Response of fauna in seagrass to habitat edges, patch attributes and hydrodynamics

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Abstract This study has investigated the taxon-specific responses of fauna to patch edges, and how these relate to patch attributes (patch size, seagrass biomass and water depth), and hydrodynamics in the seagrass habitat. Faunal abundances were sampled at the edge, 2 m in from the edge, and in the middle of 10 seagrass patches of variable size in Port Phillip Bay, Australia. Five of nine taxa showed edge effects. There were higher abundances at the edge compared with the middle for porcellid harpacticoids, and an increase in abundance from the edge to the middle of the patches for tanaids and isopods. For caprellid and gammarid amphipods, the edge effect varied across patches. Changes in current within the patch and patch size were related to the variability in the edge effect pattern of caprellids. None of the measured environmental variables (seagrass biomass, current and water depth) or patch size had a role in the variable edge effect pattern of gammarid amphipods. At the patch level, the distribution of six of nine taxa in this study, namely isopods, polychaetes, 'other harpacticoids', porcellid harpacticoids, cumaceans and gammarid amphipods, was related to differences in average water depth, average seagrass biomass and patch size. Our study indicates that the faunal response to edges cannot be generalized across seagrass habitat, and the implications of habitat area loss will vary depending on the taxon under consideration.

Key words: edge effect, fauna, habitat area loss, seagrass.

INTRODUCTION

In terrestrial systems, fragmentation and habitat area loss are considered to be among the biggest threats to biodiversity (Henle *et al.* 2004). The reduction in habitat structure from fragmentation and habitat area loss influences the abundance and distribution of animals and changes the ecological processes within the patch by reducing connectivity between patches, reducing patch area and increasing the amount of edge habitat (Fagan *et al.* 1999). Edge effects, which refer to the distinctive species composition and abundance in the outer portion of the habitat fragment (Fagan *et al.* 1999), are the result of a change in habitat configuration during fragmentation. The effect of the edge habitat increases with a decrease in patch area, as the ratio of habitat perimeter to habitat area increases (Murcia 1995; Ranta *et al.* 1998). The abiotic and biotic processes at the edge of a fragment can be different from the interior of a patch. This can result in high biodiversity and productivity at the edge of habitats (Davies-Colley *et al.* 2000); however, habitat edges can also allow for an increase in predation and an invasion of exotic species to the detriment of some species (Harrison & Bruna 1999; Flaspohler *et al.* 2001).

In the marine environment, seagrass meadows add complexity to soft sediments, provide food and refuge for numerous animal species, and increase the biodiversity and productivity of coastal waters (Healey & Hovel 2004). Seagrass habitat is often naturally patchy, but it is also vulnerable to further fragmentation and habitat area loss by such factors as eutrophication (Short & Burdick 1996), dredging (Erftemeijer & Lewis 2006) and propeller scarring (Uhrin & Holmquist 2003; Burfeind & Stunz 2007). Studies of edge effects in seagrass meadows have found few patterns that are consistent among species and over time, and reviews tend to emphasize the variability in species responses to edges (Bostrom *et al.* 2006; Connolly & Hindell 2006).

Variable results from previous edge effect studies on seagrass fauna suggest that there may be an interaction between, or a combination of, factors operating in the seagrass patches. These factors may include habitat configuration (Eggleston *et al.* 1998; Healey & Hovel 2004), proximity to adjacent habitats (Skilleter *et al.* 2005; Jelbart *et al.* 2007), physical environment and hydrodynamics (Bologna & Heck 2002) and internal patch attributes (Bologna & Heck 2002; Tanner 2005; Bologna 2006). There is evidence of a combined, yet variable, role of patch attributes and the physical environment on nekton in the seagrass ecosystem (Connolly & Hindell 2006). For example, the correlation between survival rate of crabs and patch size is not consistent, as the effect of patch size varies between regions depending on the interaction between habitat complexity and hydrodynamics (Hovel 2003). Physical factors, such as water depth and currents, have been shown to influence the distribution of nekton within patches (Hovel *et al.* 2002; Jackson *et al.* 2006). The direct influence of physical factors may override the effect of patch attributes, such as seagrass biomass, on edge effect patterns (Connolly & Hindell 2006). Little is known about the relative importance of patch attributes and the physical environment in determining faunal abundances in the seagrass habitat.

