

Fish Responses to Experimental Fragmentation of Seagrass Habitat

PETER I. MACREADIE,^{*†**} JEREMY S. HINDELL,^{‡††} GREGORY P. JENKINS,^{*‡}
ROD M. CONNOLLY,[§] AND MICHAEL J. KEOUGH^{*}

^{*}Department of Zoology, University of Melbourne, Parkville, Australia

[†]Victorian Marine Science Consortium, Queenscliff, Australia

[‡]Marine and Freshwater Systems, Department of Primary Industries, Queenscliff, Australia

[§]Australian Rivers Institute: Coast & Estuaries, and School of Environment, Griffith University, Gold Coast Campus, Australia

Abstract: *Understanding the consequences of habitat fragmentation has come mostly from comparisons of patchy and continuous habitats. Because fragmentation is a process, it is most accurately studied by actively fragmenting large patches into multiple smaller patches. We fragmented artificial seagrass habitats and evaluated the impacts of fragmentation on fish abundance and species richness over time (1 day, 1 week, 1 month). Fish assemblages were compared among 4 treatments: control (single, continuous 9-m² patches); fragmented (single, continuous 9-m² patches fragmented to 4 discrete 1-m² patches); prefragmented/patchy (4 discrete 1-m² patches with the same arrangement as fragmented); and disturbance control (fragmented then immediately restored to continuous 9-m² patches). Patchy seagrass had lower species richness than actively fragmented seagrass (up to 39% fewer species after 1 week), but species richness in fragmented treatments was similar to controls. Total fish abundance did not vary among treatments and therefore was unaffected by fragmentation, patchiness, or disturbance caused during fragmentation. Patterns in species richness and abundance were consistent 1 day, 1 week, and 1 month after fragmentation. The expected decrease in fish abundance from reduced total seagrass area in fragmented and patchy seagrass appeared to be offset by greater fish density per unit area of seagrass. If fish prefer to live at edges, then the effects of seagrass habitat loss on fish abundance may have been offset by the increase (25%) in seagrass perimeter in fragmented and patchy treatments. Possibly there is some threshold of seagrass patch connectivity below which fish abundances cannot be maintained. The immediate responses of fish to experimental habitat fragmentation provided insights beyond those possible from comparisons of continuous and historically patchy habitat.*

Keywords: artificial seagrass, disturbance, edge effects, habitat fragmentation, habitat loss, patchiness, Port Phillip Bay, *Stigmatopora*

Respuestas de Peces a la Fragmentación Experimental de Hábitat de Pasto Marino

Resumen: *La comprensión de las consecuencias de la fragmentación del hábitat ha provenido principalmente de comparaciones de hábitats fragmentados y continuos. Debido a que la fragmentación es un proceso, su estudio es más preciso mediante la fragmentación activa de áreas continuas en múltiples fragmentos más pequeños. Fragmentamos hábitats de pasto marino artificiales y evaluamos los impactos de la fragmentación sobre la abundancia y riqueza de especies en el tiempo (1 día, 1 semana, 1 mes). Los ensambles de peces fueron comparados entre cuatro tratamientos: control (fragmentos individuales continuos de 9 m²), fragmentado (fragmentos individuales continuos de 9 m² divididos en cuatro fragmentos discretos de 1 m²); prefragmentado/fragmentado (cuatro parches discretos de 1 m² con el mismo arreglo que fragmentado) y control de perturbación (fragmentado e inmediatamente restablecido a parches continuos de 9 m²). El pasto marino heterogéneo tuvo menor riqueza de especies que el pasto marino fragmentado activamente (basta*

^{**}email petermacreadie@gmail.com

^{††}Current address: Arthur Rylab Institute, Department of Sustainability and Environment, Melbourne, Australia.

Paper submitted March 16, 2008; revised manuscript accepted September 8, 2008.

39% menos especies después de 1 semana), pero la riqueza de especies en los tratamientos fragmentados fue similar a los controles. La abundancia total de peces no varió entre tratamientos y por lo tanto no fue afectada por la fragmentación, la heterogeneidad ni la perturbación causada durante la fragmentación. Los patrones de riqueza y abundancia de especies fueron consistentes 1 día, 1 semana y 1 mes después de la fragmentación. La disminución esperada en la abundancia de peces por la reducción de la superficie de pasto en los tratamientos fragmentados y heterogéneos pareció ser compensada por la mayor densidad de peces por unidad de área de pasto marino. Si los peces prefieren vivir en los bordes, entonces los efectos de la pérdida de hábitat sobre la abundancia de peces pudieron haber sido compensados por el incremento (25%) del perímetro de pasto marino en los tratamientos fragmentados y heterogéneos. Posiblemente hay un umbral de conectividad de pasto marino debajo del cual las abundancias de peces no pueden ser mantenidas. Las respuestas inmediatas de los peces a la fragmentación experimental del hábitat proporcionaron conocimientos más allá de los obtenidos con comparaciones de hábitat continuo e históricamente heterogéneo.

Palabras Clave: Bahía Port Phillip, efectos de borde, fragmentación de hábitat, heterogeneidad, pasto marino artificial, perturbación, *Stigmatopora*

Introduction

The literature on the effects of habitat fragmentation is vast and dominated by observational studies (Fahrig 2003). Most researchers use patchiness as a proxy for fragmentation; that is, patchy habitats are used to represent a postfragmented state and continuous or “reference” habitats are used to represent a prefragmented state (e.g., Robinson et al. 1992; Laurance et al. 2001; Mac Nally & Brown 2001). This retrospective approach offers a historical perspective on the effects of fragmentation and allows conservation biologists to assess the long-term effects of fragmentation. By contrast, little work has been done to assess the immediate effects of fragmentation.

