

# Seagrass patch size affects fish responses to edges

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## Summary

1. Patch area and proximity of patch edge can influence ecological processes across patchy landscapes and may interact with each other. Different patch sizes have different amounts of core habitat, potentially affecting animal abundances at the edge and middle of patches. In this study, we tested if edge effects varied with patch size.
2. Fish were sampled in 10 various-sized seagrass patches (114–5934 m<sup>2</sup>) using a small (0.5 m<sup>2</sup>) push net in three positions within each patch: the seagrass edge, 2 m into a patch and in the middle of a patch.
3. The two most common species showed an interaction between patch size and the edge–interior difference in abundance. In the smallest patches, pipefish (*Stigmatopora nigra*) were at similar densities at the edge and interior, but with increasing patch size, the density at the edge habitat increased. For gobies (*Nesogobius maccullochi*), the pattern was exactly the opposite.
4. This is the first example from a marine system of how patch size can influence the magnitude and pattern of edge effects.
5. Both patch area and edge effects need to be considered in the development of conservation and management strategies for seagrass habitats.

**Key-words:** edge effects, fish, landscape structure, patch size, seagrass

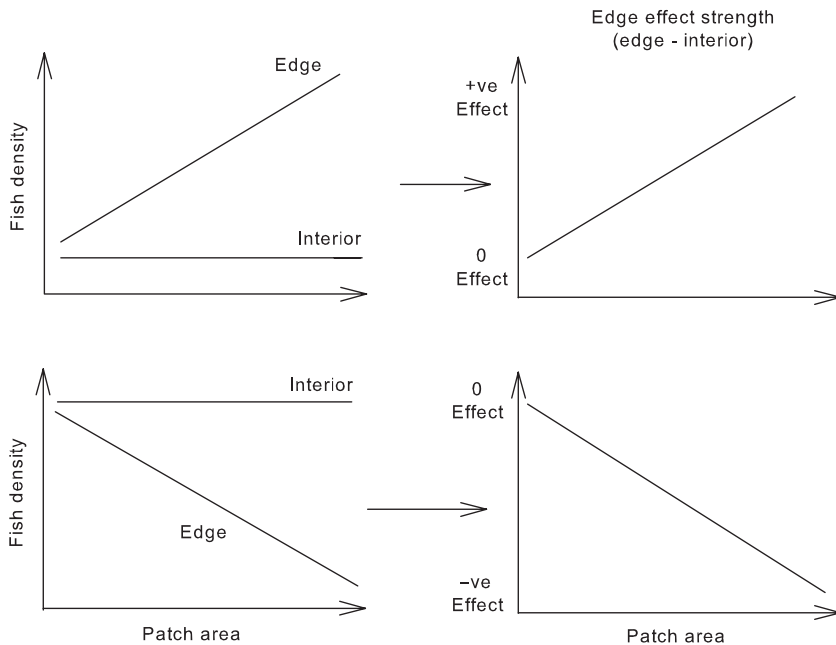
## Introduction

Habitat edges and patch size are key elements in landscape ecology, directly affecting animal abundances and distributions (Bender, Contreras & Fahrig 1998; Fletcher *et al.* 2007). Edges can influence physical parameters and species interactions, increasing and decreasing animal densities (Paton 1994; Fagan, Cantrell & Cosner 1999; Ries *et al.* 2004a). The role edges play in determining faunal distributions varies with temporal scales, patch quality, mechanisms of patch formation and contrast between patches and the surrounding matrix (Ries *et al.* 2004a; Ries & Sisk 2004b; Ewers & Didham 2006). Patch area is included in many landscape studies, but it is linked to habitat edges, and the two are often confounded and difficult to isolate (Bender *et al.* 1998; Parker *et al.* 2005; Fletcher *et al.* 2007). The few studies that have investigated the interaction between edge effects and patch size have generally found an interaction between them (Didham *et al.* 1998; Barbosa & Marquet 2002; Ewers, Thorpe & Didham 2007), suggesting that the strength and direction of edge effects may be related to patch size (Fig. 1). The relation-

ship between patch size and edge is important to ecologists because small patches generally have a greater edge to area ratio and less core habitat than larger patches, and the distance to edges is less in small patches, suggesting that edge effects could drive area effects (Malcolm 1994; Fletcher 2005; Fletcher *et al.* 2007). The relationship is fundamentally important in the conservation, restoration and management of habitats suffering from fragmentation through anthropogenic activities (Ries *et al.* 2004a; Ewers *et al.* 2007).

