

RESEARCH ARTICLE

Response of Fish Assemblage Structure and Function Following Restoration of Two Small Bahamian Tidal Creeks

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Abstract

Disruption of hydrologic connectivity via road crossings is extremely common in Bahamian tidal creeks, resulting in increased sedimentation and decreased habitat quality and quantity for biota. We restored hydrologic connectivity (i.e., tidal flow) in two small Bahamian mangrove tidal creeks in May 2004 and 2005. We observed the characteristics of fish assemblage structure (species richness) and function (secondary production and transient species utilization of restored areas) before and after restoration, and compared these data with fragmented and unfragmented reference creeks. Restoration significantly increased species richness and secondary production of resident fish species in one of the two restored creeks. Increased utilization of the previously blocked wetlands by transient fishes was

observed in both creeks. We suggest success could be attributed to the presence of adjacent nearshore recruitment sources, a more complex local seascape (i.e., high habitat heterogeneity in the creek and local nearshore), and the creation of deep upstream refugia pools. This is one of the first studies to use both structural and functional characteristics to monitor the success of restoration in mangrove ecosystems. Studies combining both structural and functional metrics in restoration monitoring are imperative in linking restoration ecology theory with practical ecological restoration efforts.

Key words: back reef, culvert, estuary, fragmentation, nursery, underwater visual census.

Introduction

Mangrove ecosystems are recognized as areas of high floral and faunal productivity (Odum 1971; Lewis et al. 1985; Wolanski & Boto 1990) as well as nursery habitat important for the maintenance of coastal fisheries (Mumby et al. 2004; Adams et al. 2006). Yet approximately one-third of the world's mangrove forests have been lost over the past 50 years due to a variety of anthropogenic activities, and remaining mangrove systems are being altered at a rapid rate (Alongi 2002). Of particular concern is disruption of *hydrologic connectivity*, the water-mediated transfer of energy, matter, and organisms throughout the hydrologic cycle (sensu Pringle 2003), via tidal flow in mangrove systems. Tidal flow is essential to the integrity of coastal wetlands, and restricting tidal connectivity alters physiochemical parameters and floral and faunal communities (Layman et al. 2004b; Ray 2005;

Lewis & Gilmore 2007; Valentine-Rose et al. 2007a, 2007b). Alteration of hydrologic connectivity in coastal ecosystems may result in overall deterioration of ecosystem function, e.g., an overall reduction in nursery value (sensu Beck et al. 2001; Dahlgren et al. 2006) for ecologically or economically important species (Pringle 2003; Ray 2005; Valentine-Rose et al. 2007b).

As ecosystems continue to be degraded, restoration ecology is increasingly acknowledged as a critical component of long-term conservation strategies (Young et al. 2005). Restoration ecology aims to assist the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004), including both structural and functional characteristics (Ehrenfeld & Toth 1997; Hobbs & Harris 2001; Bradshaw 2002). Regional-scale empirical studies have shown that reestablishment of tidal flow in fragmented coastal mangrove estuarine systems can restore estuarine *structure* within 1–3 years, including fish, invertebrate, plant biodiversity, abundance, and size–structure, as well as abiotic and morphological characteristics (Burdick et al. 1997; Raposa 2002; Lewis & Gilmore 2007). However, little has been done to document the effects of restoration of tidal flow on ecosystem *function* (McKee & Faulkner 2000). Although studies combining both structural and functional metrics are not common, these studies are imperative in the ongoing efforts to link restoration theory with practical

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ecological restoration (Ehrenfeld & Toth 1997; Palmer et al. 1997; Bradshaw 2002; Young et al. 2005).

Secondary production, the accumulation of animal biomass over time (Benke 1993), is a functional metric that incorporates all factors, both biotic and abiotic, that affect the biomass, growth, and survival of organisms. Because of its value in measuring specific components of ecosystem function in a composite fashion, secondary production can be a powerful tool in measuring the success of restoration efforts. For example, Peterson et al. (2003) used secondary production to show that oyster reef restoration could increase fish production by as much as $5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and McCay and Rowe (2003) used secondary production to model the trophic effects of restoration on entire seagrass food webs.

