Edge patterns in aquatic invertebrates explained by predictive models

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Abstract. Predictive frameworks for understanding and describing how animals respond to habitat fragmentation, particularly across edges, have been largely restricted to terrestrial systems. Abundances of zooplankton and meiofauna were measured across seagrass–sand edges and the patterns compared with predictive models of edge effects. Artificial seagrass patches were placed on bare sand, and zooplankton and meiofauna were sampled with tube traps at five positions (from patch edges: 12, 60 and 130 cm into seagrass; and 12 and 60 cm onto sand). Position effects consisted of the following three general patterns: (1) increases in abundance around the seagrass–sand edge (total abundance and cumaceans); (2) declining abundance from seagrass onto sand (calanoid copepods, harpacticoid copepods and amphipods); and (3) increasing abundance from seagrass onto sand (crustacean nauplii and bivalve larvae). The first two patterns are consistent with resource-distribution models, either as higher resources at the confluence of adjacent habitats or supplementation of resources from high-quality to low-quality habitat. The third pattern is consistent with reductions in zooplankton abundance as a consequence of predation or attenuation of currents by seagrass. The results show that predictive models of edge effects can apply to aquatic animals and that edges are important in structuring zooplankton and meiofauna assemblages in seagrass.

Additional keywords: current flow, edge distribution, plankton tube traps, predictive model, seagrass.

Introduction

A fundamental goal of community ecology is to understand how animals are distributed within their environment. This is particularly important in threatened habitats, such as those that have been fragmented. Fragmentation increases the edge-to-area ratio of patches and there is a growing body of literature on the responses of animals to increases in edge habitat (i.e. 'edge effects'). This literature has recently been used to develop models to understand the patterns and variability from edge-effect studies (Ries *et al.* 2004). Ries and Sisk (2004) predicted that when resources are concentrated around edges, or where resources are divided between habitats, there will be a 'hump' in animal abundance near the edge boundary (i.e. positive edge effect, Fig. 1*a*). Conversely, when resources are concentrated in the preferred habitat, there will be a 'transitional' decline in abundance at edges in the preferred habitat (i.e. negative edge effects, Fig. 1*b*) and an increase in animal abundance at edges

in the non-preferred habitat (i.e. positive edge effects, Fig. 1*b*). Fagan *et al.* (1999) suggested that another 'transitional' response may occur as a result of increased mortality in the preferred habitat or where edges restrict movement of animals into preferred habitat (Fig. 1*c*).

Predictive models of edge effects have been largely generated from the terrestrial literature. There are fundamental differences between terrestrial and aquatic systems, such as differences in the physical properties of wind and water currents (Denny 1990) and their capacity for facilitating dispersal (Carr *et al.* 2003; Kinlan and Gaines 2003), and there is need to validate predictive models in aquatic systems. We measured the distribution of fauna across edges in an aquatic system to see whether patterns around edges conform to any of the three previously described predictive models. We used seagrasses because they are a critical marine habitat that has undergone significant global decline as a result of fragmentation (Bell *et al.* 2001; Duarte 2002; Orth *et al.* 2006).
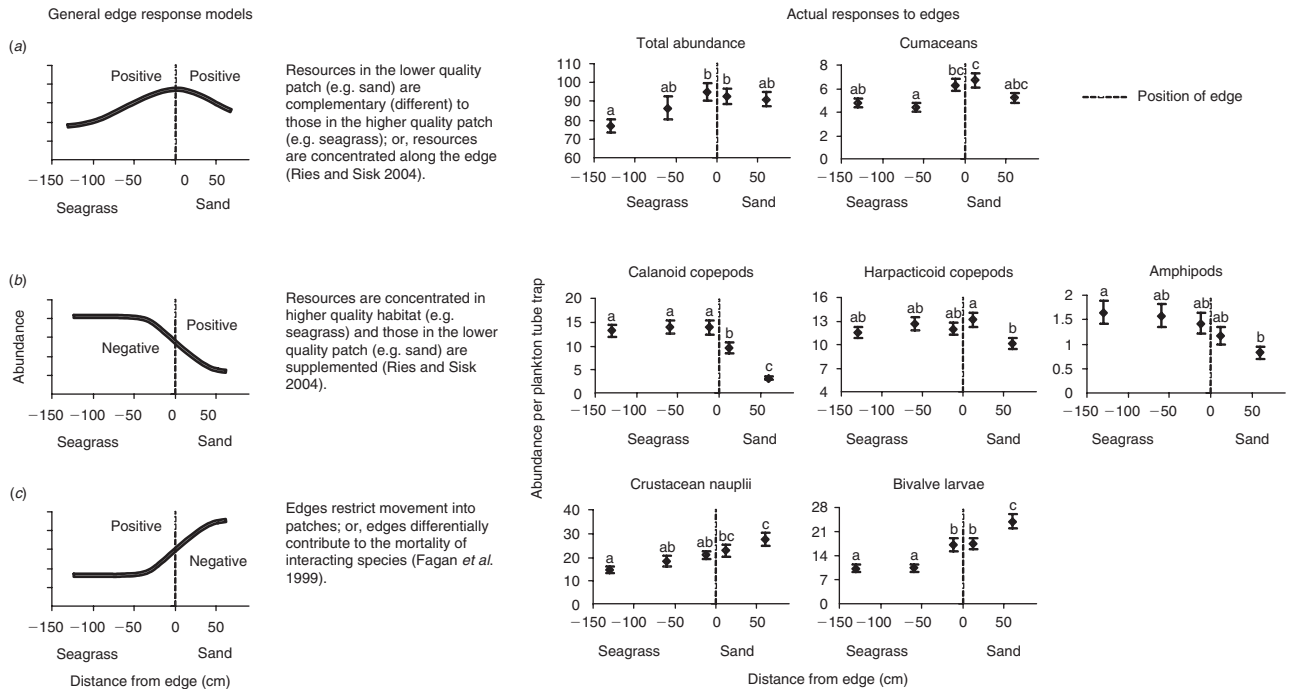
Fig. 1. Generalised models and actual distributions of meiofauna and zooplankton (mean abundance per plankton tube trap ± s.e.) across seagrass and sand edges. Responses to seagrass–sand edges may be either positive (higher abundance at edges) or negative (lower abundance at edges). Means with the same letters are not significantly different.