Fauna, such as harpacticoids, amphipods and polychaetes, are important secondary producers in seagrass habitats (Bologna & Heck 2002; De Troch *et al.* 2005; Bologna 2006). These species are also an important prey type for the majority of seagrass fish (Edgar *et al.* 1999), and their distribution within seagrass can influence the patterns of juvenile fish distribution and survival (Connolly 1994; Jenkins & Hamer 2001). Faunal abundances have been found to vary with patch size, indirectly indicating a potential edge effect (Bell *et al.* 2001; Healey & Hovel 2004). Surveys of the abundance of seagrass fauna at different positions within patches have also revealed edge effects, if somewhat sporadically (Sanchez-Jerez *et al.* 1999; Tanner 2005; Bologna 2006).

This study assessed faunal responses to seagrass patch edges and determined which environmental variables may be underlying these patterns. We aimed to answer these questions by (i) using a combination of sampling at fixed (edge and 2 m inside edge) and proportional (edge and middle) distances into seagrass patches to determine if there were faunal responses to seagrass patch edges; and (ii) focusing on four variables that we thought may have an important role in producing edge effects: patch size, hydrodynamics (currents) and patch attributes (seagrass biomass and water depth). In addition to analysis of edge effects, we also looked at the role of these variables in producing patch level variation in abundance of seagrass fauna.

METHODS

This study was conducted in Port Phillip Bay, which is a large (2000 km^2), semi-enclosed, tidal embayment in southern Australia linked to the ocean by a narrow entrance (see Jenkins *et al.* 2002 for a fuller description) (Fig. 1). We chose 10 seagrass patches of varying shape and size (mean 1265.6 m^2, range 113–5934 m^2) of the dominant seagrass, *Heterozostera nigricaulis* (leaf length 15–20 cm) at Blairgowrie, which is close to Port Phillip heads in an area strongly influenced by the tidal exchanges with Bass Strait (Jenkins *et al.* 2002) (Fig. 1). The range of seagrass patch areas was typical of that observed in the southern part of Port Phillip Bay. The seagrass cover at Blairgowrie was high in the 1990s, but has reduced in area and has fragmented since then (Ball & Heislers 2008).

At Blairgowrie, the 10 seagrass patches were sampled three times over 6 weeks in the austral Spring of 2006 at the patch edge, which was defined as seagrass within 30 cm of the sand/seagrass interface, 2 m into the bed from the patch edge and in the middle position of the patch. We measured faunal abundances at the fixed position of 2 m into the bed from the patch edge based on a previous study of edge effects patterns of small nekton conducted in these 10 seagrass patches (Smith *et al.* 2009). The middle position was at variable distances into patches, ranging from just over 2 m in the smallest patch to 25 m in the largest patch. Samples were taken with a 40-cm-long PVC tube with 9-cm internal diameter, and one end was covered with 50-μm mesh. Three samples were collected at each of the three positions in each
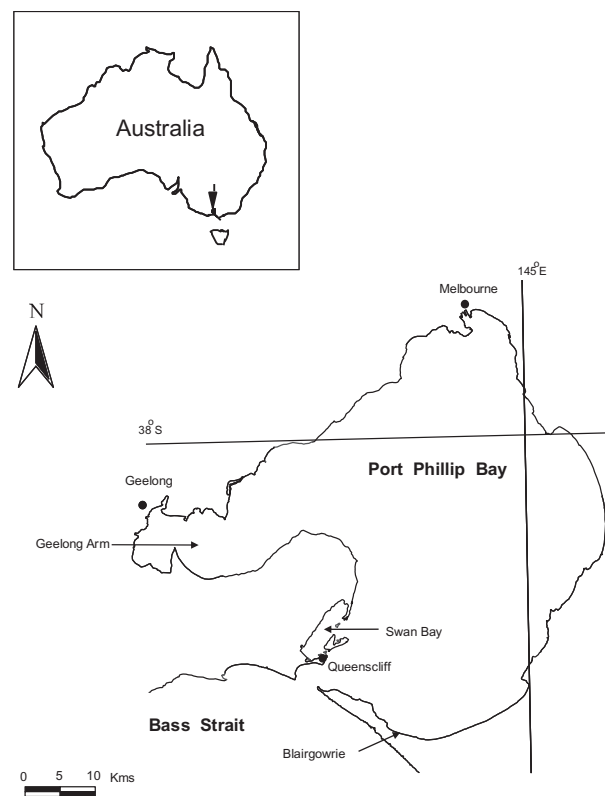

