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**Short term differences in animal assemblages in patches  
formed by loss and growth of habitat**

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**Abstract** Ecological theory predicts that habitat growth and loss will have different effects on community structure, even if they produce patches of the same size. Despite this, studies on the effects of patchiness are often performed without prior knowledge of the processes responsible for the patchiness. We manipulated artificial seagrass habitat in temperate Australia to test whether fish and crustacean assemblages differed between habitats that formed via habitat loss and habitat growth. Habitat loss treatments (originally 16 m<sup>2</sup>) and habitat growth treatments (originally 0 m<sup>2</sup>) were manipulated over 1 week until each reached a final patch size of 4 m<sup>2</sup>. At this size, each was compared through time (0 - 14 days after manipulation) to control patches (4 m<sup>2</sup> throughout the experiment). Assemblages differed significantly among treatments at 0 and 1 day after manipulation, with differences between growth and loss treatments contributing to most of the dissimilarity. Immediately after the final manipulation, total abundance in habitat loss treatments was 46% and 62% higher than controls and habitat growth treatments respectively, which suggests that animals crowded into patches after habitat loss. In contrast to terrestrial systems, crowding effects were brief (1 day), signifying high connectivity in marine systems. Growth treatments were no different to controls, despite the lower probability of animals encountering patches during the growth phase. Our study shows that habitat growth and loss can cause short-term differences in animal abundance and assemblage structure, even if they produce patches of the same size.

**Keywords:** Habitat loss, habitat growth, crowding effects, fragmentation, connectivity.

## INTRODUCTION

It is widely accepted that habitat loss causes reductions in species richness and abundance. According to a proportional area model, where animals are randomly distributed within habitat, species richness and abundance should decline linearly with habitat loss (Bender *et al.* 1998). Habitat area is therefore an important determinant of species richness and abundance for randomly distributed animals. If animals are non-randomly distributed within a habitat, then their distribution may instead be determined by the configuration of remnant patches (Eggleston *et al.* 1999; Ries and Sisk 2004). But in some situations, neither habitat area nor configuration can explain species richness and abundance (Debinski and Holt 2000). For example, Schmiegelow *et al.* (1997) detected increases in avian abundance in recently created forest fragments, that eventually declined without a change in habitat area or configuration. They attributed this to a “crowding effect” caused by the displacement of individuals from the original surrounding area.

Crowding effects are caused where animals concentrate into remnant patches from surrounding habitat after habitat loss or fragmentation (Bierregaard *et al.* 1992; Robinson *et al.* 1992), followed by community relaxation toward an equilibrium in subsequent years (Debinski and Holt 2000). If remnant patches are sampled before relaxation has occurred, then crowding effects can mask the negative effects of habitat loss (Ewers and Didham 2006). For example, Debinski & Holt (2000) surveyed the terrestrial fragmentation literature and found that the longer-term studies (≥ 14 years) revealed patterns that would have been missed in short-term investigations. Even in terrestrial systems with relatively high connectivity, crowding effects can persist for weeks or months (Parker and Mac Nally 2002). For example, Collinge & Forman (1998) recorded higher abundances of insects in experimentally fragmented grassland habitat, persisting for at least 5 weeks.

If habitat loss causes temporary increases in abundance and species richness (through crowding effects), then habitat growth should have the opposite effect. Island biogeography theory predicts that single large patches will support greater species richness than multiple smaller patches of the same total area (MacArthur and Wilson 1967). Based on species-area relationships, ‘growing’ patches will accumulate fewer animals because their smaller size reduces the likelihood of interception by passing animals (Game 1980; Gutzwiller and Anderson 1992). Recently ‘grown’ patches should therefore have fewer species and lower abundance than patches of the same size that have been stable for some time, or patches that have recently undergone habitat loss. Thus, community composition will differ in patchy landscapes depending on whether patchiness is the result of fragmentation, or patchy growth. This has important implications for studies that use patchiness as a proxy for fragmentation, because without historical data the processes responsible for patchiness cannot be known.

