Matrix composition and patch edges influence plant–herbivore interactions in marine landscapes

Jordi F. Pagès*,[1], Alessandro Gera[1], Javier Romero[2] and Teresa Alcoverro[1,3]

[1]*Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Accés a la cala Sant Francesc, 14. 17300 Blanes, Catalonia, Spain;* [2]*Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona. Av. Diagonal, 643. 08028 Barcelona, Catalonia, Spain; and* [3]*Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, 570 002 Mysore, Karnataka, India*

Summary

1. The functioning of ecosystems can be strongly driven by landscape attributes. Despite its importance, however, our understanding of how landscape influences ecosystem function derives mostly from species richness and abundance patterns, with few studies assessing how these relate to actual functional rates.

2. We examined the influence of landscape attributes on the rates of herbivory in seagrass meadows, where herbivory has been identified as a key process structuring these relatively simple systems. The study was conducted in three representative *Posidonia oceanica* meadows. The principal herbivores in these meadows are the fish *Sarpa salpa* and the sea urchin *Paracentrotus lividus*, and we hypothesized that differences in their interaction with landscape attributes would significantly influence herbivory rates.

3. We measured herbivore abundance, herbivory rates, primary production and plant quality (C:N) in seagrass patches embedded either in rock or in sand (matrix attribute), in patches either near or far from a rocky reef (distance attribute) and at the edges and interior of meadows.

4. Our results show that matrix and meadow edges significantly affected the actual levels of herbivory. Herbivory rates were higher in seagrass patches embedded in a rocky matrix compared to those on sand, and herbivory at the centre of seagrass meadows was higher than at the edges. In contrast, patch distance to rocky reefs did not affect herbivory. Neither herbivore abundance nor food quality explained the patterns across different landscape attributes. This suggests that variation in herbivory across the landscape may be related much more to behavioural differences between species in their evaluation of risk, movement and food preference in relation to the landscape structure.

5. Our results indicate that richness and abundance patterns may mask critical interactions between landscape attributes and species responses, which result in considerable heterogeneity in the way key functional processes like herbivory are distributed across the ecosystem mosaic.

Key-words: behaviour, ecosystem function, Mediterranean, movement, *Paracentrotus lividus*, *Posidonia oceanica*, *Sarpa salpa*, seagrass, seascape

Introduction

Landscape often exerts a strong influence on the functioning of systems and can mediate population structure, community composition and a range of ecosystem processes (Pickett & Cadenasso 1995). Traditionally, most landscape studies have focused on assessing the influence of landscape attributes on species distribution, abundance or richness (Diekötter *et al.* 2007). In contrast, far fewer studies have focused on the effects of these attributes on ecosystem processes, functions or indirect interactions (but see Andren & Angelstam 1988; Irlandi 1994; Cronin 2003; Diekötter *et al.* 2007; Macreadie, Geraldi & Peterson 2012) with most studies assuming that species richness and abundance patterns are a reasonable proxy for functional processes (Valladares, Salvo & Cagnolo 2006). It is unclear whether this critical assumption is always valid particularly when species with very different

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

behaviours and life histories together contribute to a single ecosystem function.

Few processes are as ubiquitous and central to ecosystem functioning as herbivory (Burkepile 2013), regulating rates of primary production and nutrient cycling (Abbas *et al.* 2012; Gera *et al.* 2013), influencing species interactions (Pringle *et al.* 2007; Pagès *et al.* 2012) and being a strong determinant of community composition, diversity and biomass (Knapp *et al.* 1999) among others. As a process, herbivory is known to be highly affected by the landscape mosaic (e.g. Diekötter *et al.* 2007; Haynes & Crist 2009), but our understanding of the influence of landscape attributes on herbivores' activity has been drawn mostly from indirect evidence such as herbivore abundance or distribution (e.g. Diekötter *et al.* 2007) or visual assessments of damaged tissues (e.g. Thies, Steffan-Dewenter & Tscharntke 2003). There is compelling evidence that herbivores do not distribute randomly across the habitat mosaic and often concentrate or disperse in space as a function of the landscape configuration, potentially generating spatial heterogeneity in herbivory function (Pickett & Cadenasso 1995; Vergés *et al.* 2011). This is due, in part, to species-specific perception abilities (Thies, Steffan-Dewenter & Tscharntke 2003). In addition, different herbivores may interact with landscapes at very different scales (Dunning, Danielson & Pulliam 1992), according to their degree of mobility (Ricketts 2001).

Mobile generalist herbivores may make foraging choices based on their social behaviour (e.g. McNaughton 1984; Black *et al.* 1992) or based on specific patch properties: choosing foraging locations as a function of patch resource availability (i.e. patch size, MacArthur & Pianka 1966), food quality (i.e. high-quality, less-defended patches are expected to be preferred; Haynes & Cronin 2004), predation risk (the so-called landscape of fear; e.g. Brown & Kotler 2004). In addition, the matrix within which the patch is embedded may also influence foraging decisions. Generalist mobile herbivores have been shown to choose landscapes where their focal habitat is embedded in a matrix with other complementary or supplementary diet elements (i.e. complementation or supplementation hypotheses, Dunning, Danielson & Pulliam 1992; Haynes, Diekotter & Crist 2007).

