

Responses of mobile epifauna to small-scale seagrass patchiness: is fragmentation important?

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Abstract Habitat fragmentation is a process involving splitting of continuous habitats into smaller, and more isolated habitat patches. To assess the effects of small-scale habitat patchiness and isolation without the confounding effect of habitat loss on benthic macrofauna, two field experiments were conducted in the Archipelago Sea, SW Finland. Using artificial seagrass units (ASUs) we contrasted continuous patches (“C”) with fragmented patches (“F”) of the same combined area as the continuous patches. The fragmentation treatment involved two isolation distances (0.5 and 3.0 m) between the ASUs (“F 0.5”) and (“F 3.0”). This design was repeated in two consecutive experiments where the patch area was 0.25 and 0.0625 m², respectively. Mobile epifauna were allowed to colonize patches for 12 days in both experiments. In both experiments, the total epifaunal density was significantly higher in the “F 0.5” treatment than in the “C”

treatment, and the three dominant taxa showed positive or neutral responses to the habitat configuration. No fragmentation effect on the number of species was detected in either of the experiments, but fragmentation had a negative effect on the epifaunal diversity (Shannon’s H') in the experiment with the largest patch area. Epifaunal diversity was significantly lower in “F 3.0” treatment than in “C” or “F 0.5” treatments in the first experiment, indicating stronger effect of isolation instead of fragmentation per se. Edge effects were indirectly tested by comparing epifaunal densities with patch edge:area ratios. The results suggest that edge effects may have a more important role than patch size for the total densities of epifaunal taxa, and that small, isolated patches have equal or higher habitat value compared to larger fragments.

Keywords Seagrass · Patchiness · Fragmentation · Isolation · ASU · Mobile epifauna

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Introduction

Fragmentation of habitats and landscapes is a global phenomenon, leading to loss of biodiversity in terrestrial (Hanski & Gilpin, 1997; Harrison & Bruna, 1999; Fahrig, 2003) and marine environments (Hastings et al., 1995; Frost et al., 1999). Habitat fragmentation consists of two separate, but strongly interrelated processes, with different impacts on biodiversity (Fahrig, 2003; Laurance, 2008). The effects of habitat

loss are mainly strong and negative, whereas habitat fragmentation per se, i.e., habitat splitting after controlling for habitat loss, results in weaker effects on diversity that can be both positive and negative (Fahrig, 2003; Healey & Hovel, 2004; Macreadie et al., 2009). Apart from reducing the amount of habitat area and the size of habitat patches, the fragmentation process creates more habitat patchiness with different degrees of isolation between habitat fragments (Taylor et al., 1993; Andr n, 1994; Fahrig, 2003). The fragmentation process results in more edge habitat in relation to core areas (Fahrig, 2003). Ecological patterns and processes may be different along patch edges compared to interior parts, a phenomenon referred to as an edge or boundary effect (Gascon & Lovejoy, 1998; Ries et al., 2004; Fletcher et al., 2007).

Fragmentation should preferentially be studied at broad spatial scales, since most of the anthropogenic disturbance occurs at the landscape scale (Freemark et al., 1995; Fahrig, 2003). However, the spatial scale of a landscape is species specific, and different taxa show different responses to habitat heterogeneity (Kolasa, 1989). Since perception ability is determined by the body size, vision and movement characteristics of an animal, the effects of increased habitat patchiness on faunal assemblages are strongly scale-dependent (Johnson et al., 1992; Eggleston et al., 1998; Attrill et al., 2000). The most appropriate spatial scale should thus be the one that best corresponds with an organism's perception ability.

In a marine setting, Eggleston et al. (1999) found that estuarine macrofauna responded to habitat heterogeneity at relatively small spatial scales (0.25–1 m²). Thus, experimental manipulations conducted at smaller spatial scales can provide valuable insights into effects of habitat heterogeneity on fauna (Wiens & Milne, 1989), and to some extent translate to other organisms and larger spatial scales (Johnson et al., 1992). The response of organisms to changes in habitat heterogeneity can also depend on life stage, since juveniles may respond differently compared to adults to the same amount of habitat heterogeneity (McCoy & Bell, 1991; Eggleston et al., 1999).

