relevant ecological process (i.e. settlement, post-settlement survival and predation) across a wide stretch of the Mediterranean coast (ca. 600km). Our results show that habitat-specific regulation is critical in determining urchin populations: each habitat limited urchin sub-populations at different life stages. Settlement was never limiting; urchins settled at similar rates in both habitats across the coast. Post-settlement survival was a clear bottleneck, particularly in seagrass meadows where no juvenile urchins were recorded. Despite this bottleneck in seagrasses, adult urchin populations were very similar in both seagrass and macroalgal habitats indicating that other processes (potentially migration) could be key in determining adult distributions across the mosaic. The fact that population regulation is clearly habitat-specific suggests that sea urchin populations may be significantly buffered from bottlenecks in mixed seascapes where both habitats co-occur. Sea urchin populations can therefore persist across the seascape despite strong habitat-specific regulation either by maintaining reproductive output in one habitat or by migrating between them. By affording these regulatory escapes to habitat-modifying species, patchy mosaics may be much more prone to herbivore outbreaks and a host of cascading effects that come in their wake.

## **Introduction**

In systems prone to alternate states, understanding how populations of a few key species are regulated is essential to predicting how close these ecosystems are to catastrophic shifts (Terborgh et al. 2001, Jackson 2001, Denno et al. 2003, Baskett and Salomon 2010, Ripple et al. 2014). Nearshore macrophyte ecosystems are particularly prone to overgrazing, shifting to heavily overgrazed barrens when herbivore populations expand without control (Wolf et al. 2007, Ling et al. 2015). When ecological roles are disproportionately distributed across the species assemblage, the health of the ecosystem is linked intimately with the population ecology of a few key species. Herbivore abundance is often strongly mediated by habitat-associated processes as individuals recruit, grow, move, feed and reproduce within the habitats they colonize and inhabit. How habitats determine the life-history processes of key species can therefore have major population consequences that can, in turn, significantly influence ecosystem function.

There is growing evidence that herbivore outbreaks are triggering a major expansion of overgrazed areas across the world's oceans, particularly in northern temperate seas (Filbee-Dexter and Scheibling 2014, Conversi et al. 2015, Ling et al. 2015). However, our ability to accurately predict impending outbreaks depends on a clear understanding of the factors influencing the arrival (recruitment and immigration), growth and loss (mortality and emigration) of individuals in a population (Ripple and Larsen 2000, Ballard et al. 2001, Ling et al. 2009, Petraitis and Dudgeon 2015), and how these drivers vary between habitats. At every life history stage, a range of habitat-contingent factors can regulate the fate of individuals in a population. While several studies have sought to determine the regulatory processes of key herbivore populations, they are often limited to a single habitat, focussing on a single major process such as larval supply (Cardona et al. 2013, Petraitis and Dudgeon 2015), predation (Sala and Zabala 1996, Estes et al. 2011, Ripple et al. 2014), or migration (Kayal et al. 2012, but see Ling et al. 2009).

Marine herbivores often use several habitats in the course of their complex life cycles, often involving an open pelagic state. Differences in settlement are likely highly dependent on inherent local or regional characteristics like nutrient availability, currents or seawater temperature (Cardona et al. 2013, García et al. 2015). Post recruitment, populations can have habitat-specific

constraints linked to the structure and species diversity of each particular habitat. Habitat choices can therefore strongly affect future life-history stages since each habitat may differ considerably in its availability of food and refugia, and in the nature and strength of species interactions (e.g. competition) to which individuals are exposed to.

Benthic herbivore outbreak events in Mediterranean macrophyte ecosystems have been linked to both unexpected increases in settlement rates (Cardona et al. 2013), and predator release (Sala 1997, Pinnegar et al. 2000). Immediately after settlement, sea urchin populations have to overcome a major bottleneck of mass mortality (López et al. 1998, Scheibling and Robinson 2008). Individuals that survive to older size classes are subject to size-specific fish and invertebrate predators, which can be important controllers of urchin populations (Sala 1997, Bonaviri et al. 2012). Additionally, there is some evidence that urchin movement and potential migration between macroalgal and seagrass habitats could drive population fluctuations within habitats (Ceccherelli et al. 2009, Prado et al. 2012).

