

Indirect interactions in seagrasses: fish herbivores increase predation risk to sea urchins by modifying plant traits

Jordi F. Pagès^{*,1}, Simone Farina¹, Alessandro Gera¹, Rohan Arthur², Javier Romero³ and Teresa Alcoverro¹

¹Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Accés a la cala Sant Francesc, 14, 17300, Blanes, Catalonia, Spain; ²Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, 570 002, Mysore, Karnataka, India; and ³Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal, 645, 08028, Barcelona, Catalonia, Spain

Summary

1. The dominant paradigm of top-down control of ecological communities through direct consumption pathways is giving way to a more nuanced understanding of trophic interactions with the recognition that subtler indirect effects can often play an important role in structuring communities. Direct and indirect trophic and non-trophic processes could well be acting simultaneously within the same food web, and their overall effects may even interact with each other.

2. We studied indirect interactions in a relatively simple trophic system comprising a single producer, two herbivores and a guild of predators. In particular, we assessed whether (i) the principal herbivore fish, *Sarpa salpa*, is capable of modifying a seagrass trait, canopy height, by grazing and (ii) whether grazing-induced habitat alteration can trigger an environment-mediated modification of the interaction between herbivorous sea urchins *Paracentrotus lividus* and their predators.

3. We tested these hypotheses with field experiments including fish herbivore-exclusion experiments (to examine the ability of *S. salpa* to modify seagrass habitats) and predation experiments using tethered sea urchins in a meadow with varying canopy heights (to test whether habitat modification can mediate urchin predation risk).

4. The effect of *S. salpa* herbivory was highly significant. Canopy height in herbivore-excluded plots was more than 3.5 times higher than in uncaged control plots. In addition, adult sea urchin predation risk in the most highly grazed plots was 4–5 times higher than plots with higher canopy heights. In contrast, predation risk on juvenile urchins was not influenced by canopy height.

5. Our results show that predation pressure on a key herbivore can be modified both by the environmental context within which it finds itself and by the actions of another herbivore that modifies the plant traits that create this environmental context. These act as two discrete pathways that interact in potentially nonlinear ways, mediating top-down control in these ecosystems. Herbivores, particularly when acting as ecosystem engineers, may have the potential to mediate and increase predation risk, as they substantially modify habitat structure, with consequences for refuge availability, among others. Assessing these indirect interactions is not just important to understand the functioning of the system itself but may have important management and conservation consequences.

Key-words: ecosystem engineering, environment-mediated, interaction modifications, *Paracentrotus lividus*, plant–herbivore interactions, *Posidonia oceanica*, *Sarpa salpa*, trait-mediated

*Corresponding author: E-mail: jpages@ceab.csic.es

Introduction

Ecological communities are structured by a complex interaction of their trophic elements, and understanding the causal mechanisms through which they operate has been a central issue in ecology (Paine 1980; Polis 1999). Quantifying the strength of these interactions is critical to understanding how natural communities are organized, and how they may respond to human interference (Bascompte, Melián & Sala 2005). Interaction networks have been widely used to decipher the structuring of ecological communities (Polis & Winemiller 1995; Ohgushi 2008). Typically, these networks are built on direct trophic interactions (feeding), with the assumption that they are the major determinants of interaction strength. Increasingly, however, there is a growing recognition that indirect trophic interactions (e.g. trophic cascades) and other trophic and non-trophic interactions, such as ecosystem engineering, may also have fundamental community-wide implications (e.g. Pearson 2010 and references therein). Direct and indirect trophic and non-trophic processes could well be acting simultaneously within the same food web, and their overall effects may even be synergistic (Jones, Lawton & Shachak 1997; Golubski & Abrams 2011).

Indirect interactions are powerful forces shaping ecological systems (Abrams *et al.* 1996). They arise when the effect of one species on another requires the presence of a third (Wootton 1994). The realization that these interactions could have community-wide influences arose with the publication of the seminal paper by Hairston, Smith & Slobodkin (1960), who proposed that indirect trophic interactions could drive trophic cascades resulting in ecosystems that are relatively dominated by primary producers ('the green world hypothesis', as it was later called). Experimental evidence on trophic cascades came early from the rocky intertidal with studies on keystone predation by Paine (1966) and further evidence provided by Estes & Palmisano (1974). From then on, top-down control, trophic cascades, and particularly, the study of tri-trophic food chains (TFCs, e.g. Bascompte, Melián & Sala 2005) with a focus on predator–consumer–producer interactions have dominated much of the research in community ecology. These have been termed 'interaction chains', and they arise by linking two (or more) direct effects together via a species involved in both interactions (Wootton 1993, 2002). Given that linked direct effects often imply that densities of the intermediary species change, these interactions have also been described as 'density-mediated indirect interactions (DMIIs)' (Abrams *et al.* 1996).

