Effects of propeller scarring on macrofaunal use of the seagrass *Thalassia testudinum*

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ABSTRACT: Propeller scarring within seagrass beds is common in shallow coastal waters. Scarring has the potential to fragment seagrass beds, resulting in habitat loss, decreased productivity, and the possibility for further erosion and degradation. We conducted a study in *Thalassia testudinum* beds in Puerto Rico to determine whether seagrass macrofauna are affected by this disturbance. Four sampling zones (propeller scar, seagrass–scar interface, homogeneous seagrass located 5 m from the scar, and homogeneous seagrass located 10 m from the scar) were compared among 10 replicate seagrass beds. Scarring modified faunal assemblages at the scale of the propeller scar; there was significantly lower total macrofaunal abundance and fewer species in scars. When individual taxa were considered, shrimp and mollusc abundances were lower in scars compared to the other sampling zones. Resident fish abundance was not significantly different among zones. Dominant shrimp species in scars differed from seagrass zones. Crabs and molluscs responded negatively to scarring as indicated by significantly lower densities of these 2 taxa up to 5 m from scars. The extent to which these results 'scale up' remains unknown and future studies should focus on larger, more intensely scarred areas.

KEY WORDS: Propeller scarring · Edge · Seagrass · *Thalassia testudinum* · Decapoda · Shrimp · Fish · Molluscs

INTRODUCTION

Fragmentation of native habitat is believed to be one of the major reasons for decreases in world biodiversity (Wilcox & Murphy 1985, Majer et al. 1997). In addition to the direct removal of structure, fragmentation modifies physical processes and landscape configuration. One such modification is the increase of edge habitat relative to interior habitat. The subsequent expansion of edge effects is thought to be the leading factor promoting ecological changes resulting from habitat fragmentation (Lovejoy et al. 1986). As the edge to perimeter ratio increases during fragmentation (Forman 1995), edge characteristics penetrate further into the interior habitat, creating the potential for changes in faunal spatial distributions and abundance patterns (Ozanne et al. 1997, Bender et al. 1998, Stevens & Husband 1998).

The effects of habitat fragmentation, especially the formation of edges and remnant patches, are of critical concern for conservation biologists (Wilcox & Murphy 1985, Saunders et al. 1991, Gascon et al. 2000). The degree to which habitat fragmentation disrupts animal dispersal depends upon organism mobility and the scale of fragmentation under investigation (Doak et al. 1992). Although terrestrial fragmentation has been widely examined, fragmentation in marine systems has received little attention (McNeill & Fairweather 1993, Strong & Bancroft 1994, Hastings et al. 1995, Frost et al. 1999, Barberá-Cebrián et al. 2002). Because seagrass beds are dominant features in the coastal zone, where human populations continue to rise, there is

tremendous potential for fragmentation resulting from disturbances linked to human activities such as wading (Eckrich & Holmquist 2000), dock and boardwalk construction (Burdick & Short 1999), boat anchoring (Walker et al. 1989, Creed & Amado Filho 1999), and boat operation in shallow water that often leads to scarring of seagrass beds by propellers (Zieman 1976, Sargent et al. 1995, Bell et al. 2002). Scarring, a unique process in which narrow trenches are created within a seagrass bed, may be severe in some regions (Gonzalez-Liboy 1979, Eleuterius 1987, Fonseca 1994, Sargent et al. 1995, Bell et al. 2002). Seagrass recolonization within scars may be slow, ranging from 2 to 10 yr for *Thalassia testudinum* (Zieman 1976, Durako et al. 1992, Dawes et al. 1997).

Because scarring events remove seagrass, and because seagrasses reduce current velocities (Fonseca et al. 1982), stabilize sediments (Orth 1977), and recycle nutrients (Fonseca 1996), scars may cause environmental modification on a local scale. For example, scarring may lead to an increase in the amount of edge-like habitat found within the seagrass bed due to the introduction of bare substrate into a meadow. Seagrass fauna would be expected to respond to this habitat modification via behavioral changes because of habitat preference.

The direct loss of habitat that normally occurs during a scarring event has led to the assumption that this type of disturbance has a detrimental effect on seagrass faunal communities. Faunal responses to natural seagrass edges are a current theme in the seagrass literature (Bologna & Heck 1999, 2002, Frost et al. 1999, Bell et al. 2001), but there is little information on the responses of fauna to scarring, although Bell et al. (2002) found few large-scale differences in fauna between scarred and unscarred areas. The paucity of data concerning this phenomenon leads to the question of whether individual scars and their associated edges are large enough to shift faunal distributions.

This study evaluates the potential impacts of individual propeller scars on Puerto Rican seagrass communities, focusing on responses of 4 macrofaunal groups: shrimp, crabs, molluscs, and fish, as these taxa have a well-documented association with seagrass and serve as prey items for local economically important species. Specifically, we tested the null hypothesis that no difference in the abundance and composition of seagrass-associated macrofauna among scar, edge, and interior regions of seagrass beds occurred.