Fig. 1. Position of sampling site within Port Phillip Bay. Inset: Position of Port Phillip Bay on Australian Coast.

patch. The tube was placed vertically over the seagrass with the open end touching the sediment. The seagrass was cut with scissors immediately under the tube, which was then sealed by sliding a steel plate underneath, and the tube was then inverted before being raised to the surface. The sample was then washed into a jar with seawater. In the laboratory, samples were washed through a 63-μm sieve with fresh water to prevent fauna from attaching to leaves (De Troch *et al.* 2005) and fixed in absolute ethanol. Samples were composited in the laboratory to provide an average of the faunal abundances of the three samples from each position (Carey & Keough 2002). The animals that passed through a 1-mm sieve but were retained on a 125-μm sieve were identified under a dissecting microscope (magnification: 12×) and enumerated. Samples were stored in 75% ethanol. Water depth was measured at each sampling point in each patch at a consistent state of the tide.

Current speed within the seagrass canopy was measured at each of the three positions in each patch (30 blocks) using the rate of dissolution of plaster of Paris current indicators (Jokiel & Morrissey 1993; Santin & Willis 2007) (Table 1). The plaster of paris current indicators were blocks of plaster 15 cm high and 6 cm wide with a steel rod inserted through the middle of the block, which allowed it to be attached to a steel picket. The blocks were attached by epoxy to a plate. Varnish was applied to all sides of the block except for the top. Rate of dissolution was estimated by weight loss (dry weight). The plaster blocks were placed below the seagrass canopy, approximately 5–10 cm above the sediment. The plaster blocks were left out for 1 week. The tidal currents in the nearshore region at Blairgowrie were likely to range up to 0.2 m s^{-1} (Black *et al.* 1993).

Seagrass biomass was measured at each of the three positions in each patch by cutting all the seagrass within a haphazardly placed quadrat of 0.25 m^2 (see methods in Smith *et al.* 2008) (Table 1). In the laboratory, the macroalgae were separated from the seagrass, the seagrass leaves and shoots were measured, and both the seagrass and macroalgae were weighed after drying to a constant weight at 60°C (Smith *et al.* 2008).

Statistical analysis

Faunal abundances within and among patches were analysed using a randomized block design where position and patch were the main factors and the blocking factor was sampling date (Quinn & Keough 2002). The analysis was coded as repeated measures in the statistical software for convenience. ANOVA assumptions were checked using box and residual plots (Quinn & Keough 2002), and where necessary abundances were log transformed to satisfy the assumptions of homogeneity of variances. Patch and date were treated as random factors, and this meant that there was no appropriate *F*-ratio to test the position main effect (Underwood 1997; Quinn & Keough 2002). We addressed this issue in three ways depending on the outcome of the initial analysis. If there were significant results for the date by patch and the position by patch interactions, there was no logical reason to test the position main effect and no test was conducted (Underwood 1997). If either of these interactions was non-significant with a probability above 0.25, we conducted post-hoc pooling that then allowed a valid test of the position main effect (Underwood 1997). Finally, if either of these interactions was non-significant, but *P*-values were less than 0.25, suggesting that post-hoc pooling was inappropriate (Underwood 1997), we used a quasi-*F* ratio to test the position main effects (Winer *et al.* 1991; Quinn & Keough 2002).