We focus on the responses of zooplankton and epi–meiofauna close to edges (the seagrass–sand interface) because this fauna is abundant (Bostrom *et al.* 2006) and the majority of work in aquatic systems has focussed on fish (e.g. Jelbart *et al.* 2006; Smith *et al.* 2008) and macroinvertebrates (e.g. Eggleston *et al.* 1999; Bologna and Heck 2002; Hovel *et al.* 2002).

Materials and methods

Study site

This study was done at Grassy Point (38°07′S, 144°41′E) in Port Phillip Bay, Victoria, Australia. Port Phillip Bay is a shallow (mostly <25 m), semi-enclosed temperate marine embayment (2000 km²). Seagrass is common (total area 60 km²) in the southern and western regions and occurs as bands of varying size and patchiness running parallel to the shore (Blake and Ball 2001). Water currents at Grassy Point move from south to north on the incoming tide, and reverse on the outgoing tide (Black *et al.* 1993).

Construction of artificial seagrass units

Seagrass patches (3 m × 3 m) were produced using artificial seagrass units (ASUs). We used ASUs to control patch size, patch shape, seagrass length and seagrass density. ASUs were designed to mimic *Heterozostera nigricaulis*, the dominant subtidal seagrass in Port Phillip Bay. ASUs were constructed by tying 5-mm-wide green polypropylene ribbon to steel mesh at a density of 3520 leaves m^{-2}. At each intersection of steel mesh (220 intersections m^{-2}), eight pieces of 1-m-long ribbon were tied to give 16 leaves, each of ∼0.45 m. Shoot density and leaf length were based on mean estimates for this area (Jenkins *et al.* 1998) and patch size was based on realistic estimates for Port Phillip Bay (Macreadie *et al.* 2009).

Experimental design

We used a randomised block design with two fixed factors, namely position (from patch edges: 12, 60 and 130 cm into seagrass; and 12 and 60 cm into sand) and orientation (in line with currents: north and south; and perpendicular to currents: east and west). Orientation was included as a factor in the design because Tanner (2003) showed that it has the potential to influence edge responses in seagrass systems. Ten patches (treated as blocks in the analyses) were constructed from ASUs on unvegetated sand at a depth of 0.5–1.5 m below mean-low-water-spring; patches were separated by 30 m. Patches were left for 1 month after construction to allow accumulation of epiphytes. Within each patch, zooplankton and meiofauna were sampled at each combination of orientation and position.

Sampling of zooplankton and meiofauna

Plankton tube traps (PTTs) are passive sampling devices that collect animals through time. We constructed PTTs according to Yund *et al.* (1991). Each PTT was a 46-cm cylindrical tube of PVC (internal diameter 5.1 cm) capped at both ends and filled with a 10% solution of formaldehyde and seawater. PTTs were attached to metal stakes, with the top end of the tube positioned immediately beneath the top of the seagrass canopy. Once they were deployed, the cap from the top end of the tube was removed.

