Hotspots of predation persist outside marine reserves in the historically fished Mediterranean Sea

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Keywords: Predator-prey interactions, Refugia, Rhizome layer, Canopy height, Paracentrotus lividus, Macroalgal communities, Posidonia oceanica, Diplodus sargus.
Abstract

The Mediterranean Sea has sustained historically high levels of fishing since pre-Roman times. This once-abundant sea has witnessed major declines in apex predators, now largely restricted to isolated pockets within marine reserves. This depletion could critically impact macrophyte communities that are strongly structured by top-down processes. We evaluated rates of predation on the sea urchin *Paracentrotus lividus*, a key herbivore of macroalgal and *Posidonia oceanica* seagrass seascapes, across a large stretch of the Western Mediterranean coastline. Fish predation was generally higher inside reserves, but was equally high at several locations outside these boundaries. Although critically low at some locations compared to reserves, predation was functionally ubiquitous in most habitats, seasons and sites. Fish were still primarily responsible for this predation with no clear evidence of meso-predator release. Macroalgal habitats were consistently subject to higher predation than in seagrass meadows, functionally critical given the vulnerability of macroalgal systems to overgrazing. Predation hotspots were clearly associated with high fish predator numbers and low refuge availability. Taken together, these results suggest that long-term overfishing may not necessarily reflect a complete loss of trophic function. Pockets of fish predation may still persist, linked to habitat complexity, predator behavioural adaptations and landscape-level features. Given the essential role top-down control plays in macroalgal communities, regulating fishing at these predation hotspots is vital to effectively conserving habitats from future hysteretic shifts. Even historically fished seas may retain areas where trophic function persists; identifying these areas is critical to preserving the remaining ecological integrity of these coastlines.
Introduction

One of the clearest signatures of the increasing human imprint on the biosphere is the gradual weakening of trophic processes as top predators decline from natural ecosystems under the combined onslaught of direct extraction and habitat loss (Ripple et al., 2014). Predation is a critical agent of community structuring (Hairston et al., 1960); the depletion of key predators leave both terrestrial and marine ecosystems increasingly prone to catastrophic and often hysteretic collapses from which recovery can be protracted. Marine macrophyte communities are particularly susceptible; uncontrolled by predation, marine herbivores can undergo major population explosions, overgrazing macrophyte-dominated ecosystems (Kempf, 1962). In a classic example, otters have been identified as principal structuring agents of kelp communities in the Eastern Pacific by regulating urchin populations (Tegner and Dayton, 2000). Similarly, the structuring of Western Mediterranean macrophytes appears to be strongly mediated by top-down control of urchins by fish predators (Pinnegar et al., 2000).

Marine ecosystem managers have long recognized the importance of conserving higher trophic functions, and regulating fishing of top predators has been the instrument of choice in managing nearshore ecosystems (Estes et al., 2011). There has been a growing call to expand networks of marine reserves and impose fishing restrictions to protect key predators and enhance the natural resilience of the ecosystems they structure (Pinnegar et al., 2000). This is predicated on the assumption that fish predator numbers link well with rates of predation, and that healthy predator populations will ensure their functional roles within the ecosystem (Clemente et al., 2010). There is growing evidence demonstrating that marine reserves have been largely effective in reversing the direct and indirect effects of trophic decline (Shears and Babcock, 2002), and they clearly enhance ecosystem functioning. However, it is becoming increasingly clear that predation is an inherently dynamic process, and predator-prey interactions can vary considerably across the seascape. The distribution and densities of predators and prey within the mosaic may be influenced by recruit supply, which may, in turn, be mediated by habitat differences (Hereu et al., 2004). Independent of numbers, predator-prey interactions may be strongly driven by how both predators and their prey use
these habitats (Farina et al., 2014). These habitat-specific factors may also interact in complex ways making predator-prey interactions often difficult to predict. Both fish predators and their prey may modify their behaviours in relation to each other’s presence, the abundance of conspecifics, the availability of refugia and the configuration of the habitat within the larger seascape. For instance, habitat structural complexity, by modifying the presence of prey refugia is fundamental in determining predation rates and, in turn, prey population structures (Farina et al., 2009; Hereu et al., 2005). Moreover, predators may also be implicated in complex indirect interactions in macrophyte communities; fish herbivores, by reducing the leaf canopy of macrophyte communities, can enhance fish predation on urchin herbivores by reducing refuge availability (Pagès et al., 2012). Further, a reduction of top predators can sometimes lead to the competitive release of benthic meso-predators that may potentially compensate rates of functional predation experienced by the system (Levi and Wilmers, 2012). This can also be highly habitat dependent since every system could be host to a very different suite of predators. Finally, both predators and prey may move between habitats in the mosaic, and predation may be strongly influenced by patterns of habitat connectivity or isolation within the larger seascape (Hitt et al., 2011).

