

Effects of landscape configuration on the exchange of materials in seagrass ecosystems

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ABSTRACT: Landscape (or seascape) attributes play an important role in modulating the flow rates of materials between habitats in the coastal marine environment. Seagrass meadows are known to both export and import organic matter, thus establishing links with other habitats. Most of those links remain unexplored, and little is known about the relevance of landscape configuration on these flows. We studied the relationships between landscape configuration (continuous meadows, patchy meadows in a sand matrix and patchy meadows in a rock matrix) and the exchange and accumulation of detrital material. Moreover, we evaluated the impact of landscape configuration on (1) plant nutrient content and (2) the diet of a model deposit feeder (holothurians). We determined detritus stocks in seagrass meadows as well as the carbon and nitrogen elemental and isotopic composition of plants, detritus and other food sources (e.g. suspended organic matter). Based on this, we identified, by applying mixing models, the different contributions of these sources to the diets of deposit feeders. Our results showed that landscape configuration influences the exchange of materials across the coastal seascape. Less accumulation of detrital seagrass leaves was found in patchy meadows, although no effects were found for allochthonous materials. In addition, patchy seagrass meadows showed significantly lower nitrogen concentrations in leaves compared to continuous meadows. Landscape configuration had no effect on the diet of the deposit feeder studied. These findings highlight the importance of landscape-level processes in coastal waters and specifically warn of the possible effects of changes in meadow size on seagrass performance.

KEY WORDS: Coastal seascape · Habitat linkages · Spatial subsidy · Deposit feeder diets · Stable isotopes · Holothuria

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INTRODUCTION

Landscape ecology has made important contributions to our understanding of ecosystem dynamics (Pittman et al. 2011). The view that spatial properties are critical for functional and evolutionary aspects of the ecosystems is a central tenet of terrestrial ecology, and concepts from landscape ecology are increasingly being applied to the marine environment. Among them, the ecological consequences of broad-scale spatial heterogeneity are receiving increasing attention (Grober-Dunsmore et al. 2007, Hinchey et al. 2008, Boström et al. 2011).

Underwater marine landscapes, or seascapes, and specifically those in the coastal zone, usually consist of an intermingled set of habitat patches that are settled in relatively small areas and often exhibit complex spatial patterns. Overall ecosystem functions in coastal seascapes and the delivery of associated ecosystem services are dependent not only on the intrinsic properties of individual habitat patches but also on the spatial configuration and functional links between the patches and their properties (Grober-Dunsmore et al. 2008, Pittman et al. 2011, Hyndes et al. 2014).

Habitat patches are linked by a range of mechanisms that function on broad spatial and temporal

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scales (Sheaves 2009). Habitat boundaries are usually crossed by organisms and materials that can carry energy, matter or information. The degree to which a given landscape facilitates such flows is called connectivity (Taylor et al. 1993). Cross-habitat linkages allow asymmetrical energy flows (Valiela et al. 2001) that can have important ecological consequences, especially by increasing productivity in the recipient area (Marczak et al. 2007, Heck et al. 2008, Mellbrand et al. 2011, Hyndes et al. 2012), which has been called a spatial subsidy (Polis et al. 1997). Habitat linkages depend on the nature and spatial arrangement of the habitats and the general setting of the physical environment. Landscape attributes such as the perimeter of focal habitats, the distance between habitats or the matrix within which they are imbedded modulate such fluxes (Polis et al. 1997, Bellido et al. 2008, Pagès et al. 2014). Thus, landscape composition and configuration will influence ecological connectivity (Mumby 2006, Grober-Dunsmore et al. 2008).

It is generally accepted that coastal ecosystems are experiencing an unprecedented set of alterations due to human pressures (Halpern et al. 2008). Most of the effects of these changes have been studied in depth, at levels ranging from the sub-individual (biochemical, physiological) through the individual and population to the community and ecosystem levels (Worm et al. 2006, Pérez et al. 2007, Hyndes et al. 2014, Vergés et al. 2014). However, much less attention has been paid to the effects of such changes on the spatial structure at the large scale; that is, to the modification of the composition and configuration of coastal seascapes resulting from human activities. Valuable habitats in the coastal ecosystem mosaic are losing cover and becoming increasingly fragmented (Macreadie et al. 2009). Fragmentation is a modification of the landscape configuration that reduces continuous ranges of habitat to small, isolated patches and can drastically change habitat structural complexity (Montefalcone et al. 2010). Habitat fragmentation increases the patchiness, which in turn causes a dramatic reduction in connectivity within habitats (Bender et al. 1998, Hovel et al. 2002) and can seriously modify the way organisms use the seascape (Boström et al. 2011, Gera et al. 2013). Changes in landscape configuration caused by human action can disrupt the natural direction or magnitude of matter and energy flows between habitats, with consequences for trophic food webs and ecosystem productivity (Howe & Simenstad 2011).