Shallow seascapes in the Mediterranean are typically complex seascapes where different habitats coexist, potentially affecting the survival of key herbivore species at different life-stages. The mosaic includes rocky macroalgal communities and *Posidonia oceanica* seagrass meadows interspersed on sandy bottoms. Outbreaks of the sea urchin *Paracentrotus lividus* have caused overgrazing events in both habitats (Pinnegar et al. 2000, Ruiz et al. 2009). Macroalgal communities are particularly susceptible to urchin herbivory that can trigger sudden, and often unpredictable, community shifts to persistent barrens (Pinnegar et al. 2000, Ling et al. 2015, Boada et al. 2017). Although there have also been cases of urchin overgrazing in *P. oceanica* meadows, these habitats appear considerably less prone to such events (Prado et al. 2007, but see Ruiz et al. 2009). Despite urchins playing a critical role across this seascape, the role that the habitat-specific processes play regulating their populations is still poorly understood. We sought to identify the principal habitat-specific processes of population control in the life history of the key herbivore *P. lividus* in a connected seascape mosaic of rocky macroalgal habitats and *P. oceanica* seagrass meadows. We explore the influence of settlement, post-settlement survival and adult predation on

*P. lividus* populations in both habitats to determine the habitat-specific strengths of these processes and its consequences for the shallow Mediterranean seascape.

## **Materials and Methods**

*Study locations and sampling design.* To assess the effect of settlement, post-settlement survival, and predation on *Paracentrotus lividus* abundance in macroalgal and seagrass *Posidonia oceanica* habitats we quantified each of these processes along a wide stretch of the Western Mediterranean coast (8 locations, ca. 600km) where both habitats co-occurred (Fig. 1). Within each location, we selected three areas where both habitats were present and all measurements were made in these connected mosaics. At all selected locations, the two habitats were generally well connected, creating complex seascapes of small to medium sized patches of seagrass and photophilic macroalgae that either abutted each other or were in very close proximity (1m to 5m distance from each other). Of the eight locations, one was inside a marine protected area (Medes Islands marine reserve) selected specifically for its high abundance of predatory fish and potentially high predation rates (Sala and Zabala 1996). In earlier study at the same locations we measured the abundance of fish and benthic predators, and established their impact on sea urchin predation (Boada et al 2015a). At each location, we measured settlement, post-settlement survival and predation rates on *P. lividus* at each habitat at a fixed depth of 5 to 8 meters, where its populations are normally at their highest (Boudouresque 2001). We measured post-settlement survival and predation impact at two different times; summer (i.e. August and September) and winter (i.e. January and February) to include any potential seasonal variation.

*Settlement rates.* We used artificial collectors (i.e. 18x10 cm wooden brushes) to estimate *P. lividus* settlement rates. This method has been successfully used to determine settlement rates in seagrasses and macroalgal substrates with the assumption that it reflects the natural settlement rates that occur in those habitats (Hereu et al. 2004, Prado et al. 2012). We placed one collector in each area and habitat within each location at two times in the peak settlement period (May-June, see Tomas et al. 2004). The collectors were weighed down to the bottom and floated ~20 cm in the water column, fixed to a buoy at one end to maintain the collector in a vertical position. After 15

days we recovered the collectors from the water (T1) and replaced them with new ones at the same location. After an additional 15 days (T2) we recovered the new collectors (1 collector x 2 times x 3 areas x 2 habitats x 8 locations = 96 collectors). We used this procedure to maximize the probability of capturing the peak settlement period, which is related to seasonal increases in seawater temperature (Tomas et al. 2004). Once in the laboratory, we washed the collectors under flowing water and filtered the water through a 250  $\mu\text{m}$  mesh net. We fixed the filtered samples in 70% ethanol and counted urchin settlers in each sample with a binocular microscope. This method provides a robust estimate of pre-settlement larval availability in the water column (Prado et al. 2012).