Changes in habitat structure (i.e. shape and area) have been a major focus of terrestrial studies because of their implications for the conservation of biodiversity (Fagan *et al.* 1999; Fahrig 2003), but they are no less important in the sea. Seagrass is a critical marine habitat that is becoming increasingly fragmented and is in significant global decline (Orth *et al.* 2006). Seagrasses’ natural propensity to form variable-sized patches (Robbins and Bell 1994) make them an ideal system for testing theories about

animal responses to changes in landscape structure (Connolly and Hindell 2006; Hinchey *et al.* 2008; Tanner 2005). Our aim was to compare the effects of habitat loss and habitat growth on fish and decapods in seagrass using realistic sized patches. Patch sizes were decreased (habitat loss treatments) and increased (habitat growth treatments) until they reached the same final size. They were then compared through time against controls which remained the same final size as treatments throughout the experiment. In habitat loss treatments, we predicted that abundance and species richness would be higher immediately after manipulation due to crowding in remnant patches. In habitat growth treatments, we predicted that abundance and species richness would initially be lower because the chance of encountering small patches during the growth phase was lower. Furthermore, we predicted that seagrass specialists with a high propensity for site attachment will be more likely to crowd and less likely to colonize growing patches than generalist or highly mobile species.

## MATERIALS AND METHODS

### Artificial seagrass

Habitat structure of natural seagrass can vary within patches (Bologna 2006). We therefore used artificial seagrass in our experiment to avoid potentially confounding micro-scale variation in seagrass structure (e.g. shoot density, leaf length and thickness) and to control patch size, shape, orientation, position, and time of habitat establishment. In addition, using artificial seagrass avoids having to destroy or cultivate natural seagrass. Seagrass patches were produced using artificial seagrass units (ASUs) as building blocks, which were constructed by tying 5 mm wide green polypropylene ribbon to 1 m<sup>2</sup> squares of steel mesh at a density of 3 520 leaves m<sup>-2</sup>. Shoot density and leaf length of ASUs were based on mean estimates for *Heterozostera nigricaulis* in this area (Jenkins *et al.* 1998), as were patch sizes (Macreadie *et al.* 2009). At each intersection of steel mesh (220 intersections m<sup>-2</sup>), 8 pieces of 1 m long ribbon were tied to give 16 leaves each of approximately 0.45 m length. Like natural seagrass, ASUs provide food, shelter and protection from predators and are thus considered good mimics of natural seagrass. Several studies have shown they attract fauna similar to that of natural seagrass (Bell *et al.* 1985; Sogard 1989; Upston and Booth 2003; Virnstein and Curran 1986).

### Study site

Artificial seagrass patches were deployed at Grassy Point (38°07'S, 144°41'E) in Port Phillip Bay, a large shallow embayment in temperate southeastern Australia. ASU patches were established on unvegetated sand at a depth of 1-2 m below Mean Low Water Spring. Each patch was separated by 30 m from other patches, and 5 - 10 m from natural seagrass. All ASUs were left for 3 weeks of conditioning to allow epiphyte growth and faunal colonization before the manipulation commenced. We have previously shown that 3 weeks is sufficient duration to reach an equilibrium in fish (Macreadie *et al.* 2009) and meiofaunal (Warry *et al.* 2009) abundance.

## Experimental design

Habitat loss treatments ( $n = 6$ ) started as single  $16 \text{ m}^2$  patches, and were reduced to  $4 \text{ m}^2$  by removal of ASUs. This treatment was designed to mimic boat propeller scarring which instantaneously removes seagrass habitat (Bell *et al.* 2002; Burfeind and Stunz 2006; Uhrin and Holmquist 2003). The removal process involved lifting (by hand) ASUs out of the water, shaking them (to remove fauna), and then transporting them (by boat) to shore. Habitat growth treatments ( $n = 6$ ) were expanded from  $0 \text{ m}^2$  (unvegetated sand) to areas of  $4 \text{ m}^2$  by addition of ASUs. Control patches ( $n = 6$ ) remained as  $4 \text{ m}^2$  patches throughout the experiment. The manipulation of habitat loss and growth treatments took place in two even stages over 6 days during February 2007 (i.e. habitat loss:  $16 \text{ m}^2 \rightarrow 10 \text{ m}^2 \rightarrow 4 \text{ m}^2$ , habitat growth:  $0 \text{ m}^2 \rightarrow 2 \text{ m}^2 \rightarrow 4 \text{ m}^2$ ). Once manipulations were complete (i.e., within 2 hours), treatments and controls were sampled for fish and decapod crustaceans (shrimp, crabs). We have previously shown that disturbance during manipulation (removal and replacement) of ASUs has no effect on fish abundance (Macreadie *et al.* 2009). Therefore, fish responses to habitat loss and habitat growth should reflect changes in patch size rather than the process of removal and addition of ASUs.