Fragmentation is a process, not a state, and the most accurate way to capture immediate effects of fragmentation is to actively fragment habitat. Few researchers have experimentally fragmented habitat probably because it is costly and labor intensive. To date, experimental fragmentation research has been dominated by grassland studies (but see Caley et al. 2001; Grez et al. 2004), where fragmentation is more easily manipulated than in most other habitats (e.g., Hovland et al. 1999; Summerville & Crist 2001; Parker & Mac Nally 2002). The importance of experimental fragmentation is stressed by Debinski and Holt (2000), who identified (only) 20 experimental fragmentation studies in the terrestrial literature and found that many reveal effects contrary to theoretical predictions derived from retrospective approaches. They also note that experimental fragmentation offers good experimental controls and properly randomized designs, which are often difficult to achieve in observational studies.

Seagrass is a critical marine habitat that is becoming increasingly fragmented and is in significant global decline (e.g., Duarte 2002; Orth et al. 2006). The effects of habitat fragmentation on seagrass have only recently been investigated (Bostrom et al. 2006; Connolly & Hindell 2006). These studies have predominantly been retrospective comparisons of continuous and fragmented

habitats and have included investigations of the effects of fragmentation on fishes (e.g., Bell et al. 2001, 2002; Fernandez et al. 2005) and macroinvertebrates (e.g., Eggleston et al. 1999; Hovel 2003; Reed & Hovel 2006), although Johnson and Heck (2006) experimentally fragmented a seagrass habitat and measured fish and decapod responses. But, like comparable terrestrial studies (e.g., Schmiegelow et al. 1997), their study areas were embedded within larger continuous landscapes, which may potentially dampen any local-scale impacts of fragmentation (Haila 2002).

We used seagrass habitat as a model system to study the effects of experimental fragmentation on fish. We chose this system because artificial seagrass can be created and manipulated to simulate fragmentation. Artificial seagrass has been used as a surrogate for natural seagrass for almost 30 years (Barber et al. 1979) because it standardizes potentially confounding microscale differences and avoids the need for destruction of natural seagrass (Bologna & Heck 1999; Tanner 2003). We modeled our study on an actual fragmentation event that occurred in Port Phillip Bay, Victoria, Australia. Patch sizes (9 m²) and degree of fragmentation (approximately 50%) were based on realistic fragmentation scenarios. Seagrass habitat fragmentation can occur at much larger scales (tens of meters to kilometers), and fish responses may differ at these larger scales (Jackson et al. 2001), depending on their mobility and perception windows (Attrill et al. 2000). In assessing the effects of fragmentation on fish through time, we tested 2 predictions: the abundance and species richness of fish will be lower in seagrass treatments that have undergone fragmentation compared with controls and will be different in treatments that have actually undergone fragmentation compared with those that already exist in a prefragmented (patchy) state. Our simulation of fragmentation includes a simultaneous loss of habitat, so we could not separate the effects of habitat loss from fragmentation per se (i.e., the breaking apart of habitat after controlling for habitat loss; Fahrig 2003).

Methods

Study Site

We performed this study at Grassy Point (38°07'S, 144°41'E) in Port Phillip Bay, Victoria, Australia. Port Phillip Bay is a shallow, semi-enclosed, temperate marine embayment (2000 km²) bordered by a large urban population (approximately 4 million). Seagrass is common in the southern and western regions of the bay and occurs as bands of varying size and patchiness, running parallel to the shore. We based our study on an actual fragmentation event that occurred at Rosebud (38°21'S, 144°52'E) in Port Phillip Bay during 2001–2004. From aerial photographs and the GIS software ArcView 3.3, we found that the mean patch size in this region was reduced from 13.3 m² (SE 4.8) to 4.6 m² (SE 2.7). This was accompanied by an increase in the number of patches and an approximate doubling of the overall perimeter-to-area ratio.

Construction of Artificial Seagrass Units

Artificial seagrass is intended to mimic the dominant subtidal seagrass in Port Phillip Bay, the fine-leaved *Heterozostera nigricaulis*. We produced seagrass patches (3 × 3 m) with artificial seagrass units (ASUs) as building blocks. The ASUs ($n = 125$) were constructed by tying 5-mm-wide green polypropylene ribbon to steel mesh (1 m²) at a density of 3520 leaves/m². At each intersection of the steel mesh (220 intersections/m²), 8 pieces of 1-m-long ribbon were tied to give 16 leaves, each approximately 0.45 m long. Shoot density and leaf length were based on mean estimates for this area (Jenkins et al. 1998). Results of previous studies show that abundances of fish are not significantly different between bare frames and unvegetated sand (Jenkins et al. 1998) and that fish assemblages are similar in artificial and natural seagrass (Upston & Booth 2003).

Experimental Design

To test the effects of fragmentation of seagrass on fish, we used a factorial design with 2 main factors: fragmen-

tation and time since fragmentation. Fragmentation consisted of 4 treatments (Fig. 1): control (C): single, continuous, 9-m² patches; fragmented (F): single, continuous, 9-m² patches fragmented into 4 discrete 1-m² patches; prefragmented (PF): 4 discrete 1-m² patches with the same arrangement as fragmented; and disturbance control (DC): fragmented then immediately restored to continuous 9-m² patches. Fragmentation involved removing ASUs by hand, lifting them out of the water, shaking them, and then transporting them to shore. The ASUs in the disturbance controls were treated the same, but were restored to their original position immediately after they were shaken. Disturbance controls were included to provide information on the effects of disturbance caused by the fragmentation process. Fish were sampled from treatments 1 day, 1 week, and 1 month after fragmentation, giving the second experimental factor. Our experimental fragmentation of seagrass habitat involved both loss of habitat and the breaking apart of continuous habitat into smaller patch sizes. Although these processes generally occur together in nature, the effects of fragmentation per se are confounded because they are accompanied by effects of habitat loss. Therefore, we examined the effects of both fragmentation and its accompanied habitat loss.