MATERIALS AND METHODS

Study area and sampling design. This study was conducted between May and November 1999 off the south-

west coast of Puerto Rico near La Parguera (17° 58' N, 67° 03' W; Fig. 1). The area consists of a number of inshore and offshore coral reefs, scattered mangrove islands, and seagrass beds within the inner insular shelf. The dominant seagrass species is *Thalassia testudinum*, but beds may be interspersed with *Halodule wrightii* and/or *Syringodium filiforme*. Historical and recent data collected from US Tidal Reference Station 975-9110 at Isla Magueyes indicated that the daily tidal flux in this region was minimal, with a mean daily flux of 0.15 m for days when sampling occurred.

By sampling existing propeller scars, we were able to assess conditions over a wide (albeit unknown) range of scar ages. Scars were readily recognized as recent injuries (<6 mo old), with no signs of additional erosion beyond that of the original scar path. Ten monospecific *Thalassia testudinum* beds were chosen based upon level of scarring and amount of contiguous seagrass within the bed. Water depth ranged from 0.5 to 1.6 m. Each site contained a single propeller scar that was bordered by at least 20 m of continuous seagrass on one side (to allow for designation of sampling zones and to prevent influence from the natural edge of the bed) and 10 m on the other (again, to buffer against natural edge influence). Scars ranged from 4 to 129 m in length, 0.25 to 0.76 m in width, and 0.03 to 0.12 m in depth. We sought to include a range of scar morphologies in order to make our results more generally applicable. Scars ≥30 m in length were subdivided into 10 m divisions with one of the divisions chosen randomly as the sampling area. Four sampling zones were distinguished per site: propeller scar (bare sand trench resulting from prop dredging), edge (seagrass within 0.25 m of the scar), 5 m interior (distance of 5 m from the scar), and 10 m interior (distance of 10 m from the scar). Seagrass zones were designated on the side of the scar containing the greatest amount of contiguous seagrass. The scars were measured for length and divided into 10 equal-length sections, each marked with a piece of surveyor's tape attached to a galvanized nail to enhance the visibility of each section from above the water's surface. Sections were marked in the same manner in the edge zone. Two parallel lines, the same length as the scar, were established 5 and 10 m from the scar. The lines were divided into the same equal-length sections as the scar and edge zones. Three different sections from within each zone (scar, edge, 5 m, 10 m) were randomly chosen for faunal sampling. Because scar lengths varied, sampling locations varied in proximity. Each site was completely sampled over a maximum of 5 d. To ensure that the scar–seagrass transition was well sampled, scar and edge samples were taken as close as possible to scar margins.

Fauna. Seagrass fauna were sampled using a drop trap modified from that of Holmquist (1997). The di-

mensions of the trap were reduced to 0.25×0.25 m to allow the trap to fit into each scar without including any seagrass. These types of traps have proven to be highly efficient for sampling small organisms (decapods and small fish) and are the recommended method for faunal surveys in subtidal unvegetated habitats as well as seagrass (Rozas & Minello 1997). Although drop traps efficiently sample demersal seagrass canopy fauna, sediment surface dwellers and highly mobile fishes are generally under-sampled (Sogard et al. 1987). Target organisms for this study included decapods, small fish, and molluscs, as these taxa commonly occur in seagrass beds and are efficiently captured via drop trap. No attempt was made to quantify larger species as the required sampling gear can be disruptive, ineffective in vegetation (Rozas & Minello 1997), and too large to exclude seagrass from scar samples. Three random sections from within each zone were selected for sampling with the restriction that there was a minimum 2-section distance between samples taken from adjacent zones. Sampling times of 08:00, 12:00, and 16:00 h were randomly assigned to each of 3 sampling days to encompass daily fluctuation, if any, in animal abundance; thus avoiding temporal pseudoreplication (Hurlbert 1984). There was a minimum of 24 h between samplings. On each day, 1 section from within each zone was trapped.

It was necessary to lower rather than throw the trap because of the precision of placement required. In order to minimize disturbance, the trap was lowered with a 1.5 m PVC handle. The handle gripped the trap with a Vise-Grip® locking panel clamp. Using the handle, the trap was carried to the appropriate zone section by field personnel, placed on the substrate, and pushed 1 to 2 cm into the sediment. A weighted screen was placed over the trap aperture, which was easily lifted and lowered during the clearing process. The trap was held in place with lead weights suspended from each corner. Fauna were cleared from the trap by passing a 0.25 m wide, handled net (2 mm mesh) through the trap at the water–sediment interface. The net was emptied of its contents into a 19 l plastic bucket filled with seawater. Ten net passes were made in each trap, removing ~95% of target fauna (A. Uhrin pers. obs., Holmquist 1997, Eckrich & Holmquist 2000, Bell et al. 2002). Buckets were transported to the laboratory where shrimp, fish, crabs, and molluscs were sorted live, enumerated, and identified to species,

with the exception of crabs, which were grouped as either Brachyura or Anomura. Total faunal abundance (abundance of individuals from all groups combined) and abundances within each group were determined and scaled to per m^2 values. Number of species per $0.25\ m^2$ was also calculated. Shrimp species comprising less than 9% of the total number of individuals collected were pooled for some analyses. Molluscs and fish were treated similarly.