*Post-settlement survival.* We estimated the abundance of juvenile sea urchins (less than 3 cm test diameter, TD) at each of the eight locations (see above) to estimate post-settlement survival. Within each habitat and location, we selected three areas to measure the abundance of *P. lividus* individuals. Sea urchins were counted within each area in two different time periods to account for possible seasonal differences (summer and winter) using five 50x50 cm quadrats, placed haphazardly in each area (5 quadrats x 2 times x 3 areas x 2 habitats x 8 locations = 480 quadrats). Sea urchin densities (individuals $\cdot\text{m}^{-2}$ ) were then calculated from abundances in quadrats.

*Predation impact.* We used a tethering technique to measure predation impact on the adult sea urchin *P. lividus* (>3cm, i.e. ~4cm TD). This technique is the most extensively used method to assess predation in marine ecosystems of temperate and tropical seas and we have discussed its principal methodological benefits and constraints elsewhere (see Boada et al. 2015b). We threaded urchins with a thin nylon line by piercing the test with a fine hypodermic needle. We then knotted the line to create a harness for the urchin; harnesses were attached to a brick or a metal stake to tether urchins in rocky or in the sandy seagrass habitats respectively. Lines were long enough (50 cm) to allow sea urchins to find a shelter. We distributed twenty tethered sea urchins randomly in each habitat in groups of 5 at each location. This allowed us to measure predation impact after 15 days from the start of the experiment, based on the percentage of urchins preyed on in each group. This experiment was repeated in summer and winter to account for potential seasonal variations in predation impact (20 urchins x 2 habitats x 2 seasons x 8 locations = 640 urchins). We also

estimated the identity of the predators indirectly, using the distinctive marks they leave on the sea urchin test, and directly, using GoPro cameras at some of the locations. The results indicate that the main predators were visual fish predators, mostly *Diplodus sargus* (results published elsewhere Boada et al. 2015a, see Supplementary 1). In addition, to determine that predation impact was related to the fish population, we conducted visual estimates of refuges present in each of the locations and areas. Specifically, we accounted for the potential refuges available for each tethered urchin. Results show a clear relationship between predator numbers, number of refuges and predation impact (results published elsewhere Boada et al. 2015a and see analyses presented in the Supplementary 1).

*Adult population densities.* Along with juvenile urchins, we measured adult sea urchin abundances within the quadrats described above. Studies concerning the ecology of *P. lividus* generally divide the adult population into two size classes: young adults between 3-5 cm and adults >5 cm. For the sake of the investigation we combined them into one overall adult population. These measurements were conducted at the same areas within the eight locations at two times (summer and winter) to account for the adult population densities across the year. Sea urchin numbers were counted in five randomly placed 50x50 cm quadrats in each of the selected areas (5 quadrats x 2 times x 3 areas x 2 habitats x 8 locations = 480 quadrats) to estimate adult sea urchin densities (individuals·m<sup>-2</sup>).

*Statistical analyses:*

*Processes regulating populations at the two habitats.* We explored how life cycle related processes varied between habitats. We did this using a series of generalized linear mixed models (GLMMs). For settlement, we used a GLMM with ‘Habitat’ as a fixed factor (2 levels, macroalgal habitats and seagrass meadows), ‘Location’ (8 levels) and ‘Time’ (2 levels) as random factors. We also included the factor ‘Area’ nested within location (3 levels) in the analyses for predation impact. We used the same analyses to test for differences in the adult sub-population with ‘Habitat’ as a fixed factor (2 levels, macroalgal habitats and seagrass meadows), ‘Location’ as a random factor (8 levels), ‘Area’ (3 levels) as a random factor nested within location and ‘Time’ as a random factor (2 levels). We could not use any GLMM to test for differences in post-settlement survival since no

juveniles were found within seagrass meadows. We used a Poisson distribution for all statistical analysis since we were dealing with count data (Zuur 2009).