While interaction chains are now relatively well studied, our understanding of other indirect interactions is much patchier, even though they may be as important in their ecosystem consequences. It has been shown, for instance, that when a species modifies the interaction between two other species ('interaction modification'; Wootton 1993), it results in sometimes significant community-wide

consequences (e.g. Kauffman, Brodie & Jules 2010). Species in an ecosystem can modify an interaction in at least two separate pathways. For one, a species can change the environmental context in which two other species interact, thereby modifying the interaction between them. These interactions have been labelled 'environment-mediated interaction modifications' (Wootton 1993) and generally involve the participation of a foundation species (e.g. macrophytes reducing predation pressure on prey by providing hiding places; Crowder & Cooper 1982).

The second way, by which interaction modification may arise, occurs when one species changes the traits (i.e. a particular property of individual organisms) of another species, and these altered traits modify how the second species interacts with the third (Wootton 1993). These so-called trait-mediated indirect interactions (TMIIs) (Abrams *et al.* 1996) may be behavioural (in which there has been much interest in recent years, see Werner & Peacor 2003 for a review), morphological, chemical, etc. Non-behavioural TMIIs have been recently reassessed, particularly for plant communities (Ohgushi 2005; Pringle *et al.* 2007; Caccia, Chaneton & Kitzberger 2009; Pearson 2010). Ohgushi (2008) argues that it is critical to account for the impact of these lesser-explored interactions in analysing interaction webs because they are likely more common and important in a wide variety of ecosystems than earlier considered, where they influence community structure and, ultimately, species diversity. Among them, non-lethal herbivory plays a central role in many indirect interactions (Ohgushi 2005; Huntzinger, Karban & Cushman 2008; Pringle 2008). In effect, herbivores can induce a great variety of responses on plants (Karbon & Baldwin 1997), some of which alter their traits resulting in TMIIs.

Non-lethal herbivory is more frequent in terrestrial systems than in aquatic ones. This is because terrestrial herbivores usually feed on a part of the plant, whereas marine herbivores tend to consume the producer as a whole (e.g. zooplankton feeding on phytoplankton) or almost in entirety (e.g. sea urchins feeding on algae). Marine herbivores remove 51% of primary production on average, three times higher than their terrestrial counterparts (Cyr & Pace 1993). Aquatic vascular plants represent an exception to this pattern, with removal rates similar to that of terrestrial vegetation (Cyr & Pace 1993), making TMIIs much more likely in these systems. It has recently been shown that seagrasses can endure substantial herbivory pressure without lethal impacts (Prado *et al.* 2007; Planes *et al.* 2011). This, together with the fact that they are relatively simple systems (with few trophic links), makes seagrass meadows an excellent model system to explore indirect interactions. Evolutionarily derived from terrestrial plants, these species have several morphological adaptations (meristemic growth, protected rhizomes, mechanical defences, etc. Heck & Valentine 2006), as well as physiological responses (compensatory growth, chemical defences; Verges *et al.* 2008; Planes *et al.* 2011) to deal

with the impacts of herbivory. Given the increasing recognition of the direct impact herbivory has to the functioning of these ecosystems (Heck & Valentine 2006), it is vital to understand whether herbivory can additionally influence other trophic processes through indirect pathways. We examined how changes in seagrass structure by a herbivorous fish influenced predation risk of other species. We tested this main question by attempting to separately assess the interactions present in the system: (i) Are fish herbivores capable of changing canopy structure, a seagrass trait? And if so, (ii) does this habitat structure modification affect another herbivore, a sea urchin, by triggering a change in its size-specific predation risk?