Data analysis. Comparisons for total macrofaunal abundance, number of species, and abundance of individual species were made among the following zones: scar and edge, scar and 5 m, scar and 10 m, edge and 5 m, edge and 10 m, 5 and 10 m. Normality was tested using the Shapiro-Wilk test (SAS Institute 1999). Bartlett's test and the F-max test (SAS Institute 1999) were used to test for homogeneity of variances. In order to meet the above assumptions various transformations were necessary. Total fauna abundance and total number of shrimp were $\sqrt{(y + 0.5)}$ transformed. Abundances of *Thor manningi*, *Hippolyte zostericola/pleuracanthus*, *Periclimenes americanus*, *Latreutes fucorum*, *Cerithium eberneum*, *Cerithiopsis greenii*, *Tricolia bella*, and *Modulus modulus* were log $(y + 1)$ transformed, as were pooled shrimp species, total molluscs, and pooled mollusc species. Variables that met the assumptions were examined by paired Student's t-tests (2-tailed). Non-parametric Wilcoxon sign rank tests were used for the remaining variables. The sequential Bonferroni correction was used to reduce multiple comparison testing error (Holm 1979). Rank-abundance plots were constructed as a representation of community diversity. All statistical analyses were performed using SAS Version 8.0 (SAS Institute 1999).
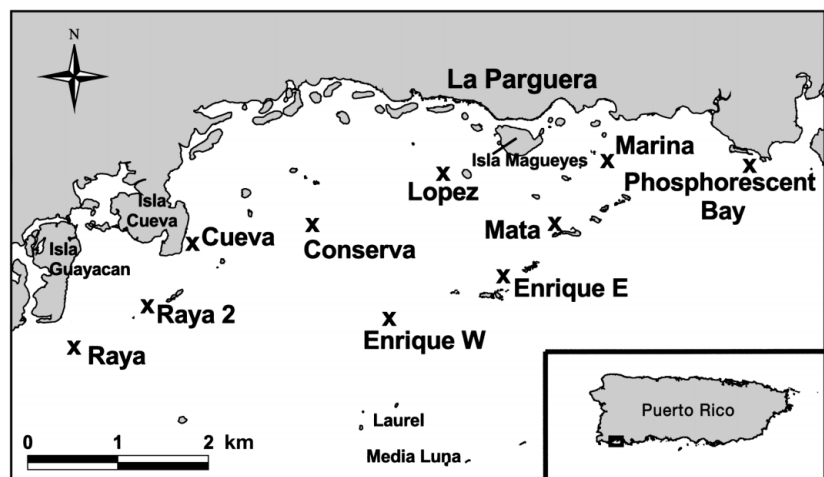

Fig. 1. Map of the shoreline and associated reefs near La Parguera, Puerto Rico. **x**: location of each study site

Table 1. Summary of total macrofauna and decapods (no. m^{-2} ± SE) and total species collected from within each seagrass-bed (*Thalassia testudinum*) zone (n = 10)

Taxonomic group	No. of individuals	% of total	Scar	Edge	5 m	10 m
Total macrofauna			67.7 (18.3)	200.0 (41.1)	203.2 (43.5)	283.2 (23.8)
Total no. of species			1.6 (0.3)	5.0 (0.7)	5.2 (0.7)	6.2(0.5)
Total shrimp	559	100	23.5 (4.5)	89.6 (21.2)	78.0 (14.7)	105.5 (20.0)
Thor manningi	137	24.5	1.6 (1.6)	25.0 (6.5)	15.5 (5.1)	29.3 (10.1)
Hippolyte zostericola/ pleuracanthus[a]	128	22.9	1.6 (1.1)	21.3 (10.5)	17.1 (6.0)	28.3 (21.9)
Alpheus normanni	109	19.5	8.0 (3.0)	12.3 (5.4)	19.7 (4.1)	18.1 (7.0)
Periclimenes americanus	75	13.4	4.3 (2.1)	12.3 (5.2)	9.1 (2.6)	14.4 (6.3)
Latreutes fucorum	71	12.7	1.1 (0.7)	14.4 (4.6)	13.9 (4.3)	8.5 (4.2)
Trachypenaeus sp.[b]	14	2.5	4.3 (3.2)	1.1 (0.7)	1.1 (0.7)	1.1 (1.1)
Processa bermudensis[b]	12	2.1	1.6 (1.1)	1.1 (1.1)	0 (0)	3.7 (1.4)
Leander tenuicornis[b]	6	1.1	0 (0)	1.6 (0.8)	0 (0)	1.8 (0.9)
Latreutes parvulus[b]	2	0.4	0 (0)	0.5 (0.5)	0.5 (0.5)	0 (0)
Tozeuma carolinense[b]	2	0.4	0.5 (0.5)	0 (0)	0 (0)	0.5 (0.5)
Sicyonia laevigata[b]	1	0.2	0 (0)	0 (0)	0.5 (0.5)	0 (0)
Farfantepenaeus duorarum[b]	1	0.2	0 (0)	0 (0)	0.5 (0.5)	0 (0)
Metapenaeopsis goodei[b]	1	0.2	0.5 (0.5)	0 (0)	0 (0)	0 (0)
Pooled shrimp	39	7.0	6.9 (3.0)	4.3 (1.7)	2.7 (1.2)	6.9 (1.1)
Total crabs	369	100	29.9 (10.8)	39.5 (10.6)	44.3 (7.6)	83.2 (13.7)
Brachyura	251	68.0	22.9 (7.3)	31.0 (9.1)	31.5 (5.1)	48.5 (7.2)
Anomura	118	32.0 (4.1)	7.0 (9.3)	8.5 (14.2)	12.8 (14.9)	34.7