*Processes regulating adult subpopulations within each habitat.* We also used generalized linear mixed models (GLMMs) to study the relative contribution of each habitat-specific process (see below) to the adult classes for each habitat separately, with the response variable being the adult sea urchin densities. We tested settlement rates, post-settlement survival (only in macroalgal communities since we found no recruits in seagrass meadows) and predation impact as explanatory variables in both cases. To compare all the variables within the same model we pooled the replicates within the areas and the time (number of replicates: 8 location x 3 areas). This was necessary since the number of replicates or the timing was different for each of the variables measured. A negative binomial distribution was chosen as the best method to deal with overdispersion (Zuur et al. 2009). We performed a multimodel averaging method using ‘MuMIn’ package in R to infer the relative importance (sum of Akaike weights over all possible models) of the studied processes (Whittingham et al. 2006, Grueber et al 2011). All statistical analyses were performed using ‘lme4’ package (Bates et al. 2014) in the open source software R (R Development Core Team 2013).

*Data accessibility.* Data used in this work have been uploaded to the Dryad repository.

## **Results**

*Comparing sea urchin settlement between habitats.* Settlement varied greatly between studied locations with average values ranging from less than 5 settlers brush<sup>-1</sup> in some locations to a maximum of 232 settlers brush<sup>-1</sup> in other locations (per sampling interval). Settlement in *P. oceanica* seagrass meadows (mean value 22 settlers brush<sup>-1</sup>  $\pm$  3.2 SE) and macroalgal habitats (mean value 31 settlers brush<sup>-1</sup>  $\pm$  3.6 SE) was very similar (though statistically different), showing consistent differences across all locations (Fig. 2a; Table 1).

*Comparing sea urchin post-settlement survival between habitats.* Post-settlement survival (densities of individuals < 3 cm TD) differed substantially between habitats (Fig. 2b, Table 1). In fact, we found no juveniles in any of the 8 seagrass meadows we sampled across the coast. In

contrast, we recorded an average of  $2 \pm 0.4$  SE sea urchin juveniles per  $m^2$  in macroalgal habitats. Nevertheless, we found strong differences in juveniles between locations within macroalgal habitat, ranging from 1 to more than 12 juveniles per  $m^2$  (Fig. 2b).

*Comparing predation impact between habitats.* Predation on adult urchins differed substantially between locations and habitats, and was highly habitat specific (Fig. 2 c). While predation in *P. oceanica* meadows ranged from around 5% to 60% of individuals consumed after 15 days, predation in macroalgal communities was considerably higher – ranging from 35% to 90% of individuals consumed. The highest predation values in both ecosystems were observed in Medes Islands marine reserve (Fig. 2c). Mean predation impact was on average substantially lower in *P. oceanica* meadows, with values close to 22.5% ( $\pm 5$  SE) than in macroalgal habitats 55.5% ( $\pm 3$  SE) (Fig. 2c, Table 1).

*Comparing adult populations between habitats.* Adult populations also differed significantly between locations; while we recorded no adult urchins inside the marine reserve (i.e. Medes Islands) at other locations we found densities of up to 8 urchins per  $m^2$  (across both habitats). However, across all locations, the average number of adult urchins was 4.2 individuals per  $m^2$  ( $\pm 0.6$  SE) in *P. oceanica* meadows, and 3.9 ind. $m^{-2}$  ( $\pm 0.4$  SE) in macroalgal habitats with no significant differences between habitats (Fig. 2d, Table 1).

*Sub-population regulation within each habitat.* Predation was the most important process determining adult sub-populations in seagrass and macroalgal systems (Table 2, Fig. 3). Despite this, the number of urchins surviving after settlement was a key determinant of adult populations in macroalgal systems (relative importance of 0.37 in macroalgal systems, Table 2). In seagrass meadows, settlement was of relatively minor importance in determining urchin numbers even though seagrasses had high associated post-settlement mortality (Table 2, Fig. 3).