Seagrass is a common nearshore ecosystem with a propensity to form patches of various sizes interspersed with unvegetated sand (Robbins & Bell 1994) and that is susceptible to anthropogenic disturbance (Orth *et al.* 2006). The influence of seagrass edges and patch area on fish densities and distributions in seagrass is unclear, with the majority of species showing no apparent effect (Bell *et al.* 2001; Connolly & Hindell 2006). Recent work, however, suggests that edges play a role in structuring the composition of seagrass fish assemblages (Jelbart, Ross & Connolly 2006; Smith *et al.* 2008), and indicates that patch size may explain some of the inconsistencies among studies (Jelbart *et al.* 2006). Jelbart *et al.* (2006) found that fish species richness did not differ between the interior and edge of small patches, but was lower at the edge of large

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**Fig. 1.** Schematic representation of changes in strength and direction of edge effects as patch size increases if edge effects and patch area interact.

patches; suggesting that small patches may have no suitable core habitat for fish, and that edge effects may drive area effects in seagrass patches. However, patch size and edge effects did not interact to influence fish density; only one species showed an edge effect, while eight showed an area effect. This indicates that edge and area effects may function independently of each other to influence the abundance and distribution of individual fish species. Inconsistencies among the results of studies that have assessed edge effects in seagrass may be related to the size of the patches sampled. For example, Smith *et al.* (2008) found that total fish density and the density of three individual species showed an edge effect, but they sampled smaller patches than Jelbart *et al.* (2006).

The strength of edge and patch effects on faunal composition and abundances can be affected by the surrounding landscape (Tanner 2006; Ewers & Didham 2006). Landscape variables, such as distance to nearest neighbour, to shore and to other patch types, can affect species-abundance patterns (Heithaus *et al.* 2006; Jelbart, Ross & Connolly 2007), which may in turn affect abundance at the patch edge. In addition, changes to the attributes of seagrass patches may influence fish abundance within and between patches (Boström, Jackson & Simenstad 2006). Indeed, variation in the structure and depth of seagrass can affect the distribution of fish within a patch (Jackson, Attrill & Jones 2006; Smith *et al.* 2008). Differences in within patch seagrass structure therefore also need to be considered when assessing edge and area effects.

The definition of seagrass patch edge–interior varies among studies, often varying with study organism and patch size. The seagrass interior can be represented as: a fixed distance into a patch (e.g. 5 and 10 m, Uhrin & Holmquist 2003; > 10 m, Bologna 2006; 6–8 m, Jelbart *et al.* 2006), which is consistent regardless of patch size, or at the halfway point across each individual patch (e.g. Bowden, Rowden & Attrill 2001; Smith *et al.* 2008). Variation in definitions of the sea-

grass interior may explain some of the inconsistencies among studies investigating seagrass edge effects.

We hypothesized that, in small patches, edge effects are small because edge and core habitats are similar, and that as patch size increases, edge effects will increase as the edge and core become more dissimilar. We tested this by determining if differences in fish densities between the edge and interior of seagrass patches are influenced by patch size. We also determined if fixed or proportional distances into patches differ in representing the interior of patches, and tested whether seagrass structure explained fish variables not responding to patch size.

## Materials and methods

### STUDY SITE

Sampling was carried out in May and October 2006 at Blairgowrie on the south-eastern coast of Port Phillip Bay, a large (2000 km<sup>2</sup>) embayment in Victoria, Australia. Blairgowrie supports patches of the seagrass *Heterozostera nigricaulis* of various shapes and sizes, interspersed by 10s of metres of sand, to a depth of 1.5 m. In recent years, the area of seagrass has declined (Ball *et al.* 2006), and seagrass habitat has become increasingly patchy.