We were also interested in how faunal abundances varied with environmental variables (average seagrass biomass, average current and average water depth) and patch size (log transformed). When there was a significant difference in abundances among patches but no interaction, we were interested in how faunal abundances across the whole patch differed among patches in relation to a change in environmental variables. For this analysis we summed taxon abundances from all positions in a patch and pooled across dates. We did a Pearson correlation test among the four variables and none of the four variables was strongly correlated with each other ($R < 0.15$). We therefore used all four variables in a forward stepwise-linear multiple

Table 1. Patch area, current flow and seagrass biomass in each of the 10 patches at the edge, 2 m and middle positions into the patch

| Patch	Patch area (m^2)	Current flow (g h^{-1})			Seagrass biomass (g)		
		Edge	2 m	Middle	Edge	2 m	Middle
1	3098	9.3	8.8	7.6	168 (±61)	327 (±131)	226 (±84)
2	461	9.1	9.0	8.9	31 (±25)	38 (±23)	50 (±16)
3	268	7.9	8.6	8.7	286 (±96)	305 (±157)	268 (±29)
4	5934	8.7	9.0	9.0	203 (±162)	183 (±48)	41 (±11)
5	1126	8.1	8.9	8.9	207 (±75)	229 (±43)	144 (±30)
6	113	9.1	8.1	8.1	232 (±120)	261 (±86)	261 (±86)
7	521	8.7	8.9	9.0	90 (±35)	96 (±25)	96 (±26)
8	485	7.8	8.7	7.5	130 (±43)	109 (±19)	120 (±44)
9	238	9.7	8.9	8.8	210 (±52)	214 (±24)	134 (±33)
10	412	9.0	8.4	7.7	75 (±29)	70 (±13)	68 (±15)

±SD for seagrass biomass.
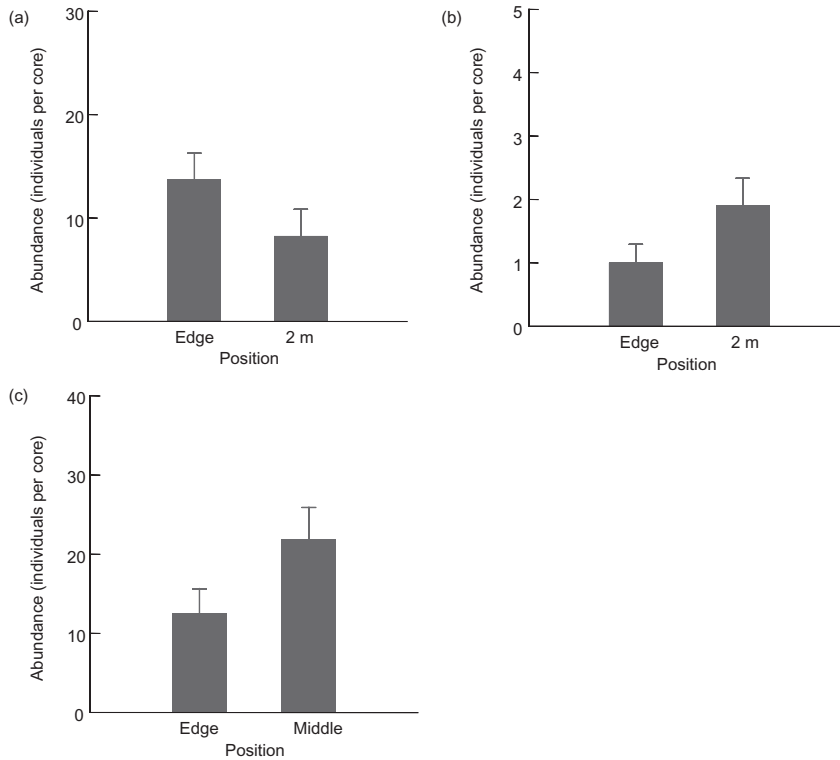
Fig. 2. The pattern of edge effects for (a) porcellid harpacticoids, (b) tanaids and (c) isopods showing a consistent response among 10 seagrass patches (mean ± SE).

regression, with a tolerance of 0.1 (Quinn & Keough 2002), to determine which variable(s) explained differences among patches. Where an interaction between patch and position was found, we were interested in how environmental variables and patch size influenced edge effect patterns of fauna. In this case the difference in abundance of the taxon at the edge and 2 m or the edge and middle positions was regressed against patch size and the differences in environmental variables between the two positions of interest. This test indicated whether differences in environmental variables between the edge and interior of patches were positively or negatively related to differences in faunal abundances between the edge and interior of patches.