Two macrophyte habitats dominate the North Western Mediterranean: *Posidonia oceanica* seagrass meadows and shallow macroalgae-dominated rocky habitats, both potentially structured by top-down control of the herbivorous sea urchin *Paracentrotus lividus* (Fig. 1) (Verlaque, 1987). The Mediterranean has been seriously overfished for millennia (Sala et al., 2012), and determining if predation still plays a functional role is essential to planning conservation actions across the region (e.g. creations of marine reserves, management of coastal development, etc.). While it is well established that predation intensity is relatively high inside existing protected areas (Sala and Zabala, 1996) it is unclear to what extent this function is conserved beyond their boundaries, although it is generally assumed to be low because of this historically sustained fishing pressure (Guidetti et al., 2010). However, there is little information available on the factors that influence predation in different macrophyte habitats. The decline of fish predators could have triggered a functional substitution by other benthic predators. In addition, given that reserves are principally established to
enhance predator numbers, understanding how predation activity is linked to fish predator abundance is critical. To answer these questions, we measured relative rates of sea urchin predation by fish and benthic predators at eight representative locations across a large stretch of the NW Mediterranean coast in both algal communities and seagrass meadows in different seasons. In addition, we attempted to identify if predator habitat use or habitat-specific factors (presence of refuges) can drive functional rates of predation in these dominant macrophyte habitats.
Materials and Methods

Study system

The shallow seascape of the Western Mediterranean is dominated by rocky macroalgal communities and *P. oceanica* seagrass meadows. Although the sea urchin *P. lividus* is a key herbivore in both habitats, they may differ considerably in their susceptibility to urchin herbivory (Boudouresque and Verlaque, 2001). In macroalgal systems, urchin overgrazing can cause ecosystem barrens from which recovery is often protracted (Pinnegar et al., 2000). Predators likely play a vital role in regulating sea urchin populations (Supplementary, A1), preventing these ecosystem shifts (Guidetti, 2004; Sala, 1997). While *P. oceanica* meadows may experience very similar rates of urchin herbivory, they may cope better with this offtake because of their inherent evolutionary adaptations (Vergés et al., 2008). However, heavy eutrophication could make meadows susceptible to overgrazing (Ruiz et al., 2009). Several fish species prey on *P. lividus*, and many of these are important commercial and recreational fishery targets (Guidetti, 2006). Additionally, benthic predators including starfish and some gastropods may also be important contributors to sea urchin predation (Boudouresque and Verlaque, 2001).