### SAMPLING METHODS

Ten patches were sampled within an hour of low tide (Table 1) during two seasons: autumn (May) and spring (October). Samples were taken at three positions within each patch: the seagrass edge, within 1 m of the seagrass/sand interface (edge); fixed seagrass interior, 2 m from the seagrass edge (2 m); and half way across the seagrass patch at the proportional seagrass interior (middle), between 2 and 60 m from the seagrass edge. During each season (autumn, spring), samples were collected on eight occasions (four days, four nights). On each occasion, samples were taken from only one or two of the three positions (selected at random to limit disturbance of nearby

**Table 1.** Landscape characteristics of each patch sampled

Patch	Area (m <sup>2</sup> )	Nearest neighbour (m)	Distance to shore (m)
1	5934	4	30
2	3098	43	19
3	1126	4	91
4	522	17	94
5	485	17	108
6	461	20	21
7	413	29	99
8	269	10	46
9	239	30	56
10	114	8	66

positions). At the smallest patch, the middle and 2-m positions were located at the same distance into the patch.

Fish were caught using a 1 × 0.5 m push net, with 1 mm mesh, which was pushed parallel to the patch edge for a distance of 5 m. All fish were identified and counted. Seagrass structure (above-ground biomass, shoot length, density, epiphyte biomass) was quantified by taking four seagrass samples at each position within each patch during each season (4 samples × 3 positions × 10 patches × 2 seasons = 240 samples). Seagrass samples were taken by cutting all seagrass within a 0.25-m<sup>2</sup> quadrat. The number of seagrass shoots in each sample was counted to estimate seagrass shoot density, and the length of 10 randomly selected shoots measured. Seagrass and epiphytic algae biomass were measured by weighing these plant components separately after drying to constant weight at 60 °C. Epiphytic algae consisted of small filamentous brown algae and thin sheet-like red and green algae that contributed little to the structure of the meadows.

Water depth was measured at the point of each fish sample. Seagrass patch area, distance to shore and distance to nearest neighbour for each patch were measured on rectified aerial photographs using GIS software (ESRI ArcView Gis 3.3). Distance to shore was measured as the distance from the high tide mark to the centre of the patch, and nearest neighbour as the smallest distance between seagrass patches.

#### DATA ANALYSIS

Any interaction between sampling positions and patches would suggest that variation between patches may be affecting edge effects. To assess if positions and patches interacted, species richness and the density of the two most abundant species were each analysed using a three-factor, repeated-measures ANOVA. Separate analyses of the same test were carried out to compare the positions: (i) edge and 2 m, and (ii) edge and middle. Season, time of day and patch were treated as between-patch subjects, where season (autumn, spring) and time of day (day, night) were treated as fixed factors and patch as a random factor. Position was treated as the within-subjects factor. Data were assessed for assumptions of homogeneity and normality by viewing box plots and plots of residuals; where these assumptions were not met, data were log transformed and reassessed.

Where there was a significant interaction between position and patch, the difference in the response variable between positions (i.e. edge – 2 m or edge – middle) was tested against predictor variables (i.e. patch area and other seagrass measures); depth and seagrass density were analysed by first calculating differences between positions (i.e. edge – 2 m or edge – middle). Stepwise multiple linear regressions

were used to assess the relative contribution of patch characteristics in determining variation in abundances of fish across positions and patches. Where there were significant differences among patches (and no interaction), regression analyses were carried out between predictor variables and fish densities for each patch. Patch area, distance to shore, distance to nearest neighbour, depth, seagrass biomass, density, shoot length and epiphyte biomass were used as predictor variables in regression analysis. Predictor variables were tested for collinearity. Distance to shore, seagrass biomass, shoot length and epiphyte biomass were correlated with other predictor variables ( $r$  values > 0.3) and were removed from analyses. For the same reason, nearest neighbour data were removed from all analyses except for spring densities, and depth was removed from analyses of interactions between position and patch. Therefore, only patch area, seagrass density, the nearest neighbour in spring, and depth, when there was no interaction between patch and position, were used as predictor variables in regression analyses.