[a] Treated as a complex of the 2 species (Gore et al. 1981)
[b] Pooled shrimp

RESULTS

Total fauna

Propeller scars had fewer animals than the surrounding seagrass (Tables 1 & 2). In addition, the edge and 5 m zones contained fewer total animals than the 10 m zone (Table 2). Scars also had fewer species than the other zones (Tables 1 & 2).

Decapods

Fourteen shrimp species (Decapoda) were collected (Table 1); 5 species accounted for 92.2% of the total number of shrimp (Table 1). The total number of shrimp per m^2 was lower in scars when compared to the edge, 5 m, and 10 m zones (Tables 1 & 2). No other zone comparisons were different (Table 2). Shrimp species densities were generally lower in the scars than in the other zones (Table 2). There were no significant differences in *Periclimenes americanus* densities among any of the zones (Table 2). Shrimp assemblages in scars differed from the adjacent seagrass (Fig. 2, Table 2). *Thor manningi* and *Hippolyte zostericola/pleuracanthus*, dominant seagrass occupants, were not as proportionally abundant in the scars as in the seagrass. *Alpheus nor-*

manni and *Trachypenaeus* sp. represented the highest proportion of shrimp in scars. Rank abundance plots indicated low evenness across all zones, although scars were more even than seagrass (Fig. 2).

Brachyurans were the dominant crab group, comprising 68.0% of the total crabs collected (Table 1). Brachyuran densities were significantly lower in the scar and 5 m zones than in the 10 m zone (Table 2). Anomuran densities exhibited no significant differences across zones (Table 2). There were significantly lower numbers of total crabs in the scar, edge, and 5 m zones than in the 10 m zone (Table 2).

Molluscs

Four species accounted for 60.7% of the total molluscs (Table 3). Total mollusc density was significantly lower in scars versus all other zones, and densities in the edge and 5 m zones were significantly lower than the 10 m zone (Table 4). There were no significant differences among zones for *Cerithium eberneum* (Table 4). No *Cerithiopsis greeni* were collected from scars (Table 3). *Modulus modulus*, the third most abundant mollusc, had significantly lower densities in scars than in the 10 m zone (Tables 3 & 4). *Tricolia bella* densities were significantly lower in the scar versus all

Table 2. p-values resulting from paired, 2-tailed *t*-tests comparing differences in mean total macrofauna (no. m^{-2}), mean total species (0.25 m^{-2}), and mean no. of decapods m^{-2} between pairs of seagrass-bed zones. *significant at the per-contrast error rate ($\alpha = 0.05$); **significant after correcting for multiple comparisons

Taxonomic group	Scar vs edge	Scar vs 5 m	Scar vs 10 m	Edge vs 5 m	Edge vs 10 m	5 vs 10 m
Total macrofauna	<0.0001**	<0.0001**	<0.0001**	0.965	0.002**	0.004**
Total no. of species	0.0004**	0.0001**	<0.0001**	0.602	0.135	0.203
Total shrimp	0.006**	0.002**	0.002**	0.506	0.236	0.126
Thor manningi	0.001**	0.027*	<0.0001**	0.104	0.850	0.141
Hippolyte zostericola/ pleuracanthus[a]	0.006**	0.008**	0.0004**	0.616	0.197	0.154
Alpheus normanni	0.564	0.023*	0.252	0.238	0.066	0.824
Periclimenes americanus	0.173	0.151	0.116	0.901	0.616	0.454
Latreutes fucorum	0.029*	0.013*	0.075	0.746	0.570	0.431
Pooled shrimp[b]	0.213	0.122	0.399	0.434	0.030*	0.005**
Total crabs	0.457	0.261	0.020*	0.711	0.031*	0.003**
Brachyura	0.505	0.359	0.041*	0.952	0.092	0.023*
Anomura	0.364	0.489	0.074	0.971	0.148	0.074