## Sampling

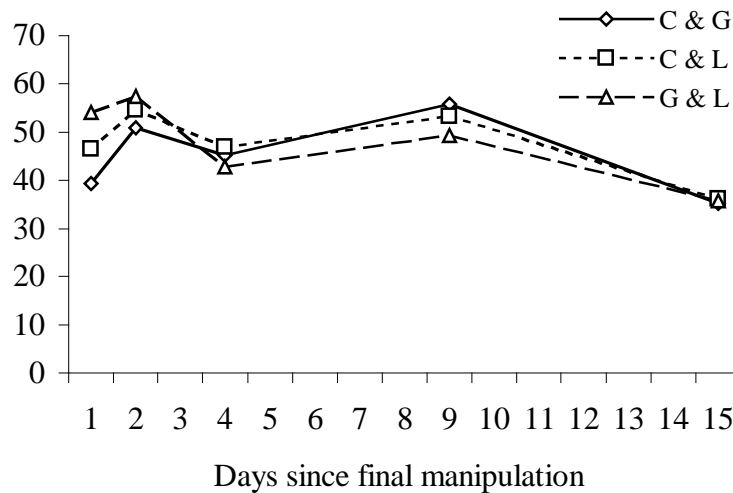
To sample fish and decapods, we used a seine net consisting of a buoyant head-rope and weighted foot-rope (6 m wide with 3 m bridles, 2 m drop and 1 mm mesh size). We set the net around the perimeter of each treatment and then hauled it over the treatment in one direction. We ran three consecutive hauls of the net over each replicate within 2 hours of the final manipulation. Animals were held within a flow-through holding net in the field and returned to treatments once identified and counted. Although seagrass fish appear to be relatively resilient to seagrass disturbance (Macreadie *et al.* 2009), we made every effort to minimize the potential disturbance effects of repeated sampling of patches. For example, during the release process we placed fish within drop nets ( $1 \text{ m}^2$  with 2 m drop and 1 mm mesh size) over treatments and allowed them to acclimate within seagrass for 20 min before drop nets were removed to minimise their vulnerability to predation or being carried away by currents. All sampling was performed during daylight hours at low tide to limit the potential influence of time of day, depth, and tide.

## Data analysis

Data were analysed with multivariate (PRIMER 5) and univariate (Systat 12) statistical techniques. Differences in fish and decapod assemblages among treatments were tested using ANOSIM (Bray-Curtis similarity matrix with raw data), and the SIMPER routine was used to measure dissimilarity between pairs of treatments (Clarke and Warwick 1994). Sampling times were analysed separately since repeated measure tests for similarity data do not exist. For univariate analyses, response variables were animal abundance and species richness (defined as the total number of species per treatment). Individual taxa were analysed if they were sufficiently abundant, otherwise they were combined into higher taxonomic groups for analysis. We compared response variables

among treatments using repeated measures ANOVA, with ‘treatment’ and ‘time’ since final manipulation as fixed and repeated factors, respectively. Taxa with significant time  $\times$  treatment interactions were analysed further with *post hoc* Tukey tests to determine which treatments differed, at each time after manipulation. The time  $\times$  treatment interactions provide information about the effects of time since manipulation on treatments, so our analyses focus on this interaction.

## RESULTS



**Fig. 1.** Levels of dissimilarity in assemblages (average %, calculated using SIMPER routine in PRIMER) between pairs of treatments at each time. Controls (C,  $n = 6$ ), habitat growth treatments (G,  $n = 6$ ), and habitat loss treatments (L,  $n = 6$ ). Asterisks indicate a significant difference ( $P < 0.05$ ) in assemblages between pairs for a given time.