## Results

Fifteen species of fish from nine families were sampled. During autumn and spring, 802 fish from 9 species and 961 fish from 14 species respectively were sampled. The pipefish *Stigmatopora nigra* (Kaup) was the most abundant species (904 individuals), followed by the goby *Nesogobius maccullochi* (Hoese & Larson) (425). These two species contributed 70% of all fish sampled, and represent species with affinities for seagrass canopy (*S. nigra*) and unvegetated sand (*N. maccullochi*).

#### SPECIES RICHNESS

Species-richness edge effects did not vary with patch size, but increased with seagrass density. Species richness varied inconsistently amongst patches between seasons at the edge and middle positions (Table 2), but predictor variables explained little of this variation. At the edge and 2-m positions, there was a highly significant difference in species richness amongst patches ( $F_{9,40} = 11.5$ ,  $P < 0.001$ ). Seagrass density was positively correlated with species richness ( $P = 0.033$ ), explaining 38% of the variability across patches (Fig. 2). Species richness did not vary between the edge and middle positions (Table 2) or between edge and 2-m positions. A greater number of species was sampled at the edge and middle positions at night (Table 2), and at the edge and 2-m positions at night in spring ( $F_{1,40} = 8.5$ ,  $P = 0.017$ ).

#### PIPEFISH

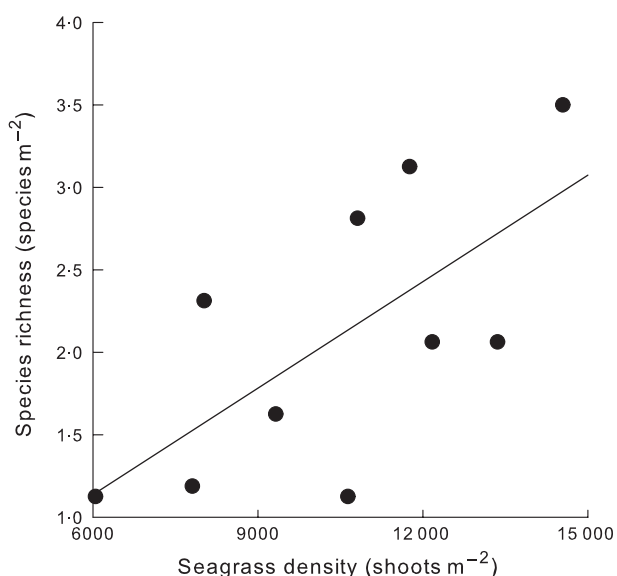
Densities of *S. nigra* at patch edges relative to the middle of patches increased as patch size increased. Differences in *S. nigra* densities between the edge and middle positions varied among patches (position × patch interaction, Table 2); 56% of this variation was explained by patch size ( $P = 0.041$ ), with greater densities at the edge of large patches (Fig. 3). *Stigmatopora nigra* densities were greater at edge (Table 2) than middle positions during the day in autumn, and at 2 m than edge positions at night in autumn ( $F_{1,40} =$

**Table 2.** Repeated-measures analysis between the edge and middle for fish density, species richness, *Stigmatopora nigra* and *Nesogobius maccullochi*