Common habitats in the coastal seascape include rocky reefs dominated by different species of macro-

algae, seagrass beds and unvegetated sedimentary bottoms dominated by infauna as well as mangroves and coral reefs, among others. Different linkages have been explored between such habitats and their importance for the functioning of the overall system assessed (Wernberg et al. 2006, Howe & Simenstad 2011, Hyndes et al. 2014, Pagès et al. 2014). However, despite these recent efforts, the effects of landscape configuration and its ecological significance for the linkages between habitats within the coastal seascape are still poorly understood.

While coral reefs and mangroves in tropical areas seem to play a central role in ecosystem functioning, seagrass meadows constitute one of the most important structural and productive habitats in coastal waters worldwide (Hemminga & Duarte 2000). Seagrass meadows are linked to other coastal habitats through multiple processes, both as subsidizer and as subsidized habitat. Seagrasses play an important nursery role (Boström et al. 2011) and can play an important role in the ontogenetic migrations of many organisms (Mumby et al. 2004). Together, primary and derived secondary seagrass production represents an important trophic subsidy for several coastal habitats (Heck et al. 2008) and even for deep sea (Vetter & Dayton 1998) and terrestrial systems (Mellbrand et al. 2011). Seagrass meadows are in turn subsidized by other habitats, such as rocky reefs with macroalgae (Hyndes et al. 2012), which are frequently detached during periods of high wave action and transported passively to seagrass habitats (Wernberg et al. 2006). Moreover, they also induce deposition of particles suspended in the water column (Gacia et al. 1999, Kennedy et al. 2010), thus stretching the benthopelagic links. All of these imported allochthonous materials have the potential to enhance primary seagrass productivity by supplying nutrients but also to feed trophic webs by increasing food availability to consumers. Among consumers, deposit feeders can benefit greatly, as allochthonous sources are generally more palatable and easily assimilated and therefore preferred over seagrass as a food resource (Olsen et al. 2011, Poore & Gallagher 2013).

Seagrasses can grow either as large, continuous meadows or in the form of patches of different shapes and sizes interspersed with unvegetated sand or rocky habitats with macroalgal cover (Robbins & Bell 1994, Jackson et al. 2006), with the latter especially common in shallow waters. These patterns are driven by natural biotic (e.g. growth rate and the expansion of rhizomes) and abiotic (e.g. hydrodynamics) factors (Fonseca & Bell 1998, Hovel 2003, Mills & Berken-

busch 2009), to which anthropogenic forcing (e.g. eutrophication or physical removal) is added (Short & Wyllie-Echeverria 1996, Duarte 2002, Boström et al. 2006). Therefore, these ecosystems (and the seascapes they are embedded in) are excellent models to explore and test hypotheses about the influence of landscape attributes on ecosystem processes.

The fate of the high production of seagrass meadows has been widely studied (Mateo & Romero 1997, Cebrián et al. 2000, Pérez et al. 2001). Aboveground production (mostly leaves) can either enter the food web directly through leaf grazing or temporarily accumulate as leaf litter and then decompose or be exported (Romero et al. 1992, Cebrián et al. 1997). Meanwhile, the bulk of belowground production remains buried as dead organic matter (OM) in the sediment (Mateo et al. 1997). Despite previous work, little is known about how landscape configuration modulates energy flow via the export of seagrass detritus or the import of allochthonous OM, such as particles suspended in the water column or macroalgae from surrounding habitats within the coastal seascape (Valiela et al. 2001, Heck et al. 2008).

To help fill this gap, in this study we explored the relationships between landscape configuration and the exchange of materials across a temperate coastal seascape dominated by *Posidonia oceanica* (L.) Delile seagrass meadows as well as the impact of landscape configuration on both plant nutrient content and the diets of consumers. *P. oceanica* is a habitat-forming seagrass species that can grow as patchy meadows, especially in shallow areas, and can be found growing either between rocky substrates or in sandy areas (Pagès et al. 2014). In this study, we used a patch matrix model approach (Boström et al. 2011) with the seagrass *P. oceanica* as the focal habitat to compare the 3 most frequent landscape configurations: large continuous meadows, small patches intermingled in rocky habitats (patches embedded within a rock matrix) and small patches in sedimentary bottoms (patches embedded within a sand matrix).

We evaluated detritus stocks accumulated in seagrass meadows to understand how landscape configuration modulates the flux of materials between seagrass and the surrounding habitats. We hypothesized that (1) detrital seagrass leaves will accumulate in greater quantities in continuous meadows than in seagrass patches and (2) landscape matrix composition will influence the type of material entering the focal habitat. At the community level, we assessed whether landscape configuration influenced the nutrient content of seagrass leaves and the propor-

tions of food sources in the diet of a model deposit feeder (holothurians). We hypothesized that (1) nutrient content will be lower in seagrass patches due to low material accumulation rates and (2) the proportions of food sources in the diets of deposit feeders will change by differences in the flux of materials between habitats.