In contrast, low-mobility herbivores likely respond to landscape features very differently. They are much more prone to be affected by the presence of edges, which may be a barrier for their movement (Ricketts 2001). In these cases, patch-specific patterns may dominate, and recruitment-mortality processes within the patch may become the main driver of herbivore abundance and eventually of herbivory pressure. Indeed, herbivores may either avoid habitat edges, as often predation (or perceived risk) has been found to be more intense at the edges of habitats than in the centre (e.g. Andren & Angelstam 1988; Irlandi 1994; Macreadie, Geraldi & Peterson 2012), or aggregate in areas close to habitat edges (e.g. Haynes & Cronin 2003; Macreadie, Geraldi & Peterson 2012), both mechanisms

generating potential edge-related heterogeneities. Again, the composition of the matrix has been shown to be crucial in determining how edges will be perceived (Cronin 2003; Haynes & Cronin 2003). If the matrix habitat contrasts strongly with the patch habitat, edges may be perceived as hard, thus inhibiting migration; conversely, less contrasting matrix types, with similar structure to patch habitat, may favour softer patch edges (i.e. low contrast), with higher permeability (Stamps, Buechner & Krishnan 1987). These factors will influence the movement and abundance distribution patterns of low-mobility herbivores, thus affecting the processes they contribute to within focal habitat patches (Haynes & Cronin 2003, 2006).

Underwater landscapes in the coastal zone (seascapes), like many other linear habitats (riverine ecosystems, mountain ridges, among others), are characterized by being relatively small patches of habitat isolated from each other by matrices of a different nature and with a tendency of being miniaturized (Goodsell, Chapman & Underwood 2007). This makes them ideal candidates to study ecosystem processes at a scale that is relevant for the landscape. However, seascapes have specific features that make them unique. They are generally more connected than terrestrial systems and potentially less affected by barriers, particularly during larval and dispersal phases (Tanner 2006). However, many shallow-water systems have significant hard edges which become particularly important for adult life stages of animals with restricted movement (e.g. echinoderms, Hereu 2005).

Seagrass meadows are a common nearshore vegetated ecosystem, frequently interspersed with rock or sandy habitats and with a propensity to form differently sized patches, especially in shallow coastal waters (i.e. 0–10 m). They create a seascape mosaic that raises critical questions of how ecological functions are distributed across the habitat. It is known that seagrass patch size influences within-patch species richness and abundance (e.g. MacReadie *et al.* 2009), that patches embedded in different matrices display contrasting species abundances (e.g. Tanner 2006), that edges can modify within-patch species abundance and distribution (Smith *et al.* 2010) and that seagrass patches display shorter canopies near coral reefs than away from them (Valentine *et al.* 2007). More recently, ecosystem processes, such as primary production and nutrient cycling, have also been observed to change as a result of seagrass patch size (Gera *et al.* 2013), and specifically, herbivory increases with the reduction of the meadow size (Prado *et al.* 2008). However, studies dealing with the effects of landscape attributes on seagrass ecosystem processes are scarce, and those assessing the effects of landscape attributes other than patch size, on seagrass functioning, are, to our knowledge, very limited.

We take advantage of a relatively simple plant–herbivore system with one primary producer (the Mediterranean endemic seagrass *Posidonia oceanica*) and its two dominant consumers, a fish and an echinoderm. Both are generalists and interact strongly between them (Pagès *et al.*
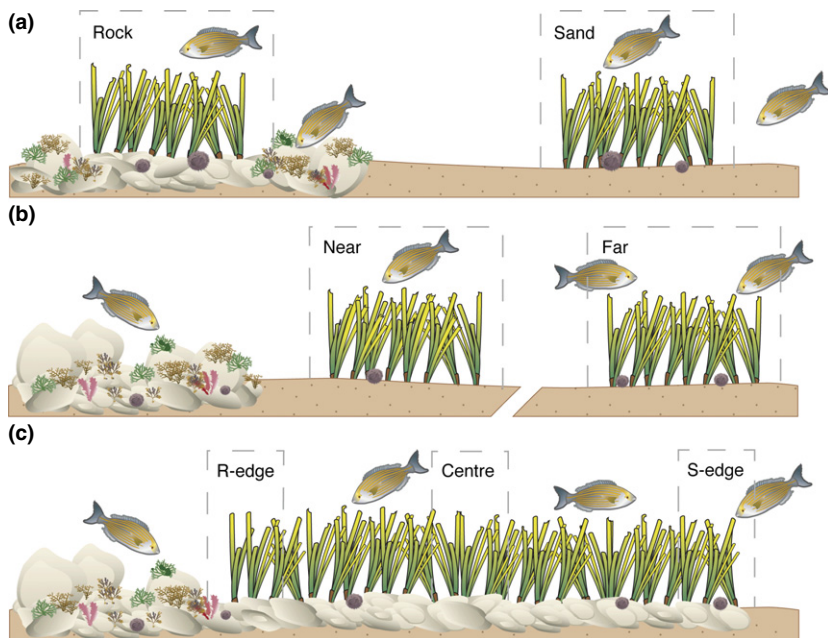
Fig. 1. Experimental design. (a) Matrix experiment consisted of measuring ecological features from seagrass patches embedded in a rock matrix ($n = 4$) and patches in a sand matrix ($n = 4$), in three sites. (b) Distance experiment involved measuring ecological parameters from seagrass patches embedded in a sand matrix and either near (~5 m, $n = 4$) or far (~20 m, $n = 4$) from a rocky reef, in three sites. (c) In the edge experiment, we measured ecological features in five plots at the centre of a meadow and five plots at the rock and sand edges, also in three sites.