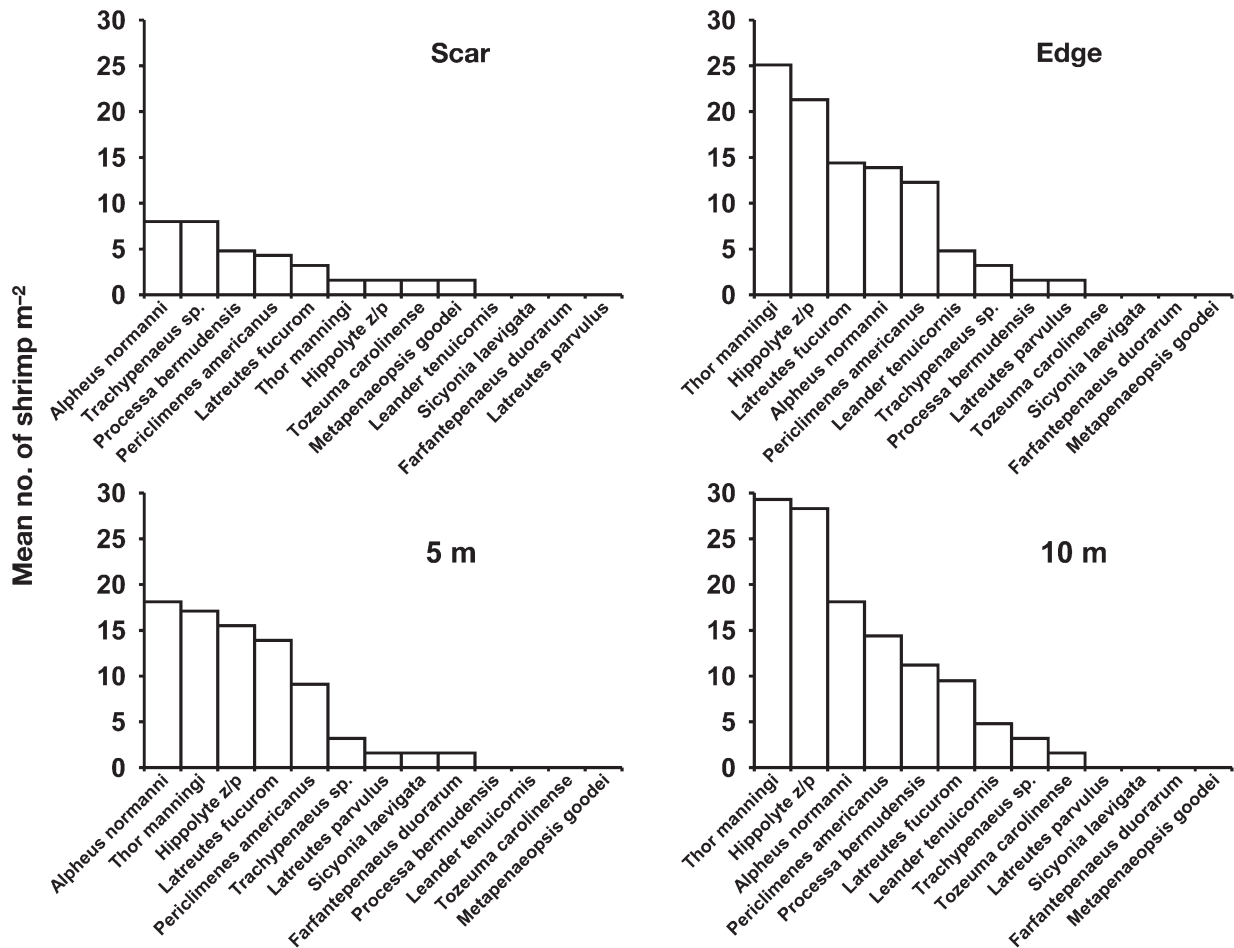[a]Treated as a complex (Gore et al. 1981)
[b]Pooled shrimp as in Table 1

Fig. 2. Shrimp rank abundance plots for all seagrass-bed zones. Absence of bars indicates no individuals were collected. *Hippolyte z/p = Hippolyte zostericola/pleuracanthus*

Mar Ecol Prog Ser 250: 61–70, 2003

Table 3. Summary of molluscs (no. m^{-2} ± SE) collected from within each seagrass-bed (*Thalassia testudinum*) zone (n = 10)