Habitat fragmentation and loss is of great concern in seagrass landscapes (Duarte, 2002; Orth et al., 2006; Waycott et al., 2009). Along with natural ecological and hydrological processes (Vacchi et al., 2010), anthropogenic events such as coastal development and

eutrophication may increase the degree of patchiness in seagrass habitats (Jackson et al., 2001; Heck et al., 2003; Montefalcone et al., 2010).

Seagrass fragmentation experiments are often limited to comparisons of epifaunal diversity and density (McNeill & Fairweather, 1993; Eggleston et al., 1999; Reed & Hovel, 2006), larval settlement (Bologna & Heck, 2000) and survival (Irlandi et al., 1995; Hovel & Lipcius, 2001, 2002; Hovel, 2003) between patches of different sizes, making conclusions regarding effects of fragmentation per se difficult. McNeill & Fairweather (1993) found that species richness per unit area was greater in numerous small patches than in one large patch of the same area. The role of fragmentation per se without changes in patch area remains poorly understood, although Healey & Hovel (2004) experimentally studied the effects of seagrass fragmentation per se by comparing artificial seagrass units (hereafter ASUs) with similar surface area but different degrees of patchiness. They found that epifaunal density and diversity correlated with increasing patchiness, but responses were highly variable among taxa and in time. Results from edge effects in seagrass habitats have so far shown inconsistent patterns (Connolly & Hindell, 2006). Most taxa show no pattern with edge (Bell et al., 2001; Connolly & Hindell, 2006), but both positive (Bowden et al., 2001; Bologna & Heck, 2002; Healey & Hovel, 2004; Tanner, 2005; Warry et al., 2009) and negative (Hovel & Lipcius, 2002; Bologna & Heck 2002; Uhrin & Holmquist, 2003) responses of seagrass-associated fauna have also been reported. Along with increasing habitat heterogeneity, the isolation of patches may also influence organisms (Goodsell & Connell, 2002; Goodsell et al., 2007). However, patch isolation may be mediated by drifting algae, and algal mats may play an important role for epifaunal colonization and dispersal in patchy seagrass landscapes (Holmquist, 1994; Norkko et al. 2000; Brooks & Bell, 2001). The survival of juvenile blue crabs has been shown to be lower in small, isolated seagrass patches compared to larger, connected patches (Eggleston et al., 1998; Hovel & Lipcius, 2002), although opposite findings have also been reported (Hovel & Lipcius, 2001). As small, isolated seagrass patches can be structurally less complex compared to larger patches (Irlandi, 1994, 1997), the influence of landscape attributes on faunal patterns and dynamics is difficult to interpret. Such confounding effects can be avoided by using ASUs (e.g., Hovel & Lipcius, 2002).

In this study, we experimentally tested the importance of seagrass habitat fragmentation per se and patch isolation for mobile epifaunal colonization using ASUs. Specifically, we tested for fragmentation effects by comparing epifaunal abundance and diversity of continuous patches with four fragments of the same total area as the continuous patch, thus excluding potential habitat area effects. Isolation effects were assessed by comparing fragments isolated by two distances (i.e., 0.5 and 3.0 m). To assess if epifaunal responses to fragmentation are consistent across patch sizes, two sizes of continuous patches were fragmented into smaller patches in two consecutive experiments. Even though habitat fragmentation is a process, our design with a static arrangement of isolated patches of different sizes did not allow for tests the effects of active, ongoing habitat fragmentation (see Macreadie et al., 2009), but rather aims at assessing how mobile epifauna respond to differences in small-scale patchiness. We predicted (1) higher density and diversity of mobile epifauna in fragmented treatments, because with equal surface area and patch shape the smaller fragments have higher perimeter:area (P:A) ratios and thus a larger proportion of edge, and consequently a higher probability of species encounter; (2) lower species density and diversity in fragmented treatments with longer distances between fragments relative to short distances, because of an isolation effect; (3) more drift algal trapping, and thus enhanced macrofaunal densities in several small patches than in one large.

Materials and methods

Study site and experimental design

The study was carried out during the most productive period (July–August 2006) in the northern Baltic Sea on the island of Fårö (59°55,219'N and 21°47,711'E) located in the Archipelago Sea, SW Finland. The experiments were conducted by SCUBA-diving on a uniform, unvegetated (300 m²), shallow (1–1.3 m) sandy bottom adjacent to a mixed (*Zostera marina*, *Potamogeton pectinatus*, *Potamogeton perfoliatus*) seagrass bed growing offshore at 2–6 m depth. The summer water temperature ranges typically between 10 and 20°C and the salinity is ~6‰.