Table 1. Three-factor ANOVAs comparing animal abundances and taxon richness among blocks (B), positions (P) and orientation (O)

Only taxa with a mean of >1 individual per plankton tube trap are presented. Bold indicates significant ($P < 0.05$) differences

Parameter	Residual MS error	*P*-value					
		B	P	O	B × P	B × O	P × O
d.f.	108	9	4	3	36	27	12
Total abundance	575	**<0.001**	**0.015**	0.118	6.083	0.121	0.193
Calanoid copepods	29	**<0.001**	**<0.001**	0.174	**<0.001**	**0.001**	0.102
Harpacticoid copepods	18	**<0.001**	**0.034**	0.277	0.254	0.189	0.796
Crustacean nauplii	121	**<0.001**	**<0.001**	**0.007**	0.085	0.059	**0.008**
Cumaceans	7	**<0.001**	**0.002**	0.274	0.420	0.193	0.289
Amphipods	1	0.360	**0.024**	0.785	0.473	**0.003**	0.297
Isopods	7	0.737	0.192	0.311	0.622	0.521	0.343
Ostracods	1	0.081	0.080	0.709	0.916	0.494	0.191
Polychaetes	7	**0.004**	0.881	0.787	0.183	0.464	0.413
Bivalves	78	**<0.001**	**<0.001**	0.070	0.904	**0.039**	0.050
Nematodes	8	**<0.001**	0.194	0.525	0.976	0.879	0.852
Cnidarians	111	**0.001**	0.273	0.610	0.441	**0.035**	0.208
Taxon richness	5	**0.006**	0.414	0.982	0.492	0.255	0.433

The formalin was dyed so that we could monitor its concentration throughout the experiment. PTTs were deployed for 3 days during October 2007. Once collected, PTTs were taken back to the laboratory, and the contents were passed through a 63-μm sieve. All animals were identified and counted.

Data analysis

Response variables were zooplankton and meiofaunal abundance, and taxon richness. Abundance of individual taxa were analysed only if they had a mean of >1 animal per sample. Treatments were compared in a three-factor ANOVA with block (B) treated as a random factor, and position (P) and orientation (O) as fixed factors. Taxa with significant position effects were compared using Tukey's HSD. Statistical analyses were performed using Systat (version 12).

Results and discussion

Crustaceans dominated (60%) the collection and were composed of nauplii (23%), harpacticoid copepods (15%), calanoid copepods (12%), cumaceans (6%), amphipods (2%) and isopods (2%). Other abundant taxa included bivalve larvae (18%), cnidarians (7%), polychaetes (7%), nematodes (3%) and gastropod larvae (2%). Most taxa varied significantly among blocks (patches) (Table 1). Abundances of calanoid copepods varied differently among positions across blocks (Table 1) because of weaker trends in 3 of 10 blocks (data not shown). Effects of orientation also depended on blocks for calanoid copepods, amphipods, bivalve larvae and cnidarians (Table 1), but no obvious patterns emerged when individual blocks were analysed (data not shown).

Effects of position and conformity to predictive models

Abundances of 6 of 11 taxa, as well as total abundance, varied with position whereas the remaining five taxa showed no effect, nor did taxon richness (Table 1). The taxa that were not affected by position consisted of isopods, ostracods, polychaetes, nematodes and cnidarians. Those affected by position were calanoid copepods, harpacticoid copepods, crustacean nauplii, cumaceans, amphipods and bivalve larvae. Each of these latter taxa showed position effects that were comparable with one of the predictive models, as follows: (1) increases around the seagrass–sand boundary (total abundance and cumaceans, Fig. 1*a*); (2) similar abundances across seagrass, with a decline onto sand with distance from edge (calanoid copepods, harpacticoid copepods and amphipods, Fig. 1*b*); or (3) increases from seagrass interiors to distant sand (crustacean nauplii and bivalve larvae, Fig. 1*c*).

The first pattern (Fig. 1*a*, higher abundances at edges) was also reported by Tanner (2005), who measured infaunal and epifaunal abundances around edges of fragmented seagrass meadows in Gulf St Vincent, South Australia. We have also recorded the higher abundance of meiofaunal crustaceans at seagrass edges before (Warry *et al.* 2009). This pattern was represented by total abundance and cumaceans, although it should be noted that cumaceans were not sufficiently abundant to have caused the pattern for total abundance. Instead, total abundance represents a combination of all taxa, none of which is overly dominant. Therefore, the pattern for total abundance fits Model 1 but cannot be explained by Model 1. The reason we included total abundance as a community metric in our analyses is because of its relevance as a food source for fish living in seagrass. As for cumaceans, the underlying mechanism to explain their distribution is most likely to be a concentration of resources around the seagrass and sand edge (Ries *et al.* 2004). We suspect that this pattern is indirect and may be caused through a trophic cascade. There are many cases where higher abundances of one species at edges cause higher abundances of another; a situation often referred to as 'cascading edge effects'. A case in point is the woodland brown butterfly (*Lopinga achine*) that concentrates at

edges because its host plant is most abundant there, which is a result of the microclimate at edges being ideal to support the host plant in the first place (Bergman 1999). A similar situation may exist for cumaceans where nutrients concentrate at edges, causing an increase in the deposition of organic matter and an increase in the abundance of cumaceans which feed on organic matter.