Materials and methods

STUDY SYSTEM AND EXPERIMENTAL DESIGN

Posidonia oceanica (L.) Delile, an endemic seagrass species in the Mediterranean sea, forms extensive monospecific meadows along the coasts of the whole basin (Procaccini *et al.* 2001). It is a habitat-forming seagrass that provides shelter, food and substrate to a great number and variety of species (Mazzella, Scipione & Buia 1989; Francour 1997; Martínez-Crego 2008). It has two principal herbivores, the fish *Sarpa salpa* (L.) and the sea urchin *Paracentrotus lividus* (Lam.) (Prado *et al.* 2007). Both together have been reported to remove 50% of the annual plant primary production on average (Prado *et al.* 2007), despite most of this grazing is exerted by *S. salpa*, which is even capable of causing overgrazed patches in certain meadows (Tomas, Turon & Romero 2005). Trophic interactions in sea urchins, as in many age- or size-structured populations, change considerably with the stage of their life cycle as their vulnerability to particular predators varies (Sala 1997; Hereu *et al.* 2005). The principal predator of juvenile *P. lividus* (<1 cm test diameter without spines, TD) is the labrid fish *Coris julis* while other species are of secondary importance (in order of relevance: *Diplodus sargus*, *Thalassoma pavo*, *Labrus merula*, *Diplodus vulgaris*; Hereu *et al.* 2005). For adult sea urchins, the spard *D. sargus* is by far the principal predator (Sala 1997), although *Sparus aurata* has also been observed frequently preying on them (personal observations).

In this study, we tested the existence of interaction modifications in seagrass meadows. We first assessed whether the herbivore *S. salpa* can modify seagrass traits through herbivory (trait-mediated interaction modification), which in turn, can modify the environment in which a predator–prey interaction takes place (between the sea urchins and their predators). To assess these interactions, we conducted two different experiments. The first was a herbivore-exclusion experiment to test the capacity of *S. salpa* to modify a morphological plant trait. The second one was designed to test the relationship between size-specific predation risk and plant traits. These experiments were conducted separately for different urchin size classes to test whether indirect effects detected were modulated by individual size.

All field experiments were carried out in the Medes Islands marine protected area in the northern part of the Catalan coast (42° 2' N, 3° 13' E), where fishing has been prohibited since 1983 and fish abundance is very high (García-Rubies & Zabala 1990; Hereu *et al.* 2005). The region has a large continuous *P. oceanica* meadow extending from 3 to 14 m depth. Our experiments were conducted in summer, from August to September 2010, after a grazing peak that takes place in July–August (Prado *et al.* 2007) and corresponding to a seasonal peak in predatory fish activity (García-Rubies 1997).

EXPERIMENT 1: HABITAT STRUCTURE MODIFICATION

To test the first hypothesis ('herbivorous fishes are able to modify plant traits and habitat structure'), we established herbivory enclosures by fencing off areas of the seagrass meadow and compared these to the surrounding, exposed habitat. We deployed three enclosures in the meadow (*c.* 5 m depth) a month before the beginning of the summer grazing peak (i.e. in May 2010). Each cage consisted of a plastic mesh (cage size 150 × 150 × 100 cm, length × width × height) attached to four metal stakes, with a transparent nylon net on the top to protect the leaves and reducing light as little as possible. Mesh openings were sufficiently large (2 × 2 cm) to allow free movement of small fish and invertebrate mesofauna, but small enough to prevent the entrance of *S. salpa* fish. Cages were maintained for 2 months, during which natural leaf elongation was possible (Alcoverro, Duarte & Romero 1995), without suffering any losses to herbivory. The areas outside the cages were subject to intense *S. salpa* grazing. After 2 months, we compared habitat structure inside and outside the cages by measuring canopy height in the three experimental plots and three additional plots selected at random in adjacent areas of the meadow. To measure canopy height, we grabbed a large handful of plants, extended the leaves to their maximum height, and ignoring the tallest 20% of leaves, measured from the sediment to the height of the top of the remaining 4/5 of this bundle (80% of the leaves) (Duarte *et al.* 2001).