## **Discussion**

*Summary of the results.* Habitat-specific processes contribute to determining sea urchin population dynamics, with predation essential in driving regulation processes in both seagrasses and macroalgae. Critically, urchin sub-populations were limited at different life stages in each habitat. Post-settlement survival was a clear bottleneck, particularly in seagrasses, where we found no juveniles in any of the locations; in macroalgal habitats, in contrast, juveniles were present but at low densities. This is particularly relevant given that that settlement was very similar between habitats. Despite such high early life-history mortality, adult urchins were abundant in both habitats, posing a conundrum, particularly stark in seagrass meadows, of how these populations continued to be maintained. It is possible that, in connected matrices, populations could potentially find demographic refuge in adjacent habitats where predation pressure is less prevalent. These habitat-specific life-history bottlenecks could thus allow populations that use connected landscapes to thrive despite strong predation pressure in each habitat.

*Settlement between and within habitats.* Although many marine populations are strongly recruitment limited, our results show that settlement did not strongly predict adult urchin numbers. Urchin larvae have proved to be related to the number of recruits in both habitats by previous studies (Prado et al 2012). Here, larvae were most likely derived from the same regional pool, subject to larger oceanographic processes; settlement rates were similar in both habitats and the marginally higher settlement in macroalgal habitats did not amount to a clear demographic control between habitats. When settlement rates do become limiting, peaks of settlement can have a significant role determining urchin demography, with major flow-on consequences for macroalgal communities (Cardona et al. 2013). However, our results indicate that settlement was a weak predictor of adult urchin abundances in macroalgae and only partially predicted adult abundances in seagrass meadows. This, despite the fact that settlement rates in seagrass meadows were relatively high in most locations, suggesting that recruitment limitation was not a factor. This adds to the growing consensus that the nearshore benthic systems of the Western Mediterranean may not be significantly recruitment limited (see Prado et al. 2012).

*Post-settlement mortality between and within habitats.* Habitat-specific post-settlement processes are clearly critical in regulating urchins in seagrass and macroalgal systems. Our study documents a distinctly different life-history bottleneck for the urchin, contingent on the habitat in which it is found: post-settlement survival in seagrass meadows was disproportionately low compared with macroalgal habitats. While we could not identify the specific processes driving this trend, several other studies suggest that early-in-life predation or sediment burial can be particularly strong mortality processes for urchin settlers (Prado et al. 2009, Hunt and Scheibling 1997, Bonaviri et al. 2012). Although we recorded no settlers in seagrass meadows, it is likely that very low levels of successful recruitment (below our detection abilities) may still have occurred. In an earlier study using the same methods, Prado et al. (2009) found that in seagrass meadows with unburied seagrass mat (a mixture of live and dead rhizome and roots) which possibly serve as refuge, a few juvenile urchins do manage to survive. This indicates that although sea urchin larvae choose seagrass habitats to settle, their main bottleneck may be the presence of suitable, stable, substrate when rhizomes are completely buried (Prado et al. 2009). These sparse survivors may be especially important to the population, particularly in completely isolated seagrass patches where migration between habitats is practically absent. In our study, however, we found no juveniles in any sampled meadow and we could not include post-settlement survival as a factor in the predictive model of adult sea urchin sub-populations in seagrass habitats. In contrast, post-settlement survival was a critical factor explaining adult populations in macroalgal habitats. As shown in previous studies on *P. lividus* (López et al. 1998, Tomas et al. 2004, Prado et al. 2012) and other benthic species (Hunt and Scheibling 1997), post-settlement mortality can represent an important filter of adult communities at this stage.