2012). They also show very different adult mobility patterns, which we expect to be highly influenced by landscape configuration, with consequences for how their rates of herbivory are distributed across the mosaic. In this study, we examined whether landscape configuration could drive patterns of herbivory by these two herbivores across the meadow. Specifically, we assessed actual levels of herbivory of each herbivore (i) in seagrass patches embedded either in rock or in sand matrices (hereafter matrix attribute), (ii) in seagrass patches embedded in a sand matrix, either near or far from rocky reefs (hereafter distance attribute) and (iii) at the centre and edges of seagrass meadows bordered on one side with rock (rock edge) and on the other with sand (sand edge; hereafter edge attribute) (Fig. 1). Additionally, we evaluated plant production and nutrients in each of these patches to test whether forage quality differences could help explain observed patterns of herbivory across the seagrass mosaic.

Materials and methods

STUDY SYSTEM

Posidonia oceanica (L.) Delile is a habitat-forming seagrass whose meadows, considered among the most productive communities in the Mediterranean (Cebrian *et al.* 1996), provide shelter, food or substrate to a large diversity of species (Francour 1997). This seagrass typically grows as patchy meadows, especially in shallow areas, and can be found growing either between rocky substrates (i.e. embedded within a rock matrix) or in sandy areas (i.e. embedded within a sand matrix). The macroherbivore guild is limited in this system, with just two key species responsible for the bulk of the herbivory: the sparid fish *Sarpa salpa* (L.) and the sea urchin *Paracentrotus lividus* (Lam.) (Tomas, Turon & Romero 2005). Both are generalist herbivores and can have significant impacts on macrophyte communities, consuming on average more than 40% of seagrass leaf production (Prado *et al.* 2007). The activity of

both species peaks during summer months and is concentrated in the upper infralittoral zone (Prado *et al.* 2007).

The sparid *S. salpa* is a roving herbivore with home ranges that often span several hectares (Jadot *et al.* 2006; Pagès *et al.* 2013). It is a generalist fish capable of connecting distant habitats (several kilometres apart, Pagès *et al.* 2013). Adults tend to prefer seagrass leaves (but they also feed frequently on macroalgae), while juveniles typically consume macroalgae (Verlaque 1990). *S. salpa* fishes travel in large shoals of hundreds of individuals and have few (if any) extant predators. In contrast, the adults of the sea urchin *P. lividus* display a considerably restricted movement pattern (average distance from initial position after 3 months = 1·5 m, Hereu 2005) and generally do not cross sandy areas (Dance 1987). The *P. lividus* diet is also varied and includes different species of macroalgae, as well as seagrass leaves. In addition, both adults and the juveniles of this species are highly predated by a wide variety of fishes (Sala 1997). The differences in movement, behaviour and predation risk between the two predominant Mediterranean herbivores, which determine their ability to forage in different landscape configurations, may influence their overall impacts on the ecosystem.

FIELD DESIGN

To assess the importance of different seascape attributes (matrix, distance to neighbouring habitats and matrix-dependent edge effects) in determining herbivory rates, we selected three shallow *P. oceanica* seagrass meadows (5–8 m depth) with similar seascape configurations. The sites, separated by few kilometres, are situated along the northern Catalan coast (NW Mediterranean). At each site, we tested the influence of seascape attributes on actual herbivory rates. For the matrix attribute, we selected eight seagrass patches of similar sizes (mean ± SE = 5·1 ± 0·9 m^2) embedded in two different matrices: four patches in 'rock' and four patches in 'sand' (Fig. 1a). For the distance attribute, we selected another set of eight seagrass patches of similar sizes (mean size ± SE = 4·1 ± 0·5 m^2) all embedded in a sand matrix, either 'near' (four patches, mean distance from a rocky reef ± SE = 5·6 ± 0·7 m) or 'far' from a rocky reef (four patches, mean distance from a rocky reef ± SE = 23·1 ± 2 m) (Fig. 1b). For the edge attribute, we selected 15 plots (~5 m^2) within a continuous

meadow: five at the centre of the meadow, five at edges bordered with rock ('rock edge') and five at edges bordered with sand ('sand edge') (Fig. 1c).

At each of the selected patches or plots, we measured total herbivory rates and herbivore-specific herbivory rates (fish or sea urchin). To compare impacts of herbivory between patches/plots, we measured primary production at every patch/plot. In addition, we measured herbivore abundance to test whether rates of herbivory were related to site-specific or attribute-specific herbivore numbers. Additionally, to test whether plant quality was responsible for any of the observed patterns, we analysed plant tissues nutrient content (carbon : nitrogen ratio) from every patch/plot.