MATERIALS AND METHODS

Study site

The study was performed at 3 sites along the NE coast of Spain (NW Mediterranean): Aiguablava (41° 56' N, 3° 12' E), Giverola (41° 44' N, 2° 57' E) and Rustella (42° 14' N, 3° 13' E) (Fig. 1). These sites were selected for their similar geomorphological conditions (e.g. area, bathymetry and degree of exposure) and also for having a similar underwater ecosystem mosaic including rock, sand and seagrass habitats. The 3 landscape configurations under study were present in all 3 sites, thus minimising sources of variability among configurations other than the configuration itself. We considered continuous seagrass meadows where seagrasses covered an area of more than 100 × 100 m, while seagrass patches in either a rock or a sand matrix covered approximately 2 × 2 m. All landscape configurations were situated at similar

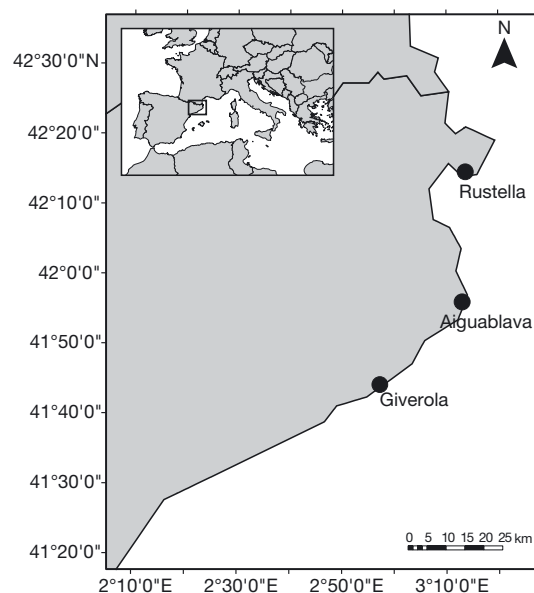


Fig. 1. Sampling locations along the Catalan coast, Spain, NW Mediterranean. Each of the sites presented similar seagrass landscapes, with continuous meadows and small patches in sand and rock habitats at the same depth range

depths in all sites (5 to 8 m) and, for each site, at a maximum distance of 50 m from each other. At these depths, fragmentation of seagrass habitats has been associated with, apart from anthropic impacts, big storms that occur sporadically and in general have a long return time (Montefalcone et al. 2010, Alcoverro et al. 2012). To discard confounding factors (other than landscape configurations), shoot density was measured in 3 replicate 40 × 40 cm quadrats in each landscape configuration within each site. Results were analysed using a 2-way mixed-effects ANOVA, with site and landscape configuration as factors, and there were no significant differences among sites and configurations ($p > 0.05$, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m532p089_supp.pdf), with an overall mean of 548 ± 29 shoots m^{-2} (\pm SE).

Sampling

Samples were collected in October 2012 (fall season in the northern hemisphere), at the end of the period of leaf fall and, consequently, the period for which leaf litter accumulation is at its maximum (Romero et al. 1992). No storm or high hydrodynamic event, potentially distorting results, occurred before or during the sampling. At each site, 5 replicate sampling points (each consisting of 1 to 1.5 m^2) were randomly selected inside the continuous meadows, and 1 sampling point was selected in each of 5 randomly selected seagrass patches in both a rock and a sand matrix, for a total of 15 sampling points per site. Scuba divers haphazardly placed a 40 × 40 cm square at each sampling point and used hand-held corers (40 mm diameter) to collect undisturbed sediment (upper 2 cm) for OM determination. Then, all of the detrital material inside the square was collected using a suction device for 1 min and sieved through a 1 mm mesh attached to the collector end of the suction device. Each sample was then placed inside a plastic bag, sealed and later transported chilled to the laboratory. Five seagrass shoots were then collected from within each square for elemental and isotopic composition analysis of living plants. Finally, 1 individual sea cucumber, either *Holothuria poli* or *H. tubulosa-mamatta* complex (Borrero-Pérez et al. 2009), was captured as close as possible to the sampling square for elemental and isotopic composition analysis. Holothurians were used as a model organism, as they are known to feed on a variety of detrital sources (bulk sediment and leaf litter of different sizes), and they constitute the largest and most

conspicuous detritivore in seagrass habitats (Massin & Jangoux 1976).

The entire sampling programme resulted in a total of 45 samples of each class, corresponding to 3 landscape configurations in 3 replicated sites, with $n = 5$ replicates per experimental condition. Additionally, 2 l of seawater (from 1 m depth) was collected in triplicate from each site and filtered into prewashed and precombusted (450°C, 4 h) Whatman GF/F filters within 2 h of collection for later elemental and isotopic composition analysis of suspended particulate organic matter (SPOM). All samples were kept frozen at -20°C until analysis in the laboratory.