In order to keep patch area, shoot density and shoot length constant, ASUs were constructed of a plastic

mesh (Tensar[®]-geowebbing, 40 mm mesh size) and green polypropylene ribbon. Each “shoot” consisted of two separate “blades” with a length of 30 cm (width 5 mm). ASU shoot density corresponded to 784 shoots m⁻², which is within the range of natural seagrass beds in the study area (500–1200 shoots m⁻², Boström et al., 2003).

Effects of fragmentation were analyzed in a simple randomized design ($n = 5$) consisting of the following treatments: (1) “Continuous”, i.e., a continuous patch (hereafter referred to as “C”), (2) “Fragmented 0.5”, i.e., 4 fragments isolated by 0.5 m and of the same combined area as the continuous patch (hereafter referred to as “F 0.5”) (3) “Fragmented 3.0”, i.e., 4 fragments isolated by 3.0 m and of the same combined area as the continuous patch (“F 3.0”; see Fig. 1). This design allowed separation of fragmentation and isolation effects on epifaunal density and diversity. To see if results were consistent between patch sizes, this design was repeated in two consecutive experiments conducted during a 4 week period (July 15–August 15). Thus, the size of the continuous patch was 0.25 m² (fragment size = 0.0625 m²) and 0.0625 m² (fragment size = 0.01562 m²) in Experiment 1 and 2, respectively (Fig. 1). These patch sizes and configuration patterns are commonly found in the natural seagrass beds in the study area.

Artificial seagrass units were buried in the sediment (~3 cm deep) using metal hooks in a completely randomized design with replicates separated by at least 4 m of unvegetated sediment. In both experiments, the ASUs were left to colonize for 12 days, whereafter they were retrieved by carefully enclosing the entire patch into a netbag. The method is very efficient and we did not observe any swimming macrofauna within 5 s after sampling. Each sample was transported to a boat where plants and animals were transferred to glass jars and preserved in a 70% alcohol–seawater solution.

Laboratory analyses

In the laboratory, animals were counted under a dissecting microscope (×10 magnification) and identified to the lowest practical taxonomic level (usually genus or species). The genus *Idotea* consisted of two species, *Idotea baltica* and *I. chelipes*, but due to similar ecological preferences of both species, and the low contribution of *I. chelipes* to the total abundance,

