

# Differences in predator composition alter the direction of structure-mediated predation risk in macrophyte communities

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Structural complexity strongly influences the outcome of predator–prey interactions in benthic marine communities affecting both prey concealment and predator hunting efficacy. How habitat structure interacts with species-specific differences in predatory style and antipredatory strategies may therefore be critical in determining higher trophic functions. We examined the role of structural complexity in mediating predator–prey interactions across several macrophyte habitats along a gradient of structural complexity in three different bioregions: western Mediterranean Sea (WMS), eastern Indian Ocean (EIO) and northern Gulf of Mexico (NGM). Using sea urchins as model prey, we measured survival rates of small (juveniles) and medium (young adults) size classes in different habitat zones: within the macrophyte habitat, along the edge and in bare sandy spaces. At each site we also measured structural variables and predator abundance. Generalised linear models identified biomass and predatory fish abundance as the main determinants of predation intensity but the efficiency of predation was also influenced by urchin size class. Interestingly though, the direction of structure-mediated effects on predation risk was markedly different between habitats and bioregions. In WMS and NGM, where predation by roving fish was relatively high, structure served as a critical prey refuge, particularly for juvenile urchins. In contrast, in EIO, where roving fish predation was low, predation was generally higher inside structurally complex environments where sea stars were responsible for much of the predation. Larger prey were generally less affected by predation in all habitats, probably due to the absence of large predators. Overall, our results indicate that, while the structural complexity of habitats is critical in mediating predator–prey interactions, the direction of this mediation is strongly influenced by differences in predator composition. Whether the regional pool of predators is dominated by visual roving species or chemotactic benthic predators may determine if structure dampens or enhances the influence of top–down control in marine macrophyte communities.

As a key ecological driver, predation strongly influences community structure and ecosystem processes (Menge 2000). Besides controlling direct trophic pathways, the presence of predators in a system can also influence other species interactions and have cascading effects to lower trophic groups, with far-ranging consequences for the overall functioning of the ecosystem (Schmitz et al. 2004). However, the ability of predators to influence ecosystem structuring is far from universal, and in many ecosystems, predation plays a relatively small role (Matson and Hunter 1992). Several factors contribute to explaining the importance of predation within a community, including predatory guild composition within a region, habitat structural complexity or site-specific predatory strategies.

The ability of predators to control ecosystem processes is strongly mediated by the architectural or structural complexity of habitats, which can, paradoxically, work both to enhance or reduce predation, depending on the circumstance (Bartholomew et al. 2000). Specifically structure can significantly lower predation risk when it serves as a refuge for prey (Masahiro et al. 2013) but can also increase susceptibility to predators that use structure for ambush or camouflage (Hoese et al. 2006, Rawlins 2011). In many ecosystems, both terrestrial and marine, sessile biotic elements (trees, erect algae, kelp, coral, etc.) are the main structural agents in the habitat, and their value as a refuge is often strongly dependent on the relationship between the density of these habitat dominants and the predator–prey community that

inhabits the ecosystem (Manatunge et al. 2000, Scheinin et al. 2012).

Whether structure facilitates or dampens the strength of predation pressure in ecosystems is heavily dependent on the dominant predatory strategies employed by the carnivore guild. Predators that depend on vision and speed in sighting and capturing their prey are often seriously disadvantaged by habitat complexity (Crowder and Cooper 1982, McGinley et al. 2009). This is because highly structured environments do not only significantly reduce a visual predator's hunting efficiency (Duffy and Hay 2000), but also provide plenty of shelter for prey species (Gotceitas and Colgan 1989). In contrast, predators that use cryptic sit-and-wait or sit-and-pursue strategies perform much better in structurally complex environments (Preisser et al. 2007). Because of these differential evolutionary strategies, the composition of the predator guild can make all the difference to the strength and type of predation occurring within an ecosystem, depending on whether the dominant predators benefit from, or are hampered by, increasing habitat complexity.

Terrestrial and aquatic systems differ considerably in the generation times of their principal primary producers which potentially explain why aquatic systems are generally more strongly influenced by top-down processes than terrestrial systems (Shurin et al. 2006). This has served to make them ideal model systems to test the influence of predatory processes on community organization (Orth et al. 1984). In these systems, as on land, predator composition is determined by a suite of interacting forces operating at different scales, from local habitat-specific resource availability and, inter-specific competitive interactions, to larger scale variations in juvenile recruitment, population dynamics and migration (Connolly and Roughgarden 1999). In addition, variations at biogeographic scales arising from historical distribution patterns and evolutionary history can also strongly influence predator guilds and predator-prey interactions (Jackson et al. 2001). These

affect the ability to predict the importance of predation at a particular location.

In this study, we examined the importance of habitat and biogeographic differences in predatory guilds in modifying structure-mediated predation patterns across a range of macrophyte habitats. Apart from being among the most productive nearshore communities in temperate and subtropical seas, macrophyte habitats encompass widely different levels of structural complexity, from thin filamentous algae to large vertical expansions. We quantified structure-mediated predation patterns in eleven macrophyte habitats distributed across three ocean basins (Indian Ocean, Mediterranean Sea and Gulf of Mexico), representing a range of structural types with widely varying predator communities. Predation risk was estimated inside the habitat, at habitat edges and outside. Generally edges are less structurally complex than the interior of habitats allowing greater access to roving predatory fish (Gorman et al. 2009), but can still provide a certain degree of refuge from roving predation compared with totally exposed sandy areas.

We used standard sea urchin tethering techniques to assess the relative influence of predation by habitat-associated and roving predators at every zone (Fig. 1). To determine if predation patterns were mediated by prey size, we quantified predation rates on small and medium size classes of sea urchins. At each location we measured biomass and canopy heights to estimate habitat complexity (Orth et al. 1984) and predator abundance to determine the relative importance of macrophyte habitat structure and regional predatory guild composition in determining the strength of predation across these three distinct biogeographic areas.