EXPERIMENT 2: SIZE-SPECIFIC PREDATION RISK

To test the relationship between the size-specific predation risk and habitat structure, we took advantage of the heterogeneous canopy height caused by the foraging behaviour of the herbivore fish *S. salpa*, which is known to produce small-scale variability in meadow canopy height (i.e. on the order of tens of metres, see Tomas, Turon & Romero 2005). We used two complementary approaches, one categorical and one continuous. For the first approach, three different treatments (i.e. canopy height, conditions of sea urchins' exposure) were selected: 'mowed' (canopy height = 7 ± 1 cm), 'short' (canopy height = 26 ± 0.2 cm) and 'long' (canopy height = 47 ± 3 cm). Shoot density differed slightly between treatments (*P*-value < 0.05, Table 1). Shoot density was 490 ± 36, 589 ± 58 and 353 ± 10 shoots m⁻² in mowed, short and long treatments, respectively. A total of nine plots per category were chosen for each treatment and assigned randomly to three different sea urchin size classes (juveniles, ≤ 1 cm TD, young adults, 3–5 cm TD, and adults, > 5 cm TD), resulting in a total of three replicate plots for treatment and urchin size. Each replicate (plot) was 150 × 150 cm in size, marked with metal stakes and with a plastic mesh surrounding its perimeter (20 cm height, 2 cm mesh openings). This was carried out to exclude potential benthic predators, as our objective was to assess only visual predation (i.e. by predatory fish). Although the fences could have drawn attention of visual predators to the urchins, potentially leading to artificial predation rates, predation rates on this experiment were very similar (for a given canopy height) to those in the gradient-based continuous approach (without fences, see below and results). Plots were deployed in areas where rhizomes were covered with sand (to avoid the potential shelter, rhizomes can offer to urchins, which would obscure our results; Farina *et al.* 2009). All plots were located at the same depth (*c.* 5 m), within tens of metres of each other, and within an area < 20 × 20 m. We can therefore safely assume that every plot was exposed to the same predator fish community.

Sea urchins were collected from rocky substrates using SCUBA. For each experimental plot, 10 individuals of the same size class were pierced through the test with a hypodermic needle, threaded

Table 1. Summary of the different analyses performed. *P*-values correspond to those provided by an *F*-test

Variable	Effects	d.f.	% variance	<i>P</i> -value
ANOVAS				
Canopy height	Treatment	2	97.01	0.0000
	Error	6	2.99	
Shoot density	Treatment	2	74.54	0.0165
	Error	6	25.46	
ANCOVAS				
Percentage of juveniles preyed	Shoots	1	–	n.s.
	Treatment	2	–	n.s.
	Shoots × Treatment	2	–	n.s.
	Error	3	100	
Percentage of young adults preyed	Shoots	1	–	n.s.
	Treatment	2	93.6	0.0078
	Shoots × Treatment	2	–	n.s.
	Error	3	6.4	
Percentage of adults preyed	Shoots	1	n.p.	n.s.
	Treatment	2	n.p.	0.0061
	Shoots × Treatment	2	n.p.	n.s.
	Error	3	n.p.	

d.f., degrees of freedom; n.p., nonparametric; n.s., non-significant.

with monofilament line (nylon, 30 cm length) and tied to metal pegs. Each tethered urchin was uniquely identified with a number and placed randomly inside the plot, after verifying that the plot was free of bottom predators. While it is true that this is a rather invasive method, given that it implies the perforation of the test, most studies acknowledge very few detrimental effects (e.g. McClanahan & Muthiga 1989; Aronson & Heck 1995; Sala & Zabala 1996). Indeed, tethering has been effectively applied to estimate predation rates on sea urchins in coral reefs, rocky reefs and seagrass habitats (McClanahan & Muthiga 1989; Sala & Zabala 1996; Shears & Babcock 2002; Farina *et al.* 2009). We attributed sea urchin mortality to two sources: (i) predation by fish (characterized by missing sea urchin tests with an intact nylon loop or broken tests with firmly attached spines) and (ii) mortality attributable to manipulation-induced stress (intact test with loosely attached spines and faded test colour) (Bonaviri *et al.* 2009). Mortality owing to the tethering manipulation itself was 2.5% (similar to rates found in other studies, e.g. Sala & Zabala 1996). These individuals were removed from any further analysis. Urchins were monitored everyday to correctly attribute sea urchin mortality to one of the sources above.

In addition to the 27 treatment plots inside the meadow (three treatments × three urchin sizes × three replicates), three more plots (one for each size class) were established on a bare sand patch as a time control, with the urchins totally exposed, to determine the endpoint of the experiment. Complete urchin predation in the sand patch took place within 5 days, after which pegs were removed and the remaining sea urchins counted in all plots.

For the gradient-based, continuous approach, 20 tethered urchins of each size class (namely juveniles, young adults and adults) were distributed randomly (as independent replicates) on a large area inside the meadow (outside the fences, *c.* 250 m²) with the aim of capturing the heterogeneity of canopy heights in which urchins might shelter. These urchins were visited daily to assess their survival time (in days). The total number of urchins per size-class was *n* = 30, because, in addition to these 20 urchins, one urchin from each experimental and sand plot was also used in the analyses.