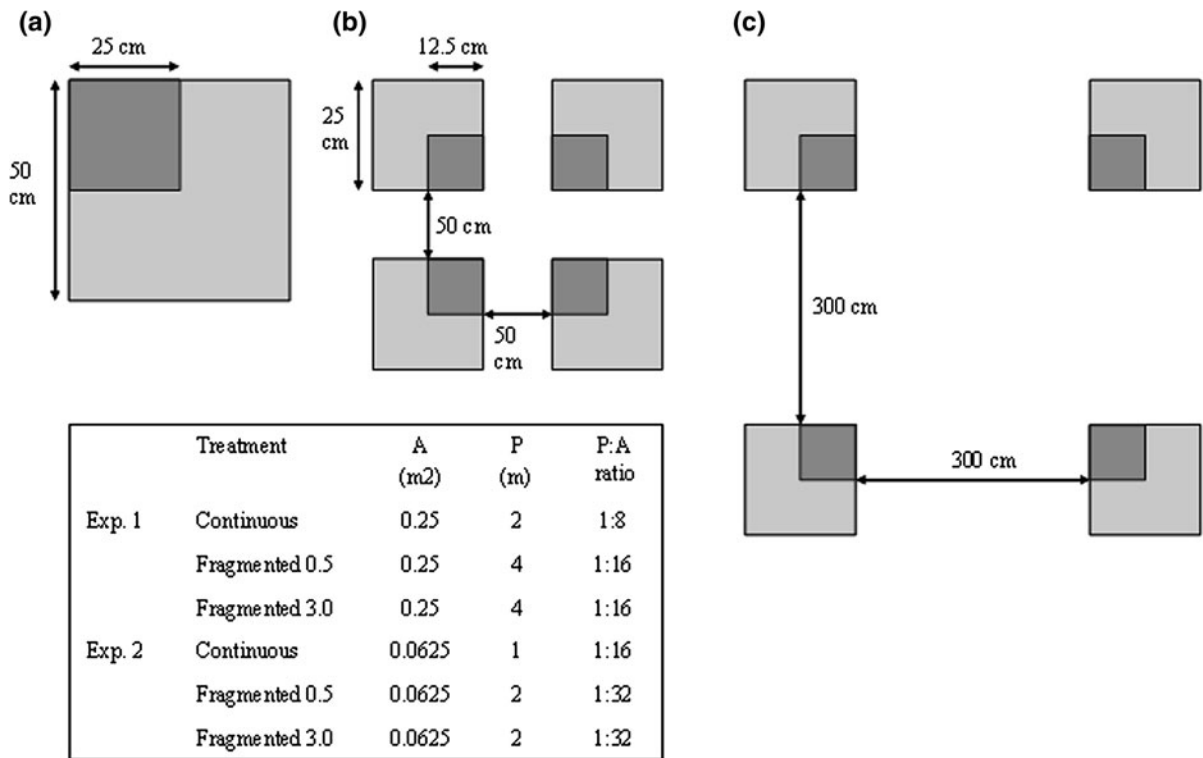


Fig. 1 Schematic representation of the experimental design and treatments. **a** Continuous “C”, **b** Fragmented 0.5 m “F 0.5”, and **c** Fragmented 3.0 m “F 3.0”. Table summarizes patch

area (A), perimeter length (P), and P:A ratios in the two experiments. Dark grey areas indicate patch sizes in the second experiment

these species were combined and are reported as *Idotea* spp. Juvenile Idoteids can not be identified to species level, therefore Idoteids <5 mm are reported as “*Idotea* spp. <5 mm” (Table 1) and included in the total abundance of *Idotea* spp. Similarly Gammarids <5 mm are reported as “juveniles” and included in the total abundance of *Gammarus* spp. In order to compare the amount of drift algae with the density of mobile epifauna (Experiment 1 only, no drift algae recorded in Experiment 2), drift algae was carefully cleaned from animals and dried to constant weight for 48 h in 60°C.

Data analyses

The abundance, number of species and algal biomass of the four individual fragments was pooled in all analyses and compared with the “C” treatments and are reported per metre square. Epifaunal diversity was analyzed using the Shannon index (H'). Both experiments were analyzed separately, using a one-way analysis of variance (ANOVA), with total abundance,

species richness, epifaunal diversity (Shannon H'), abundance of *Idotea* spp., *Gammarus* spp. and *Hydrobia* spp. as dependent variables. Levene’s test was used to test for heterogeneity of variances and normality was tested with Kolmogorov–Smirnov’s test. When necessary, data transformations ($\log_{10}(x + 1)$) were carried out to meet the assumptions for parametric testing (Underwood, 1997). Comparisons among means were performed using the Dunn–Sidak procedure for multiple comparisons (Dunn, 1961). Pearson’s correlation analysis was used to investigate relationships between drifting algal biomass and epifaunal abundance. All means are reported as ± 1 SD.

Results

Total abundance varied between 858 and 1891 individuals m^{-2} , with generally much higher densities in Experiment 2, while species richness showed less variability and ranged between 6.2 (SD ± 1.789) and

Table 1 Total number of individuals (left column) and the relative contribution (right column) of each taxa sampled in the continuous (C) and the two fragmented (F 0.5 and F 3.0) treatments in the first and second experiment in July–August 2006