RESPONSE VARIABLE ASSESSMENTS

We measured direct herbivory rates and leaf growth (as a surrogate of primary production) in July 2011, when herbivory is at its seasonal maximum (Prado *et al.* 2007), on the same *P. oceanica* shoots. Primary production was estimated using a modified Zieman's method (Zieman 1974; Pérez & Romero 1994), and herbivory was assessed with a tethering technique similar to the one used in Prado *et al.* (2007). SCUBA divers marked five shoots per patch for matrix and distance experiments [five shoots per patch, four patches, two conditions, three sites, resulting in a total of 120 marked shoots for each experiment (matrix and distance)] and three shoots per plot for the edge experiment (three shoots per plot, five plots, three positions, three sites, resulting in a total of 135 marked shoots). In each shoot, we marked the base of the leaves (piercing the leaf with a needle) to measure leaf elongation. We also counted the initial number of leaves, measured the initial leaf length and recorded the state of the apical part of each leaf (broken, eaten by fish, eaten by sea urchin or intact). 15 days later, all marked shoots were collected and transported to the laboratory for sorting. For each shoot, we counted the number of leaves, and for each leaf, we measured its length and examined the state of its apex. For each leaf, the new leaf tissue produced (between the pierced mark and the ligula) was also measured (i.e. leaf elongation). Primary production (cm shoot^{-1} day^{-1}) of pierced shoots was determined by dividing the cm of new tissue produced by the number of days elapsed since marking. Shoot herbivory rates (cm shoot^{-1} day^{-1}) were estimated for each of the collected shoots by adding leaf elongation (cm of new tissues produced) to the initial length and subtracting this total from the final leaf length, finally divided by the number of days elapsed since marking (Prado *et al.* 2007). Only leaves that had clear herbivore bite marks were assigned to herbivory, and the rest were discarded to avoid herbivory overestimates. Given that the prevalence of lateral bite marks on leaves was low, we assumed that our calculations reflected mostly actual consumption, not just defoliation (plant tissue lost, but not consumed). Both herbivores leave bite marks of distinctly identifiable shapes (e.g. Tomas, Turon & Romero 2005), and we were able to separately estimate seagrass removal rates for sea urchins and for fish (herbivore-specific herbivory rates). To calculate herbivore-specific herbivory rates, we have to assume that the likelihood of one herbivore grazing a leaf already grazed by the other species is low. In statistical analyses, the mean of these 3–5 marked shoots was taken as the primary production and herbivory rate of each experimental unit [i.e. patch (matrix, distance experiments) or plot (edge experiments)]. Production–herbivory balances were obtained by subtracting herbivory (cm shoot^{-1} day^{-1}) from production (as leaf elongation, cm shoot^{-1} day^{-1}) to assess whether shoot length (and, consequently, canopy height) was overall increasing (if production outpaced herbivory) or decreasing (if herbivory was greater than production) for the period considered (July, i.e. early summer).

We estimated sea urchin density at each experimental location by counting adult sea urchin abundance (test size ≥ 3 cm) in 40 × 40 cm quadrats randomly placed in each patch for matrix and distance experiments (three quadrats per patch, four patches, two conditions, three sites, resulting in a total of 72 quadrats for each experiment) or plot for the edge experiment (two quadrats per plot, five plots, three positions, three sites, resulting in a total of 90 quadrats). In statistical analyses, the mean of these 2–3 quadrats was taken as the sea urchin density of each experimental unit [i.e. patch (matrix, distance experiments) or plot (edge experiments)]. We did not assess fish herbivore abundance in each condition as *S. salpa* are very mobile and display a home range greater than our experimental scale (i.e. on the order of hectares; Jadot *et al.* 2006; Pagès *et al.* 2013). We therefore assume that within each site, every patch or plot is equally likely of being visited by *S. salpa* fishes with no physical barriers restricting their movements. As a result, potential differences in fish herbivory between matrices, distances to the rocky reef or plots will be the result of behavioural choices made by these fishes.

To assess food (plant) quality, we measured leaf nitrogen (% N) and carbon (% C) to obtain C : N ratios from leaves at each site (see for e.g. Haynes & Cronin 2004). To obtain adequate leaf biomass for these analyses, we pooled 3–5 shoots together resulting in one sample per experimental unit [i.e. per patch (matrix and distance experiments, four patches, two conditions, three sites, 24 samples in total) or per plot (edge experiment, five plots per position, three positions, three sites, 45 samples in total)]. Leaf nitrogen and carbon concentration were measured using an Elemental Analyser EA1108 (Carlo Erba Instruments) at Unidade de Técnicas Instrumentais de Análise (Universidade de Coruña).

STATISTICAL ANALYSES

We used linear mixed-effects models to determine how seagrass response variables [i.e. total herbivory rates, herbivore-specific herbivory rates, sea urchin density, primary production, production–herbivory balance and plant quality (C : N ratio)] varied across the different landscape attributes studied (i.e. matrix composition, distance to the nearest rocky reef, edge effects). For the matrix attribute, 'matrix' was considered a fixed factor with two levels (rock and sand); for the distance attribute, 'distance' was considered a fixed factor with two levels (near and far); and for the edge attribute, 'position' was the fixed factor with three levels (rock edge, centre, sand edge). In addition, we included the random effect 'site' into all models to account for the variance between measurements taken from the same site [three levels, the three sites (except for the variables related to herbivory in the edge experiment, which only had two suitable sites, as the third showed virtually no herbivory, possibly due to a problem with the shoot-marking technique)], despite this random effect was negligible in most cases. In those attributes that involved patches (matrix and distance attributes), patch size (m^2) was also included into the models as a covariate to control for this possible source of variation. Finally, to assess the response variable herbivore-specific herbivory rate, 'animal' was included into the model as a fixed factor with two levels (fish and sea urchin). We always started model selection from a full model including all explanatory variables and their interactions for each response variable. Then, each effect was dropped one by one, and we selected the best model using the Akaike Information Criterion and the likelihood ratio test statistic (Zuur *et al.* 2009).

We conducted multiple comparisons using Tukey's HSD on those dependent variables that showed a significant effect in our linear mixed-effects analyses. This enabled us to test pairwise differences between variables. Normality and homogeneity of variances were checked graphically by inspecting residuals and fitted values. Some response variables did not follow the assumption of normality and were thus transformed (see Tables S1, S2, S3 in Supporting Information). In addition, whenever model residuals were clearly

heteroscedastic, their variance structure was modelled with weights within the linear mixed-effects models and the best weighted model was selected using Akaike Information Criterion (AIC) (Zuur *et al.* 2009) (see Tables S1, S2, S3 from the supplement). All data were analysed with the package nlme in the statistical software R (Pinheiro *et al.* 2011; R Development Core Team 2012).