*Predation between and within habitats.* Predation on adult urchins differed substantially between habitats, representing an additional habitat-specific regulatory process. Many fish predators concentrate in macroalgal habitats and potentially contribute to the bulk of urchin predation (Boada et al. 2015a). In contrast, benthic predators (i.e. starfish and whelks) in seagrass meadows likely contribute to overall predation in seagrasses (Boada et al. 2015a, Farina et al. 2014). In addition, the presence of refuges also clearly differs between habitats. Seagrass meadows with

large canopies protect sea urchins from predation much more than low macroalgal canopies or turf algae (Farina et al 2009, Farina et al 2014), although in this habitat the presence of refugia reduces predation impact since sea urchins tend to stay in small crevices (Boada et al. 2016). While it is not particularly surprising that predation is so important in regulating urchin populations, it is of particular relevance for macroalgal communities, given their susceptibility to shift to overgrazed, unproductive barrens (Pinnegar et al. 2000). Interestingly, results show that sea urchins in seagrass meadows are also heavily affected by predation, although predation impact is much lower. Our study shows that this pattern is consistent at wide regional scales (hundreds of kilometers), and that predation remains the major factor determining population numbers of the key herbivore *P. lividus* across the Western Mediterranean.

*Adult populations in seagrass and macroalgal habitats.* Beyond the importance of predation or settlement in explaining adult populations in seagrass meadows, there still remains the unresolved question of how adult urchins are found in seagrass habitats despite the absence of juveniles. In our view, this could arise through two mutually non-exclusive pathways (i) differential growth of the ones that survive and (ii) migration from macroalgal beds. We have not directly measured either of these in our study. However, for the first to be true, it would require that the few urchins that continue to survive are likely sufficient to maintain adult populations (something that a long-term monitoring of the variability of settlement rates and post-settlement survival could probably respond) – and that urchins grow differentially faster in seagrass meadows. At a subset of our study locations we examined if habitat-specific growth can explain these patterns (supplementary material). Results show that growth is very similar between both habitats and, if anything, slightly higher in macroalgal habitats. Thus, while differential growth is likely not a factor, lower predation pressures at later life stages may allow for a gradual accumulation of occasional survivors to contribute to adult populations in seagrass meadows. In sediment-deficient seagrass meadows with high-unburied rhizome layers, this survival may be particularly important since it is known to decrease predation risk (Prado et al. 2009). On its own however, this gradual accumulation seems unlikely to account for the relatively high urchin abundance we recorded in seagrass habitats. Perhaps the most parsimonious alternative (pathway ii) is that occasional

migration (of adults and juveniles) from adjacent macroalgae supplements urchin sub-populations in seagrass meadows. Unpublished observations from an earlier study lend support to this explanation. Comparing connected macroalgal and seagrass habitats across several locations, we observed that juvenile sea urchins were only present close to macroalgal habitat (few meters apart), and were almost absent from the rest of the meadow (see supplementary material). The need to find refuge from intense predation may increase the probability that urchins move to more complex adjacent habitats within a landscape where predation is less prevalent (Farina et al. 2009, Pagès et al. 2013). Given the strong difference in predation pressures between habitats, it is likely that urchins seek a potential escape from predation by migrating to seagrass habitats (Farina et al. 2009). This ability to move between habitats could be an important strategy to avoid habitat-specific survival risks as urchins seek food or refuge in more complex nearby habitats (Farina et al. 2009, Farina et al. 2017). This refuge-seeking behaviour is relatively common in terrestrial systems, where the ability of species to migrate between habitats can be critical in mediating population numbers (Sinclair and Arcese 1995, Lima 1998). In addition to protection, it is possible that mobile organisms may selectively switch between habitats to maximize foraging intake (Fretwell and Lucas 1969). This means that predation pressure could influence the numbers of sea urchins in seagrass meadows both directly by predation as well as indirectly by controlling the number of available migrants in the adjacent macroalgal subpopulation (see supplementary material).

