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Integrating edge effects into studies of habitat fragmentation: a test using meiofauna in seagrass

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Abstract Habitat fragmentation is thought to be an important process structuring landscapes in marine and estuarine environments, but effects on fauna are poorly understood, in part because of a focus on patchiness rather than fragmentation. Furthermore, despite concomitant increases in perimeter:area ratios with fragmentation, we have little understanding of how fauna change from patch edges to interiors during fragmentation. Densities of meiofauna were measured at different distances across the edges of four artificial seagrass treatments [continuous, fragmented, procedural control (to control for disturbance by fragmenting then restoring experimental plots), and patchy] 1 day, 1 week and 1 month after fragmentation. Experimental plots were established 1 week prior to fragmentation/disturbance. Samples were numerically dominated by harpacticoid copepods, densities of which were greater at the edge than 0.5 m into patches for continuous, procedural control and patchy treatments; densities were similar between the edge and 0.5 m in fragmented patches. For taxa that demonstrated edge effects, densities exhibited log-linear declines to 0.5 m into a patch with no differences observed between 0.5 m and 1 m into continuous treatments. In patchy treatments densities were similar at the internal and external edges for many taxa. The strong positive edge effect (higher densities at edge than interior) for taxa such as harpacticoid copepods implies some benefit of patchy landscapes. But the lack of edge effects during patch fragmentation itself demonstrates the importance of the mechanisms by which habitats become patchy.

Keywords Landscape ecology · Harpacticoid copepod · Seagrass · Edge effects · Fragmentation · Artificial seagrass units

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Introduction

The role of geometric properties and spatial arrangement of habitat patches in shaping ecological patterns and processes has influenced the development of theoretical ecology, including island biogeography (MacArthur and Wilson 1967), patch dynamics (Picket and White 1985) and boundary effects models (Schonewald-Cox and Bayless 1986). As habitats are increasingly modified by anthropogenic activity, improving prediction of the consequences of changes in habitat configuration has become a prominent goal for ecologists.

Habitat fragmentation involves the simultaneous loss of habitat and alteration of habitat configuration (Villard et al. 1999; McGarigal and Cushman 2002) through the division of patches into smaller, more numerous units with proportionally more edge to interior (Fahrig 2003). The effects of fragmentation on faunal assemblages depend on organism responses to, and preferences for, edge and interior conditions (Bender et al. 1998), which can be manifested as edge effects, whereby proximity to the habitat boundary elicits some change in the response variable.

Empirical work has provided a much better understanding of the effects of fragmentation in terrestrial than aquatic systems despite the propensity for aquatic systems to be fragmented. Seagrass is valuable habitat for marine fauna as it provides the basis of a detrital food chain, sediment stabilisation, nutrient cycling and a refuge from predation for small and juvenile fish and macroinvertebrates (Orth et al. 2006). Seagrass habitats worldwide are under threat of fragmentation from anthropogenic disturbances, and have a natural propensity to form discrete patches of varying size (Ramage and Schiel 1999; Short and Wyllie-Echeverria 1996). This spatial heterogeneity results from the internal regulatory mechanisms of clonal and sexual reproduction and external mechanisms which regulate patchiness and fragmentation through abiotic and disturbance factors (Boström et al. 2006). Seagrass fragmentation assumes two main forms, occurring through the creation of: (1) patches of unvegetated sand within a matrix of seagrass or (2) unvegetated channels dividing continuous tracts into smaller individual patches (Boström et al. 2006). The value and vulnerability of seagrass, in conjunction with the applicability of terrestrial approaches (Robbins and Bell 1994), has motivated studies of habitat fragmentation and edge effects in seagrass systems (e.g. Bell et al. 2001; Tanner 2005, 2006; Reed and Hovel 2006).

Studies of edge effects in seagrass systems have thus far provided inconsistent findings (Connolly and Hindell 2006). Positive (Tanner 2005), negative (Hovel and Lipcius 2002), and neutral (Summerson and Peterson 1984; Tanner 2006) responses to habitat edges have been documented for seagrass-associated fauna. Inconsistencies in results may reflect taxa specific responses, the different spatial and temporal scales considered by different studies (Stephens et al. 2003), and/or inadequacies of experimental design (see reviews by Boström et al. 2006; Connolly and Hindell 2006).

To date, most studies have assessed fragmentation effects on fauna using a static arrangement of patches (Boström et al. 2006; but see Reed and Hovel 2006), and have not considered how the active process of fragmenting habitat actually influences fauna (Boström et al. 2006; Fahrig 2003). Manipulative experiments that actively fragment habitat allow the process of fragmentation to be separated from patterns associated with habitat patchiness (McGarigal and Cushman 2002), but these are rarely done due to logistical and ethical constraints. Furthermore, given the increase in the proportion of edge through fragmentation, understanding how faunal assemblages change from patch edges to interiors will generally strengthen our interpretation of effects of fragmentation on fauna. The study by Reed and Hovel (2006) is one of the few to actively fragment seagrass patches. They found that fragmentation reduced epifaunal abundance and species richness in large plots with 90% habitat removal, but did not attempt to address the interaction between fragmentation and edge effects.