## Material and methods

We used the survival ratio of the most common species of sea urchin in each region as model prey, using tethering

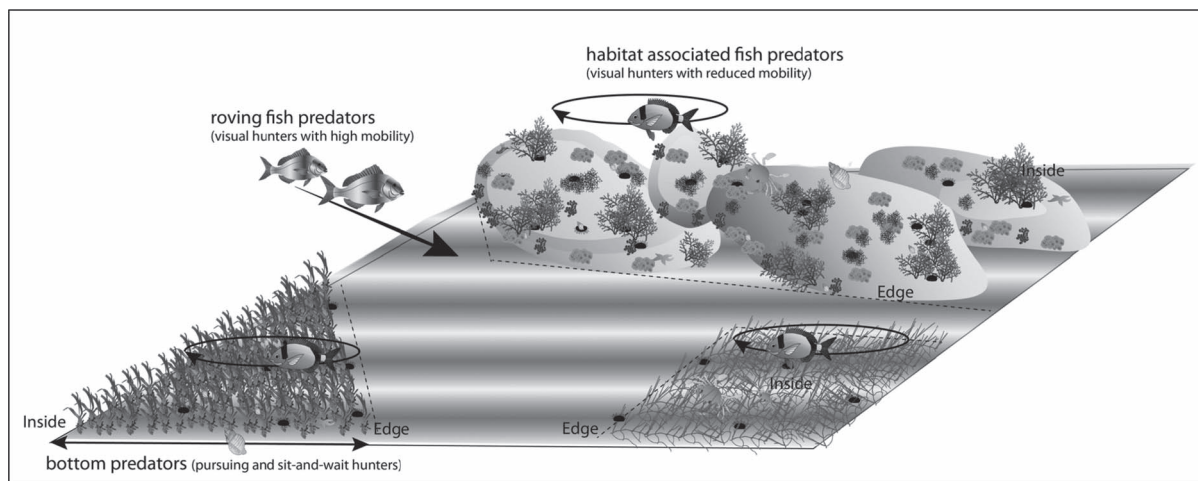


Figure 1. Diagrammatic representation of a typical seagrass and algae benthic mosaic and its associated predator guild, including roving predatory fish, habitat-associated fish predators and bottom predators. Under natural conditions, sea urchins are found largely inside the habitats, but also along habitat edges. Bottom-dwelling habitat-associated predators typically inhabit the structurally complex habitats, but the dense vegetation may inhibit visual predators like fish. The edges of the habitats in contrast may still be accessible for both predatory fish as well as habitat-associated predators.

techniques to quantify prey survival. We used both small (juveniles) and medium (young adults) size classes of urchins as prey, since they are the most vulnerable to predators, whereas larger adult urchins are rarely preyed on by extant predator communities (Guidetti 2004, Sala 1997). In order to expose urchins to different conditions of structure and predator complexes, we estimated survival ratios in three treatments: 1) prey placed within vegetated habitat (structure present, habitat-associated predators and roving predatory fish present); 2) prey placed at the edge of vegetated habitat (no structure, habitat-associated predators and roving predatory fish present); and 3) prey placed in sandy open space away from vegetated habitats (no structure and no habitat-associated predators, roving predatory fish present; Fig. 1). Thus, predation assays were designed to estimate the influence of habitat structure on predation while still exposing model prey to specific habitat-associated predators, using habitat edges and nearby sandy open spaces as proxies of predation processes that occur independent of structure (Smith et al. 2010).

## Study area and study design

This study took place in the western Mediterranean Sea (Catalonia, Spain), eastern Indian Ocean (Perth, Western Australia) and northern Gulf of Mexico (Florida, USA) (see Supplementary material Appendix 1 for geographical references). In each region, we selected a range of dominant and representative macrophyte habitats with varying levels of structural complexity, and performed urchin predation assays at two replicate locations for each habitat (site A and B) except for the northern Gulf of Mexico, where predation was measured in only one location (site A). For this reason, we restrict our comparisons to the western Mediterranean Sea and the eastern Indian Ocean, and use observations from the northern Gulf of Mexico to supplement and reinforce our principal results. We compared predation rates inside the habitat, at the edge, and outside the habitat for every macrophyte community in each site and region in order to evaluate the relative importance of habitat-associated and roving predators for each structural type in each bioregion (Fig. 2 details the study design for each region).

### Western Mediterranean Sea (WMS)

Predation assays and surveys were carried out in two locations 4 km apart along the Costa Brava (Spain): site A (Fenals) and site B (Canyelles). We tested the survival ratio of small (less than 3 cm test diameter, TD) and medium (3 to 5 cm TD) sized *Paracentrotus lividus* that can grow to approximately 7 cm diameter (Boudouresque and Verlaque 2001) in four of the most representative macrophyte habitats of the region between 5–10 m depth. In the WMS, these comprised two types of seagrass meadows, *Posidonia oceanica* and *Cymodocea nodosa*, and two algae assemblages, namely: ‘turf-forming algae’, consisting of bushy and sparsely-branched, small filamentous algae (e.g. Cladophoraceae, Rhodomelaceae), and ‘erect algae’, consisting of erect algal growth forms such as Dictyotaceae and Stypocaulaceae (Ballesteros 1992, Sala et al. 2012).

### Eastern Indian Ocean (EIO)

The study was performed in two locations 45 km apart in Perth (Western Australia): site A (Marmion reef) and site B (Bird Rock). We measured the survival ratio of small (around 3 cm TD) and medium size (5–6 cm TD) classes of the sea urchin *Helicoidaris erythrogramma*, which can reach 9 cm diameter in Australia (Keesing 2007), in four of the most representative macrophyte habitats in the region at 5 m depth. The habitats used in EIO were: meadows of the seagrasses *Posidonia sinuosa* and *Amphibolis griffithii*, and two algal-dominated reef habitats comprising the kelp *Ecklonia radiata* and ‘turf-forming algae’ assemblages (e.g. Sargassaceae, Dasyaceae).

### Northern Gulf of Mexico (NGM)

The study was conducted at the T. H. Stone Memorial Park in St. Joseph Bay, in the northeastern Gulf of Mexico (Florida, USA). The survival ratio of small (< 3 cm TD) and medium sized (3 to 3.5 cm TD) sea urchin, *Lytechinus variegatus*, which can grow to 9 cm diameter (Watts et al. 2001), were evaluated in three representative shallow seagrass habitats (1–1.5 m depth): *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme*.

## Habitat structure

We classified biotic structural complexity of macrophyte habitats based on canopy height and shoot biomass (Heck and Crowder 1991, Orth et al. 1984) without considering the heterogeneity of the substrates on which algae grew. Abiotic shelters, such as crevices and holes, were carefully avoided when sea urchins were placed on rocky bottoms to ensure that our between-habitat comparisons in complexity were largely due to their macrophyte assemblages.