Overall differences in fish and decapod assemblages among treatments were observed at 0 days (ANOSIM: Global  $R = 0.32$ ,  $P = 0.009$ ) and 1 day ( $R = 0.19$ ,  $P = 0.027$ ) after final manipulation, but no differences were observed after 3 days ( $R = 0.01$ ,  $P = 0.397$ ), 8 days ( $R = -0.07$ ,  $P = 0.811$ ), or 14 days ( $R = 0.05$ ,  $P = 0.264$ ). SIMPER analyses indicated that most of the dissimilarity among treatments occurred at 0 and 1 day after manipulation. At 0 and 1 day after manipulation, dissimilarity was greatest between growth and loss treatments, but loss and control treatments also had high dissimilarity, and were more dissimilar than growth and control treatments (Fig. 1).

Our first prediction, that abundance would initially be higher in habitat loss treatments than controls due to crowding effects, was true for 3 of 7 taxa analysed: the decorator crab *Naxia aries*, monacanthid fish (leatherjackets), and spotted pipefish *Stigmatopora argus* (Table 1). *Post hoc* comparisons for monacanthids and *N. aries* showed that crowding effects were only present immediately after the final manipulation (i.e. 0 days after manipulation, 90 and 86% more abundant respectively), whereas for *S.*

*argus*, crowding effects lasted up to 1 day after manipulation (46 and 56% more abundant at 0 and 1 day respectively, Table 1, Fig. 2). Crowding effects were also observed for total abundance immediately after habitat loss, and this pattern was largely driven by *S. argus* which represented 68% of the total catch (Table 1, Fig. 2). Species richness was 31% higher in habitat loss treatments compared to controls, but this difference was not significant (Table 1, Fig. 2). No effect of crowding was found for *Idiosepius notoides* (southern pygmy squid), *Macrobrachium* sp. (grass shrimp), *Platycephalus* spp. (flathead), or *Stigmatopora nigra* (wide-bodied pipefish).