Marine meiofauna play an integral role in the transfer of energy from primary producers to higher trophic orders (Bell and Hicks 1991; Buffan-Dubau and Carman 2000; De Troch et al. 2006), and are also important in the diets of small and juvenile fish (Jenkins et al. 1996; Kendrick and Hyndes 2005). Meiofauna are thought to respond to disturbance regimes at the scales of metres, and are a useful model on which to focus when investigating fragmentation and edge effects at small spatial scales. Understanding the response by meiofauna to seagrass fragmentation and edge effects is also critical in the development of models about changes in the assemblage structure of seagrass-associated animals from higher trophic orders.

In the present study, artificial seagrass units were used to experimentally evaluate how meiofaunal assemblages respond to patch edges, and whether edge effects vary with habitat fragmentation in the form of continuous patches being divided with a matrix of unvegetated sand. Specifically, we tested hypotheses that the assemblage structure of meiofauna would vary: (1) between the edge and 0.5 m into patches, as 0.5 m into seagrass patches represents an important transition point in the sub-canopy flow field (Gambi et al. 1990; Peterson et al. 2004), if proximity to the edge had an effect; (2) in different ways across the edges of patchy and continuous habitats, if habitat configuration had an effect; (3) in different ways across the edges of patches that had undergone fragmentation and those that were originally patchy or continuous, if the process of fragmentation had an effect; and, (4) in different ways across patch edges depending on the location of an edge within a patchy habitat and the spatial resolution of sampling.

Materials and methods

Study area

This study was carried out in a region (Grassy Point: 38°07′S; 144°41′E) of Port Phillip Bay, a large (1,950 km^2),

semi-enclosed tidal embayment linked to the ocean by a narrow rocky entrance (see Black et al. 1993). The seagrass *Heterozostera nigricaulis* (Kuo 2005) occurs intermittently in shallow waters (<5 m deep) around the margins of Port Phillip Bay (Bulthuis et al. 1992), and in the study region occurs in patchy configurations, as a result of anthropogenic and natural phenomena, close to the shoreline.

Study design

Three complementary experiments in the austral summer (September 2006–March 2007) investigated how assemblages of meiofauna associated with artificial seagrass units (ASUs) varied across patch edges and with fragmentation. ASUs facilitate the manipulation of habitat that would be difficult in natural systems, and enable habitat structure (e.g. shoot density, length) to be held constant. ASUs are colonised rapidly (within a week) by meiofaunal invertebrates (Virnstein and Curran 1986), and support fish and invertebrate assemblages similar to those of natural seagrass (Sogard 1989; Upston and Booth 2003).

ASUs used in the current study were made of square 1 × 1 m wire mesh (mesh size 50 × 70 mm), with 16, 40 mm long by 5 mm wide lengths of green, polypropylene ribbon tied to each intersection. This arrangement approximated the leaf morphology and density of shoots measured for the seagrass *H. nigricaulis* in the study area (Jenkins et al. 1998).

Experiment 1: effects of fragmentation on edge effects

ASUs were used to create four treatments (Fig. 1): (1) continuous (C)—nine 1 m^2 ASUs placed together to produce a 3 × 3 m continuous plot; (2) procedural control (PC)—nine 1 m^2 ASUs placed together to produce a 3 × 3 m continuous plot, after 1 week, five ASUs were lifted (leaving the four corner ASUs untouched) and immediately replaced; (3) fragmented (F)—nine 1 m^2 ASUs placed together to form a 3 × 3 m contiguous patch, with five ASUs removed after 1 week leaving only the four corner ASUs each separated by 1 m of unvegetated sand; and (4) patchy (P)—four 1 m^2 ASUs each separated by 1 m of unvegetated sand. Treatments were left for 1 week prior to fragmentation to allow epiphytic growth and faunal colonisation to occur (Virnstein and Curran 1986; Bologna and Heck 2000; Upston and Booth 2003).

The fragmentation experiment was done using a randomised block design with four factors: treatment (C, PC, F, P); time (after fragmentation—1 day, 1 week and 1 month); position (edge of ASU against sand, 0.5 m minimum distance, into the plot); and block (three blocks, each spanning 5 weeks and composed of each treatment × position × time combination). Each block was set up on unvegetated sand, with individual plots (treatment by time combinations, i.e. a set of four or nine ASUs as defined by treatment to be sampled 1 day, 1 week or 1 month after fragmentation) positioned 30 m apart and <10 m from natural seagrass. ASUs were removed, cleaned (using high pressured fresh water) and redeployed between blocks.