RESULTS

Nine taxa were common enough (more than 100 animals) to examine distribution patterns: gammarid ampipods (pooled total: 10 942), caprellid amphiods (pooled total: 5548), porcellid harpacticoids (pooled total: 10 016), 'other' harpacticoids (pooled total: 30 098), isopods (pooled total: 4655), tanaids (pooled total: 371), cumaceans (pooled total: 1266), polychaetes (pooled total: 6753) and nematodes (pooled total: 3460). These nine taxa include both epifauna and infauna because sediment was present in the majority of our samples.

Edge effects

Three taxa showed consistent edge effects among all patches. Porcellid harpacticoids were more abundant at the edge than the 2 m position ($F_{1,29} = 6.624$, $P = 0.015$) (Fig. 2a), while tanaids were more abundant at the 2 m position ($F_{1,20} = 6.688$, $P = 0.029$) (Fig. 2b), and isopods were more abundant at the middle position ($F_{1,29} = 4.66$, $P = 0.039$) (Fig. 2c).

There was a patch by position interaction at the edge and 2 m positions for caprellid amphipods ($F_{9,18} = 2.898$, $P = 0.026$) and gammarid amphipods ($F_{9,18} = 2.634$, $P = 0.038$) (Fig. 3). For caprellids, this difference in abundances between the edge and 2 m positions was related to patch size, and difference in currents between the edge and 2 m positions within the patches, using a forward stepwise regression. Caprellid amphipods had a positive relationship with patch size with more caprellids at the edge of larger patches and more caprellids at the 2 m position in smaller patches ($F_{2,7} = 5.135$, $P = 0.042$) (Fig. 4a). Caprellid amphipods had a negative relationship with current, as there were more caprellids at the edge or 2 m position, depending on where the current was weaker ($F_{2,7} = 5.135$, $P = 0.042$) (Fig. 4b). For gammarids, none of environmental variables (seagrass biomass, water depth and current) or patch size explained the patch by position interaction ($P > 0.05$ for all four variables).

Table 2.   Significant stepwise multiple regression relationships between faunal abundances and patch size, average water depth, average current and average seagrass biomass

Taxon	Measurement	Patch attribute	P-value	R^2
Gammarids	Proportional	Depth (+)	0.032	0.46
Porcellid harpacticoids	Proportional	Seagrass biomass (+)	0.007	0.84
Isopods	Fixed	Depth (−)	0.003	0.88
Cumaceans	Fixed	Seagrass biomass (+)	0.001	0.75
Polychaetes	Fixed	Seagrass biomass (+)	0.001	0.92
		Depth (−)	0.002	
		Patch size (+)	0.049	
Porcellid harpacticoids	Fixed	Seagrass biomass (+)	0.007	0.57
Other harpacticoids	Fixed	Seagrass biomass (+)	0.012	0.88
		Patch size (+)	0.039	
		Depth (+)	0.040	