Study site and Sampling design

The study was conducted along the NW Mediterranean (~600km). Eight sites were selected along the coast, characterized by shallow seagrass *P. oceanica* habitats and photophilic macroalgae on rocky substrates (Fig. 2). Sites were not randomly selected since all sites required both habitats to be present and at least one unfished reserve was required for the study objectives. Fishing is permitted at all sites except the Medes Island Marine Protected Area, which has been a marine reserve since 1990, and partially controlled in Portlligat since 2006 as part of the Cap de Creus Natural Park but with low fishing regulation. The reserve is characterized by a high abundance and biomass of predatory fish (Garcia-Rubies et al., 2013). In each habitat we assessed predation on the sea urchin *P. lividus*, the most important key herbivore in NW Mediterranean macrophyte habitats (Harmelin et al., 1980). We evaluated predation impact by fish and benthic predators (see below) in each of the selected sites in summer and winter. In addition, we estimated the habitat use by the most important
urchin predators, and evaluated habitat characteristics that could constitute an effective predation refuge for the urchin (i.e. canopy height in both habitats, crevices in rocky substrates and bare root-rhizome layer in seagrass meadows) (Orth et al., 1984). All measurements were recorded within a depth range of 3 to 8 meters for both habitats.

**Predation impact**

Predation impact was measured using tethering techniques (Boada et al., 2015; Aronson and Heck, 1995) on adult urchins. This comparative method has been used extensively to assess predation in Mediterranean and other temperate ecosystems (Farina et al., 2009; Guidetti and Sala, 2007) and coral reefs (McClanahan and Muthiga, 1989; Pederson and Johnson, 2006). The urchin was harnessed by threading a thin nylon line through its test. The harness was then attached to a brick or metal stake, which were deployed in rocky reefs or meadows respectively. The harness left the urchin a 50 cm radius space to move from its point of attachment. Within this radius, the urchin could actively seek available shelters as it would in natural conditions. To assess tethering-related mortality before the experiment we tracked the survival of caged urchins (to exclude predators); none of the 14 tethered urchins died in the 12 days of this assessment. Twenty urchins were placed in groups of 5 at each site and habitat (total of 4 replicated groups) in two different seasons (i.e. summer and winter). Predation impact was measured 15 days after the start of the experiment.

Predation impact was calculated for each group of urchins using the percentage of dead urchins with respect to the initial number (0, 20, 40, 60, 80 and 100% predation). Fish or benthic predators leave clearly distinguishable bites/marks on sea urchin carcasses (Shears and Babcock, 2002) and we carefully examined dead urchin tests to assign predation impact to their respective consumers; fish predator impact (FPI) and benthic predator impact (BPI).

**Predator abundances and habitat use**

We measured the habitat use of the most common identified benthic predators of *P. lividus* within the two selected habitats, *Hexaplex trunculus* and *Marthasterias glacialis* (Boudouresque and Verlaque, 2001). We frequently found these benthic predators still attached to the prey. In addition
we recorded a few predation events by the starfish *Coscinasterias tenuispina* (S. Farina pers. obs.) and added this species to our sampling. Benthic predator habitat use was estimated through accounting the abundance of benthic predators at each site and habitat along 4 underwater visual belt transects (10 m x 2 m). These were used to calculate benthic predator densities per square meter for each site.

We also investigated the habitat use by fish predators during daylight hours, when predators are most active (Savy, 1987). We used underwater video cameras in each habitat and season (i.e. GoPro Hero 2, 10Mp) (Harasti et al., 2014) to record 4 fixed videos of 20 minutes within each site. We used underwater buoys to mark a 5 x 5 m area in front of the camera and counted the number of individuals of the principal predators and scavengers of medium and large sea urchins (*Diplodus sargus*, *D. vulgaris*, *Sparus aurata* and *Labrus merula*) (Guidetti, 2004; Sala, 1997) and two more potential predator or scavenger species of the genus *Diplodus* (*D. puntazzo* and *D. cervinus*) seen traveling through the marked area. This was then multiplied by the total time each species spent within the zone and divided by the total observed area. Habitat use \( (U) \) was calculated as follows:

\[
U = \frac{\sum (T_i)}{T \cdot A}
\]

where \( i \) is the number of predators observed during the sampling interval, \( T_i \) is the total time each predator species spent in the area, \( A \) is the total area observed in each video and \( T \) is the video recording time (approx. 20 minutes each).