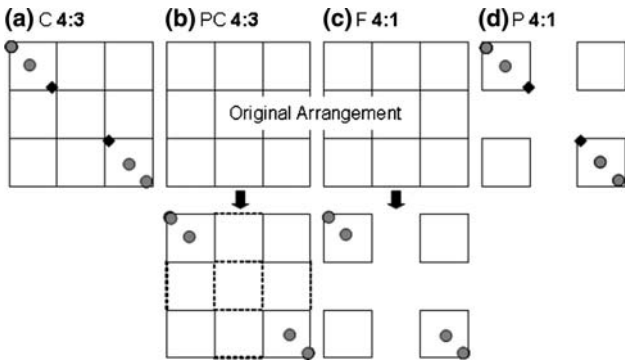

Fig. 1 Schematic of **a** continuous (*C*), **b** procedural control (*PC*), **c** fragmented (*F*), and (**d**) patchy (*P*) treatments constructed from 1 m^2 artificial seagrass units (ASUs). Corresponding perimeter-to-area ratios are shown. Empty 3 × 3 diagrams in panels **b** and **c** represent the original arrangement of PC and F treatments for the week prior to disturbance or fragmentation. In panel **b**, *dashed lines* represent ASUs that have been removed and then immediately replaced. *Grey circles* Location of samples in experiment 1, *black diamonds* location of the additional 1 m samples from C and P treatments in experiment 2

Meiofauna were sampled with a corer (150 mm diameter × 400 mm long, covered at one end with 63 µm mesh) placed vertically over 16 pre-determined shoots. The ribbon was cut immediately above the substratum, and a metal plate was used to seal the core before it was inverted and raised to the surface, where the contents were washed into a jar and preserved in ethanol. Two sub-samples were taken from each position in each plot. In the laboratory, samples were washed through a 63 µm sieve, and retained meiofauna counted and identified to the lowest taxonomic level possible. Difficulty with identification prohibited animals being identified to species.

Experiment 2: extent of edge effects

A second experiment investigated whether meiofauna changed between (1) the internal and external edges of P plots, and (2) the edge and 1 m (minimum distance) into C plots (Fig. 1). Four replicates of treatments C and P were established 1 week prior to sampling. Because the fragmented treatment from experiment one did not demonstrate an edge effect, neither F nor PC were included in experiment 2. Meiofauna were sampled at three positions in each plot: edge (sand/seagrass interface); 0.5 m (minimum distance) into the plot; and 1 m (minimum distance) into the plot (Fig. 1) using the methods described earlier. Two

sub-samples were taken from each plot, and were processed as above.

Experiment 3: shape of edge effects

A final experiment investigated whether the shape of edge effects varied between continuous and patchy treatments. Four replicates of C and P were set up 1 week prior to sampling (as in experiment 2). Because densities of meiofauna did not differ between internal and external edges of P plots, or between 0.5 and 1 m into C plots in experiment 2, samples were taken only as far as 0.5 m into plots. Meiofauna were sampled at five positions (edge, 12.5, 25, 37.5, and 50 cm, minimum distance, into plots), and samples were processed as above.

Statistical analyses

Assumptions of normality and homogeneity of variances were checked using box-plots and plots of residuals, respectively (Quinn and Keough 2002). Data that failed to meet these assumptions were $\log_{10}(x + 1)$ transformed and reassessed. Taxa occurring in >50% of samples were analysed separately. Sub-samples were averaged prior to analyses.

Experiment 1

Four-factor, repeated measures ANOVAs were used to compare densities of meiofauna among treatments (fixed), times (fixed), positions (repeated measure, because the edge and 0.5 m samples were taken from the same plots) and blocks (random). The blocking factor was included to provide replication in assessing variance among treatments, times after fragmentation and positions, so the focus for all results is confined to these main effects.

Two series of a priori comparisons were used to answer subtly different questions about edge effects and fragmentation. First, to assess whether the presence of an edge effect differed with fragmentation, the edge and 0.5 m were compared for each treatment separately. Second, to assess whether the magnitude of edge effects differed with fragmentation, differences in meiofaunal densities across the edge (edge–0.5 m) were compared between pairs of treatments. C treatments were first compared to PC to test for experimental artifacts. If this test was not significant ($P > 0.05$), the average of C and PC was compared to each of F and P, separately. Post hoc power analyses, based on a 100% effect size, were used to assess confidence in detecting a difference between C and PC. If, however, C and PC were different, or power was low, then PC was compared to F, and C to P. F was compared to P as a test of fragmentation versus patchiness.