We repeated this design on 3 occasions (each 5 weeks in duration, one after the other, September–December 2006), which formed the blocks of a randomized block design. Blocking was necessary because of the large number of ASUs needed to replicate treatments at any one time and because of limitations at the study site (there was limited bare sand adjacent to seagrass to accommodate treatments). Within each block, 1 of each of the 12 treatments were established randomly on bare sand at a depth of 1–2 m below mean low water spring (MLWS), with each treatment separated by 30 m, but located within 5–10 m of natural seagrass. Treatments were left for 1 week to allow epiphyte growth and faunal colonization before fragmentation. Once all treatments were sampled, ASUs were removed, cleaned (with freshwater from a high pressure hose) and redeployed in different blocks. The ASUs were always randomly assigned among treatments in each block.

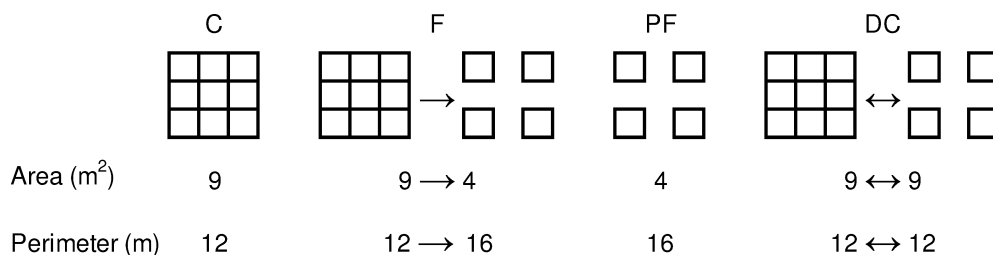


Figure 1. Treatments for the fragmentation experiment were constructed from artificial seagrass units (1 m²) and included: control (C), a continuous 9-m² patch; fragmented (F), a 9-m² patch fragmented to 4 single 1-m² patches (resulting in a 56% loss of seagrass habitat); prefragmented (PF), 4 single 1-m² patches; and disturbance control (DC), fragmented and then immediately restored to a continuous 9-m² patch.

Fish Sampling

To sample fish, we used a seine net with a buoyant head-rope and weighted foot-rope (10-m wide with 5-m bridles, 2-m drop, and 1-mm mesh) and a “pursing” technique. This involved setting the net around the perimeter of each treatment and then hauling the net over the treatment by pulling on the bridles in one direction. We ran 3 hauls of the net per treatment (although ASUs were arranged differently within treatments, the overall area of each was the same, i.e., 9 m²). Capture efficiency with seine nets over ASUs is high for the main species targeted in this study (Jenkins & Sutherland 1997). We performed all sampling during daylight hours at low tide to limit the potential influence of time of day, depth, and tide.

Data Analyses

Response variables were fish abundance, density, and species richness (defined as the total number of species per treatment). We compared each of these among treatments with a 3-factor randomized block design with treatment (*T*), block (*B*), and time after fragmentation (*TAF*) as factors. Block was treated as a random factor and *T* and *TAF* were treated as fixed factors. We used box plots and normal probability plots to test the assumptions of analysis of variance (ANOVA) (Quinn & Keough 2002), and to meet the assumption of homogeneity of variances we transformed the data to $\log_{10}(x + 1)$ where necessary. Replication was gained by pooling data from blocks ($n = 3$). Factors were compared in a 3-way ANOVA and planned comparisons were made among treatments for abundance, density per square meter of seagrass, and species richness. Controls were first compared with disturbance controls to determine whether there was an effect of disturbance during fragmentation. If no difference was found, then these were pooled and compared with fragmented treatments (control + disturbance control vs. fragmentation) to increase our power to test for fragmentation effects. Otherwise, if there was a difference between controls and disturbance controls, then fragmented treatments were compared with disturbance controls alone. Fragmented and prefragmented treatments were then compared to assess whether patchiness is a suitable proxy for fragmentation. Multivariate analyses were also performed; however, these analyses showed nothing of interest that was not apparent in the univariate analyses, so results are not presented.

Fish abundance data were analyzed only if a species occurred in >50% of samples. This criterion served to exclude taxa that were insufficiently abundant for statistical analyses. Taxa not meeting this criterion comprised <10% of the total fish sampled and were generally present in only a single block (replicate). Those fish that did not meet this criterion were combined into higher taxonomic groups for analysis. Pelagic fishes such as atherinids, which schooled in treatments between net hauls after

being attracted by netting activity, caused large variability in the data and were omitted from analyses to avoid masking patterns in total abundance relating to fragmentation. To convert abundance per treatment to density per square meter of seagrass, controls and disturbance controls were divided by 9 and fragmented and prefragmented treatments were divided by 4. All taxa, including atherinids, were included in the species-richness analysis. Species richness was measured per treatment rather than per square meter of seagrass so as to include any fish present on the sand between the 4 discrete seagrass patches in fragmented and prefragmented treatments.