Source	d.f.	Species richness		<i>Stigmatopora nigra</i>		<i>Nesogobius maccullochi</i>	
		<i>f</i>	<i>P</i>	<i>f</i>	<i>P</i>	<i>f</i>	<i>P</i>
<b>Between subjects</b>							
Season (S)	1	28.1	< 0.001	7.0	<b>0.026</b>	10.2	<b>0.011</b>
Time of day (TOD)	1	13.4	<b>0.005</b>	0.2	0.664	4.7	0.059
Patch (P)	9	11.5	< 0.001	18.3	< 0.001	6.2	< 0.001
S × TOD	1	3.7	0.085	2.5	0.145	0.9	0.355
S × P	9	2.5	<b>0.021</b>	3.4	<b>0.004</b>	1.2	0.340
TOD × P	9	1.6	0.161	0.9	0.521	2.8	<b>0.012</b>
S × TOD × P	9	1.1	0.386	0.6	0.748	0.6	0.772
Error	40						
<b>Within subjects</b>							
Position	1	0.1	0.761	10.6	< 0.001	0.9	0.380
Position × S	1	4.2	0.071	2.0	0.138	0.9	0.364
Position × TOD	1	0.4	0.522	1.6	0.212	0.1	0.716
Position × P	9	0.9	0.563	3.0	< 0.001	2.2	<b>0.042</b>
Position × S × TOD	1	< 0.1	0.847	4.8	<b>0.009</b>	0.4	0.529
Position × S × P	9	0.6	0.779	1.3	0.176	0.9	0.510
Position × TOD × P	9	0.8	0.648	0.8	0.789	0.5	0.852
Position × S × TOD × P	9	0.5	0.835	0.9	0.544	1.1	0.404
Error	40						

Significant results in bold.

8.7,  $P = 0.016$ ), but there was little difference for other combinations of season and time of day. Densities of *S. nigra* at the middle and 2-m positions also varied amongst patches, but this variation depended on season ( $F_{9,40} = 10.5$ ,  $P < 0.001$ ). No predictors significantly contributed to patch differences during autumn. In spring, however, depth explained 47% of *S. nigra* variation among patches ( $P = 0.029$ ).



**Fig. 2.** Relationship between mean species richness and seagrass density across patches at the seagrass edge and 2 m (pooled).

## GOBIES

Densities of *N. maccullochi* at the patch edges decreased relative to the middle of patches as patch size increased. Differences in densities of *N. maccullochi* between edge and middle positions varied among patches (Table 2); 42% of this variation was explained by patch area ( $P = 0.026$ ), with greater densities in the middle of large patches (Fig 3). Densities of *N. maccullochi* at edge and middle positions were greater in spring than autumn (Table 2). At the edge and 2-m positions, densities of *N. maccullochi* varied among patches ( $F_{9,40} = 2.1$ ,  $P = 0.049$ ) but differences were not explained by patch area, water depth or seagrass density. *Nesogobius maccullochi* densities were greater in spring than autumn ( $F_{1,40} = 5.8$ ,  $P = 0.040$ ), and during the night than day ( $F_{1,40} = 10.5$ ,  $P = 0.017$ ).

## Discussion

Edge effects and patch size are key elements of landscape ecology, but they potentially interact and their influences can be difficult to separate (Fletcher 2005; Parker *et al.* 2005; Fletcher *et al.* 2007). We have shown that the strength and direction of edge effects on two common fish species in seagrass patches could be explained by patch size, which has a positive (for *S. nigra*) and negative (for *N. maccullochi*) effect on densities at the edge. Our findings contrast with those of previous work on seagrass fish, which found that species richness interacted with patch size, but that the densities of *S. nigra* (Jelbart *et al.* 2006) and invertebrates (Tanner 2006) did not. Patch size and edge width were smaller in this study