Species/taxa	Continuous				Fragmented 0.5				Fragmented 3.0			
	Exp 1		Exp 2		Exp 1		Exp 2		Exp 1		Exp 2	
	n	%	n	%	n	%	n	%	n	%	n	%
<i>Idotea</i> spp. total	536	49.9	274	83.8	837	47.1	450	76.1	1040	60.8	7315	74.8
<i>Idotea balthica</i>	8	0.7	6	1.8	5	0.3	15	2.5	8	0.5	7	1.7
<i>Idotea chelipes</i>	48	4.5	152	46.5	58	3.3	225	38.1	62	3.6	209	49.6
<i>Idotea</i> spp. <5 mm	480	44.7	116	35.5	774	43.5	210	35.5	970	56.7	99	23.5
<i>Gammarus</i> spp.	229	21.3	26	8.0	442	24.9	57	9.6	367	21.4	35	8.3
<i>Hydrobia</i> spp.	189	17.6	9	2.8	307	17.3	58	9.8	181	10.6	35	8.3
<i>Lymnea</i> spp.	53	4.9	4	1.2	58	3.3	11	1.9	48	2.8	7	1.7
<i>Mytilus trossulus</i>	29	2.7	4	1.2	80	4.5	5	0.9	32	1.9	2	0.5
<i>Piscicola geometra</i>	14	1.3	5	1.5	21	1.2	4	0.7	27	1.6	4	1.0
<i>Theodoxus fluviatilis</i>	6	0.6	3	0.9	8	0.4	6	1.0	6	0.4	19	4.6
<i>Sygnathus typhle</i>	6	0.6	0	0	6	0.3	0	0	3	0.1	0	0
<i>Crangon crangon</i>	0	0	1	0.3	8	0.4	0	0	1	0.1	1	0.2
<i>Gasterosteus aculeatus</i>	3	0.3	0	0	0	0	0	0	0	0	0	0
<i>Pungitius pungitius</i>	0	0	0	0	4	0.2	0	0	2	0.1	1	0.2
<i>Nerophis ophidion</i>	5	0.5	0	0	3	0.2	0	0	1	0.1	0	0
Mycidacea	1	0.1	0	0	0	0	0	0	3	0.1	1	0.2
<i>Jaera albifrons</i>	2	0.2	1	0.3	0	0	0	0	0	0	0	0
<i>Palaemon adspersus</i>	0	0	0	0	1	0.1	0	0	0	0	0	0
<i>Pomatoschistus minutus</i>	0	0	0	0	1	0.1	0	0	0	0	0	0
<i>Limapontia capitata</i>	0	0	0	0	0	0	0	0	0	0	1	0.2
Total	1073	100	327	100	1776	100	591	100	1711	100	421	100

Idotea spp. total consists of the two identified species (*I. balthica* and *I. chelipes*) and unidentified juvenile idoteids <5 mm in length

9.6 (SD \pm 2.074) species in both experiments (Fig. 2). *Idotea* spp., *Gammarus* spp., and *Hydrobia* spp. dominated the macrofaunal community, and made up >90% of the total abundance in both experiments (Table 1).

Experiment I

Total epifaunal density differed between the continuous and the fragmented treatment ($F_{2,14} = 5.6$, $P = 0.019$), with the “F 0.5” treatment having significantly more individuals than the “C” treatment (Fig. 2a). There was no difference between the “C” and “F 3.0” or between the “F 0.5” and “F 3.0” treatments. The number of species did not differ among treatments ($F_{2,14} = 0.02$, $P = 0.982$, Fig. 2b). Shannon’s index of diversity was significantly lower in the “F 3.0”

treatment than in the “C” and “F 0.5” treatments ($F_{2,14} = 8.8$, $P = 0.004$), while the “C” and “F 0.5” treatments did not differ from each other (Fig. 2c). No significant differences were detected in the density of *Idotea* spp. ($F_{2,14} = 3.2$, $P = 0.078$) (Fig. 3a). The density of *Gammarus* spp. was significantly higher in the “F 0.5” treatment compared to the “C” treatment ($F_{2,14} = 4.4$, $P = 0.037$) (Fig. 3b). The highest density of *Hydrobia* spp. was in the “F 0.5” treatment (Fig. 2c), but this difference was not statistically significant ($F_{2,14} = 4.0$, $P = 0.078$). In Experiment 1, juveniles (<5 mm) dominated the abundances of *Idotea* spp. and *Gammarus* spp. Drift algae consisted of unattached *Pylaiella* spp., *Ectocarpus* spp. and *Cladophora* spp. The “C” treatment collected more drifting algae than the fragmented treatments, however, the difference between treatments was not significant