Results

Fish assemblages were dominated numerically by pipefish of the species *Stigmatopora argus* and *S. nigra* (83%), and these species occurred in every treatment. *Stigmatopora* recruits were recently settled individuals (<30 mm) that were too small to identify to species. Other commonly occurring fish species were recently settled individuals of leatherjacket (*Acanthaluteres* spp.; 7%), goby (*Nesogobius maccullochi*; 2%), and Pleuronectids (flounder; 1%). Commonly sampled invertebrates included the grass shrimp (*Macrobrachium* sp.) and the southern pygmy squid (*Idiosepius notoides*).

Abundances of *S. argus* and *Acanthaluteres* recruits, total abundance, and species richness increased with each occasion the experiment was repeated (blocks), coinciding with increases in water temperature (Table 1; Fig. 2). In contrast, Pleuronectids and *S. nigra* decreased in abundance with blocks (Fig. 2). The 2 species of *Stigmatopora* showed opposite trends in their abundance with blocks (Fig. 2). Treatments varied consistently 1, 7, and 30 days after fragmentation (Table 1). During the fragmentation process, fish from ASUs being lifted out of the water and shaken were observed swimming into untouched ASUs from the same treatment.

Fish abundance did not vary among treatments when data were analyzed per treatment; however, significant differences were found when abundance data were adjusted to the density of fish per square meter of seagrass (Table 1; Fig. 3). According to planned comparisons, there was no difference between controls and disturbance controls for fish abundance per treatment ($p = 0.483$) or density ($p = 0.585$). When these treatments were pooled and compared against fragmented treatments (control + disturbance controls vs. fragmentation) no difference was found in fish abundance per treatment ($p = 0.942$), but fish density per square meter of seagrass was significantly higher in fragmented treatments compared with controls ($p \leq 0.001$). No difference was found in fish abundance per treatment ($p = 0.499$) or fish density ($p = 0.562$) between fragmented

Table 1. The p values for 3-factor analyses of variance (ANOVA) comparing abundance and species richness of fish per treatment^a and per square meter of artificial seagrass sampled among blocks (B), treatments (T), and different times after fragmentation (TAF , 1 day, 1 week, 1 month).^b

	Per treatment						Per m ² of seagrass					
	B	T	TAF	$B \times T$	$B \times TAF$	$T \times TAF$	B	T	TAF	$B \times T$	$B \times TAF$	$T \times TAF$
	2	3	2	6	4	6	3	3	1	9	3	3
<i>Stigmatopora argus</i>	<0.001	0.105	0.675	0.645	<0.001	0.713	<0.001	<0.001	0.721	0.663	<0.001	0.794
<i>S. nigra</i>	0.181	0.685	0.692	0.612	0.076	0.925	0.413	0.014	0.728	0.873	0.092	0.838
Pleuronectidae	0.111	0.301	0.892	0.084	0.097	0.583	0.222	0.358	1.000	0.201	0.176	0.584
<i>Acanthaluteres</i> recruits	<0.001	0.172	0.061	0.671	0.036	0.495	<0.001	0.422	0.127	0.769	0.094	0.715
Total abundance	<0.001	0.378	0.379	0.845	<0.001	0.794	<0.001	<0.001	0.440	0.945	<0.001	0.888
Species richness	<0.001	<0.001	0.097	0.968	0.152	0.898						

^aThe 9-m² plot area, including sand between seagrass patches within fragmented and prefragmented treatments.

^bWith the exception of the species richness analysis, only fish groups present in >50% of samples are presented. Where appropriate, species were grouped into family level. Whole numbers under treatment types are df .

or prefragmented treatments. All patterns observed were consistent after 1, 7, and 30 days (Table 1; Fig. 3).

Species richness (total number of fish species per treatment) was significantly different across treatments (Table 1; Fig. 4). Planned comparisons showed no differences ($p = 0.136$) between controls and disturbance controls. These treatments were therefore pooled and compared against fragmented treatments, but no significant difference was found ($p = 0.726$). There was a significant

difference between fragmented and prefragmented treatments, with fewer species in prefragmented treatments ($p = 0.019$). This pattern was consistent after 1, 7, and 30 days.

Discussion

Several models have been developed from terrestrial landscapes that predict patterns in animal abundance following habitat fragmentation (Bender et al. 1998; Delin & Andren 1999). According to the proportional-area model, fish abundance in fragmented treatments should decrease linearly with seagrass loss. In our study the process of fragmentation had no effect on fish abundance. This finding was consistent after 1, 7, and 30 days and went against our main prediction that fragmentation would reduce fish density. On the basis of proportionality, we expected abundance to approximately halve in fragmented treatments given that approximately 56% of the seagrass was removed (i.e., 9 m² was fragmented to 4 m²). The lack of change in abundance with fragmentation was therefore surprising and indicates that the proportional-area model did not predict fish abundance. Similarly, Delin and Andren (1999) found that Eurasian red squirrel (*Sciurus vulgaris*) density did not decline in fragmented forest. They suggest that a combination of shorter distances and less hostile surroundings accounted for differences between their findings and those from other squirrel studies.