STATISTICAL ANALYSES

All calculations were performed using the open-source statistical software R (R Development Core Team 2010).

For both categorical experiments, we treated each plot as the experimental unit with three replicates each. The variables canopy height and shoot density were evaluated with a one-way ANOVA with 'canopy height' as a fixed factor with three levels (mowed, short, long). The variables per cent of juveniles preyed on, per cent of young adults preyed on and per cent of adults preyed on were evaluated with a one-way ANCOVA with 'canopy height' as a fixed factor with three levels (mowed, short, long) and including shoot density as a covariate (as it differed slightly between treatments and may also affect sea urchin visibility and thus predation risk). Before analysis, data were tested for normality and homoscedasticity using the Shapiro–Wilk's and Bartlett's test respectively. The percentage of adults preyed upon was analysed with a nonparametric equivalent of ANCOVA (Quade 1967), as this variable was neither normal nor homoscedastic. All other variables met the normality and homoscedasticity assumptions necessary for the ANOVA and ANCOVA. Whenever an ANOVA or ANCOVA was significant, a multiple range contrast test was applied (Tukey HSD) to determine treatment-specific differences.

For the continuous approach, data exploration revealed a non-linear relationship between sea urchin survival and canopy height. To describe this relationship, we used a generalized additive model (GAM) (Hastie & Tibshirani 1990) with a log link function (using the Poisson distribution) to evaluate how urchin survival time (in days) varied in relation to the explanatory variable canopy height. We used the LOESS smoother from the GAM package in R (R Development Core Team 2010; Hastie 2011), which applies a weighted linear regression within a moving window of a specified size (we selected a span containing the 80% of data, as it was considered the optimal choice after residuals inspection; see Zuur *et al.* (2009)).

Results

EXPERIMENT 1: HABITAT STRUCTURE MODIFICATION

Canopy height was more than 3.5 times higher inside herbivore exclusion cages than outside (*P*-value < 0.01, Table 1). The average canopy height inside enclosures was 96 ± 4 cm, while outside, in the presence of herbivory, canopy height was 24 ± 11 cm on average. Seagrass shoots outside the enclosures also showed clear signs of intense fish herbivory (see Fig. 1).

EXPERIMENT 2: SIZE-SPECIFIC PREDATION RISK

The percentage of juveniles preyed upon was not significantly different between canopy treatments (Fig. 2a, Table 1). In contrast, a strong effect of the factor canopy height was detected both for young and adult sea urchins predation (Table 1). In both cases, predation in the lowest canopy treatment (i.e. mowed) was significantly higher than in the short and long leaves treatments (confirmed by Tukey HSD, see Fig. 2b,c). Specifically, the percentage of predation on young and adult urchins was 4–5 times higher in mowed treatments than in long-leaved ones. The effect of the covariate shoot density was not significant for any of the size classes (*P*-values > 0.3 in all cases).



Fig. 1. Photograph showing the contrast between a heavily grazed area (foreground; canopy height around 20 cm) and a caged plot just after cage removal (background), with a canopy height more than 3.5 times longer than uncaged areas.

The continuous approach confirmed that juvenile survival was not influenced by canopy height: both linear and additive models failed at describing this relationship (Fig. 3a). In contrast, the survival of young adults and adults showed a nonlinear relationship with canopy height that was successfully described by the GAM (young adults: $\chi^2 = 14.582$, P -value = 0.0003; adults: $\chi^2 = 17.806$, P -value = 5.10^{-05}). For both young and adult sea urchins, low survival times were observed in short-canopy heights. Survival times increased with increasing canopy heights (gradually for young and abruptly for adults) until a plateau was reached for canopies above *c.* 25 cm (Fig. 3b,c). Adult survival time appears to decrease again after the plateau, although confidence intervals become wider and edge effects may occur at the margins of data sets (Zuur *et al.* 2009).