Recently, structural and functional differences between fragmented (via road crossings) and unfragmented tidal creeks have been documented throughout the Bahamas, including decreases in fish, plant, and invertebrate biodiversity (Layman et al. 2004a; Valentine-Rose et al. 2007a), disruption of food web structure and dynamics (Layman et al. 2007), and erosion of ecosystem function via reduced fish secondary production (Valentine-Rose et al. 2007b). Fragmentation of tidal flow via road crossings results in loss of hydrologic (tidal) connectivity, altered physiochemical characteristics, and diminished floral and faunal recruitment as a result of a distinct feedback cycle (Fig. 1, modified from Whisenant 1999, 2002 and King & Hobbs 2006). Hydrologic fragmentation, even if some portion of the historic creek channel remains, continually alters the function of tidal creeks through decreased water flow and increased sedimentation. Sedimentation reduces substrate heterogeneity (e.g., covers exposed rock habitat) and decreases overall channel depth, thereby decreasing the quantity and quality of available aquatic habitat (Valentine-Rose et al. 2007a). Sedimentation also drives increased mangrove settlement at the fringes of the creek channel, further slowing the water velocity and decreasing hydrologic connectivity. This results in decreased species richness and growth rates of ecologically and economically important species in fragmented creeks (Valentine-Rose et al. 2007a, 2007b), and thus decreased ecosystem function via decreases in fish secondary production (Valentine-Rose et al. 2007b).

Previous qualitative observations have suggested rapid shifts in faunal diversity and food web structure following restoration of hydrological connectivity in these Bahamian tidal creek systems (Layman et al. 2004a). In the present study, we provide a rigorous framework for quantifying shifts in ecosystem structure and function, using species richness, secondary production, and transient species movements as our core metrics of study. We hypothesized that restoration of hydrologic connectivity would restore ecosystem structure (species richness) and ecosystem function (secondary production and transient species utilization of restored areas) to levels (1) similar to unfragmented reference creeks and (2) significantly greater than fragmented reference creeks. Our results demonstrate how relatively simple restoration projects can result in substantial benefits at the ecosystem scale. These results serve as a foundation for specific recommendations as

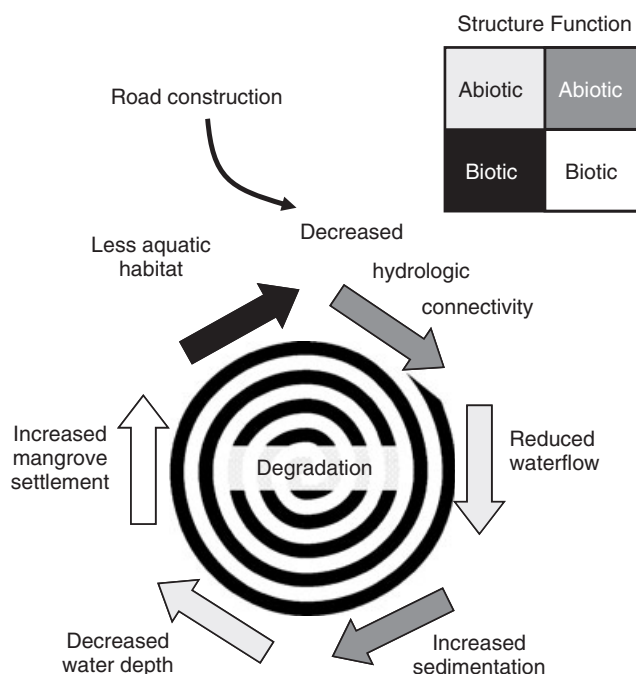


Figure 1. Conceptual model, modified from King and Hobbs (2006) and Whisenant (1999, 2002), demonstrating the degradation feedback cycle following anthropogenic fragmentation of tidal creeks. The shading of the arrows represents the category of the effect following the box in the upper right hand corner.

to how such small-scale projects can provide for maximum benefit with respect to nursery function in tropical mangrove systems.