We propose that no fragmentation effect was observed because positive edge effects (defined as increases in abundance at seagrass and sand edge) compensated for area loss. Fish densities differed across treatments and appeared to be a function of patchiness. Fragmented and prefragmented patches, which consisted of 4 single 1-m² patches, had significantly higher densities of fish compared with controls and disturbance controls, which consisted of a single 9-m² patch. There are many examples

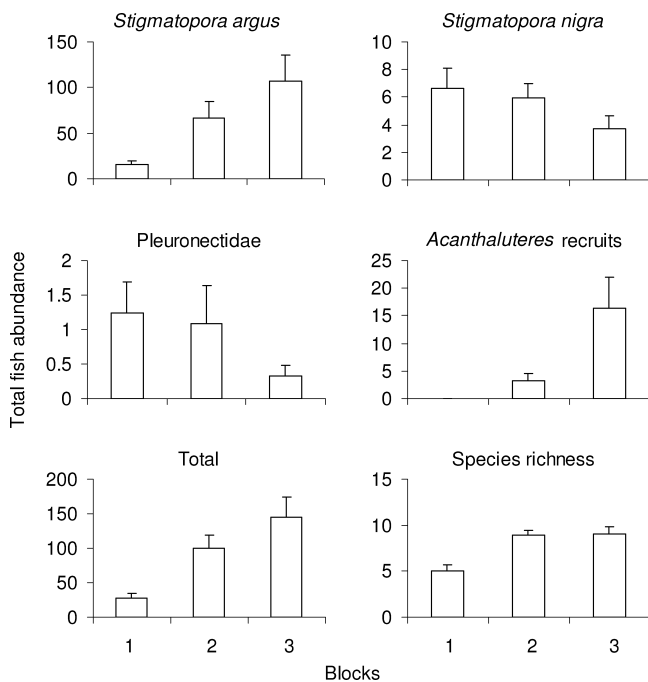


Figure 2. Total fish abundance and species richness (mean SE) pooled across treatments during each time block in 2006. Each time block was 5 weeks long (block 1, September through October; block 2, October through November; block 3, November through December).

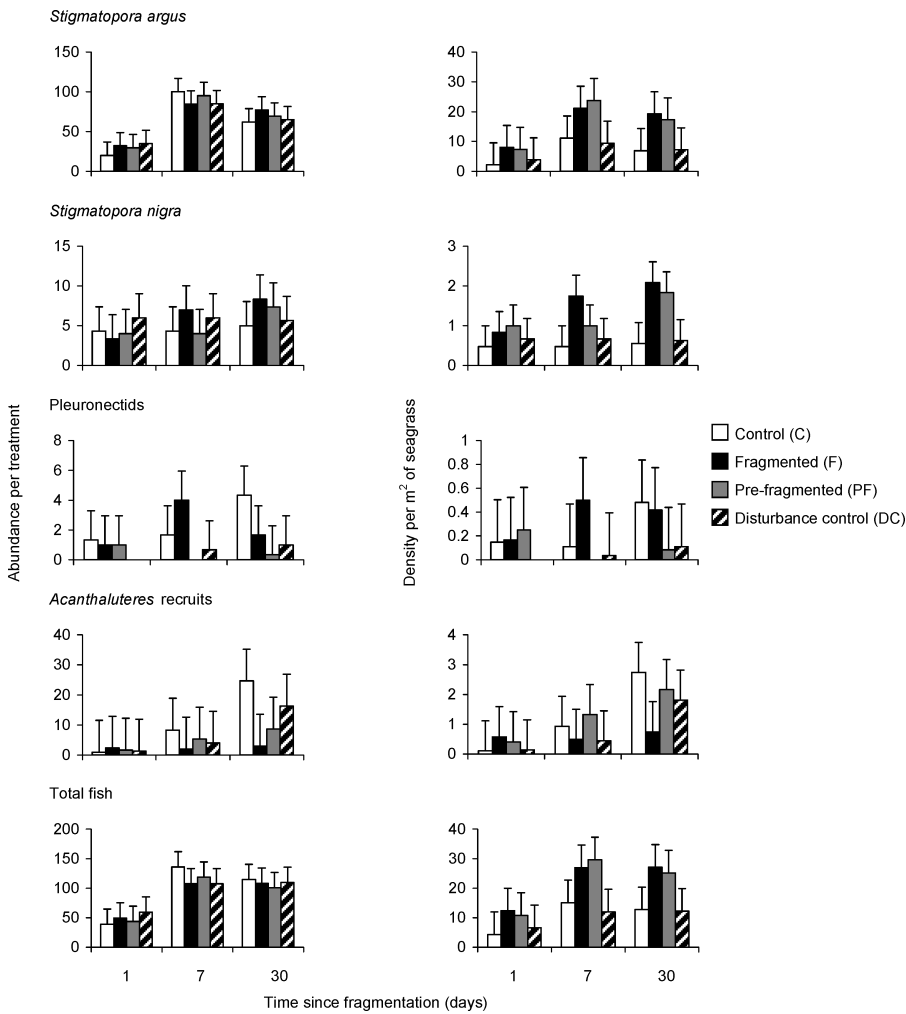


Figure 3. Mean fish abundance (per treatment, on left) and density (per square meter of artificial seagrass, on right) in treatments following manipulations (error = $\sqrt{\text{mean square}_{\text{block} \times \text{treatment}}}$). [Correction added after publication 12 January 2009: Errors in the shading of the figures were amended.]

of smaller patches supporting higher densities of animals per unit area than larger patches in both terrestrial systems (e.g., Bender et al. 1998; Doak 2000; Laurance et al. 2006) and aquatic systems (e.g., Sousa 1984; McNeill & Fairweather 1993; Salita et al. 2003). One explanation

is that edge-to-area ratios increase with increasing patchiness, and habitat edges can support higher abundances of fauna through positive edge effects (Fagan et al. 1999). In our study the perimeter-to-area ratio increased 3-fold with fragmentation (1.25–4). Assuming perimeter equates to edge, and edge is the preferred habitat of the fish caught in this study, then the potentially adverse impacts of fragmentation may have been offset by positive edge effects. This explanation is best addressed by considering species-specific responses to fragmentation.