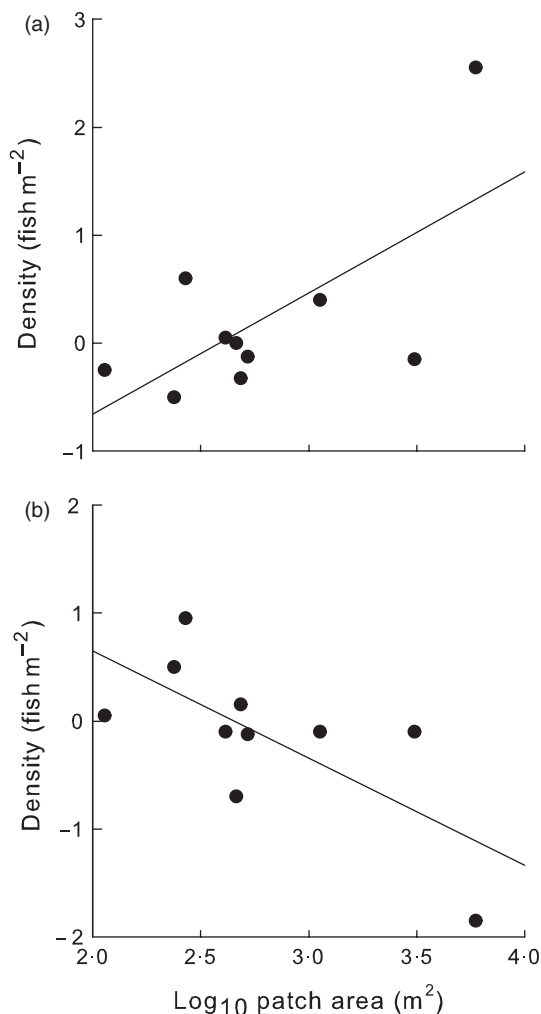


Fig. 3. Relationship between the difference in density at the edge and interior (edge-interior), and seagrass patch area ( $\log_{10}$ ) for (a) the pipefish *Stigmatopora nigra* and (b) the goby *Nesogobius maccullochi*.

than in Jelbart *et al.* (2007), and possible consequences are discussed below. Our findings are, however, consistent with terrestrial studies that have found that edge effects and patch size interact to influence abundance (Didham *et al.* 1998; Barbosa & Marquet 2002; Ewers *et al.* 2007). Changes in the strength of edge effects as patch size increases suggest that edge effects are driving area effects (Parker *et al.* 2005; Ewers *et al.* 2007; Fletcher *et al.* 2007). The lack of an edge effect for both *S. nigra* and *N. maccullochi* in small patches supports the hypothesis that, in small patches, there is little core habitat to sustain differences in densities between the edge and interior (Ewers *et al.* 2007). In contrast, in larger patches where there is more core habitat, and a greater distance between the edge and middle positions to promulgate changed conditions, a larger edge effect can result (Barbosa & Marquet 2002; Ewers *et al.* 2007). The detection of few inconsistent differences in species abundance between positions at the edge and 2 m into seagrass patches lends further support to the theory that small patches provide little or no core habitat for fish.

Edge effects are known to vary in marine and terrestrial systems (Ries *et al.* 2004a; Ewers *et al.* 2007), including seagrass habitats (Boström *et al.* 2006; Connolly & Hindell 2006). Differences in patch conditions and attributes can explain some of the variability amongst studies (Donovan *et al.* 1997; Ewers *et al.* 2007), and the interaction between edge and patch area is an important component of this variability (Jelbart *et al.* 2006). Differences in densities of *S. nigra* between the middle and edges of seagrass patches were greater in large than small patches (i.e. there were relatively more fish at the edge in large patches than in small patches). This contrasts with Jelbart *et al.* (2006), who found no difference in *S. nigra* densities between the edge and middle of seagrass patches regardless of patch size. Small patches in their study were similar in size to our large patches; it would therefore be expected that greater densities of *S. nigra* would be sampled at patch edges in their study. Inconsistencies between patterns of *S. nigra* distributions in Jelbart *et al.* (2006) and our study may relate to difference in patch characteristics (i.e. seagrass species, length, water depth), landscape variables (i.e. patch location, nearest neighbour) or sampling position within patches. Jelbart *et al.* (2006) considered the edge to be 4 m wide, and thus may have included some interior habitat in edge samples. Large-scale landscape characteristics such as position within a landscape, the role of corridors and patch aggregation have only recently been considered in seagrass ecosystems (Boström *et al.* 2006), and may provide insights into inconsistencies among edge studies.