Results

Matrix composition had a significant effect on total herbivory rates (Table S1). Meadows embedded in a rock matrix sustained herbivory rates more than twice as high as those surrounded by sandy habitats (Fig. 2a), and this effect was significantly modulated by patch size (see the significant interaction Matrix × Size, Table S1). In addition, size alone also significantly affected herbivory rates, with smaller patches being more grazed (Fig. S1a). Although fish herbivory (mean ± SE = 57 ± 15%) appeared to be somehow higher than sea urchin herbivory in both matrices (Fig. 2b), the animal effect was not significant (Table S1). We did not find any shift in the proportion of herbivory caused by each herbivore species according to matrix composition (Matrix × Animal effect was dropped, Fig. 2b, Table S1). Sea urchin density and seagrass primary production were not significantly different across matrices (Fig. 2c,d, Table S1). In contrast, we found significant differences in the production–herbivory balance of shoots from patches within the rock matrix, with a daily mean of leaf length loss (± SE) of 0·82 ± 0·3 cm, compared to shoots from sand patches, which showed a neutral balance between herbivory and production (Fig. 2e, Table S1). Patch size also modulated the production–herbivory balance (Table S1). There were no differences in plant quality between seagrass patches on sand or rock matrices (Fig. 2f), although differences were evident between matrices for some size ranges (significant Matrix × Size interaction, Table S1).

Patch distance from rocky reefs did not influence total herbivory rates, with very similar values between patches near and far from rocky reefs (Fig. 3a, Table S2). Fish herbivory was significantly higher than urchin herbivory (significant 'animal' effect, Table S2). Fish herbivory rates were especially higher in patches 'far', where they made up three-quarters of the total herbivory (Fig. 3b). Distance to rocky reefs did not have an effect on sea urchin densities (Fig. 3c, Table S2), while sea urchin density was significantly affected by the covariate patch size (Table S2, see also Fig. S1b). We found no effects of distance on primary production, production–herbivory balances or plant quality (Fig. 3d,e,f, Table S2), but again we detected a significant effect of the covariate patch size on plant production (with higher production in bigger patches) and plant quality (higher quality [lower C : N ratio] in bigger patches) (Table S2, Fig. S1c,d).

Position within the meadow had a clear influence on herbivory (Fig. 4a, Table S3). Both edges showed lower levels of herbivory compared to the centre of the meadow, but differences were only significant between the rock edge and the centre of the meadow according to Tukey's HSD pairwise comparison. Specifically, herbivory rates were 3·6 times higher at the centre of the meadow compared to the rock edge (Fig. 4a). These differences were due to increased herbivory pressure exerted by fish grazers at the centre of the meadow (see the significant 'animal' effect; Fig. 4b, Table S3), which accounted for 80% of total herbivory at this position. Sea urchin density was not significantly different between positions in the meadow, despite a non-significant trend of lower sea urchin density from the rock towards the sand edge (Fig. 4c, Table S3). Primary production did not differ with meadow position (Fig. 4d,f, Table S3). Thus, given the heterogeneity in herbivory rates, significant differences in production–herbivory balances were evident (Table S3), with a highly negative balance at the centre of the meadow (shoots shortening) compared to the edges, particularly rocky edges, whose shoots showed a slightly positive balance (Fig. 4e). Plant position within the meadow did not affect plant quality.
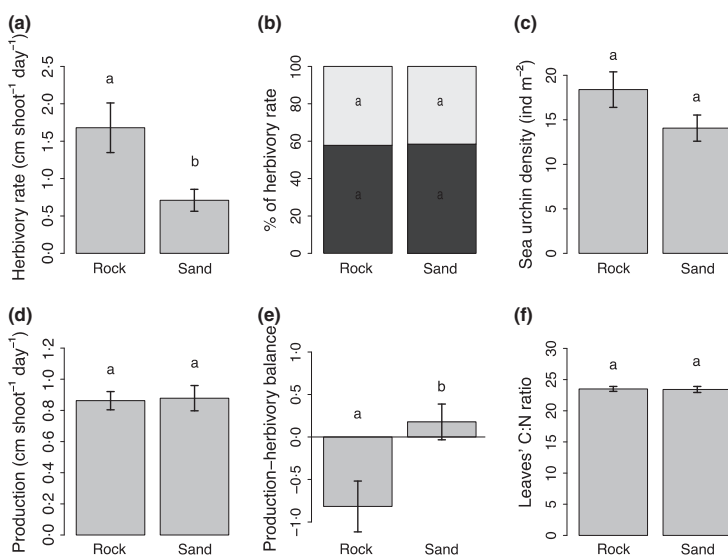