### Canopy height

We measured canopy height in situ for each macrophyte community as the maximum height of seagrass leaves or algae thalli of 35–50 haphazardly selected areas distributed within the habitat.

### Biomass

Ten replicates of seagrass shoots and three replicates of kelp fronds were randomly collected by hand. Three replicates of algae assemblages of ‘turf-forming’ and ‘erect’ algae were randomly collected with a flat-bladed paint scraper from a 0.10 m<sup>2</sup> quadrat. All samples (except kelp) were dried in an oven for 48 h at 80°C and then weighed. Since individual kelp were too big to be dried and weighed whole, its biomass was estimated using dry weights of equal circular-cut samples of stipe, lamina and lateral parts of the thallus, which were used to estimate the dry weight of the entire kelp thallus based on known proportions of these parts. The dry weights (DW) were calculated in grams per m<sup>2</sup> and multiplied by density when necessary.

## Predator abundance

We classified fish and invertebrate bottom predators dependent on their mode of predation in relation to habitat structure: 1) habitat-associated fish predators, with limited

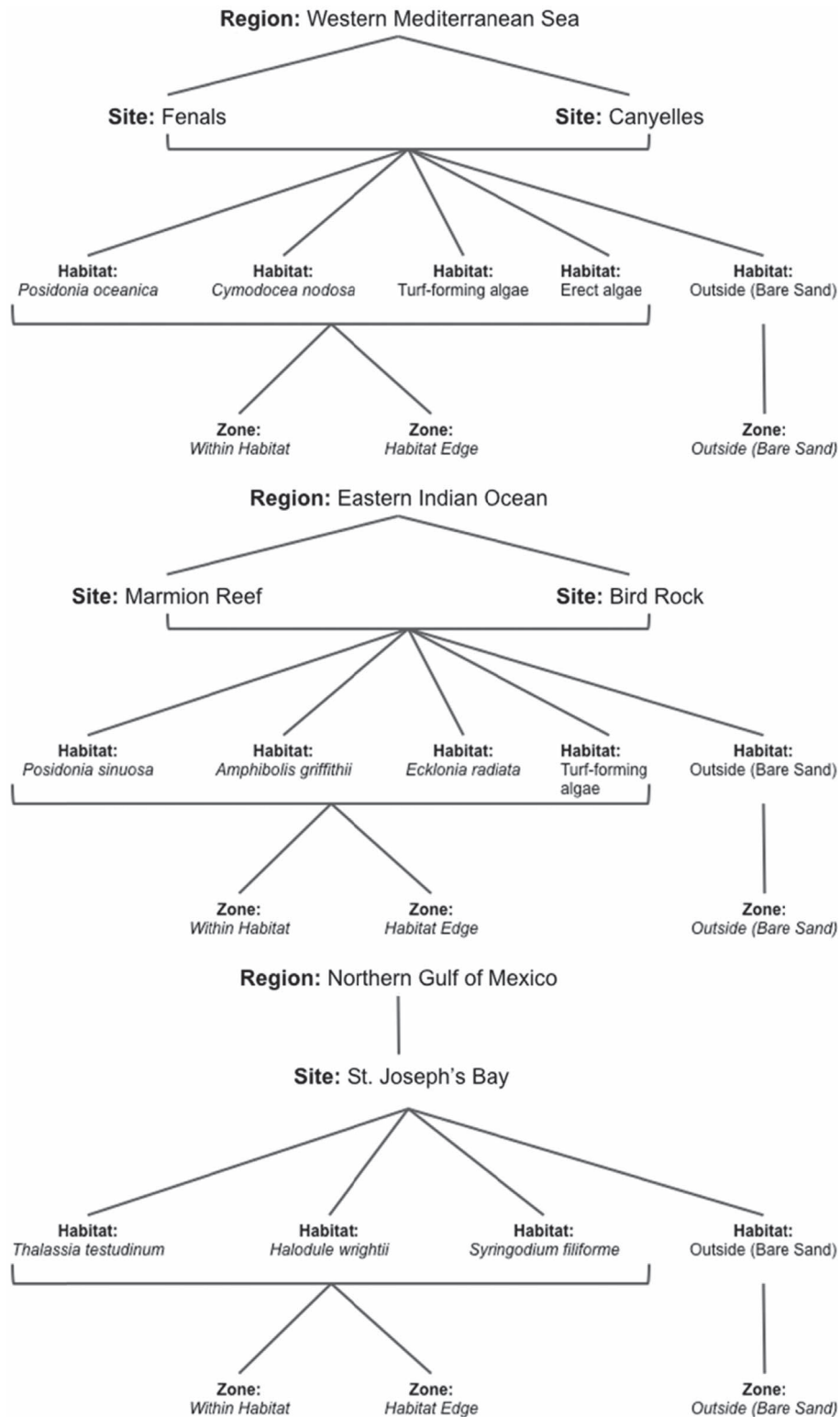


Figure 2. Study design employed in the western Mediterranean Sea, the eastern Indian Ocean and the northern Gulf of Mexico, showing the sites and habitats chosen for predation assays at each region.

movements, and largely restricted to the habitat, 2) roving predatory fish that move over large areas, often moving between habitats, and 3) habitat-associated bottom predators (cryptic invertebrate predators), such as crustaceans,

molluscs and sea stars. At each habitat, we measured the abundance of habitat-associated bottom predators and predatory fish (e.g. species of Labridae, Sparidae or Muricidae). Scuba divers estimated the abundance of predators using five



replicate underwater visual transects ( $25 \times 2$  m) as a modified version of the methodology used in García-Rubies (1997). Large size classes of roving predatory fish, such as *Sparus aurata* in the Mediterranean Sea, typically have a very high mobility and, at their extant densities outside Marine Protected Areas, are usually very difficult to estimate using standard underwater visual census techniques. We used urchin-tethering assays on bare substrates (outside habitats) to assess the potential predation of these roving predators.

Transects were conducted for each habitat independently, with the exception of turf-forming and erect algae in the western Mediterranean Sea (or turf and kelp in the case of eastern Indian Ocean) since they were interspersed within a rocky matrix. Visual transects were conducted along the inside and the edge zones of habitats.