Methods

Site Description

In the Bahamas, tidal creeks are clear-water, mangrove-lined components of the back-reef ecosystem formed from scouring of calcareous rock substrate. They are dominated by tidal exchange with little freshwater input (Buchan 2000). Tidal amplitude in these creeks is approximately 0.8 m, with water depths at high tide flooding extensive, shallow intertidal flats. At low tide, water is restricted to the main creek channels providing permanent habitat for fishes (i.e., fishes remain in the main creek channels even on the lowest tides). Main channel areas may contain multiple habitat types including mangrove, rock, seagrass, or sand and can vary substantially in microtopography among systems. Intertidal flats typically have a sandy substrate with interspersed dwarf Red mangrove (*Rhizophora mangle*) and Black mangrove (*Avicennia germinans*). Importantly, tidal creeks serve as the primary corridor between inland mangrove wetlands and nearshore habitats (such as coral reefs), and maintaining connectivity through this corridor is important to the health and ecosystem function of both wetland and marine ecosystems (Nagelkerken et al. 2000; Aguilar-Perera & Appeldoorn 2007; Mumby & Hastings 2008). For more detail on these tidal creek

systems see Layman et al. (2004a, 2004b) and Valentine-Rose et al. (2007a, 2007b).

As a part of extensive community outreach programs, two creeks were restored on Andros Island: Man-o-War (MOW, May 2004) and Conch Sound (CS, May 2005). Unlike most mangrove restorations that focus on replanting in deforested areas (Farnsworth & Ellison 1997; Alongi 2002), restoration efforts on Andros were based on restoring a more natural hydrology to fragmented mangrove creek ecosystems (see studies reviewed in Turner & Lewis 1997). Projects targeted one or both of the following: (1) reduction of ecosystem fragmentation and thus increasing hydrologic connectivity through the construction of bridges and (2) reconstruction of a more natural tidal regime by selectively removing mangroves that had encroached into the main channel as a result of the anthropogenic impact (see above description of degradation feedback cycle).

MOW tidal creek had been fragmented by a limestone rock footpath constructed approximately 60 years ago, and this footpath blocked the majority of water flow (Valentine-Rose et al. 2007a). In May 2004, we removed two, 2-m wide corridors of rock from the footpath as well as sediment and mangrove in the channel, restoring water flow between

upstream and downstream areas in the creek (Fig. 2A) (details in Layman et al. 2004a). Restoration was completed with approximately 80 total man hours and capital investments limited to two bags of concrete and two wooden plank bridges. CS had been fragmented by a small road with an undersized span bridge that significantly reduced historic tidal exchange. Owing to the substantial reduction in connectivity, mangroves completely encroached into the historic tidal channel (Fig. 2B). In May 2005, upstream and downstream channels were recarved by removing mangroves, rock, and sediment (Fig. 2B). Work was carried out by approximately 30 people, largely community volunteers, working over the course of 2 days. The project entailed no capital costs.

Both fragmented and unfragmented reference systems were included in the sampling design to assure that improvements in restored creeks approached structure and functional levels not only more similar to unfragmented tidal creeks, but also to levels greater than fragmented tidal creeks. Unfragmented reference creeks were characterized by rocky or sandy substrate at the creek mouths, channels 0.5–1.5 m deep and 2–5 m wide with a rocky substrate, and edges fringed with Red mangroves. Channels in the fragmented tidal creeks contained more organic matter and muddy sediment, and

(A)



(B)

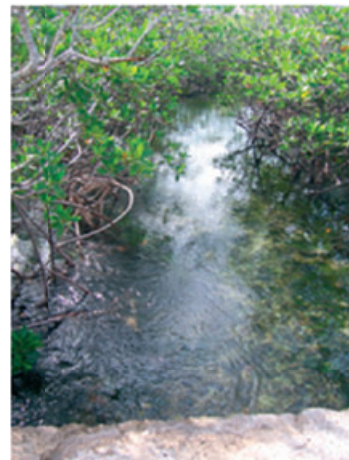


Figure 2. Pre- and post-restoration in (A) MOW and (B) CS.

upstream areas were considerably shallower (0.5 m). Baseline information on all reference and restored creeks can be found in studies by Valentine-Rose et al. (2007a, 2007b).

Sampling

Changes in ecosystem structure and function following restoration were based on separate surveys of resident and transient individuals. Resident individuals, for the purposes of this study, are those that remain in the creek at low tide and do not move in and out of the system with each tidal cycle (e.g., Gray snapper, *Lutjanus griseus*). Transient individuals were those moving upstream into the mangrove wetland on rising tides, but leaving upstream areas at low tide (e.g., Barracuda, *Sphyraena barracuda*). Surveys documenting changes in residents were based on a whole-creek sampling scale of all reference and restored creeks. Surveys documenting changes in transients were conducted in upstream areas of restored creeks with no reference creek comparisons, because natural tidal channels are too wide to allow for adequate enumeration of all migrating individuals.