Fig. 2. Matrix experiment. (a) Total herbivory rates, (b) percentage of herbivory rate accounted by each herbivore [dark grey bars correspond to fish herbivory (*S. salpa*) and light grey ones to urchin herbivory (*P. lividus*)], (c) sea urchin density, (d) seagrass primary production, (e) balance between production and herbivory (cm shoot^{-1} day^{-1}) and (f) plant quality (leaves' C:N ratio) in *P. oceanica* patches embedded in a rock or in a sand matrix. Bars labelled with the same letter do not differ significantly according to a Tukey HSD *post hoc* test.
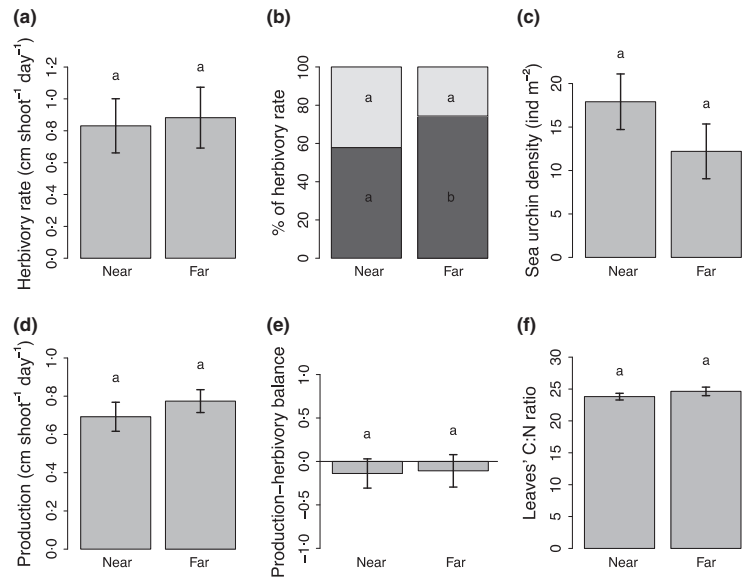
Fig. 3. Distance experiment. (a) Total herbivory rates, (b) percentage of herbivory rate accounted by each herbivore [dark grey bars correspond to fish herbivory (*S. salpa*) and light grey ones to urchin herbivory (*P. lividus*)], (c) sea urchin density, (d) seagrass primary production, (e) balance between production and herbivory (cm shoot^{-1} day^{-1}) and (f) plant quality (leaves' C:N ratio) in *P. oceanica* patches placed either near or far from a rocky reef. Bars labelled with the same letter do not differ significantly according to a Tukey HSD *post hoc* test.


Fig. 4. Edge experiment. (a) Total herbivory rates, (b) percentage of herbivory rate accounted by each herbivore [dark grey bars correspond to fish herbivory (*S. salpa*) and light grey ones to urchin herbivory (*P. lividus*)], (c) sea urchin density, (d) seagrass primary production, (e) balance between production and herbivory (cm shoot^{-1} day^{-1}) and (f) plant quality (leaves' C : N ratio) in areas placed at the rock edge, at the centre or at the sand edge of *P. oceanica* meadows. Bars labelled with the same letter do not differ significantly according to a Tukey HSD *post hoc* test.
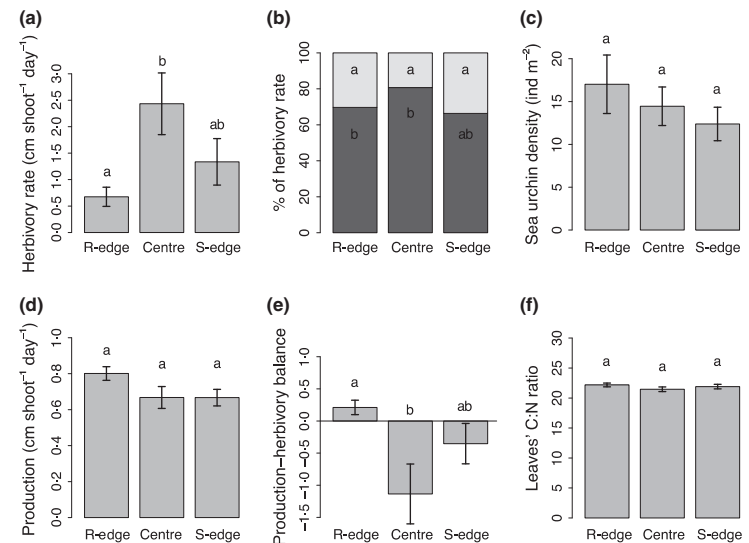
Discussion

Landscape appears to play a critical role in mediating the way ecological functions are distributed in the seagrass ecosystems we studied. Both the landscape matrix composition and edges influenced overall rates of herbivory within the meadow, while distance did not appear to affect herbivore consumption rates. Herbivory rates were higher in seagrass patches embedded in a rocky matrix compared to sandy matrices, and herbivory was higher at the centre of seagrass meadows compared to its edges. Moreover, edge effects appeared to be matrix dependent. In contrast, patch distance to rocky reefs did not play any role in determining plant–herbivore interactions or ecological processes in *P. oceanica* seagrass meadows, at least at the scale tested. Previous studies on terrestrial systems found that matrix composition affected herbivore abundances (Haynes, Diekotter & Crist 2007; Haynes & Crist 2009; Öckinger *et al.* 2012), pollinator visitation (Diekötter *et al.*

2007), herbivore movements (Ricketts 2001; Haynes & Cronin 2003) and plant damage (Thies, Steffan-Dewenter & Tscharntke 2003). Here, we show that matrix and patch edges significantly affected the actual levels of herbivory, driven largely by differences in the foraging behaviour of the two key herbivores of the system, and not by differences in food quality across the landscape as has been widely reported (Haynes & Cronin 2004).