Measurement column: proportional measurement is edge and middle position into patch; fixed measurement is edge and 2 m position into patch.
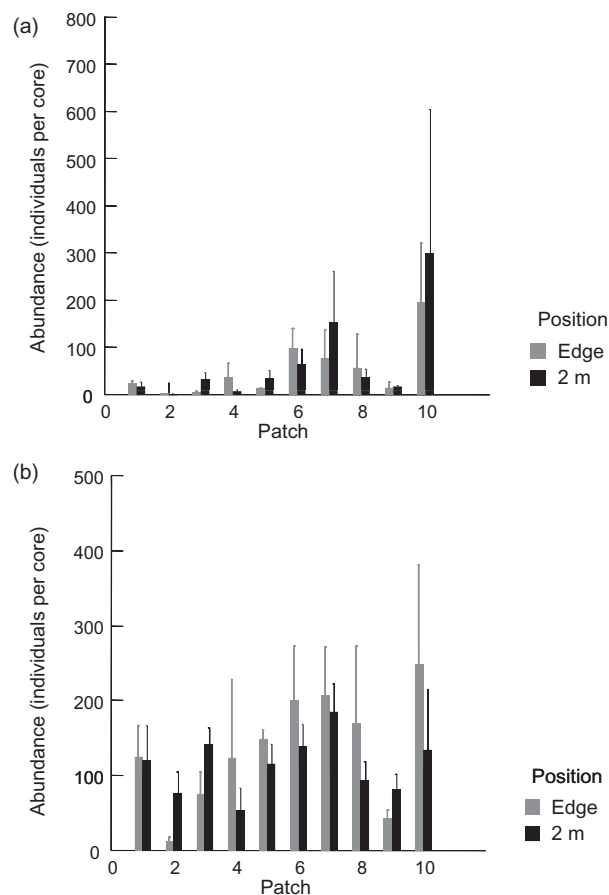

Fig. 3.   The pattern of edge effects for (a) caprellid amphipods and (b) gammarid amphipids showing a variable response among 10 seagrass patches (mean ± SE).

Patch effects

For proportional measurements (edge *vs.* middle position), significant differences in abundances among patches were found for gammarid amphipods ($F_{9,18} = 4.272$, $P = 0.004$), caprellid amphipods ($F_{9,18} = 11.845$, $P < 0.001$), porcellid harpacticoids ($F_{9,18} = 15.123$, $P < 0.001$) and nematodes ($F_{9,18} = 3.570$, $P = 0.010$). For fixed measurements (edge *vs.* 2 m position), significant differences in abundances among patches were found for isopods ($F_{9,18} = 2.796$, $P = 0.030$), porcellid harpacticoids ($F_{9,18} = 7.353$, $P < 0.001$), cumaceans ($F_{9,18} = 2.854$, $P = 0.028$), polychaetes ($F_{9,18} = 3.696$, $P = 0.005$), nematodes ($F_{9,18} = 3.696$, $P = 0.009$) and 'other harpacticoids' ($F_{9,18} = 2.457$, $P = 0.049$). Where multiple regression analyses were significant, seagrass biomass, water depth and patch size were the most important variables influencing the distribution of these taxa among patches (Table 2). The distribution of gammarids was positively associated, while the distribution of isopods was negatively associated, with water depth (Table 2). Porcellid harpacticoids and cumaceans were positively associated with seagrass biomass (Table 2). 'Other harpacticoids' made up more than 40% of our samples, and we found that their distribution was positively associated with patch size, seagrass biomass and water depth (Table 2). The distribution of polychaetes among patches was positively associated with seagrass biomass and patch size and negatively associated with water depth (Table 2).