Resident Production and Richness

Secondary production (P) of the fish community was calculated for each reference and restored creek by following the methods in Valentine-Rose et al. (2007b). P is calculated based on 25, 1-m², quantitative snapshot underwater visual census surveys of fish densities and lengths in each habitat in each creek at low tide in May 2004, 2005, and 2006. Lengths for each individual were converted to biomass in grams per square meter using both in situ-derived and published length–weight regressions. Total biomass for each species was converted to species production in grams per square meter per year by multiplying with published age-specific growth rates (gray and schoolmaster snapper growth rates were derived in situ, and different rates were used for unfragmented, downstream areas of fragmented, and upstream areas of fragmented creeks). Production values were weighted by habitat areal coverage within the entire creek system and summed for all species, resulting in total fish community P for each reference and restored creek. For sampling and calculation details see Valentine-Rose et al. (2007b).

In order to account for rare species that may have been missed during production surveys, an additional survey protocol was employed. The presence of resident fish was assessed in two randomly chosen 100 m² (10 m × 10 m) main channel plots (Layman et al. 2004b; Valentine-Rose 2007a), one in the upstream reach and the other in the downstream reach of each tidal creek, and in additional plots established in adjacent mangrove habitat and at the creek mouths ($n = 5$ per creek) (Valentine-Rose et al. 2007a) in May 2004, 2005, and 2006. In each plot, fishes were surveyed using underwater visual census with mask and snorkel (Brock 1954; Layman et al. 2004b). Each visual survey was conducted for 15 minutes at high tide while the snorkeler moved slowly throughout the

100 m² plot. Whole-creek resident species richness was determined by the total number of species identified in secondary production and presence/absence surveys combined. Fish were identified based on Robins and Ray (1986) and Human and Deloach (2002). Juvenile *Sparisoma* spp. were identified to generic level, and included Bucktooth parrotfish (*S. radians*), Redband parrotfish (*S. aurofrenatum*), and Stoplight parrotfish (*S. viride*). All *Eucinostomus* spp. (Mojarra) were also grouped at the generic level and included Slender mojarra (*E. jonesi*), Mottled mojarra (*E. lefroyi*), and Silver jenny (*E. gula*) (Layman et al. 2004b). Presence/absence, secondary production, and species richness surveys were repeated multiple times in each reference creek (see “Statistical analysis” below for details on treatments for each restored creek).

Assumptions

It is important to note that these P values are intended to be used for comparisons among tidal creeks within this study. Care should be taken in extending these numbers for comparisons with other systems. Owing to the limitations of our sampling method, they are not the exact whole ecosystem values, because they do not include in situ growth rates for every species or survival, emigration, or immigration rates. The use of published growth rates from similar environmental conditions to estimate secondary production is a common practice when in situ growth rates cannot be obtained (Waters 1977; Benke 1993; Peterson et al. 2003; Powers et al. 2003). Error in production estimates may have resulted from using the same growth rates for both fragmented and unfragmented tidal creeks for species other than Gray and Schoolmaster (*L. apodus*) snapper. However, since growth rates are likely slower in fragmented creeks (Valentine-Rose et al. 2007b; Rypel & Layman 2008), differences in secondary production estimates presented here are conservative, and we likely underestimated production differences between fragmented and unfragmented creeks. Lack of mortality estimates likely inflates our production estimates, but mortality estimates are extremely difficult to obtain in coastal and estuarine ecosystems (Adams et al. 2006). Nonetheless, production estimates may be more sensitive than abundance or biomass data alone because production adjusts those data to account for rapid growth of smaller (i.e., less biomass) species and individuals, providing for energetic equivalency and transforming those data to an energetics (i.e., functional) scale. Therefore, these limitations do not compromise the value of the estimates in this study to indicate ecosystem functional response to restoration, and to demonstrate the value of secondary production as a composite measure of this response.