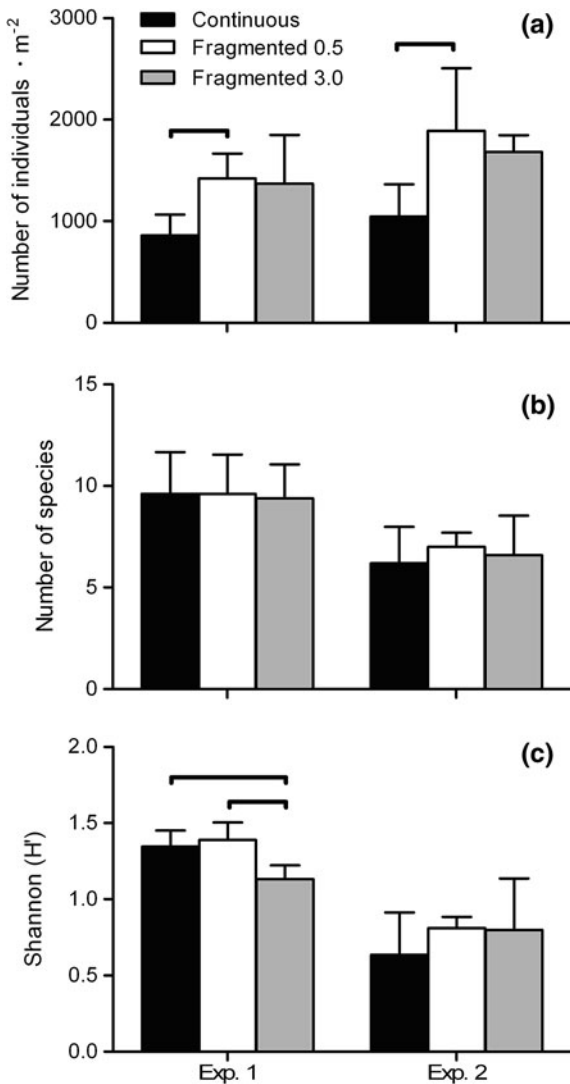


Fig. 2 Epifaunal community variables **a** density, **b** species richness, and **c** diversity (H') in the two experiments in July–August 2006. Significant treatment differences are indicated with horizontal bold lines

($F_{2,14} = 0.87$, $P = 0.445$). No significant relationships were found between the amount of drift algae and epifaunal density (total abundance: $r = -0.042$, $P = 0.88$; *Idotea* spp.: $r = -0.032$, $P = 0.91$; *Gammarus* spp.: $r = -0.239$, $P = 0.39$).

Experiment II

Total epifaunal density was significantly higher in the “F 0.5” treatment compared to the “C” treatment ($F_{2,13} = 5.3$, $P = 0.024$) (Fig. 2a). There were no