**Habitat structural parameters**

To test the influence of habitat structural parameters on predation rates, we measured habitat complexity (canopy height and number of refuges) in both habitats. We measured canopy height with a measuring tape at 20 random locations within the macroalgal and *P. oceanica* canopy at each site and for each season. In addition, we measured the depth of the total unburied rhizome layer.
(Prado et al., 2009) in *P. oceanica* meadows since this is often used as an important refuge by sea urchins in seagrass meadows (Orth et al., 1984). This was done at 20 random points at each meadow with a measuring stick inserted into the unburied matrix. In rocky macroalgal systems we counted the number of potential shelters (crevices and niches that were estimated to harbor an urchin of at least 4 cm diameter) within a 50 cm diameter range at 20 random points per site and season.

**Statistical analyses**

3-way ANOVA’s tests were performed to establish the effect of habitat, season and site on the following dependent variables: total predation impact, fish predator impact (FPI), bottom predator impact (BPI), sea urchin predator fish habitat use (U) and canopy height. The factors considered were ‘site’ (8 levels, fixed factor), ‘habitat’ (2 levels; *P. oceanica* meadows and macroalgal habitats, fixed factor) and ‘season’ (2 levels; summer and winter, fixed factor). Prior to the analyses we tested for normality (Shapiro-Wilk test) and homogeneity of the variance (Bartlett’s test). When assumptions were not met, we set the significance level to *p* < 0.01 as the F statistic is robust despite violation of these assumptions when the sampling size is large enough (Underwood, 1981). Significant differences between sites were further explored with Tukey HSD *post hoc* tests.

A continuous approach (GLM) was used to test the significance of the explanatory variables related to fish habitat use (for the three main predators) and habitat structural parameters (presence of habitat-specific refuges, see below) to explain the observed patterns of fish predation (FPI) within each habitat. We could not test this model for bottom predation impact (BPI) as the number of predation events observed was too low to reliably establish any causal link. A General Linear Model (GLM) with a Binomial distribution (and a logarithmic link function) was fitted to test significance. To describe the response of FPI within each habitat a specific analysis was performed according to habitat-specific explanatory variables. For the *P. oceanica* habitats the specific variables included in the model were canopy height (canopy), depth of the dead matte rhizome layer (matte) and the habitat use of fish of the *Diplodus* genus as the main *P. lividus* predators. For the macroalgal dominated rocky habitats the variables...
included were canopy height (canopy), number of refuges (shelters) and the habitat use of fish of the Diplodus genus as the main *P. lividus* predators. We used mean values of habitat use from the 8 replicates (summer and winter together) to better investigate the use in each location and habitat. We started with a full model considering all predator and habitat-associated variables for model selection. We then chose the best model by dropping each effect sequentially and using Akaike’s Information Criterion (AIC) and likelihood ratio tests (Zuur et al., 2009). All the statistical analyses were performed using ‘lme4’ package (Bates et al. 2014) in the open source software R (Bates et al., 2014; R Development Core Team, 2013).
Results

Spatio-temporal variation in benthic and fish predation rates: habitat, season and site.