Experiment 2

Two-factor, repeated measures ANOVAs were used to compare meiofauna between treatments (fixed) and among positions (repeated measure). Because position had >2 levels, the assumption of sphericity of variances was checked by the Greenhouse–Geisser (G–G) epsilon, and the potential for violation of this assumption to influence results was controlled by using the G-G adjusted probability values (Quinn and Keough 2002).

A priori comparisons were used to compare meiofaunal abundances among positions for each treatment separately. For C, densities of meiofauna were first compared between 0.5 and 1 m. If these did not differ, their average was compared to edge. If, however, meiofauna differed between 0.5 and 1 m, edge was compared to 0.5 and 1 m separately. For P, meiofauna were compared between the external and internal (1 m) edges, and if these were not different, their average was compared to 0.5 m. If, however, densities were different between the edge and 1 m, then 0.5 m was compared to each separately. Post hoc power analyses, based on a 100% effect size, were used to assess confidence in detecting a difference between positions where a non-significant result lead to averaging and comparison with another term. Where power was low, if the subsequent planned comparison was significant, it shows that there was a strong edge effect; where it was not significant, we provide the additional single factor comparisons.

Experiment 3

Two-factor, repeated measures ANOVAs were used to compare meiofaunal densities between treatments (fixed) and among positions (repeated measure). Assumptions of sphericity of variances were checked as above. The shape of the edge effect was investigated by assessing the response curve of position data with single degree-of-freedom polynomial contrasts. Post hoc multiple comparisons for repeated measures were conducted among levels of position, pooled across treatments. Dunn–Sidak corrections were applied to control the family wise type 1error rate.

Results

Over all experiments, meiofauna were separated into 20 taxa, predominantly crustaceans, including Harpacticoida, Calanoida, Ostracoda, Isopoda, Amphipoda, Cumacea, and crustacean nauplii and metanauplii. Smaller numbers of Gastropoda, Polychaeta and Ophiuroidea were also sampled. Samples in all experiments were numerically dominated by harpacticoid copepods and crustacean nauplii which together made up approximately 95% of all individuals.

In all experiments the only taxa that occurred in >50% of samples and thus were analysed individually were harpacticoid families, calanoids, ostracods and crustacean nauplii.

Experiment 1: effects of fragmentation on edge effects

Total meiofaunal densities varied between positions overall ($F_{(1,2)} = 55.7$, $P = 0.017$) but planned comparisons did not show differences between positions for any particular treatment (PC, C, F or P) (Table 1). Calanoids, ostracods and crustacean nauplii and metanauplii showed a non-significant response to all main effects: position, time after fragmentation, and treatment.

There were significantly greater densities of total harpacticoids and Parastenheliidae (the dominant harpacticoid family) at the edge than 0.5 m in C, PC and P plots, but not F plots (Table 1, Fig. 2). The change in harpacticoid density across the edge did not differ between C and PC treatments, or between the average of C/PC treatments and P. However, differences in total harpacticoid densities between the edge and 0.5 m for the fragmentation treatment differed significantly from the average of C/PC, but not P (Table 1, Fig. 2a). This pattern appeared consistent throughout the experiment; position × block, position × time, position × treatment × block, and position × block × time interactions were all non-significant.

Experiment 2: extent of edge effects

Densities did not vary significantly between C and P for any taxon, and the position × treatment interaction was also not significant. However, densities of many taxa varied significantly with position and this pattern was particularly strong for total meiofauna ($F_{(2,12)} = 10.3$, G–$G = 0.008$; Fig. 3a) and harpacticoids ($F_{(2,12)} = 12.4$, G–$G = 0.009$;

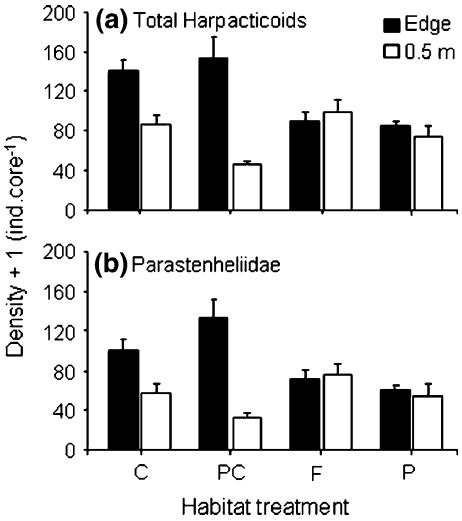

Fig. 2 Experiment 1. Density of harpacticoid taxa (mean + SE) at the edge (*black bars*) and 0.5 m into plots (*white bars*) for different habitat treatments: *C* continuous, *PC* procedural control, *F* fragmented, *P* patchy. Density is shown as the number of individuals per core where core = 150 mm diameter × 400 mm length. Samples were pooled across time after fragmentation and block, data were $\log_{10}$ transformed prior to analyses, $n = 9$. **a** Total harpacticoids. **b** Parastenheliidae