The effects of fragmentation may depend on the composition of habitat generalists and specialists in the community and their ability to use edge and interior habitat (Andren 1994). Bender et al. (1998) reviewed studies of birds, mammals, and insects living in patchy landscapes and predicted that for edge species, the decline in population size will be less than that predicted by habitat loss alone. Our samples were dominated by pipefish (*Stigmatopora* spp.), which are highly specialized fishes that rely heavily on seagrass habitat (Howard & Koehn 1985; Jenkins et al. 1997). We hypothesize that pipefish did not

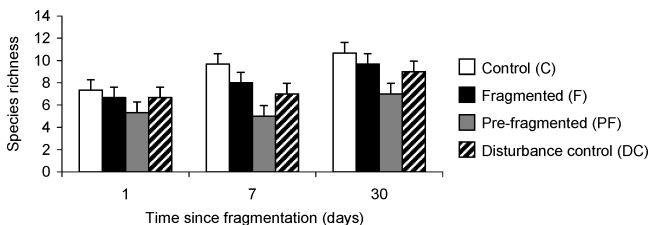


Figure 4. Mean fish-species richness per treatment following manipulations of artificial seagrass, pooled across the 3 periods (blocks) (error = $\sqrt{\text{mean square}_{\text{block} \times \text{treatment}}}$). [Correction added after publication 12 January 2009: Errors in the shading of the figures were amended.]

respond to the loss of seagrass area because of an increase in seagrass edge, which we propose is the preferred habitat of pipefish due to greater food availability. Food availability is an important process structuring fish assemblages in seagrass (Levin et al. 1997). The primary food source of pipefish is small planktonic crustaceans that are carried to seagrass patches by water currents (Jenkins & Sutherland 1997). Tanner (2005) reported positive edge effects on crustaceans inhabiting fragmented seagrass. These positive edge effects may occur where pipefish consume planktonic crustaceans before they reach patch interiors (Holt et al. 1983).

We found support for our second prediction that fish would respond differently to patches that have actually undergone fragmentation than to those that already exist in a prefragmented state. We propose a model to explain why fragmentation differed from prefragmented. At the start of the experiment, fragmentation treatments consisted of a single continuous 9-m² patch, whereas prefragmented treatments were made up of 4 single 1-m² patches. These newly created treatments were left for 1 week to allow faunal colonization. For species richness, initial colonization can depend on seagrass area (Bell & Westoby 1986; Laurel et al. 2003). Therefore, fragmentation treatments accumulated more species than prefragmented treatments. At the time of fragmentation, fish remained within fragmentation treatments rather than leaving as a result of the change in habitat configuration. We observed fish swimming from seagrass that was undergoing fragmentation into seagrass within treatments left untouched. Similar responses have been described for birds crowding into habitat fragments immediately after fragmentation (Bierregaard et al. 1992; Darveau et al. 1995; Schmiegelow et al. 1997). The results of these studies showed a drop in bird species richness in succeeding years. In our study fragmentation eventually led to lower fish species richness in seagrass, as indicated by fewer species in patchy (prefragmented) treatments. Nevertheless, this took >30 days because fish temporarily crowded into fragmented seagrass habitat.

It is important to consider the difference we found between patchiness and fragmentation because many researchers have used patchiness to represent fragmentation (Frost et al. 1999; Hovel & Lipcius 2001, 2002; Johnson & Heck 2006). Because patchiness represents the end point of fragmentation, trophic interactions are more likely to have stabilized than in habitat that is undergoing, or has recently undergone, fragmentation (MacArthur & Wilson 1967). For plant studies this can often take decades (e.g., Benitez-Malvido & Martinez-Ramos 2003). Therefore, studies that use patchiness to represent fragmentation are more likely to characterize the longer-term consequences of fragmentation. Contrastingly, experimental fragmentation provides greater opportunity to characterize patterns and processes that manifest during, and immediately after, fragmentation.

Experimental fragmentation also provides an opportunity to study the effects of disturbance caused by the fragmentation process itself. Our disturbance control tested the hypothesis that disturbance caused during the fragmentation process does not significantly affect fish. We found no difference in abundance or species richness in disturbance control compared with our control, so this prediction was supported. Although physical disturbance has been shown to alter the structure of fish assemblages in seagrass (Moran et al. 2003), the physical disturbance inflicted on disturbance control may have been insufficient to cause fish to abandon seagrass. An alternative explanation is that the risk of predation from venturing onto bare sand prevented fish from trying to reach alternative habitat (Ferrell & Bell 1991; Hindell et al. 2000). This raises the question: Why did fish rapidly colonize artificial seagrass, but not emigrate during fragmentation because of a risk of predation? We suspect that the majority of fish colonized artificial seagrass at night or with the aid of algal rafts (Thiel & Gutow 2005). The disturbance control treatment was manipulated during daylight, and there would have been limited opportunities to “hitch a ride” on passing rafts during the fragmentation process; the option to stay was therefore preferred.

Our goal was to model realistic fragmentation. In doing so, we attempted to simulate and control 3 major factors: degree of fragmentation, scale of the study (i.e., size of patches), and time for fragmentation to take place. The first factors were readily determined from aerial photographs, which gave perimeter-to-area ratios before and after fragmentation. The third factor, however, was difficult to estimate because aerial photographs were only taken annually. We therefore based our study on processes that remove seagrass instantly, such as propeller scarring (e.g., Bell et al. 2002; Uhrin & Holmquist 2003; Burfeind & Stunz 2006). Related to this issue is the time taken for the effects of fragmentation to manifest. Without previous literature on the time taken for fragmentation effects to emerge, we decided to assess the effects of fragmentation after 1, 7, and 30 days. Although our results were consistent up to 30 days, it is possible that some effects of fragmentation may take place outside of the time range of this study. There is little guidance on this in the literature, and it is worthy of further study. We therefore suggest that decisions regarding the management of seagrass habitat take into account that the effects of fragmentation on fish may take months or years to emerge. This is especially relevant where fragmentation causes indirect effects, as has shown to be the case for some forest bird species, where increased nesting success at edges is met by higher depredation and parasitism years later (Paton 1994).