Laboratory processing

In the laboratory, the detritus samples were sieved again through a 1 cm sieve and sorted into 1 fine (particles between 1 mm and 0.9 cm) fraction and 4 different coarse (1 cm or more) detrital fractions: *Posidonia oceanica* leaves, *P. oceanica* roots and rhizomes, macroalgae and material of terrestrial origin. Subsamples from the fine fraction were inspected under a dissecting microscope to estimate its origin. Detrital *P. oceanica* leaves have very low epiphyte loads, but when necessary, epiphytes were removed manually as much as possible. These fractions were dried at 60°C and weighed. The leaves from the 5 living shoots collected at each sampling point were scraped with a razor blade to remove epiphytes (Alcoverro et al. 1997a), which were kept for subsequent analysis. Once cleaned, we separated the second youngest leaf from each of the 5 shoots and pooled them. Both the epiphytes and these leaves were dried as above (Martínez-Crego et al. 2008).

Isotopic and elemental analysis was performed on samples of the coarse detrital fractions, in epiphytes and in living leaves. We did not analyse the fine detritus, as it was a mixture of the coarse detrital fractions (see 'Results'). After drying, the samples were ground to a fine powder, placed in a tin capsule and analysed for carbon (C) and nitrogen (N) elemental and isotopic composition. Prior to analysis, the detrital macroalgae and epiphytes were acidified drop by drop with HCl 2 N to remove carbonates, re-dried without rinsing and ground (Jacob et al. 2005, Carabel et al. 2006). As this chemical procedure has been reported to alter $\delta^{15}\text{N}$ values (Bunn et al. 1995), each sample was split into 2 subsamples: half of the sample was washed with acid, and the other half remained untreated. For the isotopic and elemental analysis of seston, the SPOM sample filters were

dried to constant weight, split into 2 subsamples and weighed, and half of the filter was fumed under concentrated HCl fumes (12 N) overnight at room temperature (Lorrain et al. 2003). The subsamples treated with acid were used to analyse $\delta^{13}\text{C}$, and the untreated subsamples were used to analyse $\delta^{15}\text{N}$.

The holothurians were dissected, and the retractor muscles were carefully removed and used for isotopic analysis after being rinsed in distilled water, oven dried to constant weight (for 72 h at 45°C) and ground to a fine powder. As lipids are depleted in $\delta^{13}\text{C}$ and may influence carbon isotope ratios in animal tissues (DeNiro & Epstein 1978, Post 2002), 5 samples were reanalysed after lipid removal by chloroform–methanol (2:1 ratio) extraction (Folch et al. 1957). No significant differences were found in the $\delta^{13}\text{C}$ results (data not shown) between untreated tissue and that with lipids removed, probably due to the low lipid content, and therefore untreated samples were used.

Stable isotope ratios and elemental C and N composition were measured using a MAT 253 continuous-flow isotope ratio mass spectrometer (Thermo Finnigan) coupled to an EA 1108 elemental analyser (Carlo Erba Instruments) through a Conflo III interface (Thermo Finnigan). C and N isotope ratios are expressed as δ values in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and the atmospheric air standard, respectively, according to standard notation ($\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is the ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). International Atomic Energy Agency standards were inserted every 12 samples for calibration. Replicate assays of standards indicated measurement errors of ± 0.1 and ± 0.2 ‰ for C and N, respectively. Sediment OM content was measured in triplicate as loss on ignition from sediment dry weight after combustion at 450°C in a muffle furnace for 4 h.

Data analysis

The dry weights of each detritus fraction, sediment OM content and C and N isotopic and elemental composition of living leaves and epiphytes were analysed using a 2-way mixed effects ANOVA with site (Aiguablava, Giverola and Rustella) and landscape configuration (continuous, patches in a rock matrix and patches in a sand matrix) as factors. Site was considered random, and landscape configuration was considered fixed. Where a significant ($p < 0.05$) difference occurred, a post hoc Tukey's HSD test was used to distinguish between groups. When neces-

sary, the data were fourth root transformed to meet the requirements of homogeneity of variance and normality. Non-transformed values (means \pm SE) are shown in the figures and tables. These analyses were performed using Statistica 8 software (StatSoft).

The Bayesian mixing model SIAR 4.2 (Parnell & Jackson 2013) running with R software (R Development Core Team 2014) was used to estimate the contribution of potential food sources to the diets of deposit feeders. The greatest advantage of this procedure is the incorporation of uncertainty linked to sources, consumers and trophic enrichment factors within the model (Parnell et al. 2010). This leads to the inclusion of an overall residual error term and to the generation of potential dietary solutions as true probability distributions. The model was run with 3 sources: detrital macroalgae, SPOM and a combined source of epiphytes and detrital *P. oceanica* leaves. The isotope signatures of this combined source were obtained using a weight ratio of 36:64 (epiphytes to leaves), as derived for old leaves from Alcoverro et al. (2004) and M. Pérez & J. Romero (unpubl. data). This procedure allowed us to avoid bias by reducing the number of food sources and to include epiphytes as part of the detrital material, as it was difficult to sort epiphytes from leaves in the detritus compartment. Separate mixing models were computed for each site and landscape configuration based on each corresponding set of isotope values. Within each mixing model simulation, holothurians were treated as individual consumers. We refer throughout the paper to *Holothuria* spp. (*H. poli* and *H. tubulosa-mamatta* complex), as no differences in isotope signatures were found between species (data not shown). The isotope ratios of the holothurians and food sources were analysed considering a trophic enrichment of 1.3 ± 0.3 ‰ for $\delta^{13}\text{C}$ and 2.9 ± 1.8 ‰ for $\delta^{15}\text{N}$ (adapted from McCutchan et al. 2003). Concentration dependence was incorporated into the model, as element concentrations differed between sources (Phillips & Koch 2002).