Mollusc taxon	No. of individuals	% of total	Scar	Edge	5 m	10 m
Total molluscs	460	100	11.2 (4.1)	67.7 (30.2)	76.8 (34.5)	89.6 (20.6)
Cerithium eberneum	147	32.0	4.8 (3.2)	22.9 (16.1)	24.1 (14.2)	26.6 (13.5)
Cerithiopsis greeni	48	10.4	0 (0)	7.5 (2.3)	11.7 (9.5)	6.4 (2.5)
Modulus modulus	44	9.6	1.1 (0.7)	5.3 (2.5)	6.4 (3.5)	10.7 (3.0)
Tricolia bella	40	8.7	0.5 (0.5)	4.8 (1.5)	8.5 (4.6)	7.5 (2.3)
Tegula fasciata[a]	27	5.9	0 (0)	1.6 (0.8)	3.7 (2.5)	9.1 (4.4)
Acmaea sp.[a]	22	4.8	0 (0)	3.7 (1.8)	4.3 (1.3)	4.8 (2.2)
Anachis pulchella[a]	19	4.1	0 (0)	3.7 (2.8)	1.6 (0.8)	4.3 (1.7)
Nassarius albus[a]	17	3.7	2.1 (1.4)	4.8 (3.4)	1.6 (1.6)	2.7 (1.8)
Turbo castanea[a]	16	3.5	0 (0)	3.2 (2.1)	5.3 (3.4)	1.1 (0.7)
Ischnochiton sp.[a]	14	3.0	1.1 (0.7)	0.5 (0.5)	4.7 (2.1)	0.6 (0.6)
Smaragdia viridis[a]	14	3.0	0 (0)	3.2 (2.7)	3.6 (2.5)	1.2 (0.8)
Arene tricarinata[a]	10	2.2	0 (0)	1.1 (0.7)	0 (0)	4.3 (2.5)
Bulla striata[a]	7	1.5	0 (0)	0.5 (0.5)	0 (0)	3.2 (3.2)
Acanthochitona pygmaea[a]	6	1.3	0 (0)	0 (0)	0.5 (0.5)	2.7 (1.6)
Crepidula convexa[a]	5	1.1	0 (0)	0.5 (0.5)	0.5 (0.5)	1.6 (1.1)
Crassinella guadalupensis[a]	4	0.9	0 (0)	1.1 (1.1)	0.5 (0.5)	0.5 (0.5)
Diodora sp.[a]	2	0.4	0 (0)	1.1 (0.7)	0 (0)	0 (0)
Cerithium litteratum[a]	2	0.4	0 (0)	0 (0)	0 (0)	1.1 (0.7)
Columbella mercatoria[a]	2	0.4	0 (0)	0.5 (0.5)	0.5 (0.5)	0 (0)
Engoniophos unicinctus[a]	2	0.4	1.1 (1.1)	0 (0)	0 (0)	0 (0)
Olivella floralia[a]	2	0.4	0 (0)	1.1 (1.1)	0 (0)	0 (0)
Fissurella sp.[a]	1	.2	0 (0)	0 (0)	0.5 (0.5)	0 (0)
Brachiodontus exustus[a]	1	0.2	0 (0)	0.5 (0.5)	0 (0)	0 (0)
Antillophos sp.[a]	1	0.2	0 (0)	0 (0)	0 (0)	0.5 (0.5)
Arene sp.[a]	1	0.2	0 (0)	0 (0)	0 (0)	0.5 (0.5)
Astraea phoebia[a]	1	0.2	0 (0)	0 (0)	0.5 (0.5)	0 (0)
Conus jaspidus[a]	1	0.2	0 (0)	0.5 (0.5)	0 (0)	0 (0)
Cerithiopsis emersoni[a]	1	0.2	0 (0)	0.5 (0.5)	0 (0)	0 (0)
Leucozonia sp.[a]	1	0.2	0.5 (0.5)	0 (0)	0 (0)	0 (0)
Fam. Columbellidae[a]	1	0.2	0 (0)	0 (0)	0 (0)	0.5 (0.5)
Fam. Turridae[a]	1	0.2	0 (0)	0 (0)	0 (0)	0.5 (0.5)
Pooled molluscs	181	39.3	4.8 (1.9)	27.2 (10.7)	26.1 (5.9)	38.4 (6.6)

[a]Pooled molluscs

other zones (Table 4). Scar densities of pooled molluscs were significantly lower than those in the other zones, and densities in the 5 m zone were significantly lower than those in the 10 m zone (Tables 3 & 4).

Fish

Two fish species accounted for 76.9% of the total and dominated all zones (Table 5). For total number of fish, only the comparison of the edge and 10 m zones was significantly different (Table 6). Neither of the 2 most abundant fish species exhibited differences across the zones.

DISCUSSION

The abundance and composition of seagrass fauna observed in this study are similar to those reported from other studies in Puerto Rico (Martin & Cooper 1981, Bauer 1985a,b, Eckrich & Holmquist 2000) and the Caribbean (Heck 1977). In addition, the Puerto

Rican fauna can be compared with that of temperate *Thalassia testudinum* meadows in Florida. Examining the 10 most common decapod species in Puerto Rico (Bauer 1985a,b, Eckrich & Holmquist 2000, Uhrin 2001), Florida Bay (Holmquist et al. 1989), the Indian River (Gore et al. 1981), Tampa Bay (Lewis 1984, Fonseca et al. 1996), and Apalachee Bay (Hooks et al. 1976, Lewis & Stoner 1983), one can see a general decline in similarity of species complement as latitude increases. If the presence of congenerics is considered, these systems become more similar.