DISCUSSION

Edge effects

The response of seagrass fauna, namely amphipods, isopods, tanaids and harpacticoids, to patch edges was variable, as it is for other faunal groups (reviewed in Bostrom *et al.* 2006). Five of nine taxa analysed showed edge effects either in constant patterns among
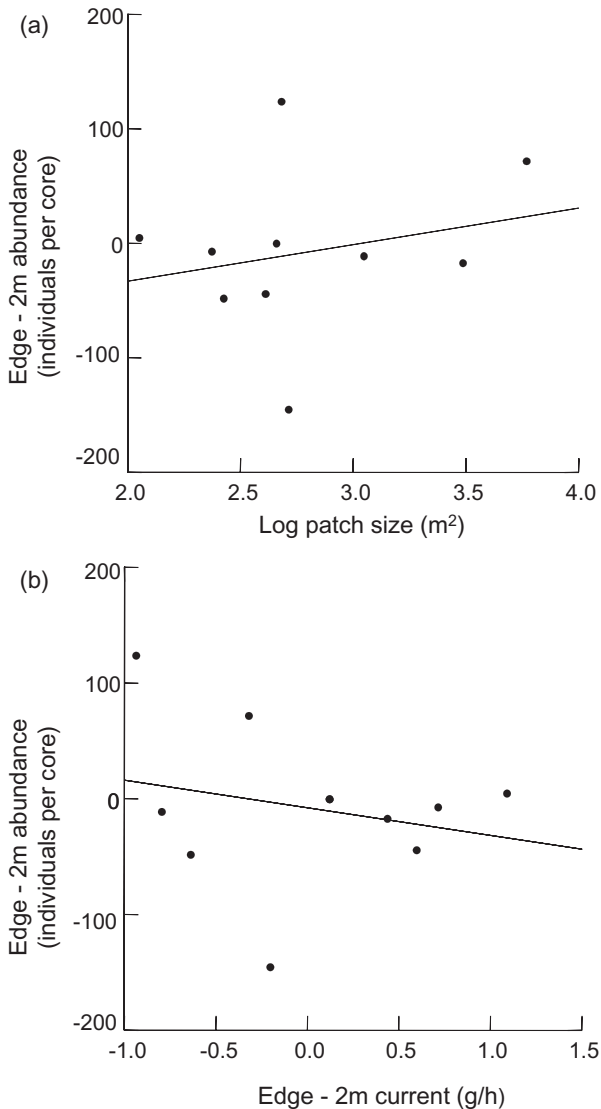
Fig. 4. (a) The relationship between the difference in abundances of caprellid amphipods at the edge and 2 m positions into seagrass patches and patch size. (b) The relationship between the difference in abundances of caprellid amphipods at the edge and 2 m positions into seagrass patches and the difference in current between the edge and 2 m positions.

all patches (isopods, porcellid harpacticoids, tanaids) or with a response that varied among patches (caprellid and gammarid amphipods). Edge effect patterns consistent over many patches have also been found for fauna in previous studies. For example, amphipods have a higher abundance at patch edges than in the middle among all patches (Bologna & Heck 2002; Tanner 2005), although they have at other times been more abundant in the middle of the patch than at the edge (Bologna 2006). In these previous studies, changes in seagrass biomass from the edge to the middle of the patches have been hypothesized as the

cause for the constant edge effect pattern (Tanner 2005; Bologna 2006), although other factors, such as currents within or among patches, were not investigated.

For two taxa, caprellid and gammarid amphipods, edge effect patterns varied among patches. The variable edge effect pattern seen in caprellids was correlated with current changes within seagrass patches and patch size. Seagrass fauna have been known to respond to changes in the physical environment, such as water depth and currents (Turner *et al.* 1999; Hovel *et al.* 2002; Jackson *et al.* 2006). Hydrodynamic differences between seasons and years may explain the variability in crustacean density by directly influencing larval settlement, feeding rates and/or locomotion of crustaceans (Hovel *et al.* 2002). Caprellid amphipods are morphologically adapted to holding onto substrata, namely seagrass stems and fronds, and they have poor swimming capabilities (Gonzalez *et al.* 2008). The higher abundances of caprellids where the current was weaker in the patches may indicate an active response by caprellids against high energy sites within the patch. Changes in patch size or hydrodynamics associated with habitat fragmentation would most likely affect the distribution of caprellids.

The importance of patch attributes

The majority of taxa in this study showed no edge effect pattern, but densities more often varied among patches. Density patterns were most influenced by differences in patch size, water depth and seagrass biomass among the 10 patches. These taxa may be habitat generalists that do not differentiate between the edge and middle of the patch and may migrate among patches depending on patch attributes (Bender *et al.* 1998). A potential controlling factor of habitat generality seen in these seagrass fauna may be refuge from predation (Duffy & Hay 1991); for example, amphipods were able to feed and take refuge in many different plant types, and habitat specialization was not evident (Duffy & Hay 1991). Furthermore, habitat generality may reduce the effect of habitat area loss and fragmentation on distributions and abundances of fauna. Habitat generalists are an important component of the terrestrial landscape, as they are able to colonize various habitats and adapt to changes in habitat configuration (Cook *et al.* 2002; Van Nouhuys 2005). In the marine environment, life history traits that included habitat generality have been used by Johnson and Heck (2006) to explain why seagrass habitat fragmentation *per se* was not of critical importance to some fish and decapods in the Gulf of Mexico, as these species were able to move between patches depending on patch attributes. On the other hand, while seagrass habitat fragmentation did not

have an effect on fish density in a recent study, as the loss of habitat area may have been compensated for by a positive effect of increased edge habitat, for fauna that are habitat generalists, and do not react positively to edge habitats, habitat fragmentation may have a potentially negative role in their distribution and abundance over time (Macreadie *et al.* 2009).