RESULTS

Concerning coarse material, detrital *Posidonia oceanica* leaves accumulated in quantities 3-fold higher in continuous meadows than in patchy ones in either a rock or a sand matrix. No landscape configuration effects were found on the accumulation of other detrital fractions (Fig. 2, Table 1, Table S1 in the Supplement). Autochthonous material (detrital seagrass leaves and root and rhizome debris)

accounted for most of the total dry weight accumulated in all of the landscape configurations studied, from 74 to 79%, while allochthonous material, including detrital macroalgae and material of terrestrial origin, represented the rest. The fine fraction (not represented) accounted for, on average, ca. 50 g dry wt m⁻², irrespective of the site or the configuration (Table 1, Table S1 in the Supplement). As indicated by the observation using the dissecting microscope, the fine fraction was made mostly of leaf fragments (especially in samples from continuous meadows) and also included algal fragments and small debris from belowground organs.

The N content of living leaves showed clear differences between landscape configurations (Fig. 3, Table 1, Table S1 in the Supplement), with plants from continuous meadows having a higher N content than those from patches in either a rock or sand matrix. There was no evidence of an effect of landscape configuration on the N content of epiphytes (Fig. 3, Table 1, Table S1 in the Supplement). In the same way, there was no evidence of an effect of landscape configuration in the C content of living seagrass leaves (overall mean of 39.99 ± 0.09%, relative to dry weight) and epiphytes (overall mean of 5.39 ± 0.18%, relative to decalcified dry weight) (Table 1, Table S1 in the Supplement). Simi-

larly, there was no evidence of an effect of landscape configuration on sediment OM content, with an overall mean of 1.39 ± 0.09%, relative to dry weight (Table 1, Table S1 in the Supplement).

Potential food sources for deposit feeders (detrital *P. oceanica* leaves and epiphytes, detrital macroalgae and SPOM) were well distinguishable using both C and N stable isotope values (Fig. 4, Table S2 in the Supplement). The δ¹³C values of the sources ranged between -12.26 and -25.50‰. SPOM was the most ¹³C-depleted source (-22.30 to -25.50‰) and

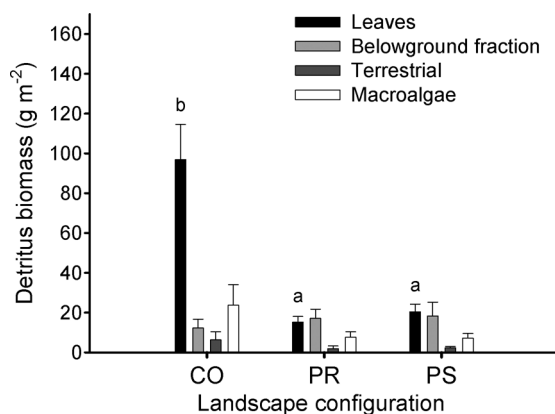


Fig. 2. Mean dry weight (±SE) of detritus stock fractions in *Posidonia oceanica* meadows from the different landscape configurations (n = 15). Bars labelled with the same letter and unlabelled bars do not differ significantly according to Tukey's HSD post hoc test. CO: continuous meadow; PR: patches embedded in a rock matrix; PS: patches embedded in a sand matrix

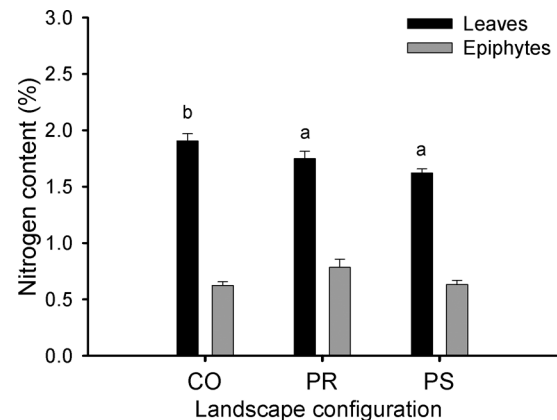


Fig. 3. Mean nitrogen content (±SE) of *Posidonia oceanica* living leaves and epiphytes from the different landscape configurations (n = 15). Bars labelled with the same letter and unlabelled bars do not differ significantly according to Tukey's HSD post hoc test. CO: continuous meadow; PR: patches in a rock matrix; PS: patches in a sand matrix