We could not conduct visual censuses for habitat-associated fish predators in the northern Gulf of Mexico, and, as a result fish data from this region were treated as absent from the statistical analysis.

### Survival ratio

The experiments were carried out during the summer in each region, when predator activity is generally highest (Heck and Valentine 1995, Sala and Zabala 1996, Vanderklift et al. 2007). Sea urchins were collected from rocky reefs near the study sites using SCUBA. Ten individual sea urchins per size class (small and medium) were marked by tethering (Ebert 1965, Aronson and Heck 1995, McClanahan 1998) and placed randomly inside the habitat, to evaluate predation risk by habitat-associated predators (inside,  $n = 10$  per size class and habitat), at the edge of the habitat, to evaluate predation risk by both habitat-associated and roving predators (edge,  $n = 10$  per size class and habitat) and on bare sandy spaces, to evaluate predation risk by roving predators alone (sand,  $n = 10$  per size class). Urchins were tied with a fishing line to metal pegs firmly fixed to soft substrates or attached to pieces of concrete brick on rocky substrates. In all cases, sea urchins were able to move within a range of approximately  $0.5 \text{ m}^2$  to seek shelter, but always within the habitat zone to which they were assigned. After the experiment was set up, we checked urchin survival every day. We considered that predation had occurred if we found the monofilament intact but without the urchin, if some urchin skeletal remains were found or when the Aristotle's lantern membrane was removed (Sala 1997, Guidetti 2004). All samples that had the nylon line broken or absent were excluded (this occurred in very few cases). The experiment was stopped when a minimum of 50% of individuals were consumed in at least one of the habitats being observed. As a result, the time of estimation of predation between bioregions was not equal and was determined based on local predation activity. Although this manipulative technique has associated artefacts such as reduced escape capacity or chemical attraction to pierced prey (Curran and Able 1998) that might affect absolute estimates, it allowed for a uniform comparison of relative predation risk between locations and structural complexities (Farina et al. 2009, Pagès et al. 2012).

### Data analysis

For each bioregion, we ranked habitats based on their structural complexity from the lowest to the highest biomass in grams of dry weight per square metre ( $\text{g DW m}^{-2}$ ) and canopy height (cm). We estimated survival as the ratio between the number of days an individual urchin survived and the total days of the experiment, expressed on a scale from 0 to 1. A linear regression model was carried out to determine the importance of the predictor variables biomass, canopy height, density of habitat-associated predators (fish and bottom predators) and the size class of prey in influencing survival ratio inside each habitat. In order to compare predation patterns at the bioregional scale, we calculated average urchin survival ratio inside, at the edge and outside habitats. Inside the habitat, prey are largely subject to predation from habitat-associated predators, while both habitat-associated and roving predators can access edge habitats (Gorman et al. 2009). Outside these habitats, on bare sand, habitat-associated predators have no influence, and we used this to assess the potential pressure of roving predatory fish in the area.

We compared differences among zones with a nonparametric Mann–Whitney U-test and we represented it in boxplots. We also generated cumulative survival curves to identify potential patterns at the habitat scale. To do this we compared survival curves between 'inside habitat' and 'habitat edge' on a daily basis (Kaplan–Meier estimation of censored survival data); differences over the time of experiments were tested with the nonparametric Coxph-test and they were summarized in boxplots. All analyses were performed using R.

## Results

### Habitat structure

We used canopy height values measured at each location to classify habitats based on their complexity. As expected, canopy height was highest in *Posidonia* spp. (average values of  $36.21 \pm 2.32$  cm in western Mediterranean Sea and  $40.60 \pm 1.71$  cm in eastern Indian Ocean) and kelp forests (average value of  $47.83 \pm 2.51$  cm) and lowest in turf algae (average value of  $1.83 \pm 0.15$  cm in WMS and  $6.9 \pm 0.5$  cm in EIO; Fig. 3a).

However, biomass was highest in the macrophyte communities dominated by erect algae and *Posidonia oceanica* in the WMS ( $1448.96 \pm 57.12$  and  $998.2 \pm 7.79$   $\text{g DW m}^{-2}$  respectively), and by kelp forests and turf algae in EIO ( $977.775 \pm 13.84$  and  $870 \pm 360.75$   $\text{g DW m}^{-2}$  respectively), while some of the smaller seagrasses had very low biomass values (e.g. *Cymodocea nodosa*  $56.73 \pm 1.655$   $\text{g DW m}^{-2}$ ; Fig. 3b).

### Predator abundance

Visual census estimation of predator composition and abundance showed large differences between regions and habitats (Fig. 4). In the WMS, *P. oceanica*, turf and erect algae assemblages had a high density of habitat-associated

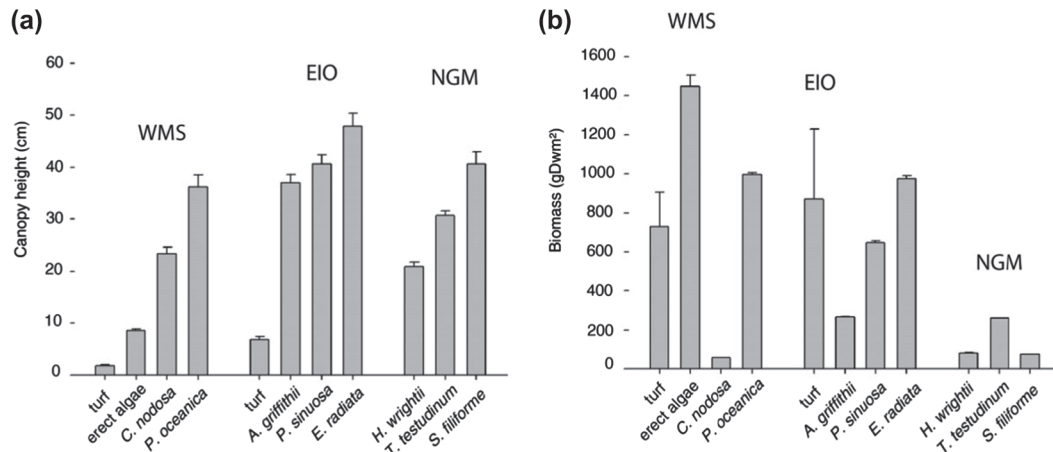


Figure 3. (a) Canopy height mean ( $\pm$  SE) and (b) biomass mean ( $\pm$  SE) are used to determine structural complexities of turf-forming and erect algae, *Cymodocea nodosa*, *Posidonia oceanica* in the western Mediterranean Sea (WMS); turf-forming algae, *Amphibolis griffithii*, *Posidonia sinuosa*, *Ecklonia radiata* in eastern Indian Ocean (EIO); *Halodule wrightii*, *Thalassia testudinum*, *Syringodium filiforme* in the northern Gulf of Mexico (NGM). Each region's habitats are listed in increasing order of canopy height, from left to right.