Predation impact varied substantially between habitats, sites and seasons (Table 1, Fig. 3). Predation impact in rocky habitats was at least double of that measured in *P. oceanica* habitats, while at some sites this difference was even more marked (Table 1, Fig. 3). On average, the predation impact in rocky reef communities was 54.9% (± 9.2%), compared with a predation impact of 17.8% (± 8.6%) in *P. oceanica* meadows (Fig. 4). The highest predation impact for both habitats was found inside the Medes Islands Marine Reserve in which fishing had been restricted for more than 2 decades. Interestingly though, other locations along the coast, outside any NTA, experienced similar predation impact both in macroalgal communities (*post hoc* Site A = B = C < D = F > E = G = H) and in *P. oceanica* meadows (*post hoc* Site A = B = E = F = G = H < C = D) (Fig. 3). In contrast, predation impact in other sites was very low in both habitats especially in a particular season (e.g. Site A or Site B, Fig. 3). While predation was generally higher in summer than in winter, this was only true for some sites (Table 1, Fig. 3). At sites where predation was very high (i.e. Site D or Site F), the difference between seasons was almost absent; where predation was low, these differences were considerably more marked (Fig. 3). Even outside the marine reserves, fish predators continued to be responsible for the bulk of predation (Fig. 3). In macroalgal habitats the few observed cases of benthic predation occurred outside the reserve. In contrast, in *P. oceanica* habitats predation by benthic predators was more prevalent, although still considerably lower than fish predation. A high peak of benthic predation was observed in the seagrass habitat in winter in Medes Islands as a result of an observed increase in the abundance of the predator starfish *C. tenuispina* (a few tethered sea urchins still had the star attached to the carcass). An interesting pattern is that season was significant when both fish and benthic predation were considered separately, but not together (Table 1, Table 2) since both predators seem to prefer distinct seasons particularly in determinate sites. Predation by fish was significantly higher in summer (41.5% ± 9.7%, Table 2), than in winter (32.3% ± 8.1%) while benthic predation was significantly lower in summer (1.0% ± 0.7%) than in winter (3.5% ± 2.2%).
Variation in predator habitat use and canopy height between habitats, sites and season.

Predator habitat use also showed clear differences between habitats (Fig. 4) and sites for certain seasons (Table 2, Fig. A2). The index of predator habitat use was more than 10 times higher in rocky habitats than in seagrass habitats, a difference not reflected in the magnitude of predation impact (Fig. 4). This suggests that although predators may use the habitat much less, predation rates continue to be relatively high in seagrass meadows.

As expected, canopy height varied considerably between macrophyte habitats; *P. oceanica* canopies were almost an order of magnitude taller (~35 cm long) than macroalgal dominated habitats (~6 cm height, Fig. 4, Table 2). Canopy height also varied between sites and seasons, although in the same direction for both habitats (Table 2, interaction between site, habitat and season, Fig. A3). Within each habitat, canopy height varied considerably between seasons, with summer canopies consistently taller than winter canopies (average values summer *P. oceanica* > average winter *P. oceanica* > average macroalgal summer and winter), a trend that was more pronounced at some sites (Table 2, interaction between site and season).

Habitat-specific refugia also varied considerably between sites (Fig. A2). In macroalgal habitats the number of refugia differed considerably between sites with a mean maximum value of 9.2 refugia per sampling and a mean minimum of 2 (ANOVA p-value < 0.001). In seagrass habitats as well, the depth of the dead matte rhizome layer could differ by an order of magnitude between sites (mean max. 14.4 cm and min. 0.8 cm; ANOVA p-value < 0.001).

Determinants of predation rates in rocky and seagrass habitats

The GLM results showed that in rocky habitats, predation rates were best predicted by the number of available shelters (p < 0.05) together with the abundance of fish predator-species of the genus *Diplodus* (p < 0.05, Table 3). The same pattern was found in *P. oceanica* meadows where the depth of the dead matte rhizome layer (p < 0.05) together with habitat use by fish species in the genus
*Diplodus* were key determinants of predation impact (*p* < 0.05, Table 3).

**Discussion**

Despite a long history of commercial, artisanal and recreational fishing, fish predation continues to be a ubiquitous process along the North Western Mediterranean coast, albeit with considerable site-level variation in intensity. While the Medes Islands marine reserve (with over two decades of fishing prohibition) unsurprisingly received the highest level of predation in both habitats, locations with no such restrictions also received comparable levels of functional predation. Fish predators continue to be the principal agent of predation in these waters with benthic predators apparently playing a relatively minor role. Perhaps most strikingly, there were strong differences in the intensity of predation between macrophyte habitats, even when separated by just a few meters. Predation impact in macroalgal habitats were at least twice as high as in *P. oceanica* seagrass meadows, even when these habitats were very closely connected, a difference that appears clearly linked to the greater abundance of predators in rocky systems. These predator-prey interactions appeared to be controlled by the same agents in both habitats, the number of available refugia as well as predator habitat use.