*Concluding remarks.* Our findings highlight the importance of evaluating potential habitat-specificity in the ecological processes that regulate the demographic fate of populations in connected seascapes. Recognizing that key populations may differ considerably in their regulatory processes between habitats and at different life stages is essential for predicting the occurrence of outbreaks and their indirect cascading effects. As we have shown, population regulation could be strongly mediated by habitat, and species may retreat to neighbouring environments within the matrix to search for potential refuges at critical stages in their life. Populations may thus persist across the seascape despite strong habitat-specific bottlenecks within the matrix. This buffering capacity of connected landscapes could have critical consequences for the functional (and dysfunctional) roles key herbivores often play, particularly in macrophyte systems. Movements

across habitat mosaics are generally ignored when studying populations of species with limited mobility (mainly because of the complexity of methods), but they could play key roles in understanding population trends. Preventing key herbivore numbers from reaching outbreak proportions, potentially triggering ecosystem collapse, requires a more holistic approach to accounting for entire seascapes rather than individual habitats.

### **Authors' contributions**

All authors conceived the idea and contributed to the experimental design. JB, SF, PP and TA collected the data in the field. JB performed the statistical analyses with contributions from the rest of the authors. JB, SF, RA, TA, PP and JR designed figures and wrote the manuscript.

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**Table 1.** Generalized Linear Mixed Models results for settlement, predation and density as response variables and habitat (fixed) and location (random) as explanatory variables. No analysis was performed for post-settlement survival as no urchins were found in seagrass meadows. Significant differences are shown in bold.

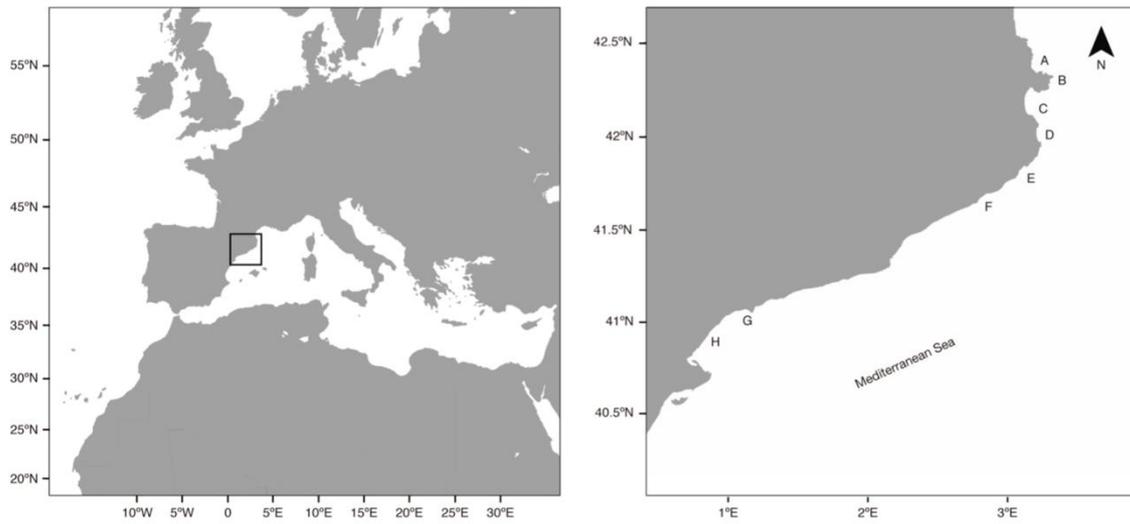
<b>Dependent variable</b>	<b>Factor</b>	<b>Df</b>	<b>Chi Square</b>	<b>P-value</b>
<b>Settlement</b>	Habitat	1	23.81	<b>&lt;0.01</b>
<b>Post-settlement survival</b>	Habitat	-	-	-
<b>Adult predation</b>	Habitat	1	73.73	<b>&lt;0.01</b>
<b>Adult densities</b>	Habitat	1	2.16	0.14

**Table 2.** Relative importance of the studied processes explaining sub-population urchin densities within each habitat. Results are from multimodel averaging of GLMMs models using package MuMIn in R (see methods). Processes within habitats are sorted according to their relative importance (sum of Akaike weight of all four considered models for macroalgae and 2 for seagrasses).