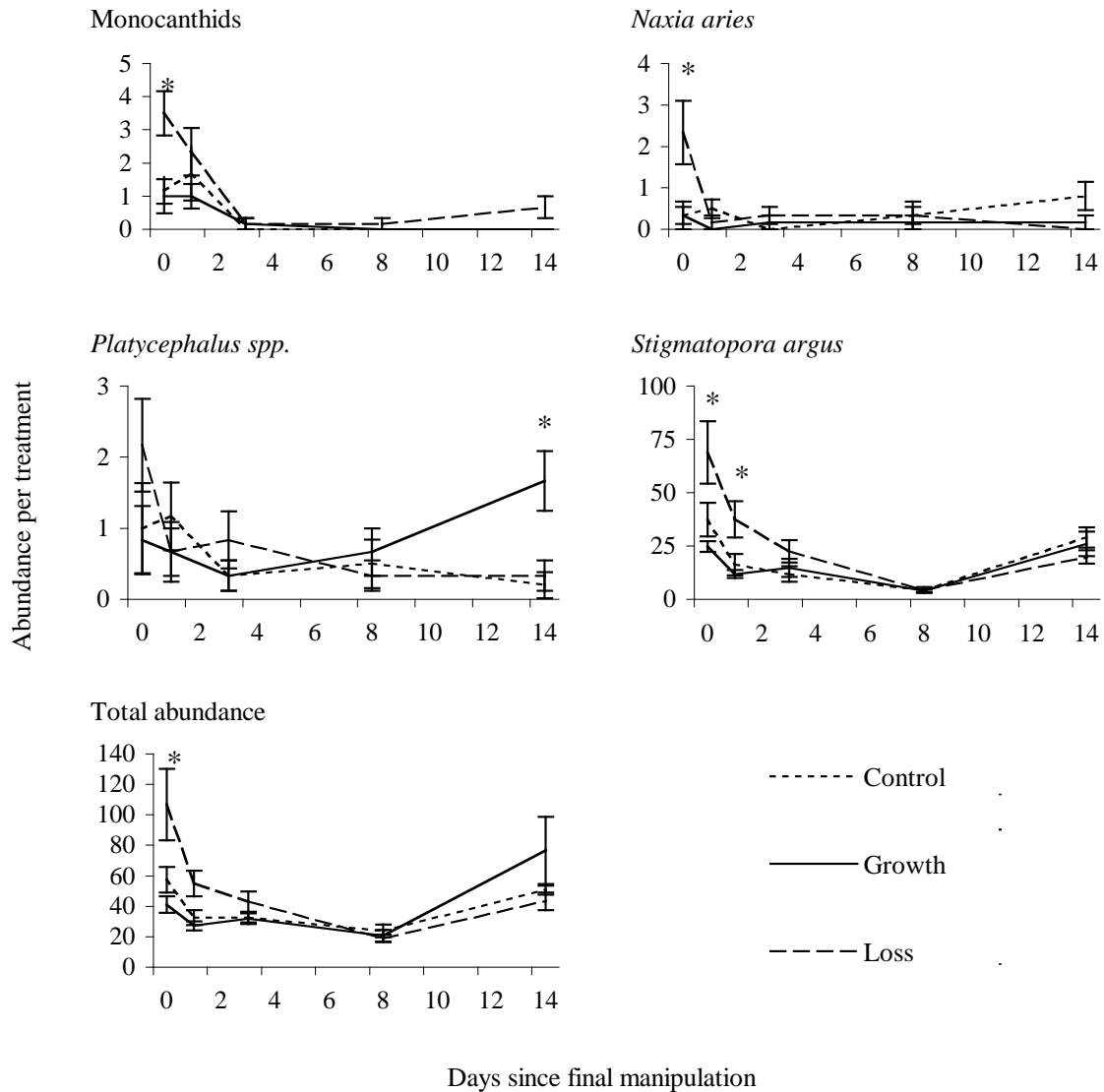
**Table 1.** Repeated measures ANOVA results (P values) comparing abundance and species richness of fish among and within treatments (L - habitat loss, G - habitat growth, and C - controls), and with time since final manipulation (0, 1, 3, 8, and 14 days). Significant P values (< 0.05) in bold. Taxa with significant Time × Treatment interactions were further analysed with Tukey *post hoc* comparisons to determine which treatments differed ( $p < 0.05$ ). NA indicates that tests were not applicable. Species that were insufficiently common for analysis were grouped into higher taxa and/or total abundance.

Source df	Total # of ind. caught	ANOVA			Tukey <i>post hoc</i> comparison	
		Between subjects	Within subjects	Time × Treatment	Time (days)	Test
		Treatment	Time			
		2	4	8	56	
Species richness	39	0.419	< <b>0.001</b>	0.092		NA
<i>Idiosepius notoides</i>	189	0.165	< <b>0.001</b>	0.173		NA
<i>Macrobrachium</i> sp.	43	0.937	0.152	0.272		NA
Monocanthids	80	<b>0.043</b>	< <b>0.001</b>	<b>0.014</b>	0	C = G < L
<i>Naxia aries</i>	35	0.146	<b>0.002</b>	<b>0.001</b>	0	C = G < L
<i>Platycephalus</i> spp.	56	0.560	0.178	<b>0.006</b>	14	C = L < G
<i>Stigmatopora argus</i>	1970	0.058	< <b>0.001</b>	< <b>0.001</b>	0 & 1	C = G < L
<i>Stigmatopora nigra</i>	116	<b>0.029</b>	<b>0.034</b>	0.284		NA
Total abundance	2901	<b>0.016</b>	<b>0.003</b>	<b>0.010</b>	0	C = G < L

Our second prediction, that abundance and species richness will be initially lower in growth treatments, was not supported. Species richness and taxa abundance in habitat growth treatments were not significantly different to controls once manipulations were completed (Table 1, Fig. 2). *Platycephalus* spp. abundance in habitat growth treatments was no different from controls at 0, 1, 3, and 8 days after manipulation, but after 14 days they were 88% more abundant in growth treatments (Table 1, Fig. 2). *S. nigra* also increased in abundance through time, but this took place across all treatments (Table 1).