	df	SS	F	p
(a) Detrital fractions biomass and sediment data				
<i>P. oceanica</i> detrital leaves	2, 36	10.39	64.62	<0.001
<i>P. oceanica</i> belowground fraction	2, 36	0.10	0.15	0.869
Terrestrial fraction	2, 36	1.64	1.20	0.390
Macroalgae	2, 36	1.39	0.48	0.640
Fine fraction	2, 36	32 183	1.15	0.404
Sediment organic matter (%)	2, 36	0.02	0.01	0.986
(b) <i>P. oceanica</i> leaves and epiphytes variables				
Nitrogen content (%)				
<i>P. oceanica</i> living leaves	2, 36	0.02	10.37	0.026
Epiphytes	2, 36	0.25	0.69	0.554
Carbon content (%)				
<i>P. oceanica</i> living leaves	2, 36	2.01	0.15	0.869
Epiphytes	2, 36	1.43	0.13	0.885

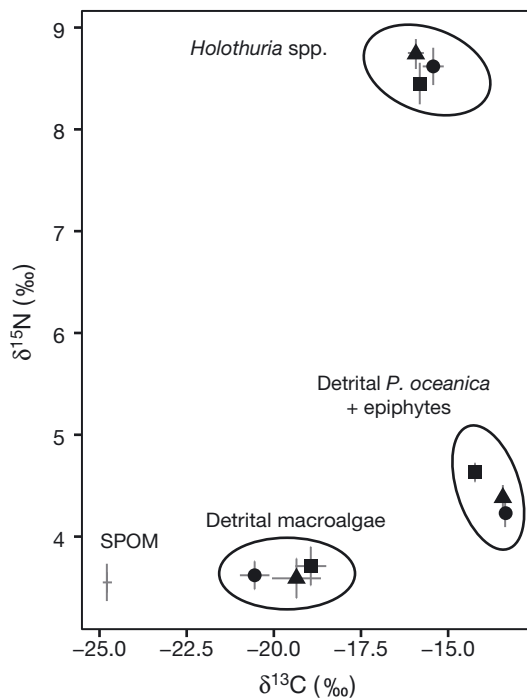


Fig. 4. Isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in parts per thousand (‰) for consumers, *Holothuria* spp. and their potential food sources (mean and standard deviation) in each landscape configuration. ●: continuous meadows; ▲: patchy meadows in a rock matrix; ■: patchy meadows in a sand matrix. SPOM: suspended particulate organic matter

showed low C:N ratios (9.60 to 10.74). The $\delta^{13}\text{C}$ values of detrital macroalgae showed intermediate values, although they presented a high variability (from -14.87 to -24.56 ‰), probably due to the presence of a range of species in different amounts. Furthermore,

detrital macroalgae had low C:N ratios (9.13 to 11.97). The combined source of detrital *P. oceanica* leaves plus epiphytes showed the most $\delta^{13}\text{C}$ -enriched values (-12.26 to -14.98 ‰) and high C:N ratios (27.12 to 30.78). The $\delta^{15}\text{N}$ values of the potential food sources were more homogeneous, between 2.10 and 5.24‰. SPOM values ranged from 2.60 to 4.60‰; detrital macroalgae ranged from 2.10 to 4.96‰; and detrital *P. oceanica* leaves plus epiphytes presented slightly higher $\delta^{15}\text{N}$ values, from 3.30 to 5.24‰, probably due to the presence of small sessile animals among the epiphytes, such as hydrozoans (*Aglaophenia harpago*, *Sertularia perpusilla*) or bryozoans (e.g. *Electra posidoniae*), among others (Prado et al. 2007).

The isotopic composition of *Holothuria* spp. was similar in the different landscape configurations studied (Fig. 4, Table S2 in the Supplement). The $\delta^{13}\text{C}$ signatures of *Holothuria* spp. ranged from -13.43 to -17.72 ‰, and the $\delta^{15}\text{N}$ values ranged from 6.94 to 9.53‰. The ranges of feasible contributions from each food source to *Holothuria* spp. diets varied slightly between landscape configurations (Fig. 5, Table S3 in the Supplement). The models suggested that the combined source of *P. oceanica* leaves and epiphytes constitutes the majority of the diet at all sites and landscape configurations, with mean values of the proportions ranging from 41 to 63%. Detrital macroalgae appeared as the second source in all of the models applied, with mean proportions in the narrow range, 29 to 36%. SPOM was also a potentially significant contributor to *Holothuria* spp. diets, with mean contributions ranging from 5 to 28%.