The now well-documented specter of trophic downgrading across the world’s oceans has raised serious questions of the continued functional resilience of important coastal ecosystems (Estes et al., 2011). On coastlines that have been dominated by heavy human extractive use for as long as the Mediterranean has, it is difficult to conceive of fish predatory functions still being ubiquitous and relevant outside the most strictly protected reserves. However, this assumption has rarely been tested at regional scales; our results are an encouraging indication that, despite the considerable trophic downgrading the Mediterranean has experienced with centuries of human use (Pauly et al., 1998), predation continues to be a relevant trophic process in its macrophyte communities. To be sure, predation was highest in the only marine reserve we studied (Medes Islands), where predatory fish guilds have increased notably in the last decades (Garcia-Rubies et al., 2013). However, a few sites along the coast without the benefit of this careful management (i.e. site F, site C) showed rates very
similar to Medes, indicating that locations across the NW Mediterranean were still able to maintain intact higher trophic functions. These sites were characterised by subtidal rocky extensions and outcrops that may attract predators (personal observation); these contingent factors may help determine how predator-prey processes vary across the coastline. Each of these processes is likely governed by a complex suite of factors acting together to determine the relative importance of predatory functions, supply side processes and bottom-up drivers in structuring macrophyte communities. For instance, while predation may be an important agent of population control, urchin populations can themselves be highly dependent on recruitment (Prado et al., 2012) and bottom-up processes controlling algal growth (Menge, 2000); these factors likely interact in complex ways to determine the capacity of predators to control the system.

What is clear, however, is that benthic predators do not substitute fish as the top trophic agents along this coast, even in sites where fish predation is very low (Site A, Fig. 2). The only observation that could potentially indicate a certain level of competitive release is seen at a seasonal level. The fish predatory guild is less active during winter, and bottom predators become more active during these months, especially in seagrass meadows. This increased winter activity may represent a competitive exclusion between predatory groups. Chemotactic benthic predators may take much longer to locate their prey than visual fish predators, and since winter temperatures constrain fish metabolic activity, benthic invertebrates may derive seasonal benefits from this reduced movement (Bonaviri et al., 2009) but see also (Farina et al., 2014). This competitive exclusion was not observed in sites where fish predation was high throughout the year and the impact of benthic predators was low (i.e. in rocky habitats from Site D and Site F). Clearly though, these appear to represent merely seasonal changes in behavior rather than any real change in community composition, and the overall predominance of fish predators indicates that these systems are not witnessing either a release of benthic meso-predators due to overfishing or competitive exclusion. This contrasts with macrophyte habitats in other fished regions (like Australia) where benthic predators dominate top trophic roles, with fish predators virtually absent (Farina et al., 2014). In other coastal ecosystems, notably
Caribbean coral reefs, the removal of large predatory fish triggers a distinct meso-predator release (Burkepile and Hay, 2007). The apparently low functional replaceability of the predator guild in the Mediterranean highlights the centrality of fish to predation pathways in these systems. This further emphasizes the importance of managing predatory fish against fishing overexploitation if this crucial process is to be preserved.