Transient Movements

Above-water visual surveys from culvert or bridge sites in restored creeks were conducted to quantify the numbers and lengths of all fish leaving the upstream restored portion of the creek on a complete falling tidal cycle (creeks were sufficiently clear to allow visual monitoring from above

the water as well as narrow enough to allow the entire channel width to be surveyed). Surveys were conducted within 2 days of new or full moons. Lengths of individual fishes were converted to biomass estimates using length–weight regressions (Valentine-Rose et al. 2007b). Transient surveys in MOW and CS were conducted in May 2005 ($n = 3$ for each creek) and 2006 ($n = 3$ for each creek). These were not intended to be comprehensive surveys of all fishes utilizing the creek systems, but to provide some information as to the extent to which fish were moving through the altered tidal channels during daytime high tides. We recognize that we are likely underestimating fish movement into upstream areas and acknowledge that such movements will vary both on diurnal–nocturnal and seasonal cycles. For example, Nurse shark (*Ginglymostoma cirratum*), Lemon shark (*Negaprion brevirostris*), and Southern stingray (*Dasyatis americana*) were observed in upstream areas of MOW on days when transient surveys were not being conducted.

Statistical Analysis

A before/after control-impact (BACI) analysis of variance (ANOVA) design, using comparisons to multiple reference sites (“beyond BACI,” Underwood 1991, 1992, 1994), was used to test for significant changes in whole-creek resident species richness and assemblage secondary production in reference and restored creeks. Separate analyses were done for MOW and CS, because we used reference systems that were most similar (microtopography, depth, etc.) to the study sites for each comparison. There were six treatments in MOW restoration, each with three replications: MOW pre-restoration (May 2004), MOW 1-year post-restoration (May 2005), MOW 2-year post-restoration (May 2006), and reference creeks pre-, 1-year post-, and 2-year post-restoration. Reference creeks sampled for comparison with changes in MOW included two unfragmented tidal creeks (Somerset and White Bight [WB]) and one completely fragmented tidal creek (Bowen). There were six treatments in CS restoration, each with three replications: CS pre-restoration (May 2005), CS post-restoration (May 2006), unfragmented reference creeks pre- and post-restoration, and fragmented reference creeks pre- and post-restoration. For CS, reference creeks included three unfragmented tidal creeks (Somerset, WB, and Buryin’ Peace) and three fragmented tidal creeks (Love Hill, Davis, and Bowen). Repeated measures ANOVA was used to compare differences in species richness and production among years in reference creeks and among years in restored creeks. Multiple production and species richness surveys in reference and restored creeks ($n = 3$ for each creek) served as replications. Significant changes in restored creeks were considered a response to restoration only if significant changes were not also seen in reference creeks. To determine if restored creeks had approached structural and functional characteristics more similar to reference creeks, one-way ANOVA was used to test for differences between species richness and secondary production in reference and restored creeks pre- and post-restoration.

When examining changes in whole-creek resident fish community assemblage composition, we used non-metric multidimensional scaling (NMDS) of plot-based presence/absence data to test if fish assemblages (1) changed significantly in reference and restored tidal creeks and/or (2) were significantly different between reference and restored tidal creeks post-restoration. The same treatments as above were used for MOW and CS. NMDS graphically represents, in two dimensions, relationships between objects in multidimensional space derived from a Bray–Curtis similarity index (Bray & Curtis 1957). In ordination plots, as the distance between the points increases, similarity of biotic species composition between the two surveys decreases. Analysis of similarities (ANOSIM), a non-parametric analog to multivariate analysis of variance (MANOVA), was used to test for significant differences in assemblage composition among tidal creeks. If ANOSIM revealed significant ($p < 0.05$) effects, then similarity percentage analysis (SIMPER, Clarke & Warwick 1994) was used to identify which species contributed to the observed differences. All NMDS, ANOSIM, and SIMPER analyses were conducted in Primer 5 (version 5.2.9, PRIMER-E Ltd, Plymouth, U.K.).

Paired t tests were used to test for changes in total upstream transient abundance, biomass, and richness following restoration. Kolmogorov–Smirnov tests were used to test for changes in transient species’ length–frequencies following restoration, which were carried out for the two most common taxa, Yellowfin mojarra (*Gerres cineures*) and *Eucinostomus* spp. (Mojarra spp.), in MOW and CS.