Fig. 3c). Densities differed between internal and external edges of P for Ectinosomatidae only, while average densities across internal and external edges were greater than those 0.5 m into plots for total meiofauna, total harpacticoids, Thalestridae, Parastenheliidae and Tisbidae (Table 2, Fig. 3). Differences were also observed across edges of continuous plots. Densities of total meiofauna, total harpacticoids, Parastenheliidae, Tisbidae, Miraciidae, and ostracods did not differ between 0.5 and 1 m into C plots, but densities at the edge were greater than the average of those at the 0.5 and 1 m positions for the afore mentioned taxa (Table 2,

Table 1 Results of a priori comparisons comparing taxa density among positions (edge and 0.5 m into a plot) and treatments (*C* continuous, *PC* procedural control, *F* fragmented, *P* patchy)

Treatment	Source	Total meiofauna			Total harpacticoids			Parastenheliidae		
		MS	*P*	Power[a]	MS	*P*	Power	MS	*P*	Power
C	E = 0.5 m	0.130	0.147		0.343	0.028*		0.749	0.024*	
PC	E = 0.5 m	0.279	0.051		0.855	0.004*		0.994	0.013*	
F	E = 0.5 m	0.003	0.809		0.005	0.747		0.041	0.496	
PC	E = 0.5 m	0.104	0.188		0.295	0.037*		0.877	0.017*	
Diff. data	C = PC	0.028	0.603	95	0.115	0.302	100	0.017	0.759	100
	Average(C/PC) = F	0.332	0.108		0.904	0.019*		0.708	0.085	
	Average(C/PC) = P	0.020	0.659		0.060	0.445		<0.001	0.988	
	F = P	0.142	0.263		0.373	0.088		0.539	0.123	

* $P < 0.05$

[a] Power (%), based on 100% effect size, given for non-significant comparisons that resulted in an averaging before comparison to another term. Data were $\log_{10}(x + 1)$ transformed prior to analysis

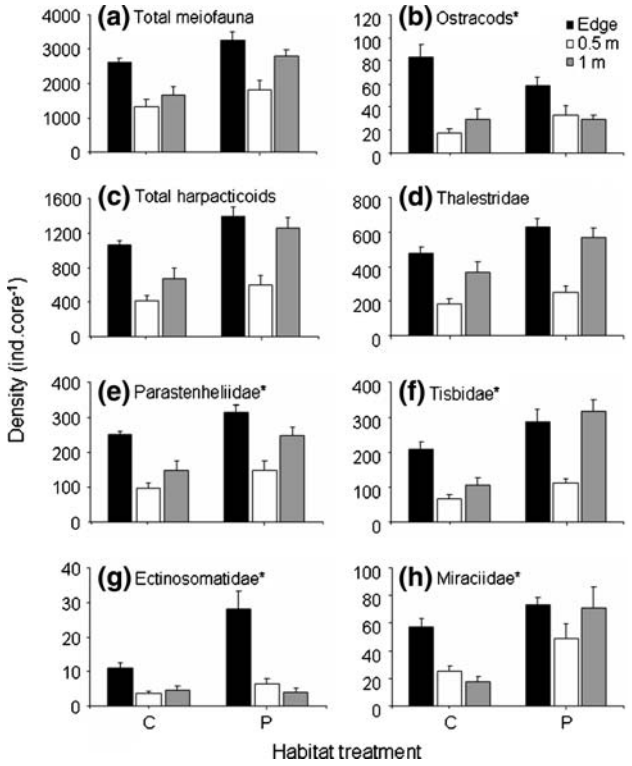

Fig. 3 Experiment 2. Density of meiofauna taxa (mean +SE) for continuous (*C*) and patchy (*P*) treatments at the edge (*black bars*), 0.5 m (*white bars*) and 1 m (*grey bars*) into the plots ($n = 4$). Data that were log10($x + 1$) transformed prior to analyses are indicated with an asterisk (*) after the taxon name. **a** Total meiofauna, **b** Ostracods, **c** total harpacticoids, **d** Thalestridae, **e** Parastenheliidae, **f** Tisbidae, **g** Ectinosomatidae, **h** Miraciidae

Fig. 3) There was no significant effect of position within C plots for Ectinosomatidae. Densities of Thalestridae at the edge differed from those 0.5 m, but not 1 m into C plots (Table 2, Fig. 3d). Planned comparisons revealed no significant effect of position within either C or P treatments for crustacean nauplii (Table 2) despite a significant effect of position in the main analysis ($F_{(2,12)} = 4.2$, G–$G = 0.048$).