predatory fish such as *Coris julis* (e.g.  $11 \pm 2.2$  ind./50 m<sup>2</sup>), *Diplodus vulgaris* ( $4.7 \pm 0.3$  ind./50 m<sup>2</sup>) and *Diplodus sargus* ( $1.9 \pm 1.1$  ind./50 m<sup>2</sup>). In contrast, bottom predator abundance was lower and we found  $0.9 \pm 0.5$  ind./50 m<sup>2</sup> of bottom predatory snails *Hexaplex trunculus* in *P. oceanica* and  $0.5 \pm 0.1$  ind./50 m<sup>2</sup> in turf and erect algae, while none of these known predator species were found in *C. nodosa* (Fig. 4a).

In the EIO, we estimated very high densities of habitat-associated bottom predators. The common carnivorous sea star *Patiriella brevispina* was found in *Posidonia sinuosa* and *Amphibolis griffithii* at average densities of  $26.6 \pm 6.1$  and  $36.6 \pm 6.14$  ind./50 m<sup>2</sup>, respectively. We also detected the large sea star *Coscinasterias calamaria* ( $0.1 \pm 0.1$  ind./50 m<sup>2</sup> in seagrasses and  $0.2 \pm 0.1$  ind./50 m<sup>2</sup> in algae habitats), as well as a few unidentified species of habitat-associated predatory fish in kelp and turf-forming algae on rocky bottoms (Fig. 4b).

Finally, we found the lowest densities of predators in the NGM. The crab *Libinia emarginata* and the predatory snail *Fasciolaria tulipa* were detected in *Thalassia testudinum* ( $0.8 \pm 0.4$  and  $0.4 \pm 0.2$  ind./50 m<sup>2</sup> respectively), and the crab *Callinectes sapidus* was found in *Syringodium filiforme* ( $0.2 \pm 0.2$  ind./50 m<sup>2</sup>; Fig. 4c). Roving predatory fish and habitat-associated predatory fish were not estimated at this location.

### Survival ratio

The linear model identified macrophyte biomass and predatory fish abundance as the most important factors explaining overall urchin survival ratio ( $p = 0.018$ ;  $R^2 = 0.33$ ), but the size class of prey also appeared to influence predator efficiency although the statistic borders on the significant ( $p = 0.051$ ; see Supplementary material Appendix 2 for the full linear model Table). In the model, that included only explanatory variables relevant to the habitats (biomass, canopy height), size class of prey and

predator composition (habitat-associated predatory fish and habitat-associated bottom predators), an important part of the variance associated with the survival ratio was still unexplained. In fact, when introducing bioregions and habitats as factors additional important differences emerged. On the whole, sea urchin predation generally differed significantly among the three habitat zones (inside, on the edge and outside macrophyte habitats), but with contrasting patterns observed in the three bioregions (Fig. 5 supported by Supplementary material Appendix 3). In the WMS and the NGM, survival ratio of the juveniles was significantly lower outside and at the edge of habitats than inside habitats. For example, in WMS an average of 30% of urchins survived inside habitats, while at the edge and outside only 10% did. The opposite trend was observed in EIO where, for both juveniles and young adults sea urchins, survival was higher outside the habitat (70 and 100%, respectively) than at the edge (10% and 40%, respectively) or inside the habitat (10% and 60%, respectively). In the WMS, there was no difference in survival ratio among habitat zones (inside-edge-outside) in medium sizes that generally survived better than small sizes in all habitats (Fig. 5). In the NGM, survival of the medium size class mirrored the effects on smaller urchins, i.e. survival was highest inside (100%) compared with the edge or outside habitats (~75%).

At the habitat scale (Fig. 6 supported by Supplementary material Appendix 4), we found that the survival of juveniles sea urchins in WMS was significantly higher inside than at the edge of all habitats with the exception of turf assemblages, where there was no difference. In contrast, for the young adults, urchin survival was not significantly different in any of the habitats. In EIO, differences in survival trends between inside and the edge of habitats were not significant for either small or medium sizes of sea urchins, with the exception of *A. griffithii*, where values were higher at the edge of habitats. The trends in urchin survival ratio in NGM for the two size classes of prey were significantly higher inside the habitat than at the edge.