Results

Changes in Whole-Creek Resident Production and Richness

Pre-restoration whole-creek secondary production in MOW was significantly lower than that in reference creeks ($F_{1,6} = 18$, $p = 0.02$) (May 2004) (Fig. 3A). Following restoration, secondary production decreased from a mean value of 215 (SD ± 55) to 67 (± 36) $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (May 2005), then increased to 146 (± 54) $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (May 2006). There was slight variation in production in reference creeks, but reference creek production ($955 \pm 189 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) remained significantly higher than MOW in all 3 years ($F_{1,6} = 22$, $p = 0.02$). Pre-restoration whole-creek secondary production in CS was also significantly lower than that in reference creeks ($F_{1,6} = 44$, $p = 0.001$) (May 2005) (Fig. 3B). Following restoration, secondary production increased significantly from 15 (± 12) to 333 (± 81) $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ($F_{5,18} = 33$, $p = 0.01$) (May 2006). This value remained significantly lower ($F_{1,6} = 15$, $p = 0.03$) than P in reference unfragmented ($813 \pm 196 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) creeks, but significantly greater ($F_{1,6} = 11$, $p = 0.04$) than P in partially fragmented ($187 \pm 67 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) creeks.

Pre-restoration species richness in MOW was significantly lower than that in reference creeks ($F_{1,6} = 14$, $p = 0.04$). Following restoration, species richness decreased from 15 (± 2) to 10 (± 4), then increased the following year to 12 (± 3), due to a fluctuation in the presence of marine species (Striped parrotfish, *Scarus iserti* and Four-eye butterflyfish,

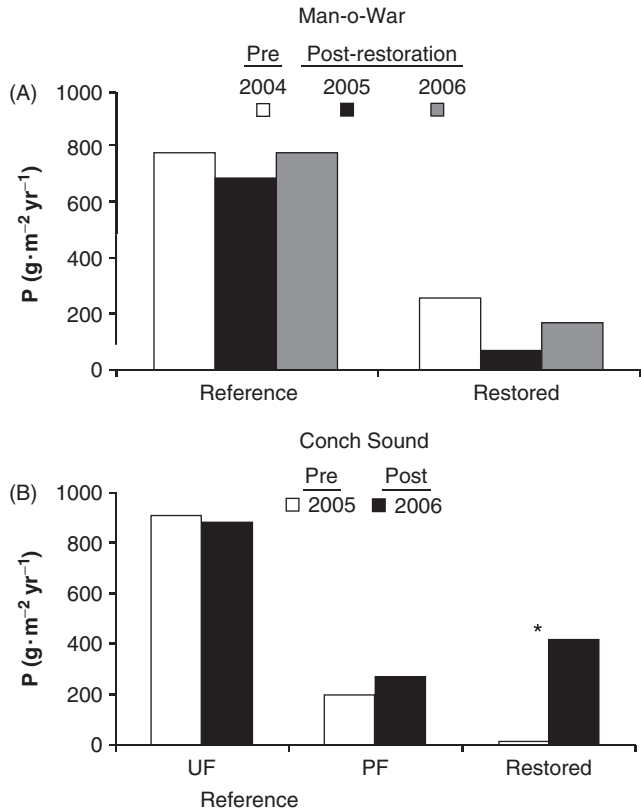


Figure 3. Pre- and post-restoration fish assemblage secondary production values (g·m⁻²·yr⁻¹) in reference and restored (A) MOW and (B) CS creeks.

Chaetodon capistratus) and grouper (Serranidae). There was a similar decline in species richness in reference creeks from year 1 to 2. Pre-restoration resident species richness in CS was also significantly lower than that in reference creeks ($F_{1,6} = 15, p = 0.04$). Following restoration, species richness increased significantly from 5 (± 0.0) to 13 (± 2) ($F_{5,18} = 24, p = 0.01$). This increase was due to the influx of snapper (Lutjanidae), grunt (Haemulidae), wrasse (Labridae), Doctorfish (*Acanthurus chirurgus*), Sergeant major (*Abudefduf saxatilis*), needlefish (Belonidae), and Barracuda (*Sphyrna barracuda*) following restoration. The increase was not significantly different from the average number of species in reference unfragmented (19 ± 7) ($F_{1,6} = 0.9, p = 0.25$) or partially fragmented (16 ± 9) ($F_{1,6} = 0.3, p = 0.12$) creeks.