Because seagrass meadows continue to decline worldwide, understanding the effects of seagrass fragmentation on associated fauna is of growing importance. We found no effect of seagrass habitat fragmentation on fish

over the duration of our study. Nevertheless, we suggest that the potential negative effects of area loss resulting from fragmentation were offset by an increase in positive edge effects. Similarly, Haas et al. (2004) found that saltmarsh fragmentation increased the abundance of brown shrimp (*Farfanepenaeus aztecus*), an edge-habitat specialist. Although edge specialists may persist after fragmentation, many generalists and interior specialists will not. Even for brown shrimp, individual-based simulation modeling showed that ultimately shrimp populations will crash when saltmarsh area drops below a certain critical threshold. Like Haas et al. (2004), we predict that the population persistence of fish in seagrass systems is governed by minimum habitat requirements.

Acknowledgments

We thank F. Warry, T. Smith, A. O'Brien, R. Watson, J. Ahern, H. Murphy, B. Loughman, G. Ryan, J. Brown, K. Baker, M. Wright, and J. Smith for field assistance, D. Ball for aerial photographs, D. Marshall and 3 anonymous referees for insightful comments on the manuscript, and the people of Roytal Enterprises for constructing ASUs. We are grateful for funding through an Australian Research Council Discovery Grant (R.C., J.H., and G.J.), a CSIRO Postgraduate Award (P.M. with D. Smith), a Nancy Millis Postgraduate Research Award (P.M.), an Australian Society for Fish Biology Michael Hall Innovation Award (P.M.), a Holsworth Wildlife Foundation Grant (P.M.), and a Norman Wettenhall Foundation Grant (P.M.). All research was conducted under University of Melbourne Animal Ethics and Department of Primary Industries Fisheries permits. Research was conducted with the facilities of the Victorian Marine Sciences Consortium.

Literature Cited

- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. *Oikos* **71**:355–366.
- Attrill, M. J., J. A. Strong, and A. A. Rowden. 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* **23**:114–121.
- Barber, W. E., J. G. Greenwood, and P. Crocos. 1979. Artificial seagrass—a new technique for sampling the community. *Hydrobiologia* **65**:135–140.
- Bell, J. D., and M. Westoby. 1986. Variation in seagrass height and density over a wide spatial scale: effects on fish and decapods. *Journal of Experimental Marine Biology and Ecology* **104**:275–295.
- Bell, S. S., R. A. Brooks, B. D. Robbins, M. S. Fonseca, and M. O. Hall. 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* **100**:115–123.
- Bell, S. S., M. O. Hall, S. Soffian, and K. Madley. 2002. Assessing the impact of boat propeller scars on fish and shrimp utilizing seagrass beds. *Ecological Applications* **12**:206–217.
- Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**:517–533.
- Benitez-Malvido, J., and M. Martinez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. *Conservation Biology* **17**:389–400.
- Bierregaard, R. O., T. E. Lovejoy, V. Kapos, A. A. dos Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments: a prospective comparison of fragments and continuous forest. *BioScience* **42**:859–866.
- Bologna, P. A. X., and K. L. Heck. 1999. Macrofaunal associations with seagrass epiphytes—relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology* **242**:21–39.
- Bostrom, C., E. L. Jackson, and C. A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: a review. *Estuarine Coastal and Shelf Science* **68**:383–403.
- Burfeind, D. D., and G. W. Stunz. 2006. The effects of boat propeller scarring intensity on nekton abundance in subtropical seagrass meadows. *Marine Biology* **148**:953–962.
- Caley, M. J., K. A. Buckley, and G. P. Jones. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* **82**:3435–3448.
- Connolly, R. M., and J. S. Hindell. 2006. Review of nekton patterns and ecological processes in seagrass landscapes. *Estuarine Coastal and Shelf Science* **68**:433–444.
- Darveau, M., P. Beauduchesne, L. Belanger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in the boreal forest. *Journal of Wildlife Management* **59**:67–78.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* **14**:342–355.
- Delin, A. E., and H. Andren. 1999. Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forest landscape. *Landscape Ecology* **14**:67–72.
- Doak, P. 2000. Habitat patchiness and the distribution, abundance, and population dynamics of an insect herbivore. *Ecology* **81**:1842–1857.
- Duarte, C. M. 2002. The future of seagrass meadows. *Environmental Conservation* **29**:192–206.
- Eggleston, D. B., W. E. Elis, L. L. Etherington, C. P. Dahlgren, and M. H. Posey. 1999. Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology* **236**:107–132.
- Fagan, W. E., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *The American Naturalist* **153**:165–182.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**:487–515.
- Fernandez, T. V., M. Milazzo, F. Badalamenti, and G. D'Anna. 2005. Comparison of the fish assemblage associated with *Posidonia oceanica* after the partial loss and consequent fragmentation of the meadow. *Estuarine Coastal and Shelf Science* **65**:645–663.
- Ferrell, D. J., and J. D. Bell. 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Marine Ecology Progress Series* **72**:15–24.
- Frost, M. T., A. A. Rowden, and M. J. Attrill. 1999. Effect of habitat fragmentation on the macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**:255–263.
- Greig, A. A., T. Zaviezo, and S. Reyes. 2004. Short-term effects of habitat fragmentation on the abundance and species richness of beetles in experimental alfalfa microlandscapes. *Revista Chilena De Historia Natural* **77**:547–558.
- Haas, H. L., K. A. Rose, B. Fry, T. J. Minello, and L. P. Rozas. 2004. Brown shrimp on the edge: linking habitat to survival using an individual-based simulation model. *Ecological Applications* **14**:132–1247.
- Haila, Y. 2002. A conceptual genealogy of fragmented research: from island biogeography to landscape ecology. *Ecological Applications* **12**:321–334.

