Fish Responses to Experimental Fragmentation of Seagrass Habitat

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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

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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., Hoiland 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 Heteroziastera 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: fragmentation 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](http://example.com/figure1.png)

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 bridle, 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 briddles 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 log₁₀(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 ≤ 0.001). No difference was found in fish abundance per treatment (p = 0.499) or fish density (p = 0.562) between fragmented...
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 m\(^2\) was fragmented to 4 m\(^2\)). 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-m\(^2\) patches, had significantly higher densities of fish compared with controls and disturbance controls, which consisted of a single 9-m\(^2\) patch. There are many examples...
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

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Fish Responses to Seagrass Fragmentation

Experimentally induced loss of seagrass can cause fish to abandon habitats that were formerly occupied (Frost et al. 1999). However, many fish species are capable of colonizing seagrass. The success of colonists depends on the rate of change in habitat configuration and on how the change affects the quality of habitat. Thus, it is important to understand the degree to which fish species respond to fragmentation. Understanding this relationship requires modeling realistic fragmentation and controlling for factors that may influence the results of studies on the effects of fragmentation on fish (Holt et al. 1983).

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 disturbance (Thiel & Gutow 2005). 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 (Farfantepena 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.

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Fish Responses to Seagrass Fragmentation

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