Herbivory was highest at the centre of seagrass patches, while edges were less grazed (rocky edges in particular). This grazing peak at the centre of meadows was accounted for by fish herbivores, which were responsible for 80% of the total herbivory rates measured at the meadow centre (Fig. 4b). Increased grazing in the interior of meadows was likely related to fish behaviour more than abundance, as we assume fish densities were relatively homogenous across the study area, given that these fish species have large home ranges (i.e. on the order of hundreds of hectares; Jadot *et al.* 2006; Pagès *et al.* 2013), which are well beyond the

scale of our study. Other studies in marine systems have proposed that similar heterogeneity in the distribution of herbivory could be driven by a greater risk of predation at habitat edges, which causes herbivores to be less abundant and reduce their feeding behaviour at these edge habitats (Macreadie, Geraldi & Peterson 2012). This mechanism is highly unlikely in Mediterranean waters, given the rarity of extant predators of *S. salpa*. Perhaps more likely, the grazing peak at the centre of meadows may be driven by the shoal feeding behaviour of this species. It may be an optimal strategy for schooling fish to start foraging from the centre of meadows, as has been observed for goose flocks (Black *et al.* 1992): because flocks land in the middle of fields and forage outwards, the centre of fields is exploited more heavily than the edges (Krebs & Davies 1993). Sea urchin herbivory, in contrast, appeared to play a minor role in explaining the observed herbivory patterns. Sea urchin abundance at the rock–seagrass edge was slightly (although non-significantly) higher than at the centre and at the seagrass–sand edge, possibly due to a migration of recruits from the rocky matrix (Prado *et al.* 2012). These differences in abundance were not reflected in total herbivory rates.

Matrix composition played a major role in influencing herbivory rates of both generalist herbivores of the system, with herbivory rates in seagrass patches embedded in rocks more than twice as high as those in seagrass patches embedded in sand. This is consistent with several studies that have observed that generalist species are more likely to be affected by the intervening matrix than specialists (Brotons, Mönkkönen & Martin 2003; Steffan-Dewenter 2003; Diekötter *et al.* 2007). Eventually, the feeding specialization of the principal herbivores of the system will determine the manner and strength with which landscape attributes affect levels of herbivory (Haynes & Crist 2009), as generalists may feed both on the focal habitat (in this case the seagrass) and in the intervening matrix (in this case, the sand or rocky matrix). As unlike the sandy matrix, rocky areas also sustain macroalgae that herbivores may complement or supplement their diet with (see Dunning, Danielson & Pulliam 1992), it is perhaps unsurprising that these matrices are favoured. Complementation or supplementation hypotheses propose that many mobile species may have a diversity of nutritional requirements that may change as they grow and which may require them to utilize multiple ecosystems, effectively linking these habitats together (Dunning, Danielson & Pulliam 1992; Haynes, Diekotter & Crist 2007).

Another factor that could potentially influence habitat use across the matrix is plant quality, which is often itself strongly influenced by landscape configuration (see Haynes & Cronin 2004 for a review). Nutrient availability, water movement, light availability and plant competitive interactions could all be heavily modified by the matrix and determine animal foraging choices (Haynes & Cronin 2004). However, plant quality did not covary with the matrix in the present study, and seagrass leaves had similar carbon and nitrogen contents in both matrices, indicating that forage quality was not a factor influencing foraging differences. Another potential reason for clearly higher herbivory rates in rocky matrix is that these may be preferred areas for sea urchins. Sea urchins recruit preferentially in rocky habitats (Prado *et al.* 2012), which provide ample shelter for the species from which they have been observed to migrate to seagrass patches (Ceccherelli *et al.* 2009). In contrast, sea urchins cannot recruit, forage or shelter in sandy areas, and they generally do not cross seagrass–sand edges (Dance 1987). Indeed, matrix type has been shown to affect edge-mediated behaviour and emigration rates of various species (Ricketts 2001; Haynes & Cronin 2003, 2006). This has been attributed to differential predation risk according to the matrix they are in. Thus, although we did not find significant differences in sea urchin abundance between patches embedded in rock or in sand, sea urchins sheltering or foraging within the rock matrix (ignored in our abundance estimates) may cross the rock–seagrass edge and feed on seagrass, further increasing herbivory in these patches. Conversely, no sea urchin immigration occurs in patches surrounded by sand, as it involves crossing a hard edge (sand–seagrass), and moving across a risky matrix (Farina *et al.* in press). These factors could further explain the differences in herbivory rates we recorded between seagrass patches embedded in rocky matrices and those embedded in sand.

Patch size significantly influenced plant primary production and plant quality in those observations that involved the use of discrete seagrass patches (matrix and distance attributes) (see Fig. S1c,d and Tables S1, S2), further complicating the relationship between landscape attributes and ecological functioning. We found reduced primary production in small fragments likely due to nutrient limitation, as small patches tended to have a lower nitrogen content (significant negative correlation between patch size and plant quality; see Fig. S1d). Our results are similar to the recent findings by Gera *et al.* (2013) with the same seagrass species. Furthermore, in the present study, we found that herbivory rates were influenced by patch size and even by interacting effects of patch size with the matrix in which patches were embedded (Fig. S1a, Table S1). These results confirm for smaller seascape scales the results of Prado *et al.* (2008), which found higher herbivory rates in smaller meadows compared to bigger ones. In the light of all these results, we would expect the strongest effects of herbivory in small patches in a rocky matrix, as they tend to be more grazed and tend to suffer from nutrient limitation leading to lower production. This would explain the significant interactive effects of matrix and patch size on the balance between production and herbivory (see Table S1). Our results thus suggest that fragmentation from continuous meadows to smaller seagrass patches may induce a higher spatial heterogeneity in herbivory function, even more pronounced if patches are embedded in different matrices.