The intensity of predation we recorded was clearly habitat dependent, even when the seascape was a patchy mosaic dominated by both habitats. Macroalgal habitats received rates of predation at least twice as high as seagrass meadows. This can, in part, be explained by higher habitat use of predators in rocky systems and the taller canopies characteristic of *P. oceanica* meadows. Surprisingly, predation impact in seagrass meadows were disproportionately high compared to predator use of these habitats. This uncoupling between predator numbers and predation impact between habitats indicates that predator-prey interactions may be highly dependent on habitat-specific traits in relation to refuge availability, predator efficiency, prey abundance, and other factors. It is well known that predatory fish abundance and habitat attributes plays a critical and often complex role in determining predation impact in marine ecosystems (Canion and Heck, 2009; Farina et al., 2009; Hereu et al., 2005). These habitat-specific differences in predation have important implications given what we know of the functioning of these ecosystems. Rocky macroalgal communities along the Mediterranean (as in several regions) appear inherently vulnerable to urchin overgrazing and may be subject to functional discontinuities once they switch to urchin barrens (Ling et al., 2014). A series of feedbacks – continued scraping by urchins preventing recolonisation by algae, urchin bioerosion of rocks creating their own refugia, etc – may make recovery very difficult past this threshold (Guidetti et al., 2003). The generally high levels of predation experienced here may be critical in ensuring that these points of discontinuity are not breached. In contrast, *P. oceanica* meadows may be less “dependent” on top-down control as a process in maintaining ecosystem function (Prado et al., 2011; Vergés et al., 2008). This may be due to the inherent ability of this seagrass to resist herbivory with its suite of coping mechanisms (Ruiz et al., 2009) unless urchin density is particularly high.
Perhaps most interestingly, predation was clearly predictable in both seagrass systems and macroalgal dominated rocky systems. Predation impact was a clear function of refuge availability and fish predators. *D. sargus* has been previously described as the main sea urchin consumer inside marine reserves (Guidetti, 2004; Sala, 1997); our results confirm that it may be a key agent of top-down control in Mediterranean macroalgal habitats even outside these protected areas. Unfortunately it also underscores the low functional redundancy these systems have, since no species appears to substitute *D. sargus* when its numbers decline. *D. sargus* may be one of few extant species in the Mediterranean capable of breaking the urchin carapace after they reach adulthood although several other fish predators can be important secondary consumers (Guidetti, 2004; Sala, 1997). This coupling of number and function validates the effectiveness of fishing restrictions in ensuring high predation in areas that require conservation. It is important however, to account for the structural complexity of these sites since, as this study and others indicate, refuge availability can critically mediate predatory-prey interactions in rocky macroalgal systems (Clemente et al., 2012; Hereu et al., 2005) and in seagrass meadows.

Our results show that fish interactions with their sea urchin prey are still prevalent across the Mediterranean coast despite centuries of human use and are highly dependent on site specificities and habitat characteristics. Given that the release from predatory functions can have cascading effects (e.g. creation of urchin barrens in rocky bottoms), it is critical to maintain and protect these higher trophic functions, particularly where they continue to be important. Identifying these hotspots of functional predation may be an essential first step when establishing new marine reserves to conserve macrophyte communities in temperate seas vulnerable to overgrazing events. This is particularly important given that meso-predators do not appear able to replace fish, even when their numbers decline, as the principal predator in coastal habitats. Our results indicate that, despite a long history of fishing, conserving functional predation may still be achievable outside marine reserves and is critical to ensure the resilience of ecosystems where top down processes still control the structuring of ecological communities.
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Acknowledgements

Authors are very grateful to J. Pagès and G. Roca for interesting discussions, A. Martínez-Ricart and L. Sastre for field support and V. Mayoral for illustration assistance. Symbols in Fig. 1 are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). This research was funded by the Spanish Ministry of Science and Innovation (projects CTM2010-22273-C02-01-02 and CTM2013-48027-C03-R) and supported J. B. (scholarship BES-2011-043630) and CSIC-201330E062 supported R. A.’s visitorship.
Table 1. Three-way ANOVAs for total and specific predation impact. p-values correspond to F-test results. d.f. = degrees of freedom.