Whole-creek resident fish assemblage composition in MOW did not change significantly following restoration ($r = 0.02, p = 0.36$) and remained significantly different from unfragmented reference creek assemblages ($r = 0.48, p = 0.01$) (Fig. 4A). Whole-creek resident fish assemblage composition in CS was significantly different following restoration ($r = 0.56, p = 0.01$) (Fig. 4B). Since only one out of seven reference streams also showed a significant difference in assemblage composition between years (WB, $r = 0.64, p = 0.01$), we attribute the assemblage composition shift in CS to restoration efforts. Furthermore, CS pre-restoration

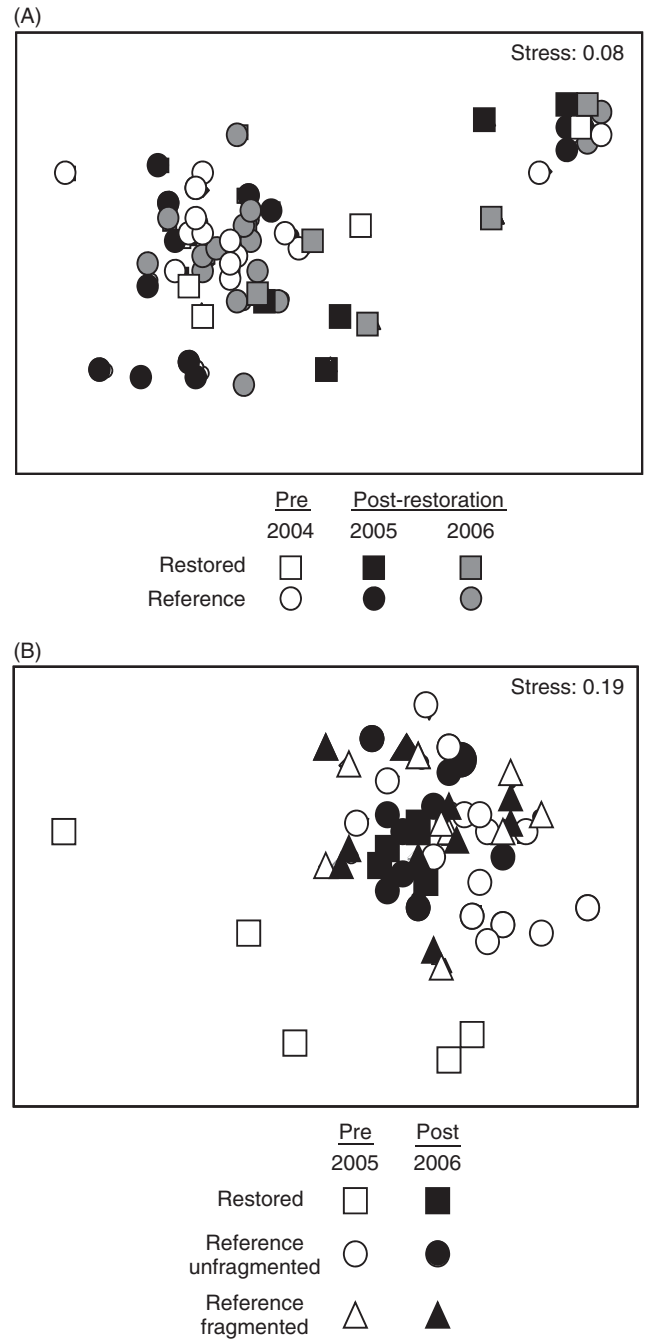


Figure 4. Pre- and post-restoration NMDS ordinations of fish assemblage production in reference and restored (A) MOW and (B) CS creeks.

assemblage composition was significantly different from all reference creeks ($r = 0.62, p = 0.01$), but was not post-restoration ($r = 0.15, p = 0.46$).

Changes in Transient Movements

We observed significant changes in transient species movement in snapshot surveys conducted the first year following restoration in MOW with an increase from 0 to 7 (± 2)

($T_{1,6} = 25$, $p = 0.01$) species. There was an additional significant increase (13 ± 2 ; $T_{1,6} = 19$, $p = 0.02$) the next year (Table 1). This increase was due to an influx of predatory (needlefish and Barracuda) and reef (Beaugregory, *Stegastes leucostictus*) species. In our surveys, transient species abundance increased significantly ($T_{1,6} = 23$, $p = 0.01$) from 0 to 261 (± 89) individuals the first year following restoration, and then to 330 (± 111) in the second year following restoration. Biomass increased significantly from 0 to 4,133 g/m² ($\pm 1,576$) ($T_{1,6} = 58$, $p = 0.001$) and then to 13,830 ($\pm 3,427$) ($T_{1,6} = 31$, $p = 0.03$) following restoration. Species richness increased significantly from 9 (± 2) to 13 (± 1) ($T_{1,6} = 11$, $p = 0.04$) following restoration in CS (Table 1). This increase was due to an influx of predatory (needlefish and Barracuda) and reef (wrasse and Doctorfish) species. Species abundance increased significantly from 76 (± 23) to 439 (± 76) ($T_{1,6} = 39$, $p = 0.001$), and biomass increased significantly from 4,636 (± 345) to 13,142 ($\pm 2,398$) ($T_{1,6} = 61$, $p = 0.003$) following restoration.