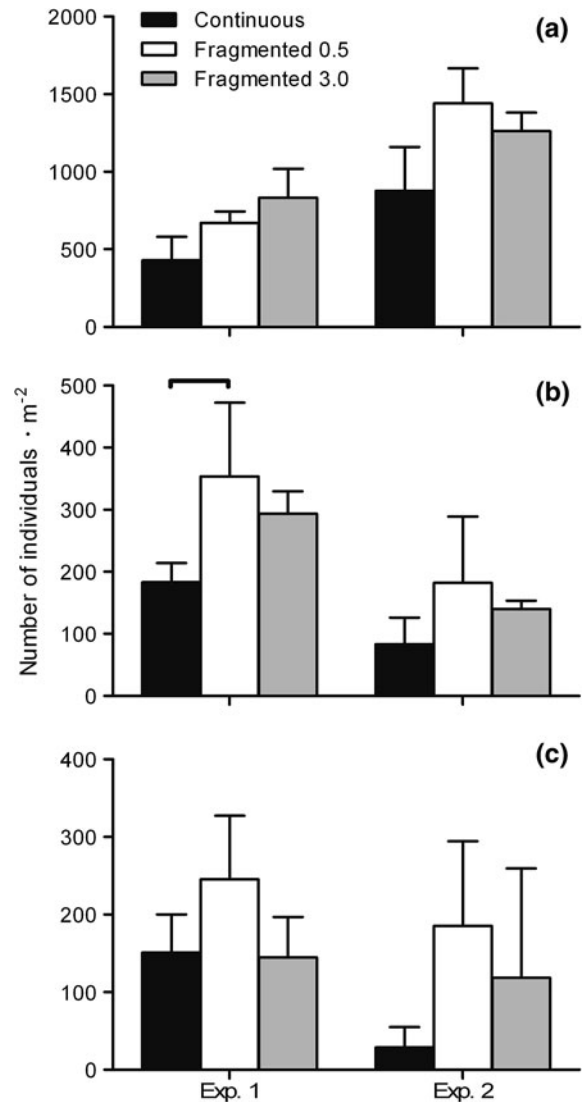


Fig. 3 Densities of dominating epifaunal taxa. **a** *Idotea* spp., **b** *Gammarus* spp., **c** *Hydrobia* spp. in the two experiments in July–August 2006. Significant treatment differences are indicated with horizontal bold lines

significant differences in abundance between the “C” and the “F 3.0” treatment or between the “F 0.5” and “F 3.0” treatment, respectively. The number of species did not differ between treatments ($F_{2,13} = 0.42$, $P = 0.666$, Fig. 2b) and there were no significant differences in diversity (Shannon H') among the treatments ($F_{2,13} = 1.6$, $P = 0.244$, Fig. 2c). Although the “C” and “F 0.5” treatments showed consistently the lowest and highest densities, respectively, no significant influence of fragmentation or isolation was evident on the densities of *Idotea* spp.

($F_{2,13} = 3.0$, $P = 0.092$), *Gammarus* spp. ($F_{2,13} = 1.1$, $P = 0.367$), and *Hydrobia* spp. ($F_{2,13} = 2.9$, $P = 0.095$), respectively (Fig. 3).

Discussion

In both experiments, epifaunal density showed a positive response to fragmentation, which was significant only when distances between habitat patches were short. This result was most probably due to positive edge effects on mobile epifauna. Surprisingly, there were no fragmentation effects on the number of species, and this result was consistent between the two experiments. The negative effect of habitat splitting on species diversity (Shannon H') was most likely due to strong dominance of *Idotea* spp. in the “F 3.0” treatment. None of the three dominating taxa showed a negative response to increased habitat patchiness. Instead, small isolated patches appeared to support higher densities regardless of taxa. Interestingly, patch size appeared to play an unimportant role for total densities of mobile epifaunal; despite the four-fold size difference in both continuous and fragmented patches between the experiments, total density was equal or even higher in Experiment 2. However, due to possible temporal differences in epifaunal abundances between the two consecutive experiments, only qualitative comparisons are possible.

Fragmentation effects

The general prediction based on terrestrial fragmentation studies is decreased density and diversity in small, isolated habitat patches contrasted to larger continuous ones, most likely due to negative edge effects, (Saunders et al., 1991; but see Quinn & Harrison, 1988). In marine environments, the situation appears to be the opposite. Thus, our results are consistent with previous seagrass studies showing that several small patches can harbor more individuals and support similar number of species compared to areas composed of one or a few large patches with approximately the same area (Bell et al., 1987; Sogard, 1989; McNeill & Fairweather, 1993; Eggleston et al., 1998; Loneragan et al., 1998; Hovel & Lipcius, 2001; Healey & Hovel, 2004; Macreadie et al., 2009). Previous studies have largely focused on the changes in habitat configuration and reduction in habitat area (Boström et al., 2006; Connolly & Hindell, 2006) as

explanatory mechanisms for changes in faunal abundance and diversity in fragmented seagrass landscapes. This study revealed positive effects of habitat fragmentation per se on total epifaunal density in both experiments, suggesting that when the variability in habitat area and structural complexity are controlled, increased habitat heterogeneity can positively influence density of mobile epifauna. These results are in line with those reported by Healey & Hovel (2004). However, these authors also found that habitat fragmentation per se had a positive effect on species richness, a result that was not evident in our study.