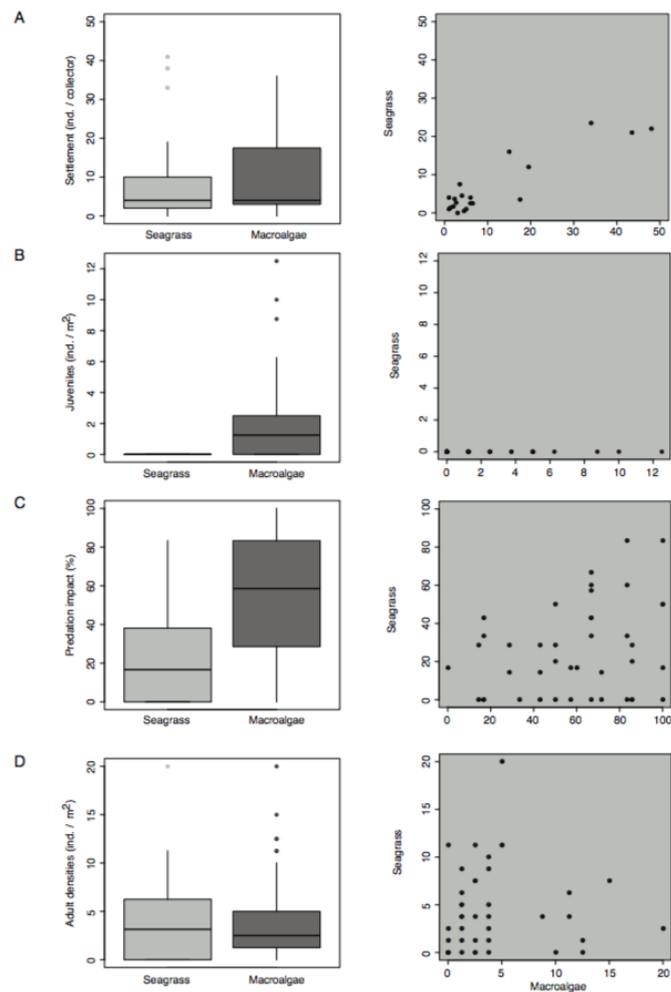
<b>Habitat</b>	<b>Factor</b>	<b>Estimate</b>	<b>Unconditional SE</b>	<b>Relative importance</b>
<b>Macroalgae</b>	Post-settlement survival	0,05	0.09	0.37
<b>Macroalgae</b>	Predation	-0,01	<0.01	0.34
<b>Macroalgae</b>	Settlement	<-0,01	<0.01	0.19
<b>Seagrass</b>	Predation	0.02	0.01	0.40
<b>Seagrass</b>	Settlement	<0.01	<0.01	0.28

## Figures

**Figure 1.** Map of the Mediterranean Sea showing the study locations within the Catalan coast (ca. 600km). Llançà (A), Portlligat (B), Montgó (C), Illes Medes (D), Giverola (E), Fenals (F), Hospitalet de l'Infant (G) and Ametlla de mar (H).



**Figure 2.** Boxplots showing habitat-specific values and scatter plots of data presented as 1 by 1 confronted replicates between habitats for A) settlement, B) post-settlement survival, C) predation on adult sea urchins, and D) adult urchin densities in each habitat. Note that in the boxplot A) outliers are out of the margins of the graph and not included for the sake of the results illustration (i.e. 117, 234 and 346 ind./collector in the seagrass habitat and 144, 155, 284 and 286 ind./collector in the macroalgal habitat).



**Figure 3.** Predicted values (blue line) plus confidence intervals (shaded grey area) for adult sea urchin densities in each habitat according to Generalized Linear Mixed Models (GLMM's) results. A) Post-settlement survival in macroalgal habitats, B) predation impact in macroalgal habitats, C) predation impact in seagrasses and D) settlement in seagrasses. Predicted values were calculated from the models proposed for each habitat. Predicted values were calculated along the range of possible explanatory variable values maintaining the rest of the variables in the model as constant. Black points represent the original data obtained in the study. Predictions were calculated and done by using the package 'visreg' in R.