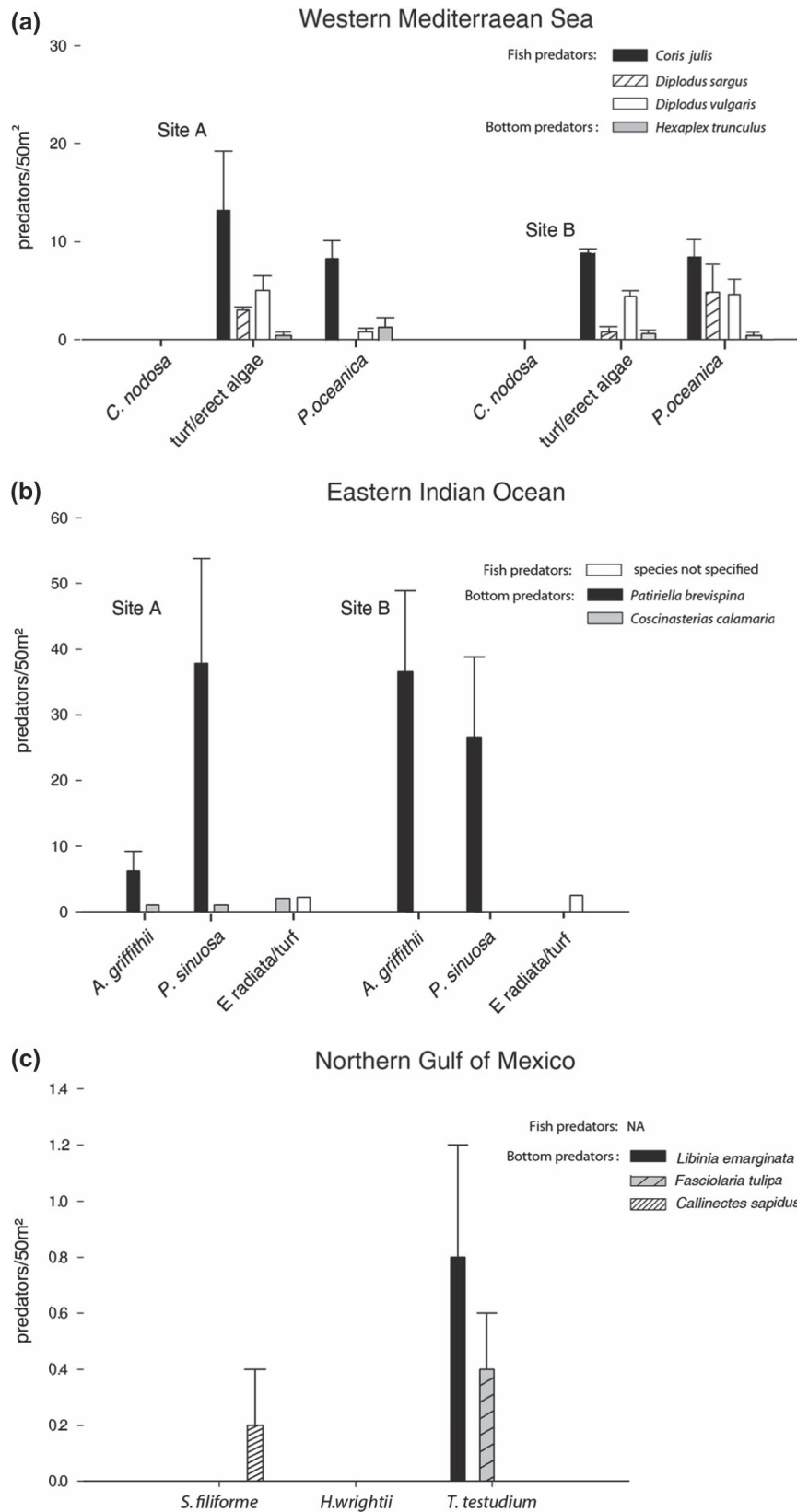


Figure 4. Abundance mean ( $\pm$  SE) of fish predators and bottom predators in 50 m<sup>2</sup>. (a) western Mediterranean Sea (*Cymodocea nodosa*, turf-forming and erect algae assemblages, *Posidonia oceanica*); (b) eastern Indian Ocean (*Amphibolis griffithii*, *Posidonia sinuosa*, *Ecklonia radiata* and turf-forming algae), and (c) the northern Gulf of Mexico (*Syringodium filiforme*, *Halodule wrightii*, *Thalassia testudinum*). Visual census was not effective in detecting roving predatory fish abundance which were underestimated, especially in the Mediterranean Sea and in the North Gulf of Mexico where urchin survival was lowest outside the habitats (see Methods for details).

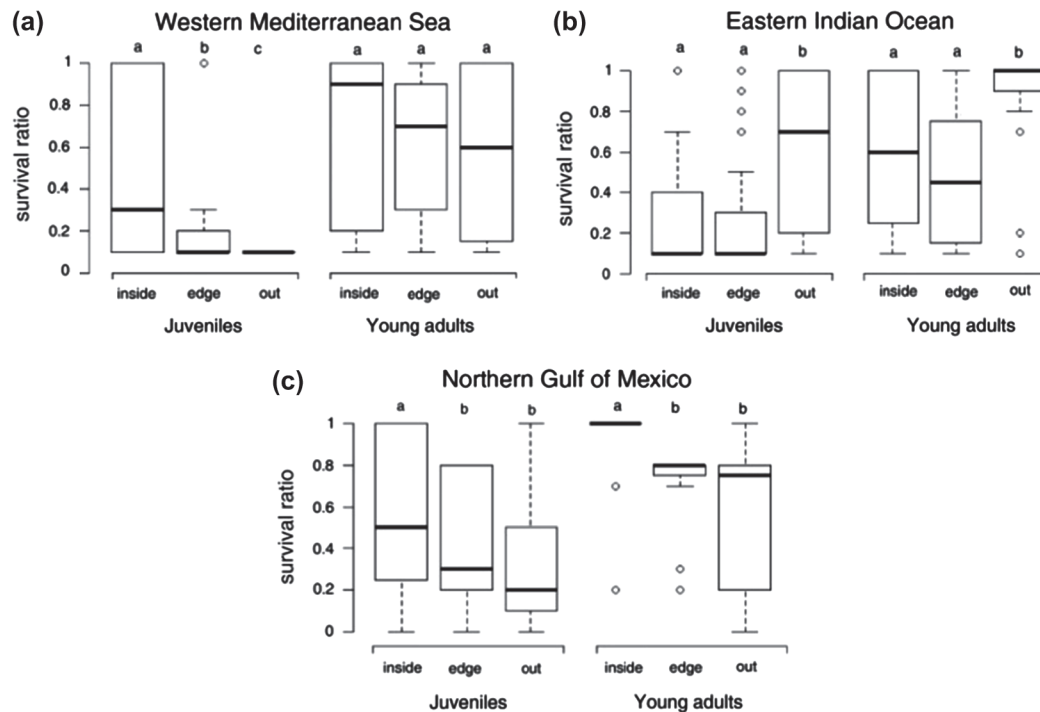


Figure 5. Boxplots (median and interquartile range) showing bioregional patterns in urchin survival ratio in the three habitat zones (inside, in the edge and outside) of a) western Mediterranean Sea; b) eastern Indian Ocean; c) northern Gulf of Mexico. Results were analysed with the non-parametrical Mann–Whitney U-test (p-level < 0.05) and significant differences were represented with lower-case letters above each bar.