Experiment 3: shape of edge effects

Densities of taxa did not vary significantly between P and C treatments, but there was a significant effect of position for many taxa, including total meiofauna ($F_{(4,24)} = 8.3$, G–$G = 0.002$) and total harpacticoids ($F_{(4,24)} = 8.1$, G–$G = 0.004$) (Fig. 4a, c). As data were log transformed prior to analyses to meet assumptions of the tests, significant single degree-of-freedom, first-order polynomial contrasts indicated a log-linear response of density to position, for total meiofauna ($F_{(1,6)} = 33.1$, $P = 0.001$), total harpacticoids $F_{(1,6)} = 43.1$, $P = 0.001$), crustacean nauplii $F_{(1,6)} = 21.5$, $P = 0.004$) and several harpacticoid families (Fig. 4). Post hoc multiple comparisons showed that the decline in

Table 2 Results of planned comparisons comparing taxa densities among positions [edge (*E*), 0.5 m and 1 m into a plot] for each treatment (continuous and patchy). *TM* Total meiofauna, *TH* total harpacticoids, *Thal* Thalestridae, *Para* Parastenheliidae, *Tisbi* Tisbidae, *Mir* Miraciidae, *Ectin* Ectinosomatidae, *Ost* Ostracods, *C Naup* Crustacean nauplii, *TNR* test not required

Source	TM		TH		Thal		Para[a]		Tisbi[a]		Mir[a]		Ectin[a]		Ost[a]		C naup	
	P	Power[b]	*P*	Power	*P*	Power	*P*	Power	*P*	Power	*P*	Power	*P*	Power	*P*	Power	*P*	Power
Continuous																		
0.5 M versus 1 M	0.425	5	0.228	5	0.125	5	0.406	100	0.344	100	0.211	100	0.570	65	0.389	100	0.791	5
(0.5 M + 1 M)/2 versus E	0.021*		0.027*		0.091		0.026*		0.002*		0.013*		0.220		0.003*		0.099	
E versus 0.5 M	TNR		TNR		0.021*		TNR		TNR		TNR		0.176		TNR		0.124	
E versus 1 M	TNR		TNR		0.330		TNR		TNR		TNR		0.272		TNR		0.078	
Patchy																		
E versus 1 M	0.280	5	0.527	5	0.597	5	0.463	100	0.673	100	0.214	100	0.031*		0.163	100	0.297	5
(E + 1 M)/2 versus 0.5 M	0.016*		0.005*		0.000*		0.026*		0.005*		0.506		TNR		0.190		0.156	
E versus 0.5 M	TNR		TNR		TNR		TNR		TNR		0.205		0.063		0.054*		0.062	
1 M versus 0.5 M	TNR		TNR		TNR		TNR		TNR		1.000		0.697		0.532		0.351	

* $P < 0.05$

[a] Data that were $\log_{10}(x + 1)$ transformed prior to analysis

[b] Power (%), based on 100% effect size, given for non-significant comparisons that resulted in an averaging before comparison to another term

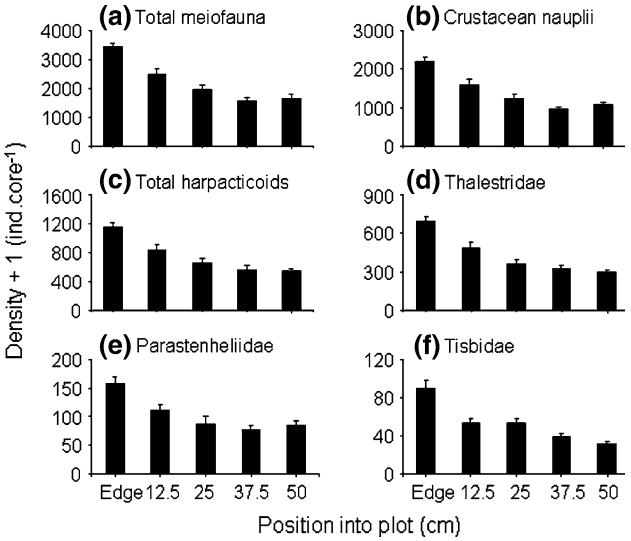

Fig. 4 Experiment 3. Density of meiofauna taxa (mean +SE) at each position: edge, 12.5 cm, 25 cm, 37.5 cm, 50 cm into a plot ($n = 8$), pooled across treatments. Data were $\log_{10}$ transformed prior to analyses. **a** Total meiofauna, **b** Crustacean nauplii, **c** total harpacticoids, **d** Thalestridae, **e** Parastenheliidae, **f** Tisbidae

density became significant ($P < 0.05$) between 25 and 50 cm for different taxa.