- Hindell, J. S., G. P. Jenkins, and M. J. Keough. 2000. Variability in abundances of fishes associated with seagrass habitats in relation to diets of predatory fishes. *Marine Biology* **136**:725-737.
- Holt, S. A., C. L. Kitting, and C. R. Arnold. 1983. Distribution of young red drums among different seagrass meadows. *Transactions of the American Fisheries Society* **112**:267-271.
- Hovel, K. A. 2003. Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. *Biological Conservation* **110**:401-412.
- Hovel, K. A., and R. N. Lipcius. 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* **82**:1814-1829.
- Hovel, K. A., and R. N. Lipcius. 2002. Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *Journal of Experimental Marine Biology and Ecology* **271**:75-98.
- Hovland, N., H. P. Andreassen, and R. A. Ims. 1999. Foraging behaviour of the root vole *Microtus oeconomus* in fragmented habitats. *Oecologia* **121**:236-244.
- Howard, R. K., and J. D. Koehn. 1985. Population dynamics and feeding ecology of pipefish (Syngnathidae) associated with eelgrass beds of Western Port, Victoria. *Australian Journal of Marine and Freshwater Research* **36**:361-370.
- Jackson, E. L., A. A. Rowden, M. J. Attrill, S. J. Bossey, and M. B. Jones. 2001. The importance of seagrass beds as a habitat for fishery species. *Oceanography and Marine Biology* **39**:269-303.
- Jenkins, G. P., and C. R. Sutherland. 1997. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: colonisation and turnover rate of fishes associated with artificial macrophyte beds of varying physical structure. *Journal of Experimental Marine Biology and Ecology* **218**:103-125.
- Jenkins, G. P., K. P. Black, M. J. Wheatley, and D. N. Hatton. 1997. Temporal and spatial variability in recruitment of a temperate, seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. *Marine Ecology Progress Series* **148**:23-35.
- Jenkins, G. P., M. J. Keough, and P. A. Hamer. 1998. The contributions of habitat structure and larval supply to broad-scale recruitment variability in a temperate zone, seagrass-associated fish. *Journal of Experimental Marine Biology and Ecology* **226**:259-278.
- Johnson, M. W., and K. L. Heck. 2006. Effects of habitat fragmentation *per se* on decapods and fishes inhabiting seagrass meadows in the northern Gulf of Mexico. *Marine Ecology Progress Series* **306**:233-246.
- Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**:105-116.
- Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. C. Andrade, P. M. Fearnside, J. E. L. Ribeiro, and R. L. Capretz. 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* **87**:469-482.
- Laurel, B. J., R. S. Gregory, and J. A. Brown. 2003. Predator distribution and habitat patch area determine predation rates on age-0 juvenile cod *Gadus* spp. *Marine Ecology Progress Series* **251**:245-254.
- Levin, P., R. Petrik, and J. Malone. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* **112**:55-63.
- Mac Nally, R., and G. W. Brown. 2001. Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. *Oecologia* **128**:116-125.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- McNeill, S. E., and P. G. Fairweather. 1993. Single large or several small marine reserves—an experimental approach with seagrass fauna. *Journal of Biogeography* **20**:429-440.
- Moran, S. M., G. P. Jenkins, M. J. Keough, and J. S. Hindell. 2003. Role of physical disturbance in structuring fish assemblages in seagrass beds in Port Phillip Bay, Australia. *Marine Ecology Progress Series* **251**:127-139.
- Orth, R. J., et al. 2006. A global crisis for seagrass ecosystems. *BioScience* **56**:987-996.
- Parker, M., and R. Mac Nally. 2002. Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation* **105**:217-229.
- Paton, P. W. C. 1994. The effect of edge on avian nest success—how strong is the evidence? *Conservation Biology* **8**:17-26.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, United Kingdom.
- Reed, B. J., and K. A. Hovel. 2006. Seagrass habitat disturbance: how loss and fragmentation of eelgrass *Zostera marina* influences epifaunal abundance and diversity. *Marine Ecology Progress Series* **326**:133-143.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* **257**:524-526.
- Salita, J. T., W. Ekau, and U. Saint-Paul. 2003. Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. *Marine Ecology Progress Series* **247**:183-195.
- Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914-1932.
- Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* **65**:1918-1935.
- Summerville, K. S., and T. O. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* **82**:1360-1370.
- Tanner, J. E. 2003. Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities. *Oikos* **100**:517-524.
- Tanner, J. E. 2005. Edge effects on fauna in fragmented seagrass meadows. *Austral Ecology* **30**:210-218.
- Thiel, M., and L. Gutow. 2005. The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanography and Marine Biology* **43**:279-418.
- Uhrin, A. V., and J. G. Holmquist. 2003. Effects of propeller scarring on macrofaunal use of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* **250**:61-70.
- Upston, J., and D. J. Booth. 2003. Settlement and density of juvenile fish assemblages in natural, *Zostera capricorni* (Zosteraceae) and artificial seagrass beds. *Environmental Biology of Fishes* **66**:91-97.