Edge effects

Faunal responses to increased habitat patchiness and edge effects are largely determined by individual dispersal abilities, which are higher in marine than in terrestrial environments (Robbins & Bell, 1994). Many animals move across edges in their search for food, mating opportunities or avoidance of predators (Schooley & Wiens, 2003). The positive effects of fragmentation per se and minor effects of habitat isolation on total epifaunal abundance give support to the idea of positive edge effects (Ries et al., 2004; Connolly & Hindell, 2006). A mosaic of small seagrass patches increases the total amount of edge and the probability of larval patch encounter, thereby increasing overall colonization of patches (Paine & Levin, 1981; Bell et al., 1987; Sogard, 1989; Eggleston et al., 1998, 1999; McNeill & Fairweather, 1993; Boström et al., 2010). Alternatively, organism preferences or active habitat choice for edges or interior parts of patches can be an important factor in their colonization of fragmented habitats (Bender et al., 1998). In this study, the 100% increase in perimeter length resulted in a 60% increase in total epifaunal abundance, and there was a clear trend of increased abundance of dominating taxa (mainly amphipods and isopods) with increasing habitat patchiness. However, epifaunal richness was consistently similar across treatments in both experiments, suggesting that species richness is insensitive to differences in patch edge-area ratios and fragmentation (Frost et al., 1999; Bowden et al., 2001; Reed & Hovel, 2006). Enhanced faunal abundances and species richness is usually explained by an increased amount of edge in relation to the patch area (i.e., higher P:A ratio) in remaining habitat fragments (Fahrig, 2003). Although edges may

be advantageous to some mobile epifauna, they are also sites of increased predation risk (Tanner, 2005). In our study area, predation risk in seagrass habitats is considered much lower compared to fully marine areas (Boström & Mattila, 1999). Thus our patches probably reached high densities over short time partly because dispersal between habitat patches in the Baltic Sea is less risky (Boström & Mattila, 1999). In addition, the presence of epifauna in small patches depends on the mobility of the species. Highly mobile taxa can disperse across habitats by swimming, whereas stationary species have more restricted capabilities to disperse in patchy habitats (Russell et al., 2005). Accordingly, the faunal assemblage in our patches was dominated by actively swimming taxa, i.e., isopods and amphipods. These taxa, and especially amphipods, can move across unvegetated areas in patchy seagrass habitats by rafting on drift algae (Norkko et al., 2000; Brooks & Bell, 2001; Salovius et al., 2005). However, contrary to our prediction, no significant treatment effects on the amount of algae were found, and algal biomass did not correlate significantly with crustacean density.

Isolation effects

Our results suggest that even very small, isolated fragments may be important for mobile epifauna (Hirst & Attrill, 2008). However, caution should be taken when extrapolating the results obtained in our artificial, small-scale vegetation mosaic to natural patches and large, continuous meadows. Bearing this in mind, our study indicates that patches consisting of a few shoots may function as important, temporary stepping-stones for actively moving invertebrates in shallow seagrass-sand mosaics. Similar results for infaunal organisms in natural *Z. marina* patches (\varnothing 17–147 cm) have also been shown (Hirst & Attrill, 2008).

The distance between habitat fragments appeared to have a minor influence on epifaunal richness and density (Fig. 2). The significantly negative isolation effect for species diversity (H') between the two fragmented treatments in Experiment 1 was due to increased dominance of *Idotea* spp. with increasing distance between fragments. Accordingly, the distance between habitats has less effect on animals with higher dispersal abilities (Andr en, 1994). In marine systems, amphipods and isopods can colonize habitats quickly

and over large distances (Virmstein & Curran, 1986; Eggleston et al., 1998). However, some species respond to isolation only when there are sufficient distances among seagrass patches (Bell et al., 2001). Thus, it is possible that the species studied here did not even perceive the “F 3.0” configuration as fragmented, although seagrass macrofauna is shown to respond to habitat heterogeneity at relatively small (0.25–1 m²) spatial scales (Eggleston et al., 1999). Hence, our results suggest that in order to identify possible thresholds in epifaunal responses to patch isolation, future experiments should incorporate larger spatial scales.

Conclusions

In conclusion, our study demonstrates that the effects of seagrass habitat fragmentation per se are not automatically deleterious for associated faunal communities. However, the degree to which increased patchiness and positive edge effects can compensate for habitat loss probably varies between systems and faunal assemblages. Our results further indicate that the unvegetated matrix between seagrass patches is an essential part of the seagrass habitat, and that small isolated patches may support significant densities of mobile crustaceans. Such configuration patterns are common at high energy sites like ours, where natural factors such as physical disturbance and clonal growth maintain the equilibrium in seagrass-sand mosaics. Thus, conservation efforts should therefore aim at preserving not only continuous vegetation, but also mosaics dominated by bare sand and small seagrass patches.

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