## DISCUSSION

As predicted, some decapod crustacean (*Naxia aries*) and fish (monocanthids, *Stigmatopora argus*) taxa crowded into patches after habitat loss. These taxa were seagrass specialists with a high propensity for site attachment (Jackson *et al.* 2001), which potentially makes them more likely candidates for crowding than generalist or highly mobile species (Schoereder *et al.* 2004). In all cases, crowding effects lasted  $\leq 1$  day. This duration was brief relative to comparable terrestrial studies. For example,



**Fig. 2.** Responses in fish and decapod abundance, and species richness (mean + SE) to habitat growth ( $n = 6$ ), habitat loss ( $n = 6$ ), and controls ( $n = 6$ ), with time since final manipulation. Asterisks indicate a significant ( $P < 0.05$ ) *post hoc* comparison among treatments for a given time.



Parker and Mac Nally (2002) suggested that crowding may explain why invertebrate abundance remained high for several months after  $15 \times 15$  m experimental grassland patches were reduced by 60 and 90% of their original size. Similarly, Collinge and Forman (1998) simulated habitat shrinkage (100  $\rightarrow$  25%) in  $10 \times 10$  m grassland patches and found that insects crowded into the remaining habitat for several weeks. It is possible that higher dispersal distances in marine systems (Kinlan and Gaines 2003) and differences in the physical properties of water and air (Denny 1990) lead to greater connectivity in marine systems and shorter crowding duration than terrestrial systems (Carr *et al.* 2003). However, it is also possible that short-term crowding effects in terrestrial systems have previously gone undetected. For example, Grez *et al.* (2004) took their first samples of insects from experimentally fragmented grassland patches after 1 week. If crowding duration were less than 1 week, as in our study, then this may explain why Grez *et al.* (2004) were unable to detect crowding effects.

Contrary to our second prediction, newly-grown seagrass patches were no different to controls in their abundance and species richness of animals. By the time the first samples were taken (i.e. 0 days after manipulation) control patches had accumulated fish and decapods over a 1 month period, whereas newly-grown patches were only 3 days old and had only just reached their final size (i.e.  $4 \text{ m}^2$ ). Despite this, total abundance in newly-grown patches was not significantly different from controls. There are two potential explanations for the lack of detectable difference. The first is that there was insufficient power to detect a change. The power to detect a 50% change in fish abundance between control and growth treatments was low (0.20). The second is that colonization was rapid, which would not be surprising given the degree of isolation from alternative habitat was relatively low (i.e., experimental patches were 5 – 10 m from natural seagrass). Since colonization to artificial seagrass is a function of distance from source (Darcy and Eggleston 2005; Sogard 1989; Virnstein and Curran 1986), connectivity in our study would have been relatively high.

This experiment focuses on the short-term responses to habitat growth and loss. Although our results show convergence of treatments over the duration of our study, it is possible that responses will change over a longer period as community dynamics and interactions change (as may be the case with platycephalid fish after 14 d) (Vasconcelos *et al.* 2008). For example, habitat loss can have generational effects that manifest through extinction debts that are paid through time as communities inhabiting fragments relax toward a new equilibrium (Brooks *et al.* 1999). In seagrass habitats, early colonizers can affect the colonization success and persistence of future colonists (Hovel and Regan 2008; Irving *et al.* 2007) and extinction debt models show a trade-off between dispersal potential and competitive ability (Banks 1997). Since colonization was rapid in our study, we suggest that competitive ability will be low, but dispersal potential will be high (Keough 1984). We therefore would not expect our findings to differ greatly had we extended the duration of our monitoring.

In summary, our study shows that habitat growth and habitat loss can cause short-term differences in animal abundance and assemblage structure, even when they produce patches of the same size. We find that samples taken from remnant patches immediately after habitat loss can have inflated densities due to crowding effects, and this has the potential to temporarily mask the negative effects of habitat loss on animal abundance.

Crowding duration was much shorter than previously reported in the terrestrial literature and this difference may reflect higher levels of connectivity in marine systems.

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