Discussion

Faunal responses to patch edges have been investigated in seagrass systems, but knowledge of the influence of habitat configuration and fragmentation on the magnitude and direction of edge effects is limited. The series of experiments presented here show strong changes in meiofaunal densities across patch edges, contingent upon the process by which patches achieved their configuration. Although some taxa showed no response to patch edges regardless of treatment, densities of harpacticoid copepods were greater at edges than 0.5 m into C, PC and P, but not F. For several taxa, densities declined in a log-linear fashion over the first 0.5 m into both C and P plots. Densities did not differ between 0.5 m and 1 m into C plots, suggesting the edge effect occurred within the first 0.5 m and few taxa responded differently to the external and internal edges of P plots.

Meiofaunal responses to seagrass edges

The direction and magnitude of edge effects observed for seagrass-associated macrofauna have been highly variable (Connolly and Hindell 2006), with many taxa showing no response to patch edges (Hovel et al. 2002; Hovel and Lipcius 2002; Tanner 2006). This variability is thought to reflect taxa specific (Boström et al. 2006) and scale-dependent (Stephens et al. 2003) responses of fauna to habitat edges. While some taxa in the present study showed little or no variation in densities across patch edges, strong differences between the edge and 0.5 m were observed for harpacticoids (in all experiments), total meiofauna (experiments 2 and 3) and for ostracods and crustacean nauplii in experiments 2 and 3, respectively. Densities of total harpacticoids (and many harpacticoid families) were significantly higher at the edge than 0.5 m into patches, and this was consistent through time and among experiments. Similar effects have been demonstrated in natural *H. nigricaulis,* where densities of total harpacticoids were greater at the edge than 2 m into patches (Murphy 2007), indicating the results from the current study are not merely an artifact of ASUs. Results from experiments 2 and 3 indicated that the decline from edge to interior occurred within the first 0.5 m into a plot, with similar densities observed at the internal and external edges of patchy plots, for most taxa. Tanner (2005) also found that much of the variation in the density of amphipods and tanaids occurred in the first 0.25–1 m into a patch. Studies using the first 1 m of patches as edge (e.g. Bowden et al. 2001; Bologna and Heck 2002) therefore, risk missing such fine-scale patterns, although the extent of any edge effect will clearly depend on the type of animals being investigated (Attrill et al. 2000).

In both continuous and patchy plots, declines in densities of many taxa from edge to 0.5 m fitted a linear function (based on log data), and this did not change between continuous and patchy plots. The spatial scale of investigations of faunal responses to habitat structure should be prescribed by the grain and extent of an animal's perception window (i.e. the scale over which an organism perceives its habitat as heterogeneous; Attrill et al. 2000; Turner et al. 2001); however, the scale at which perturbations commonly occur should also be considered. Although little is known about the movement rates of the specific taxa sampled in this study, small epifaunal organisms similar to those sampled here have been found to respond to habitat heterogeneity at scales of <1 m (Eggleston et al. 1998, 1999). Perhaps meiofauna perceived the 1 m^2 ASUs that comprised the P treatments as homogeneous habitat, accounting for the similarity of the edge effect in C and P treatments.

Recently, there has been some attention given to the development of frameworks for mechanistic explanations of edge effects (Fagan et al. 1999; Ries and Sisk 2004). Fagan et al. (1999) devised four general categories through which edges alter species interactions: edges differentially influencing the movement of individuals, edges differentially inducing species mortality, edges facilitating cross boundary subsidies, and edges creating opportunities for novel interactions. Due to the inhospitable nature of the matrix, for epiphytic meiofauna, the third category is

unlikely to explain the edge effects observed in the current study.

Seagrass is known to baffle unidirectional (Fonseca and Fisher 1986) and oscillatory (Fonseca and Cahalan 1992) currents with deceleration of flow velocity largely occurring within the first 0.5 m into the patch (Gambi et al. 1990; Peterson et al. 2004). Hydrodynamic changes across patch edges may, therefore, account for the direction and scale of meiofauna responses to patch edges in the current study through three of Fagan et al.'s (1999) general mechanistic categories. Seagrass edges may influence meiofauna movements by providing a physical barrier to dispersing individuals with poor swimming capabilities, entraining them at edges as flow decelerates further into the patch (Bologna and Heck 2000). Increased mortality through elevated predation pressure may account for lower meiofauna densities at patch interiors. Small and juvenile fish which prey on meiofauna (Jenkins et al. 1996; Kendrick and Hyndes 2005) may benefit from low-flow conditions of patch interiors that can alter feeding opportunities (Palmer 1988) and may provide protection from larger piscivores (Hindell et al. 2002). Elevated flow at patch edges may provide opportunities for novel interactions by promoting increased growth of microalgae, upon which meiofauna graze (Bell and Hicks 1991). Therefore, meiofauna may be responding to a resource base that has shown a response to patch edges; a response termed 'cascading edge effect' (Ries and Sisk 2004). If, however, hydrodynamics were exclusively influencing taxa density across edges, then it could be expected that patterns in patches with the same configuration and subject to the same hydrodynamic regime would be similar, irrespective of historical configurations.