Discussion

Our results show that even in the relatively simple assemblage of the *P. oceanica* meadow, complex interactions exist that structure the community through at least two distinct indirect pathways. Intensive grazing by the herbivorous fish (*S. salpa*) modifies an important phenotypic trait (canopy height) of the foundational species and trophic resource (*P. oceanica*) and in doing so reduces available refugia for the sea urchin (*P. lividus*) against its dominant predators (Fig. 4). Uniquely, we show that predation pressure on a key herbivore can be modified both by the environmental context within which it finds itself and by the actions of another herbivore that modifies the plant traits that create this environmental context. These act as two discrete pathways that interact in potentially nonlinear ways, mediating top-down control in these ecosystems. These interactions do not affect smaller size classes of sea urchins, as they are still able to find sufficient refuge in grazed-seagrass meadows. Taken together, our findings

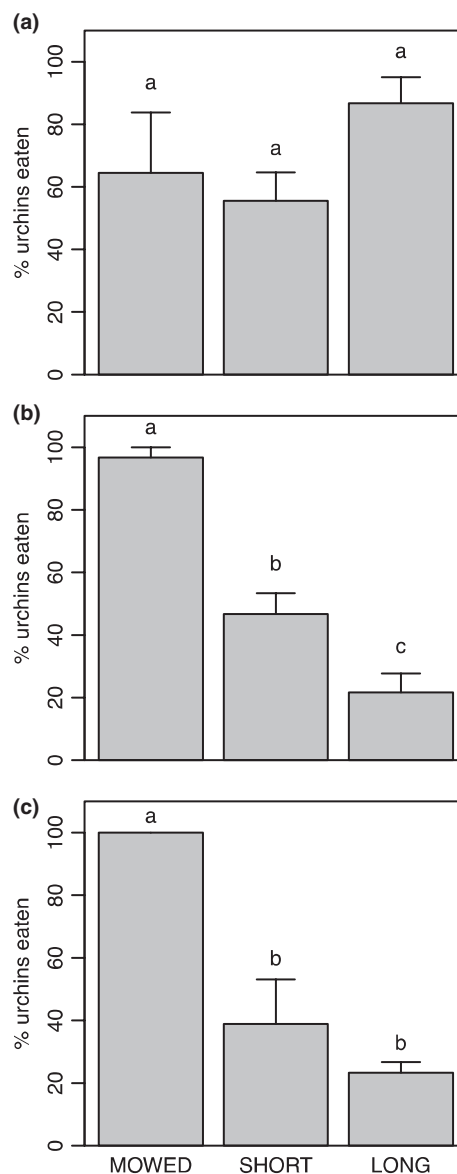


Fig. 2. Percentage of (a) juveniles, (b) young adults or (c) adults preyed in each of the canopy height treatments (mean \pm SE, $n = 3$). Bars labelled with the same lower case letter do not differ significantly according to Tukey HSD *post hoc* test.

suggest that the prevailing tenet of top-down control that has dominated ecological theory after Hairston, Smith & Slobodkin (1960) may function in complex and often much more nuanced ways.

Clearly distinguishing interaction pathways is fundamental in modelling ecological systems (Werner & Peacor 2003) as each pathway may imply very different consequences for overall system dynamics depending on the specific mechanism of action (e.g. interaction modification or interaction chain, trait- or environment-mediated). While the direct trophic pathways in our study are relatively simple (predation and herbivory), the mechanisms involved in the indirect interactions are complex: a species causes a phenotypic, trait-mediating change on a second species,