Studies investigating edge effects in seagrass have used both fixed (Uhrin & Holmquist 2003; Bologna 2006; Jelbart *et al.* 2006) and proportional (Bowden *et al.* 2001; Smith *et al.* 2008) distances into seagrass to represent the interior of patches. Abiotic and biotic differences may occur far into habitat interiors (Barbosa & Marquet 2002), and the influence of these factors may be overlooked if fixed positions are not placed far enough into patch interiors. We found little difference in fish density between our fixed distance interior (i.e. 2 m into a patch) and the patch edge. The lack of difference between the edge and fixed interior possibly points to a deficiency in the approach of choosing a fixed distance to represent the interior of a patch; although at only 2 m into the patch, the fixed position adopted in this study may still be representative of edge habitat. However, choosing the alternative approach and representing the middle of patches using proportional distances into patches provides no controls for the influence of patch area on edge effects (i.e. no difference in small patches with little core habitat). Our results suggest a constant increase in edge effects as patch size increases, although we may not have sampled enough patches, or at enough positions within patches, to detect any exponential patterns in edge effects. To separate the effects of area and edge, Fletcher *et al.* (2007) suggested sampling at multiple distances into patches of distinct categorical sizes (e.g. small, medium and large). Such sampling regimes, however, may prove difficult in sampling mobile species in small seagrass patches, which are often too small to sample at more than

one or two distances into a patch. Novel, fine-scale sampling techniques and regimes (e.g. Minello & Rozas 2002) may be required to further elucidate edge and area effects in seagrass.

Distribution of resources across habitat patches affects the magnitude of edge effects (Ries *et al.* 2004a). Food availability has been suggested as an important factor in explaining the distribution and abundance of *S. nigra* within seagrass patches (Smith *et al.* 2008; Macreadie *et al.* 2009). *Stigmatopora nigra* are a permanent seagrass species that ambush small benthic and planktonic copepod crustaceans (Steffe, Westoby & Bell 1989; Kendrick & Hyndes 2005) that vary in abundance within seagrass beds (Warry *et al.* 2009). The reduced water movement at the interior of seagrass patches (Peterson *et al.* 2004) potentially limits the flow of planktonic copepods from outside to the interior of the patch and, therefore, may reduce the abundance of prey for *S. nigra*; reduced prey densities may explain, or contribute to, differences in *S. nigra* abundance between the edge and interior of large patches. In contrast, small patches may not support enough habitat and structure to restrict flow and subsequent food supply into patch interiors. The less-significant differences in smaller patches may thus reduce the magnitude of edge effects on animals (Barbosa & Marquet 2002).

The relationship between edge and area becomes increasingly complicated in small patches, and a given distance (whether fixed or proportional) into a small patch may not behave in the same manner as in a larger patch (Ewers *et al.* 2007). Locations within small patches are closer to more edges than in large patches, and are therefore exposed to the effects of multiple edges (Malcolm 1994; Fletcher 2005). The role of multiple edges in small patches may be additive, in which case edge effects may increase exponentially (Ewers *et al.* 2007). Small patches can also encourage species aggregation (Cronin 2009), further complicating the relationship between edge and area. Patch shape can also affect animal distributions and abundance (Jelbart *et al.* 2006), and is exaggerated in small patches. Although not considered in our study, patch shape effects may have contributed to differences in edge effects between patches.

Edge effects can be driven by differential predation rates between edge and interior habitats (Lecomte *et al.* 2008), and the abundances of predators and their prey can change over time (Meyer, Sisk & Covington 2001; Ries *et al.* 2004a). In seagrass habitats, a small number of species have shown different responses to edges over time (e.g. Hovel *et al.* 2002; Smith *et al.* 2008). We found that season and time of day had little effect on the within-patch variation of seagrass fishes. Relative differences in species richness and goby density between positions in seagrass patches did not change over time, while the density of *S. nigra* varied inconsistently between positions over time, but maintained consistent patterns across patches. *Stigmatopora nigra* predator and prey abundances have been shown to vary over time (Jenkins & Hamer 2001; Hindell 2006), and may contribute to the temporal variance of edge effects on *S. nigra*.

Patch size can determine the presence and strength of edge effects. Interactions between edge effects and patch area can

influence the interpretation of landscape studies, highlighting the need for carefully planned experiments (Fletcher *et al.* 2007). Habitat fragmentation reduces patch size and increases the amount of edge habitat, making the relationship between edge and area important for conservation, restoration and management, particularly for species favouring interior habitats that are likely to be most affected. Further investigations to establish underlying mechanisms affecting the relationship between edge and area will be important for continuing conservation and management of fragmented ecosystems.

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