Effects of fragmentation on meiofaunal edge effects

Many studies of edge effects in marine habitats have considered faunal responses to patch edges to represent responses to habitat fragmentation (e.g. Bell et al. 2001; Tanner 2005), but only one has attempted to separate patchiness from fragmentation (Reed and Hovel 2006). In the present study, the direction and magnitude of the edge effect observed for total harpacticoids and Parastenheliidae (the dominant harpacticoid family) was similar in C, PC, and P. This suggests that neither the physical disturbance associated with fragmentation nor habitat patchiness affected the density of harpacticoids across patch edges. However, an edge effect was not observed in fragmented plots for total harpacticoids or Parastenheliidae, where there was a trend of higher density at 0.5 m into fragmented than other treatments.

The difference in total harpacticoid density between the edge and 0.5 m differed between F and C/PC. However, it did not differ significantly between F and P treatments, despite there being no edge effect in F plots. This suggests harpacticoid responses to edges in P plots may have been intermediate to those for C/PC and F treatments. Edge effects that vary with habitat configuration have also been documented by Donovan et al. (1997) who found higher nest predation of forest songbirds at edges than interiors in highly and moderately fragmented landscapes but not continuous. Conversely, Parker and MacNally (2002) demonstrated an edge effect for invertebrates in terrestrial grassland habitat that was consistent between continuous and fragmented treatments. These differences may reflect taxon-specific responses or fundamental differences in the processes structuring marine and terrestrial systems (Robbins and Bell 1994; Tanner 2005).

The mechanisms generating edge effects will depend on the characteristics of the edges and species involved (Fagan et al. 1999; Ries and Sisk 2004). Edge characteristics will be influenced by the mechanisms of edge creation, e.g. rapid creation through anthropogenic fragmentation or gradual formation through growth; and associated historical configurations (Boström et al. 2006). Patch size affects colonisation of seagrass habitats by invertebrates (Roberts and Poore 2005) and fish (Jelbart et al. 2006) and historical colonisers can influence the colonisation success and persistence of subsequent colonists (Irving et al. 2007). Therefore, different fish and macroinvertebrate assemblages may have established in F versus P treatments prior to fragmentation with differences persisting post-fragmentation to exert different predation and competitive pressures on meiofauna in F and P treatments. The differences observed in harpacticoid edge responses between C/PC and F treatments (which all had the same configuration prior to fragmentation) may reflect interactions between predation or competitive pressures and habitat area.

The reduction of overall habitat area through fragmentation may have produced crowding effects; the concentration of animals in remnant patches followed by community relaxation to a new equilibrium (Bierregaard et al. 1992). Crowding fish and macroinvertebrates, previously occupying 9 m^2, into a 4 m^2 habitat may have precluded any possible preferential response to edge or interior habitat due to space and resource limitations. Therefore, any influence of within patch predator preferences or physical factors on harpacticoid responses to patch edges may have been eliminated or masked in F treatments by higher densities and species diversity per unit area of these higher trophic order organisms.

Of principle interest are the timeframes involved in reaching equilibrium, whereby organism responses to edges in fragmented habitats equate to those in patchy. The effects of fragmentation on the density of total harpacticoids and Parastenheliidae appeared consistent throughout the experiment and remained apparent 1 month after fragmentation

(i.e. highly non-significant interactions between position and time after fragmentation/block). Experimental fragmentation of natural seagrass by Reed and Hovel (2006) also demonstrated that effects of fragmentation on epifaunal density and assemblage composition were similar 4 and 8 weeks after initial fragmentation. Terrestrial studies have shown crowding effects to persist for months (Parker and Mac Nally 2002) indicating the plausibility of the fragmentation effects in the current study being due to crowding effects.

Understanding of fragmentation effects in seagrass systems will be furthered by investigation over larger spatial and temporal scales, particularly to resolve questions of fragmented versus patchy habitat. In addition, as patch shape has been shown to influence animal responses to seagrass habitat (Tanner 2003) investigation into fragmentation in different shaped patches will also be beneficial.

This study has provided the first information about how edge effects for seagrass meiofauna are affected by habitat fragmentation and patchiness. Patchy habitat did not equate to fragmented habitat in terms of harpacticoid responses across patch edges and future studies must consider either experimentally fragmenting the habitat, or conducting mensurative experiments before and after predictable fragmentation events, e.g. seasonal dieback. Many meiofauna taxa, particularly harpacticoids, demonstrated significantly higher densities at patch edges, indicating that increased perimeter-to-area ratios may be advantageous. However, the processes by which a habitat achieves its configuration will affect meiofaunal responses to patch edges. Frequent monitoring of the geometric properties and spatial arrangement of seagrass habitats will thus be valuable in improving predictions of faunal responses to habitat changes.

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