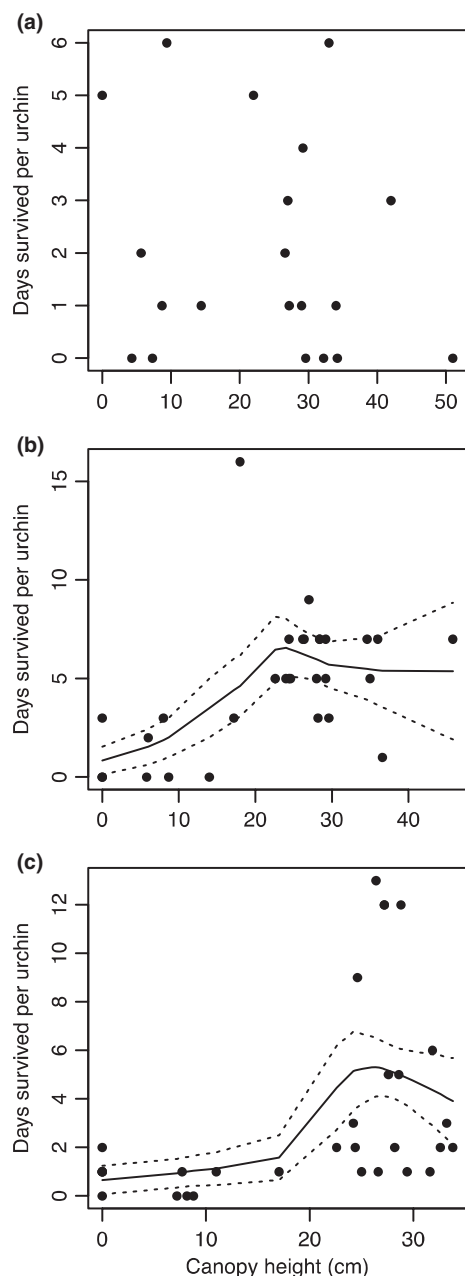


Fig. 3. Scatter plots showing the relationship between (a) juveniles, (b) young adults or (c) adults survival time (in days) and their surrounding canopy height ($n = 30$). Solid lines in (b) and (c) correspond to the generalized additive model fitted values, and dotted lines correspond to confidence intervals.

which in turn profoundly influences the environmental context of the predator–prey interaction occurring between two other species. Unusually, the indirect interactions we document are initiated by the principal herbivore in the system, and as such, are a unique reminder that species other than predators may play a greater-than-acknowledged role in shaping and modifying the system. Indeed, this type of indirect interaction is probably much more common than is recognized, particularly when initiators act as ecosystem engineers. For instance, ground squirrels,

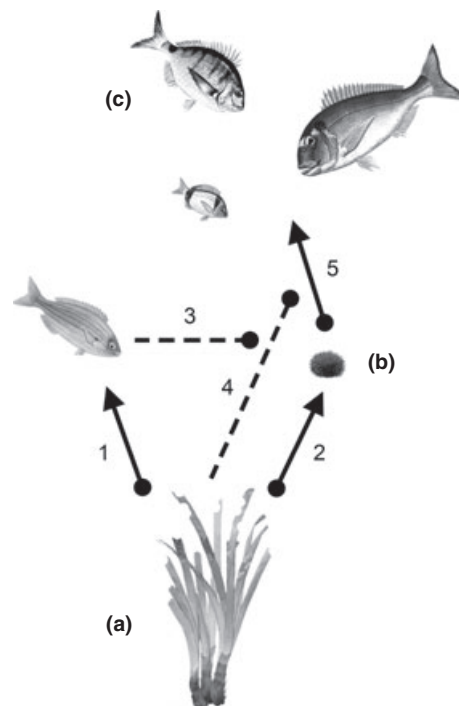


Fig. 4. Interaction web including (a) the producer *Posidonia oceanica*, (b) the herbivores *Sarpa salpa* and *Paracentrotus lividus* and (c) a guild of predators: *Sparus aurata*, *Diplodus sargus* and *Diplodus vulgaris*. Each interaction is numbered: (1) and (2) represent herbivory (direct trophic), (3) corresponds to the interaction modification mediated by a trait change in the plant that modifies the environment-mediated interaction modification (4) of the predator–prey interaction between sea urchins and their predators (5).

by constructing burrows and galleries, may reduce predation risk on other mammals (Waterman & Roth 2007). In a context much more resonant with ours, Martin, Wright & Crowder (1989) indicated that complex higher order effects could arise in a marine system when blue crabs and a fish were stocked together through the effects of crabs on the abundance of an alga, which provides refuge for the prey of the fish. As with our study, this involves two interaction modifications, one trait- and the other environment-mediated. The role of ecosystem engineers is central to these examples, each influencing predation risk of other species in the system by modifying habitat structure.

This study supports a growing literature that, in recent years, has begun to re-evaluate the importance of habitat-modifying herbivores, in initiating powerful indirect effects (Gomez & Gonzalez-Megias 2002; Lill & Marquis 2003; Ohgushi 2005; Bailey & Whitham 2006; Pringle *et al.* 2007; Pringle 2008). On the one hand, herbivores have long been known to play a significant role in reducing habitat complexity (e.g. Martin, Wright & Crowder 1989). At the same time, modifications in plant morphological traits can cause considerable functional changes in canopy characteristics, with cascading implications for the rest of the system (Huntzinger, Karban & Cushman 2008), including strong effects on predator–prey interactions (Crowder & Cooper 1982; Swisher, Soluk & Wahl 1998; Mattila *et al.*

2008; Farina *et al.* 2009). It is therefore natural to assume that any effects of consumers on plant density or structure could influence their vulnerability to predators (Werner & Peacor 2003) even though few earlier studies have made these links explicit. In this study, we show that a herbivore fish can affect the predation risk of other herbivores (urchins) by modifying a plant trait that affects the environmental context in which the predator–prey interactions between urchins and their predators take place. While we cannot be certain of how important these interactions are in non-experimental situations, the effects of fish herbivory could potentially be as dramatic as a classical trophic cascade; long-term observations at our study site indicate that, without the structural complexity required for shelter, sea urchin populations at this site are headed for a potential collapse under predator pressure (Romero, Pérez & Alcoverro *in press*).