## Discussion

While habitat structure (biogenic or otherwise) is clearly an important agent determining predation risk, our results suggest that it is strongly dependent on regional predator pools, which can drive predation risk in habitats with very similar structure in completely opposite directions, either reducing or enhancing top-down control within the ecosystem. Thus, while complex macrophyte habitats serve as an effective shelter from predation in the western Mediterranean Sea, where roving or habitat-associated fish are the dominant predators, highly structured macrophytes constitute dangerous habitats for prey in the eastern Indian Ocean due to the abundance of bottom predators. Although not replicated fully, the northern Gulf of Mexico showed similar trends as the Mediterranean, with macrophyte habitats providing efficient shelters from roving predatory fish, and urchins being safer inside rather than on the edge or outside macrophyte habitats.

The large variations in growth form and spatial configurations of dominant plant species are often a significant contributor to habitat structure in vegetated habitats (Crowder and Cooper 1982, Madsen et al. 2001). Within the same bioregion, the macrophyte communities in our study encompassed a range of biogenic structures and complexity with varying biomass and canopy heights that differ considerably in their refuge value for prey. The model indicates that structural complexity was an adequate predictor of prey survival across all bioregions (Fig. 5). In areas like the Mediterranean Sea and the Gulf of Mexico, complex habitats offered far better refuge for prey, particularly for smaller size classes. In fact, when roving and

habitat-associated fish are the dominant predators (as in the WMS), increasing structural complexity can strongly reduce predation risk. Highly structured habitats like *P. oceanica* and erect algae constitute a much safer refuge for juvenile urchins than turf algae. In the WMS, *C. nodosa* is an exception to this general trend and may be driven more by the configuration of the landscape, which has been observed to strongly influence predation depending on the spatial attributes of the habitats and the surrounding matrix within which it is housed (Farina et al. unpubl.). Meadows of *C. nodosa* in the WMS typically grow close to the coast, are very isolated from other macrophyte communities, and house very low densities of habitat-associated fish (Guidetti and Bussotti 2000), which combined, potentially explain the relatively high urchin survival here despite its structure.

In contrast with the WMS, structurally complex habitats offered very little refuge for small sea urchins in the eastern Indian Ocean. Survival rates were lower in EIO where bottom predators were more abundant than fish. Bottom predators like *Patiriella brevispina* were found inside *Amphibolis griffithii*, *Posidonia sinuosa* as well as turf habitats. It is likely that these bottom species are the dominant predators of juvenile urchins in the EIO, and their presence inside structurally complex habitats makes dense macrophyte stands very dangerous for small size classes of urchins (but see Keough and Butler 1979).

Interestingly, our results indicate that predation on large adult urchins was generally low across all habitats and bioregions. Habitat structure did not constitute a refuge for larger urchin size classes, as they were visible to predators in even the most structured habitats. However, as observed



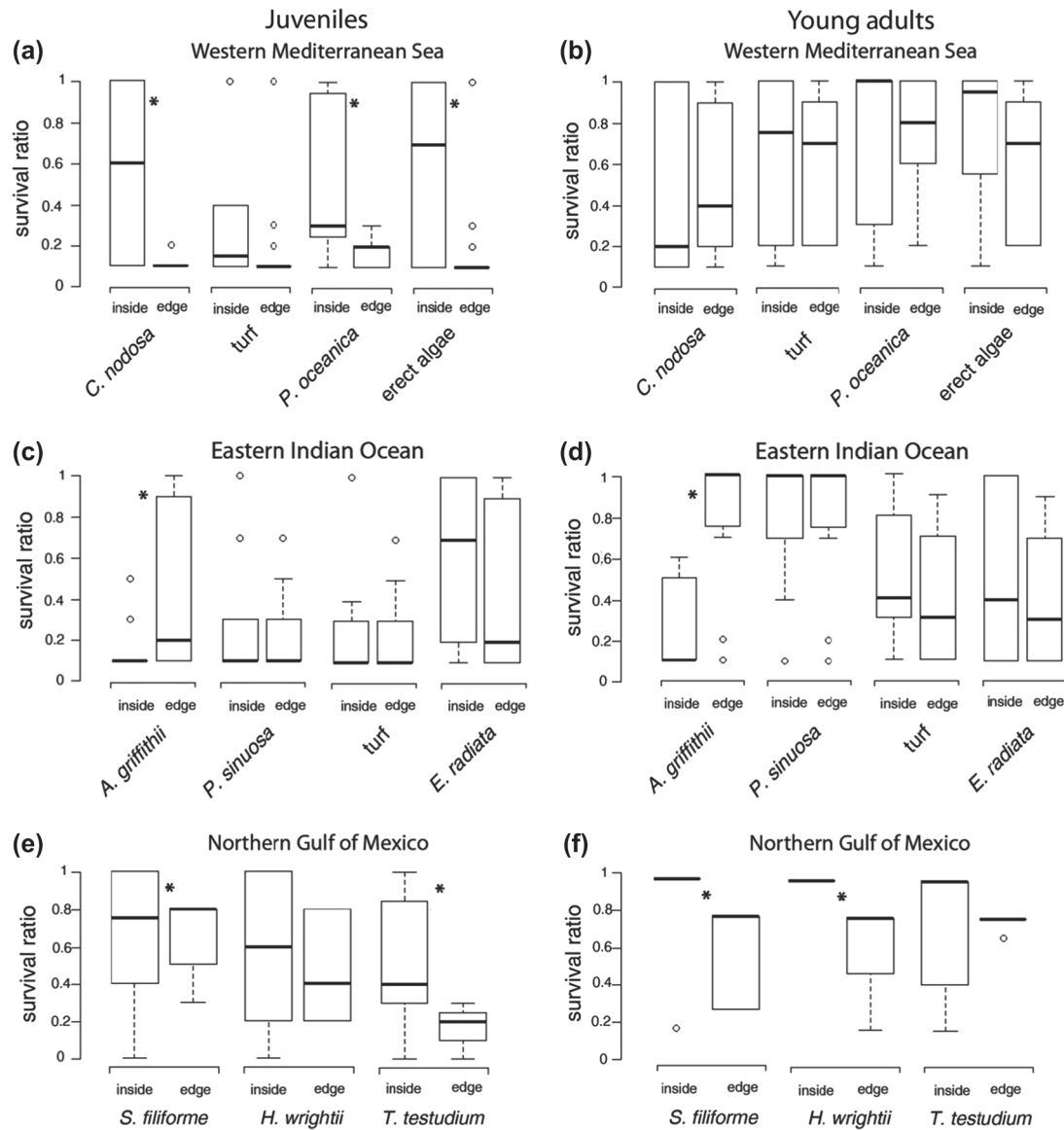


Figure 6. Boxplots (median and interquartile range) representing survival ratio of urchin size classes inside and at the edge of each habitat: (a, b) western Mediterranean Sea (*Cymodocea nodosa*, turf-forming algae, *Posidonia oceanica*, erect algae assemblages); (c, d) eastern Indian Ocean (*Amphibolis griffithii*, *Posidonia sinuosa*, turf-forming algae, and *Ecklonia radiata*) and (e, f) the northern Gulf of Mexico (*Syringodium filiforme*, *Halodule wrightii*, *Thalassia testudinum*). Significant differences were estimated comparing the cumulative curves of survivorship with the nonparametric Coxph-test (Supplementary material Appendix 4) and represented with asterisks.