In contrast, the distance of patches from rocky reefs did not play a role in determining herbivory rates despite several studies on coral reefs that have found that herbivory

is usually higher close to reefs, decreasing with distance (Valentine *et al.* 2007; Vergés *et al.* 2011). However, in this case, the distance between rocky reefs and the farthest patches was clearly insufficient to determine any pattern given the known mobility of *S. salpa*, which can connect habitats several kilometres apart (Pagès *et al.* 2013). It is interesting to note, however, that fish contributed more to total herbivory at these more distant patches compared to the patches near the rocky reef. This was possibly linked to a slightly higher (although non-significant) abundance of sea urchins in patches closer to the rocks (Fig. 3c).

This study shows that matrix and edge landscape attributes are capable of introducing considerable spatial heterogeneity in herbivory rates, a key ecological process in seagrass meadows. The high herbivory rates found in patches embedded in rock compared to sand, and at the interior of meadows compared to the edges may have important consequences for other ecological processes, particularly when these rates exceed leaf growth. This negative balance does not necessarily imply a meadow decline, as it only occurs in early summer, when herbivory is at its maximum and leaf growth at submaximum, and is largely compensated for across the annual cycle (Prado *et al.* 2007). However, the daily reduction in canopy height (at a rate of ~1 cm per shoot per day) can expose other seagrass-dwelling species (including sea urchins) to increased predation risk (Pagès *et al.* 2012). Moreover, seagrass shoots subject to these imbalances between production and herbivory have been observed to decrease shoot nutrient stocks (Vergés *et al.* 2008), likely limiting their long-term primary production (Gera *et al.* 2013) and even decreasing reproduction (Planes *et al.* 2011). In spite of the high levels of herbivory that some seagrass areas receive, we should bear in mind that herbivory in the Mediterranean is highly seasonal, with high rates during summer and low rates in winter (Prado *et al.* 2007). This seasonality may be critical for the survival of *P. oceanica* meadows in areas of the landscape where herbivory is most intense.

Overall, our results reinforce the view that a more nuanced understanding of landscape processes will require us to go beyond describing species abundance and distribution patterns across mosaics. While these may serve to provide a rough idea of how landscape configuration influences ecosystem processes, they often mask much more complex interactions. Our results show that the abundance of herbivores in a given area did not completely correspond to their functional impact: areas with very similar abundances of herbivores had very different levels of herbivory. We believe this mismatch may have been driven by differences in life history, movement and predation risk between the two dominant herbivores that resulted in very different patterns of foraging in relation to landscape attributes. These behavioural and movement patterns of the key species of the system may be fundamental to predict the spatial heterogeneity of ecological processes, which may have important consequences for plant production,

nutrient cycling, plant reproductive success and the trophic pathways of the system.

Data accessibility

Data are deposited in the Dryad repository: http://doi.org/10.5061/dryad.hr348 (Pagès *et al.* 2014).

References

Abbas, F., Merlet, J., Morellet, N., Verheyden, H., Hewison, A.J.M., Cargnelutti, B. *et al.* (2012) Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. *Oikos*, **121**, 1271–1278.

Andren, H. & Angelstam, P. (1988) Elevated predation rates as an edge effect in habitat Islands: experimental evidence. *Ecology*, **69**, 544–547.

Black, J.M., Carbone, C., Wells, R.L. & Owen, M. (1992) Foraging dynamics in goose flocks: the cost of living on the edge. *Animal Behaviour*, **44**, 41–50.

Brotons, L., Mönkkönen, M. & Martin, J.L. (2003) Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *American Naturalist*, **162**, 343–357.

Brown, J.S. & Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, **7**, 999–1014.

Burkepile, D.E. (2013) Comparing aquatic and terrestrial grazing ecosystems: is the grass really greener? *Oikos*, **122**, 306–312.

Cebrian, J., Duarte, C.M., Marba, N., Enriquez, S., Gallegos, M. & Olesen, B. (1996) *Herbivory on Posidonia oceanica: Magnitude and variability in the Spanish Mediterranean Marine Ecology-Progress Series*, **130**, 147–155.

Ceccherelli, G., Pais, A., Pinna, S., Serra, S. & Sechi, N. (2009) On the movement of the sea urchin *Paracentrotus lividus* towards *Posidonia oceanica* seagrass patches. *Journal of Shellfish Research*, **28**, 397–403.

Cronin, J.T. (2003) Matrix heterogeneity and host-parasitoid interactions in space. *Ecology*, **84**, 1506–1516.

Dance, C. (1987) Patterns of activity of the sea urchin *Paracentrotus lividus* in the bay of Port-Cros (Var, France, Mediterranean). *Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I*, **8**, 131–142.

Diekötter, T., Haynes, K.J., Mazeffa, D. & Crist, T.O. (2007) Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects. *Oikos*, **116**, 1588–1598.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.

Farina, S., Arthur, R., Pagès, J.F., Prado, P., Romero, P., Vergés, A. *et al.* (in press) Differences in predator composition alter the direction of strucure-mediated predation risk in macrophyte communities. *Oikos*. doi: 10.1111/oik.01382.

Francour, P. (1997) Fish assemblages of *Posidonia oceanica* beds at Port Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. *Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I*, **18**, 157–173.

Gera, A., Pagès, J.F., Romero, J. & Alcoverro, T. (2013) Combined effects of fragmentation and herbivory on Posidonia oceanica seagrass ecosystems. *Journal of Ecology*, **101**, 1053–1061.

Goodsell, P.J., Chapman, M.G. & Underwood, A.J. (2007) Differences between biota in anthropogenically fragmented habitats and in naturally patchy habitats. *Marine Ecology Progress Series*, **351**, 15–23.