For taxa fitting the second predictive model, the sharpness of the transition varied. For calanoid copepods, the numbers fell by 70% from the edge of the seagrass areas across the sand (Fig. 1*b*). For harpacticoids and amphipods, the pattern was similar, but the transition was more subtle and significant effects were only detected at the distant sand position (Fig. 1*b*). The carryover of fauna from higher quality habitat (seagrass) onto lower quality habitat (sand) is often referred to as the 'spillover' (Rand *et al*. 2006) or 'mass effect' (Shmida and Wilson 1985), where animals disperse from their preferred habitat into non-habitat. Differences in the dispersal distance from preferred habitat may depend on an animal's perception of edges (Attrill *et al*. 2000). For example, the responses of the two copepod taxa to edges suggested that calanoids may have a finer perception of edges (accounting for a 'narrow' edge effect) and harpacticoids may have a coarser perception of edges (a 'thicker' edge effect).

The third predictive model, of declining abundance from distant sand to seagrass interiors, as shown by crustacean nauplii and bivalve larvae (Fig. 1*c*), cannot be explained by resource distribution models (Ries and Sisk 2004; Ries *et al*. 2004) but they can be explained by two (sub)models that relate to species interactions and physical processes (Fagan *et al*. 1999). First, the larval supply model, *sensu* Bologna and Heck (2002), predicts that attenuation of current flow by seagrass will cause spatial patterns in the deposition of planktonic fauna across edges as flow conditions shift from laminar flow over sand to slower, more turbulent flow over seagrass (Fonseca *et al*. 1982; Fonseca and Bell 1998). Bologna and Heck (2002) found significant differences in the abundances of gastropod larvae between edge and interior samples, which they suggested were 'settlement shadows'. Because crustacean nauplii and bivalve larvae are primarily distributed by water currents (i.e. their distribution does not fit the *a priori* assumption that seagrass represents 'higher quality habitat' and sand represents 'lower quality non-habitat'), attenuation of current flow by seagrass may limit their penetration into patch interiors (Peterson *et al*. 2004; Hunt *et al*. 2007). Second, the distribution pattern of crustacean nauplii and bivalve larvae may be explained by higher predation rates in seagrass. The role of predation in organising community structure in seagrass is well established (Summerson and Peterson 1984), and there is ample evidence of higher predation rates at seagrass edges (e.g. invertebrates: Gaines and Roughgarden 1987; Peterson *et al*. 2001; Hovel and Lipcius 2002; and fish: Laurel *et al*. 2003) and other marine habitats (Gaines and Roughgarden 1987).

The strength of edge responses measured here might be somewhat conservative compared with natural seagrass patches. Natural seagrass patches often vary in their structural characteristics (e.g. biomass, leaf width and length) relative to distance from edge (Bologna 2006) and this may represent a potential mechanism for generating edge effects. In contrast, artificial seagrass controls for the structural characteristics of seagrass patches and this may decrease the intensity of edge responses.

Effects of orientation

Orientation had relatively weak effects on zooplankton and meiofauna. In the case of crustacean nauplii, edge effects varied with orientation (Table 1); *post hoc* comparisons showed a significant increase in abundance of individuals from patch interiors to distant sand positions on the patch side that faced water currents during the incoming tide (i.e. the southern side). Incoming (flood) currents near the shoreline persisted for much of the tidal cycle and are generally stronger than outgoing (ebb) currents (Black *et al*. 1993). This suggests that dispersal of crustacean nauplii was current-induced. A similar finding was reported by Tanner (2003), but for amphipod colonists. Tanner (2003) showed that passively dispersed seagrass epifauna responds to patch orientation when water currents (the primary dispersal mechanism) are strong, but not when they are weak, which suggests that orientation effects in seagrass are largely determined by hydrodynamic regimes. Besides crustacean nauplii, no effects of orientation were observed for any other taxa or taxon richness (Table 1).

Conclusions

Habitat edges represent an important feature of seagrass landscapes in determining the distribution of zooplankton and meiofauna across seagrass patches. The three basic patterns we observed in the distribution of zooplankton and meiofauna across seagrass–sand edges provide a platform for future models of faunal responses to seagrass edges. Increasing knowledge of resource distribution, predatory impacts and mobility of fauna living in seagrass systems will provide opportunities to build the complexity and improve the generality of the models presented here.

Acknowledgements

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