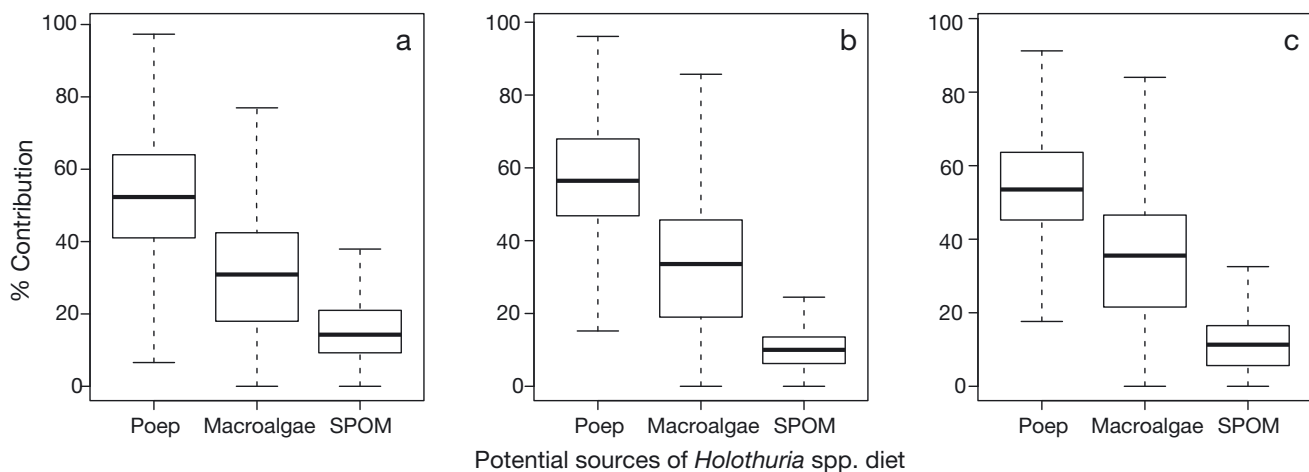


Fig. 5. Percentage dietary contributions of the 3 potential food sources for *Holothuria* spp. diets in the landscape configuration studied. (a) Continuous meadows; (b) patches in a rock matrix; (c) patches in a sand matrix. Plots show the distribution of feasible contributions from each food source to the species diet resulting from the application of the SIAR isotope model. Boxplot from top to bottom: largest observation, upper interquartile, median, lower interquartile and lowest observation. Poep: compounded source of detrital *Posidonia oceanica* leaves and epiphytes; SPOM: suspended particulate organic matter

DISCUSSION

As hypothesized, landscape configuration plays a role in modulating the flows of material between habitats in coastal marine ecosystems. Specifically, in continuous meadows, the accumulation of detrital seagrass leaves was enhanced (up to 3-fold) relative to the accumulation in seagrass patches in either a rock or sand matrix. Under such high leaf litter accumulation, *in situ* mineralization could increase nutrient availability, as suggested by the nutrient content found in leaves from plants collected in continuous meadows, which was significantly higher than that from plants in patchy configurations. Detrital seagrass leaves, including their epiphyte loads, were the main food source for deposit feeders. However, the accumulation of such materials in continuous meadows was not paralleled by a shift in the isotopic composition of the model deposit feeder (*Holothuria* spp.). This did not support the hypothesis proposed that the proportion of food sources in the diets of the deposit feeders could be modulated by differences in the flux of materials between habitats.

Accumulated detritus within *Posidonia oceanica* meadows (only coarse fraction) accounted for high organic stocks, up to 220 g dry wt m⁻² in continuous meadows and approximately 100 g dry wt m⁻² in seagrass patches. These values are of the same order as those for standing litter stocks or even higher at that time of the year (e.g. Romero et al. 1992). These values are 10-fold higher when compared with other seagrass species (e.g. *Cymodocea nodosa*) (Pérez et al. 2001) and 5-fold higher when compared with different coastal habitats such as mangroves (Woodroffe 1985). The bulk of the detritus is autochthonous, including leaf litter and rhizome and root debris. Allochthonous materials such as terrestrial detritus and macroalgae detached from rocky algal reefs were equally present in all of the landscape configurations in lower proportions (2 and 13%, respectively).

Detritus accumulation in seagrass meadows is a complex process in which biological and physical forcing interact (Romero et al. 1992). Standing litter is the result of the balance between local detritus production (e.g. leaf fall), import (of allochthonous materials but also probably of seagrass leaves from neighbouring meadows), export and decay (both mechanical, leading to the fine fraction, and biological, i.e. decomposition). All of these factors seem relevant, except maybe import. The effects of landscape configuration (specifically meadow size) seem to be

restricted to the accumulation of detrital leaves, while the other fractions (macroalgae and terrestrial detritus) seem to vary randomly across configurations. The leaf canopy of seagrass meadows attenuates water flow and reduces turbulence (Pujol & Nepf 2012). The below-canopy habitat, where detached leaves accumulate, presents low shear stress and reduced turbulence compared to the canopy–water interface region (Hendriks et al. 2008). In this study, under the same environmental conditions and with no differences in shoot density, the higher detrital leaf stocks found in continuous seagrass meadows suggest that the continuous meadows attenuate turbulence to a greater extent than patches, thus reducing the export of materials. In contrast, this does not seem to affect the import rates of allochthonous detritus.