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<td><strong>Total Predation</strong></td>
<td>Site</td>
<td>7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Habitat</td>
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<td>&lt; 0.001</td>
</tr>
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<td>Season</td>
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</tr>
<tr>
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<td>Site x Season</td>
<td>7</td>
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</tr>
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<tr>
<td></td>
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<td>Habitat</td>
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<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>1</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Site x Habitat</td>
<td>7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Site x Season</td>
<td>7</td>
<td>0.005</td>
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<td></td>
<td>Habitat x Season</td>
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</tr>
<tr>
<td></td>
<td>Site x Habitat x Season</td>
<td>7</td>
<td>0.494</td>
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<td>0.033</td>
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<td>Season</td>
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<td>Site x Habitat</td>
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<td>0.092</td>
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<tr>
<td></td>
<td>Site x Season</td>
<td>7</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Habitat x Season</td>
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<td>0.601</td>
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<tr>
<td></td>
<td>Site x Habitat x Season</td>
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<td>0.003</td>
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</table>
Table 2. ANOVA analyses for predator habitat use U (see text) and the canopy height. p-values correspond to those provided by an F-test. d.f., degrees of freedom.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source of variation</th>
<th>d.f.</th>
<th>p-value</th>
</tr>
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<tr>
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</tr>
<tr>
<td></td>
<td>Habitat</td>
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<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Season</td>
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<td>Site x Habitat</td>
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<td>&lt; 0.001</td>
</tr>
<tr>
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<td>Site x Season</td>
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<td>0.005</td>
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<td>Habitat x Season</td>
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<td>0.493</td>
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<td>Canopy</td>
<td>Site</td>
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<td></td>
<td>Habitat</td>
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<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Season</td>
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<td>&lt; 0.001</td>
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<tr>
<td></td>
<td>Site x Habitat</td>
<td>7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Site x Season</td>
<td>7</td>
<td>&lt; 0.001</td>
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<tr>
<td></td>
<td>Habitat x Season</td>
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<td>&lt; 0.001</td>
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<tr>
<td></td>
<td>Site x Habitat x Season</td>
<td>6</td>
<td>&lt; 0.001</td>
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</tbody>
</table>
Table 3. Model fitting using GLM for fish predator impact (FPI) inside rocky habitats and *Posidonia oceanica* meadows as a response variable dependent on predator species use of habitat (U) and specific structural parameters of each habitat.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Response variable</th>
<th>Full model</th>
<th>Selected model</th>
<th>Effects</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rocky habitat</td>
<td>Predation Fish</td>
<td>~Canopy + Shelters + <em>Diplodus</em> spp + <em>S. aurata</em> + <em>L. merula</em></td>
<td>~Shelters + <em>Diplodus</em> spp</td>
<td>Shelters</td>
<td>1</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Predation Benthic</td>
<td>Insufficient data</td>
<td></td>
<td><em>Diplodus</em> spp</td>
<td>1</td>
<td>0.008</td>
</tr>
<tr>
<td>Posidonia</td>
<td>Predation Fish</td>
<td>~Canopy + Matte + <em>Diplodus</em> spp + <em>S. aurata</em> + <em>L. merula</em></td>
<td>~Matte + <em>Diplodus</em> spp</td>
<td>Matte</td>
<td>1</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Predation Benthic</td>
<td>Insufficient data</td>
<td></td>
<td><em>Diplodus</em> spp</td>
<td>1</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Figure 1. Principal interactions in Mediterranean macrophyte communities. The sea urchin *Paracentrotus lividus* lives in both seagrass meadows of *Posidonia oceanica* and macroalgal dominated rocky habitats in the Mediterranean. Letters represent trophic interactions; herbivory (a) and (b), and predation (c), (d) and (e). Black arrows show the predator-prey interactions studied in the present work.
Figure 2. Map of the Mediterranean Sea showing the study locations within the Catalan Coast.

Llançà (A), Portlligat (B), Montgó (C), Medes Islands (D), Giverola (E), Fenals (F), Hospitalet (G) and Ametlla de Mar (H).
Figure 3. Mean predation impact on *P. lividus* (%) + SE in a) rocky habitats in summer, b) *P. oceanica* meadows in summer, c) rocky habitats in winter and d) *P. oceanica* meadows in winter. Filled bars represent fish predator impact (FPI) and clear bars represent benthic predator impact (BPI). Total absence of predation (0%) in sites F and H in b) and a) respectively.
Figure 4. Percentage of urchins eaten (a), index of habitat use by sea urchin fish predator guild (b) and length of the canopy height (c) in both habitats. Mean values of two seasons ± SE, n=64. Asterisk indicates significant differences based on ANOVA test.