elsewhere, adult urchins probably do not need to rely on structural complexity, their size itself being refuge enough, with few sufficiently large extant visual predators able to prey on them, even within Marine Protected Areas (Guidetti 2004). This was particularly important because predation on small sizes was very high across all three bioregions, indicating that survival of juveniles may be a critical bottleneck shaping urchin population structure.

Our results show that habitat structure can work both ways in mediating predator–prey interactions, either by reducing or enhancing top–down control. The effect is largely a function of predator identity, which determines whether habitat complexity serves as a major restriction that prevents effective hunting (through refuge) or enhances predation by providing a camouflage or hiding

space for predators (Bartholomew et al. 2000). This dual mediatory role results in a dynamic arms race among predators capable of exploiting habitats of different structural characteristics within the ecosystem mosaic. Predators in our large-scale study spanned a spectrum of predatory strategies (visual hunt, camouflage, ambush and chemotaxis). Evolutionary and behavioral predispositions enable species that rely on acute visual senses and speed to perform much better over large, relatively open expanses (Canion and Heck 2009). In contrast, species that rely more on camouflage, ambush or chemotaxis (James and Heck 1994) may be much more effective in the dense undergrowth provided by structurally complex macrophyte communities (Martin et al. 2010). A clear example of these two strategies is evident in the comparison between

the seagrasses *Posidonia oceanica* in the WMS with *Amphibolis griffithii* in EIO; both have very similar canopy height and biomass (Fig. 3), but have very different types of predators. Although *A. griffithii* has a structure characterized by tree-like fronds and an open space below its canopy that may facilitate access for medium-sized fish (Hyndes et al. 2003), predation signs found on urchin prey tests in our study were typically made by sea stars. In contrast, most predation signs in *P. oceanica* could be clearly assigned to fish that most likely hunted visually. This reflects, the dominant predator groups observed in the two regions (Fig. 4). These compositional differences appear to be critical in determining survival ratios in the community with *P. oceanica* being one of the safest habitats for urchins in the WMS, while *A. griffithii*, despite having a similar canopy height and biomass, is one of the most predation-prone habitats we observed in the EIO. Our observed trends are most likely driven by compositional differences in predators among habitats.

In our study, predation inside the refuge provided by habitat structure in the WMS and NGM was almost always lower than predation at the edges and in the sand indicating that fish predators clearly dominated the predatory pool. At least in the Mediterranean, this trend was also confirmed by our in-water surveys that showed fish predators were by far the most dominant in this system compared with bottom predators. This supports the observation that fish predators may be the main consumers of sea urchins in macroalgal and seagrass communities in the Mediterranean (Sala 1997). In striking contrast, predation inside and at the edge of the habitats tended to be higher compared to sand predation in EIO (Fig. 5), a pattern that holds in almost every habitat from simple turf forming algae to the more complex kelp *E. radiata* (Supplementary material Appendix 4). This was also related to the predator guild composition that, in this region, was characterized by a high density of bottom predators, which can move inside the structure up to habitat edges (Fig. 4b). In fact, seagrass meadows had very high densities of sea stars while fish predators were practically absent. These observations conform with similar results by Vanderklift et al. (2007) and Tuya et al. (2010), which indicate that fish were restricted to habitats close to rocky reefs and roving fish predators were very rare in the area.

While natural differences in predator composition between habitats may play a large role in determining predation rates, we cannot discount directed human harvest as an agent influencing differences in predator composition. All of our studied habitats have been subject to sustained fishing pressure (Halpern et al. 2008). As top predatory fish are selectively removed from coastal waters, there is an increasing simplification of trophic webs that can have major modifications on the predator pool in any given region (Jackson et al. 2001). In extreme cases, the removal of top predators can lead to meso-predator release (for instance, invertebrate predators), which could dramatically modify the structure–predation relationship and change the landscape of risk that prey species experience in these regions (Oksanen et al. 1981).

When the prey concerned are themselves key functional elements in the ecosystem, as sea urchins often are in

macrophyte communities (Alcoverro and Mariani 2002, Woodley 1999), these distributional differences in the predatory pool can have vital consequences for the functioning of the system. Modifications of predator guilds of sea urchins can affect the abundance and distribution of these species, and their effects may cascade and affect other ecosystem processes (top–down control). For instance, the sea urchin *P. lividus* we used in this study is among one of the most important herbivores in the Mediterranean (Hereu et al. 2005, Prado et al. 2012) and has often been observed to overgraze macrophyte communities when released from predation (Boudouresque and Verlaque 2001). In contrast, sea urchins are relatively rare in the Australian macrophyte communities we studied (Vanderklift and Kendrick 2004) and may be functionally less important to ecosystem structure. Of course, their low numbers may, at least in part, be influenced by the high levels of predation observed inside Australian macrophyte communities. Consequently, in areas that are controlled by roving and habitat-associated predatory fish (i.e. Mediterranean and Gulf of México), a much higher impact of overfishing is expected in macrophyte communities. In contrast, in areas where the main predators are bottom invertebrate predators (i.e. Australia), the impact of overfishing may not manifest so directly, although it may still appear through indirect pathways. These differences make it difficult to generalize about the nature of habitat structure–predation relationship across regions and local contexts. To fully understand and manage ecosystem function, it is therefore crucial to determine the main types of predators (fish versus invertebrate) dominant in each habitat, as structure can strongly modify ecosystem function. Whether it enhances or limits predation is contingent completely on the predatory pool, and may imply potentially very different habitat-specific management directions.

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