Natural bare substrates contain fewer total macrofauna and fewer species than adjacent seagrass (O'Gower & Wacasey 1967, Stoner 1980, Orth et al. 1984) as did the bare sand trenches created by propeller scarring studied here. These differences were also evident when comparing macrofaunal groups. For example, the shrimp sampled in this study exhibited significantly reduced abundances in propeller scars. Seagrass offers refuge from predators, and experiments have shown that some shrimp species are less vulnerable to predation in vegetated versus bare

Table 4. p-values resulting from paired, 2-tailed t-tests comparing differences in mean no. of molluscs m^{-2} between pairs of seagrass-bed zones. *significant at the per-contrast error rate ($\alpha = 0.05$); **significant after correcting for multiple comparisons; (**) denotes significance although a t-test was not possible

Mollusc taxon	Scar vs edge	Scar vs 5 m	Scar vs 10 m	Edge vs 5 m	Edge vs 10 m	5 vs 10 m
Total molluscs	0.0002**	0.0009**	0.0002**	0.691	0.014**	0.020**
Cerithium eberneum	0.109	0.197	0.031*	0.866	0.360	0.132
Cerithiopsis greeni	(**)	(**)	(**)	0.169	0.280	0.408
Modulus modulus	0.094	0.295	0.002**	0.586	0.094	0.057
Tricolia bella	0.006**	0.016*	0.003**	0.857	0.558	0.663
Pooled molluscs[a]	0.0008**	0.001**	0.0009**	0.409	0.078	0.034*
[a]Pooled molluscs as in Table 3						

Table 5. Summary of fish (no. m^{-2} ± SE) collected from within each seagrass-bed (*Thalassia testudinum*) zone (n = 10)

Fish taxon	No. of individuals	% of total	Scar	Edge	5 m	10 m
Total fish	26	100	3.2 (1.4)	2.6 (2.1)	3.2 (1.4)	5.3 (2.7)
Bathygobius curacao	14	53.8	1.1 (0.7)	2.1 (2.1)	1.1 (1.1)	3.7 (2.7)
Malacotenus macropus	6	23.1	0.5 (0.5)	0.5 (0.5)	1.6 (1.1)	0.5 (0.5)
Gobionellus saepepallans[a]	2	7.7	1.1 (1.1)	0 (0)	0 (0)	0 (0)
Fam Gobiidae[a]	1	3.9	0.5 (0.5)	0 (0)	0 (0)	0 (0)
Coryphopterus sp.[a]	1	3.9	0 (0)	0 (0)	0 (0)	0.5 (0.5)
Bryx dunckeri[a]	1	3.9	0 (0)	0 (0)	0 (0)	0.5 (0.5)
Sparisoma sp.[a]	1	3.9	0 (0)	0 (0)	0.5 (0.5)	0 (0)
Pooled fish	6	23.1	1.6 (1.1)	0 (0)	0.5 (0.5)	1.1 (0.7)
[a]Pooled fish						

Table 6. p-values resulting from paired, 2-tailed t-tests comparing differences in mean no. of fish m^{-2} between pairs of seagrass-bed (*Thalassia testudinum*) zones. *significant at the per-contrast error rate ($\alpha = 0.05$); (**) denotes significance although a t-test was not possible

Fish taxon	Scar vs edge	Scar vs 5 m	Scar vs 10 m	Edge vs 5 m	Edge vs 10 m	5 vs 10 m
Total fish	0.722	1.000	0.434	0.777	0.037*	0.541
Malacotenus macropus	1.000	0.500	1.000	0.750	1.000	0.750
Bathygobius curacao	1.000	1.000	0.500	1.000	0.500	0.500
Pooled fish	(**)	0.675	0.139	(**)	(**)	0.140
[a]Pooled fish as in Table 5						

substrates (Coen et al. 1981, Heck & Thoman 1981). Other species, such as caridean shrimp, are known to select vegetation over bare substrates (Ewald 1969, Barry 1974, Coen et al. 1981). Considering that scarring removes habitat (and shelter), shrimp probably emigrated to seagrass surrounding the scars or failed to immigrate into scar areas.

Scarring was found to modify species dominance for certain numerically abundant shrimp taxa. For example, species known to utilize the blades of seagrasses, such as *Thor manningi* and *Hippolyte zostericola/pleuracanthus*, dominated seagrass edge and interior zones but showed significantly decreased abundances in scars as might be expected. In comparison, *Alpheus normanni* and *Trachypenaeus* sp., often associated with bare sand patches (Holmquist 1992), were the most abundant shrimp in scars.

The sampled molluscs are epifaunal on seagrass blades and the associated sediment. In conjunction with the direct loss of seagrass habitat, the churning action of the propeller may displace or redistribute these organisms, and habitat selection probably plays a role as well. For example, Lovegrove (1997) found decreased abundances of taxa with restricted motility (copepods and hermit crabs) in scarred versus reference beds. We suspect the same is true for molluscs in our study.