Interestingly, our study shows that interaction modifications may be subject to strong nonlinear responses as well, with young and adult sea urchin survival plateauing beyond seagrass canopy heights of around 25 cm (see Fig 3b,c). The functional form of these ‘higher order interactions’ (requiring higher-order, nonlinear terms to model them in population equations, see Wootton 2002) may take a variety of forms likely highly dependent on context-specific natural history. For instance, Wootton (1992) described a quadratic relationship in the way barnacles modify interactions between limpets and bird predators, reducing predation pressure at lower densities but increasing it as barnacle densities increased. In the meadows we studied, heavily grazed seagrass patches expose urchins to high predation risk, where grazing is less intense, patches have a higher canopy with more prey refugia. Beyond a certain canopy height (*c.* 25 cm in the present study), the increased length does not contribute further to survival as most young and adult sea urchins are probably already well sheltered from predation. This threshold value may be difficult to generalize, because it may depend on a suite of other structural attributes of the meadow (*i.e.* shoot density, presence of mat refuges; Heck & Orth 2006; Farina *et al.* 2009). It is theoretically possible that high levels of sea urchin grazing could itself influence urchin predation risk, further complicating this interaction. However, the incidence of sea urchin herbivory is, in general, more limited compared to the pressure exerted by herbivorous fishes in *P. oceanica* meadows (Prado *et al.* 2007). More likely (although unexplored in our study) are behaviourally modified trophic interactions caused by changing structure, and indeed, *P. lividus* has been observed to modify its behaviour in the presence of predators (Hereu 2006). While these so-called ‘landscapes of fear’ have typically been described as being driven by predator presence (see Schmitz, Krivan & Ovadia 2004 for a review), our study suggests they could just as well be mediated by a structure-modifying herbivore. If present, these behavioural modifications could additionally contribute to the observed nonlinearity in functional responses.

Recent decades have seen an increasing emphasis on the role of top predators as controlling agents of ecosystems, and habitat management has focused almost exclusively on conserving these higher trophic functions, typically by managing the numbers of top predators inside protected areas or by enforcing hunting/fishing restrictions (Pinnegar *et al.* 2000; Sala & Sugihara 2005). As our study shows however, if we only pay attention to the most conspicuous interactions, that is interaction chains (linkages of direct trophic pathways), we may encounter unexpected outcomes in the long term, such as an undesirable reduction or even local extinction of certain species. This is especially true when the predators (in our case predatory fishes) and the initiators of indirect interactions (in this case a herbivore fish) are equally affected by conservation measures, as they can interact with a positive feedback. In addition, when one of the species involved is an ecosystem engineer, increases in its numbers can have broad system-level ramifications (Jones, Lawton & Shachak 1994). The dramatic decline and near extinction of sea urchin populations over the last decades in seagrass meadows in Medes Islands MPA where we conducted our field work (Romero, Pérez & Alcoverro, *in press*) is most likely a result of the kind of complex interactions we describe in this study and should serve as a powerful example of the perils of managing complex ecosystems against a single metric of success.

In conclusion, our study shows that intense grazing by a fish herbivore acting as an ecosystem engineer can have important implications for the entire community. These fish, by mediating an environment modification (through a change in the foundation species of the system), indirectly increase size-dependent predation risk on a potentially competing herbivore. Herbivores have to be recognized as potentially strong interactors capable not merely of initiating interaction cascades (as shown by Pringle *et al.* 2007) but also mediating behavioural cascades as a consequence of their ability to modify the habitat while acting as ecosystem engineers. At the same time, ecosystem-engineering species have to be recognized not just for the potential direct effects that they cause on the system, but also for the broad system-level ramifications of their actions, such as increases in predation to other species using the habitat. Bearing in mind that predation risk may not merely imply density effects to these organisms but also behavioural ones, the potential of this interaction to cause large-scale community-wide consequences is significant. Understanding how these complex interactions play themselves out in natural ecosystems may be vital in designing holistic and sustainable management plans for these ecosystems.

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