The relatively low accumulation of allochthonous detritus suggests that seagrass meadows could act as barriers, making the arrival of external materials less likely. In agreement with this, it has been shown that in relatively dense seagrass meadows, the bulk of water flow is directed to the roof of the canopy (Granata et al. 2001), and detached algae do not percolate into the canopy but pass above it (Wernberg et al. 2006). Input rates of drifting materials are considered a function of landscape variables such as patch perimeter and the distance between habitats (Polis et al. 1997), but this is not reflected in our results. This may be because the most important issue is that the probability of a moving entity entering a given habitat once intercepted is determined by the boundary permeability of the habitat (Polis et al. 1997).

Interestingly, the nutrient content of seagrass leaves was higher in continuous meadows than in patchy ones, suggesting an association between nutrients and leaf detritus accumulation. Seagrasses meet their N requirement mainly via 2 mechanisms (Romero et al. 2006): uptake from either the water column or pore water (through leaves and roots, respectively) and internal recycling (i.e. resorption and remobilization of nutrients from old leaves or rhizome pools). For the species *P. oceanica*, internal recycling has been estimated to be high enough to meet 40% of annual needs (Alcoverro et al. 2000, Lepoint et al. 2002). As demonstrated by Hyndes et al. (2012), seagrass uptake of leached nutrients from detrital sources can account for part of the remaining 60%, thus linking detritus accumulation and nutrient availability, as is known for terrestrial systems (Swift et al. 1979, Vogt et al. 1986).

The differences found in this study in the N content of plant leaves, albeit small, could have profound

consequences for plant performance. As in other seagrasses, growth rates of shallow *P. oceanica* meadows are usually limited by nutrients, usually N (Alcoverro et al. 1997b, Lepoint et al. 2002, Invers et al. 2004). The N content threshold suggested to indicate N limitation, either for this species or for seagrasses in general (Duarte 1990, Alcoverro et al. 1997b, Invers et al. 2002, Lepoint et al. 2002), is within the range of values reported here for small patches. This suggests that even small increases in N availability, if these take place close to the values involving N limitation, can stimulate plant performances (e.g. leaf growth, Alcoverro et al. 1997b), thus linking patch size and nutrient deficiency, as proposed by Gera et al. (2013) and Pagès et al. (2014) in previous works. Those authors attributed their results to increased fish herbivore activity in small patches. However, we found low densities of herbivorous fish in our study areas (authors' pers. obs.), suggesting that although the herbivorous hypothesis cannot be ruled out, detritus accumulation seems to be a better explanation in our case. Regardless, the explanations are not mutually exclusive, and further studies are needed to evaluate their (probably) site-specific relative importance. The conclusion emerging from the available evidence is that meadow fragmentation, in addition to other functional and structural effects (Montefalcone et al. 2010), could result in reduced plant performance due to nutrient shortage.

The feeding behaviour of holothurians is still poorly understood, and traditionally they have been considered non-selective feeders (Massin & Jangoux 1976). In this study, the main food source for *Holothuria* spp. was detrital *P. oceanica* leaves, including epiphytes, followed by macroalgae and SPOM in all landscape configurations. Interestingly, the contribution of detrital leaves and macroalgae to the diets did not parallel the standing biomass found in the landscape configurations studied. Some studies stress the capacity of holothurians to discriminate between nutrient-rich and nutrient-poor particles and also their particle size selection capacity, at least in some species (Massin & Jangoux 1976, Mercier et al. 1999, Mezali & Soualili 2013). Our results suggest that the diets of holothurians, irrespective of landscape configuration, are mainly supported by materials detached from the seagrass meadow, particularly leaves and epiphytes. These materials can be ingested not only as very small decaying fragments mixed with the sediments but also as large (up to 1 cm²) pieces, as confirmed by our observation of holothurian stomach contents. Both seagrass leaves

and epiphytes seem to contribute to holothurian nutrition. However, the assimilation of epiphytes seems to be prevalent, as suggested by the isotope signatures found in holothurians, maybe due to their higher nutritional value (Tomas et al. 2006). This confirms previous findings, in which the contribution of seagrass epiphytes to seagrass trophic webs is not in strict relation to their abundance (Tomas et al. 2006, Park et al. 2013). Although it has been pointed out that alterations at the landscape scale could potentially disrupt or divert the natural direction of energy flows between adjacent ecosystems and hence influence food web pathways (Polis et al. 1997, Puth & Wilson 2001, Howe & Simenstad 2011), this does not seem to be occurring in the seagrass deposit feeders studied here, at least not at the spatial scale studied.

The findings reported here confirm the importance of landscape configuration in modulating flows of material within the coastal ecosystem mosaic. These effects mainly concern seagrass leaf litter accumulation and the associated effects on nutrient availability for plants but not on the food sources for deposit feeders. Importantly, seagrass patches accumulating less foliar detritus are poorer in N content than continuous meadows, which could lead to nutrient limitation. This is of particular concern in future scenarios where synergistic effects between water quality and climate change could further modify coastal seascapes, especially under the assumed worldwide seagrass decline (Waycott et al. 2009), where habitat loss will promote habitat fragmentation or increasing seagrass patchiness and potentially reduce plant performance, with consequences for the entire ecosystem.

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