The positive relationship between polychaete and 'other harpacticoid' abundances and patch size indicated changes in habitat area in seagrass patches could have negative effects on the abundances of these two taxa. Epibenthic and interstitial harpacticoids are an important food source for seagrass-associated small fish (Gee 1989; Coull 1990; Jenkins *et al.* 1996), and a decrease in abundance of these important secondary producers could have a large impact on trophic interactions and the distribution and abundance of their predators in seagrass patches (Levin *et al.* 1997). A more detailed taxonomic analysis of the 'other harpacticoids' may have provided us with more information about changes in the distribution of specific harpacticoid families among patches (Warry *et al.* 2009). Furthermore, our scale of measurement into the patches may have been too coarse to have detected a response of 'other harpacticoids' to patch edges (Warry *et al.* 2009). Polychaete and 'other harpacticoid' abundance patterns across patches were not only influenced by patch size, but also by changes in seagrass biomass and water depth. This suggests that patch size in this system may act in combination with water depth and seagrass biomass to influence abundance patterns of infaunal and epibenthic taxa.

Differences in water depth across patches also had an important role in the distribution of fauna. The influence of water depth on faunal abundances has been seen for fish and decapods, where the relationship with depth has been positive (Bell *et al.* 1992; Jackson *et al.* 2006), negative (Francour 1997), or both negative and positive, depending on the species (Smith *et al.* 2008). In this study, the differences in water depth between patches partly explained the variability in abundances of gammarid amphipods and isopods across patches. Gammarids had a positive relationship and isopods had a negative relationship with water depth. Predation pressure by fishes may explain this variable relationship with water depth, as these seagrass fauna may be located in the water depth that is least favourable for their predators (Smith *et al.* 2008). Understanding the ecology of these crustaceans may allow us to predict their behaviour in varying physical environments.

Seagrass biomass was an important patch attribute in this study. Distribution patterns of cumaceans, polychaetes, 'other harpacticoids' and porcellid harpacticoids had a strong positive relationship with seagrass biomass among the 10 patches. Seagrass habitats provide structural complexity, including shoots, roots and rhizomes, which is thought to provide living space, food and refuge for epifauna and infauna (Sirota & Hovel 2006). Perception of seagrass biomass suitability may be taxon-specific, and perception by animals may not always be at the scale of leaf and stem, but at the patch level as well (Attrill *et al.* 2000). In the terrestrial environment, patch attributes, such as microclimate and floral structure, can have as much influence on animal abundances as edge effects when considering the effect of fragmentation (Crist *et al.* 2006; Grimbacher *et al.* 2006). A reduction in plant biomass in seagrass patches could have a direct negative effect on the abundances of these four taxa. Moreover, a reduction in seagrass biomass may have a flow-on effect of changing the hydrodynamics and area of seagrass patches, which could affect the abundances of other seagrass fauna.

Summary

Habitat area loss and habitat fragmentation occur naturally in seagrass ecosystems (Robbins & Bell 1994); however, dredging, eutrophication, anchoring, propeller scarring and other anthropogenic activities are causing further habitat loss in this vulnerable ecosystem (Bostrom *et al.* 2006). Our study has shown that patch edges altered the distribution of some taxa, while other taxa were influenced by differences in patch size, seagrass biomass and water depth. The majority of these seagrass taxa appear to be habitat generalists, and further fragmentation and habitat area loss may have negative effects on their distributions and densities over time (Macreadie *et al.* 2009). It is important to develop a greater understanding of the ecology of seagrass fauna in order to determine how they may react to habitat fragmentation and habitat area loss.

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