For more mobile organisms, scars may not present a significant boundary to movement. Highly mobile species may be less sensitive to boundaries and patch configuration (Wiens et al. 1985, Kotliar & Wiens 1990, Wiens 1992), which appears to be the case for some seagrass fauna (Holmquist 1998). Bell et al. (2002) observed pinfish utilizing propeller scars in seagrass beds as corridors. The fish in our study may not have

responded to the patch scale (0.3 to 0.8 m wide trenches) produced by propeller scars.

Crabs and molluscs exhibited a negative edge effect with significantly decreased abundances of these taxa up to a distance of 5 m from scars. Changes in predation rates at scar edges may play a part in structuring the distribution of crabs and molluscs in scarred areas. Peterson et al. (2001) found significantly shorter survival times for tethered crustaceans in *Thalassia testudinum* edge habitat (<2 m from unvegetated substrate) versus the interior (>5 m from the edge) of the bed. Larger fish, such as snapper and grunts, were observed in scars, especially scars with exposed rhizomes at the margins (A. Uhrin pers. obs.). Perhaps these larger predators, known to consume crustaceans and molluscs (J. Holmquist pers. obs., Bölke & Chaplin 1968), utilize scars as alleys, with quick forays into the fringing seagrass to feed (e.g. Bell et al. 2002). This behavior has also been observed in salt marsh predators that use unvegetated channels in the marsh as alleyways (Peterson & Turner 1994, Kneib 2000). Examination of the responses of less vagile organisms to natural seagrass bed edges is limited and yields mixed results. Bologna & Heck (1999) found higher densities of scallops in natural seagrass bed edges (within 1 m of the sand–grass interface) versus the bed interior (10 m from the interface) from *T. testudinum* beds in the northeast Gulf of Mexico, even though higher scallop predation rates were observed in the edges. The authors suggested that scallops trade off higher predation rates for the significantly higher growth rates obtained at seagrass edges (Bologna & Heck 1999). Bell et al. (2001) reported significantly reduced densities of the infaunal polychaete, *Kingbergonuphis simoni*, at *T. testudinum* edges (1 m from the sand–grass interface) compared to densities 9 m from the interface in Tampa Bay, Florida. In contrast with our study, Bologna & Heck (2002) found that pagurid crabs exhibited no significant density differences between natural seagrass bed edges and interiors.

The creation of edge habitat via scarring was not reflected by changes in shrimp abundance within seagrass surrounding scars. The intact seagrass surrounding the scars provides a deep pool of immigrants. For example, caridean shrimp have been shown to be highly mobile (Howard 1985, Stoner & Lewis 1985, Sogard 1989) and it is possible that shrimp congregate in the seagrass surrounding scars when exposed to bare substrate (active refuge seeking; Sogard 1989, Bell et al. 2002). Our findings are similar to results from natural seagrass edges. Bologna & Heck (2002) found no difference in caridean shrimp densities between edge (within 1 m of the sand–grass interface) and interior (10 m from the interface) portions of a *Thalassia*

testudinum bed in the northeast Gulf of Mexico. Interestingly, Eggleston et al. (1998, 1999) found that for isolated seagrass patches within a sand matrix, grass shrimp *Palaemonetes* spp. densities increased with decreasing sizes of seagrass patches, indicating that these species were responding positively to edges. Shrimp in unvegetated areas would tend to seek protection in the nearest available habitat ('nearest refuge' hypothesis; Virnstein & Curran 1986); in this case, isolated seagrass patches. In contrast, the propeller scars in our study represent only a small area of unsuitable habitat surrounded by intact seagrass. The 'nearest refuge' hypothesis is unlikely to produce a positive edge effect near propeller scars.

The results of our study are directly applicable to the assessment of seagrass community injuries. Our results show that ecological changes resulting from propeller scarring are not limited to the footprint of the scar, but can extend some distance away from the scar depending upon the faunal taxa under consideration. Some apparent effects were seen 5 m from scars. In seagrass beds with extensive scarring, there is the potential for sensitive taxa to disappear because significant amounts of the bed would be within this 'edge' habitat. When considering an injured bed for restoration, the distributions of fauna in comparable, undisturbed areas should first be established in order to determine which species have been impacted negatively and to what extent. As restoration proceeds, the distributions of impacted fauna can be monitored for recovery.

This study addressed issues pertaining to single scar disturbances. In contrast, when areas become riddled with scars, there is proportionally less seagrass coverage and biomass, and more edge habitat. Bed edges erode, leading to increased sediment suspension, and current flow may be altered (Walker et al. 1989, Fonseca 1996). Given that current patterns and velocities have the potential to shape seagrass beds (Fonseca et al. 1983), continual scarring may further degrade and restructure beds, leading to fragmentation of once continuous meadows (see Walker et al. 1989). Will the faunal effects observed in our study scale-up linearly, exponentially, or not at all? Initial work by Bell et al. (2002) at larger spatial scales suggests that the answers may be complex.

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