Length–frequency shifts in MOW showed an increase in larger individuals of *Gerres cineures*, Yellowfin mojarra ($D = 0.86$, $p = 0.03$), and other Mojarra species ($D = 0.77$, $p = 0.04$) (Fig. 5A & 5B) between the first year and second year after restoration. Length–frequency shifts in these two species were also significant in CS: Yellowfin mojarra ($D = 0.73$, $p = 0.04$) and other Mojarra species ($D = 0.79$, $p = 0.04$) (Fig. 5C & 5D).

Discussion

Restoration projects often are labor intensive and high-cost endeavors. Here, we provide an example of how individual components of the vast back-reef mosaic (Adams et al. 2006), that is, individual tidal creeks and associated

mangrove wetlands, can be significantly enhanced through simple restorative activities. Restoration of tidal flow through foot-bridge construction and selective removal of mangrove trees significantly increased secondary production of resident fish species in one of the two focal restoration projects. Increased utilization of the previously blocked wetlands by daily transient fishes was observed in both creeks. Such small-scale restoration endeavors may provide an important part of larger conservation/management initiatives in tropical and subtropical mangrove communities. We discuss specific aspects of enhanced ecosystem function in our study systems, and provide recommendations as to the most important components of successful restoration projects at this scale.

Whisenant et al.'s (1995) theory of thresholds in restoration ecology reasons that an ecosystem should set upon a trajectory of self-recovery in structure and function upon removal of an abiotic threshold that initiated degradation of original ecosystem structure and function. If Whisenant et al.'s (1995) theory was supported by our data then a reversal in the direction of one arrow (i.e., hydrologic connectivity) achieved through restoration should result in the subsequent reversal of all arrows (i.e., ecosystem structure and function). Our data support this theory in one of the two systems (CS). In CS, restoration increased nursery value via increases in both diversity and secondary production of fish assemblages. There were also significant changes in transient fishes (mostly predators) that utilize upstream areas of creeks at high tide, likely for foraging. Similar success to restoration of tidal flow have been described by Burdick et al. (1997), Brockmeyer et al. (1997), and McKee and Faulkner (2000). Furthermore, in the current study, the number of herbivorous marine species increased, suggesting an addition of functional groups to the food web. As such, functionally simplified food webs of fragmented creeks (Layman et al. 2007) can become rapidly

Table 1. Changes in total transient upstream area species richness, abundance (N), and biomass (B) in two restored Bahamian tidal creeks.

Species	Man-o-War						Conch Sound			
	N			B			N		B	
	Pre	Post-1 yr	Post-2 yr	Pre	Post-1 yr	Post-2 yr	Pre	Post	Pre	Post
Gray snapper	0	6	24	0	42	1,007	21	42	498	1,071
Schoolmaster	0	0	7	0	0	35	24	31	764	739
Cubera	0	0	9	0	0	769	2	4	212	62
Bar jack	0	0	3	0	0	367	0	0	0	0
Slippery dick	0	0	0	0	0	0	0	1	0	4
Beaugregory	0	0	1	0	0	0.5	2	6	3	0.5
Mojarra spp.	0	200	189	0	750	1,971	3	90	59	360
Yellowfin mojarra	0	16	71	0	510	7,455	1	207	208	689
Sergeant major	0	0	3	0	0	13	1	7	0.5	3
Checkered puffer	0	23	7	0	2,775	650	19	36	2,888	2,694
Barracuda	0	0	3	0	0	55	0	2	0	158
Doctorfish	0	0	0	0	0	0	0	1	0	1
Needlefish	0	16	16	0	56	104	3	10	3	151
Total	0	261*	330	0	4,133*	13,830*	76	439*	4,636	13,142*
Total species	0	5*	11*				9	13*		

*A significant (Paired t test, $p < 0.05$) increase in richness, N , or B following restoration. Year = yr.

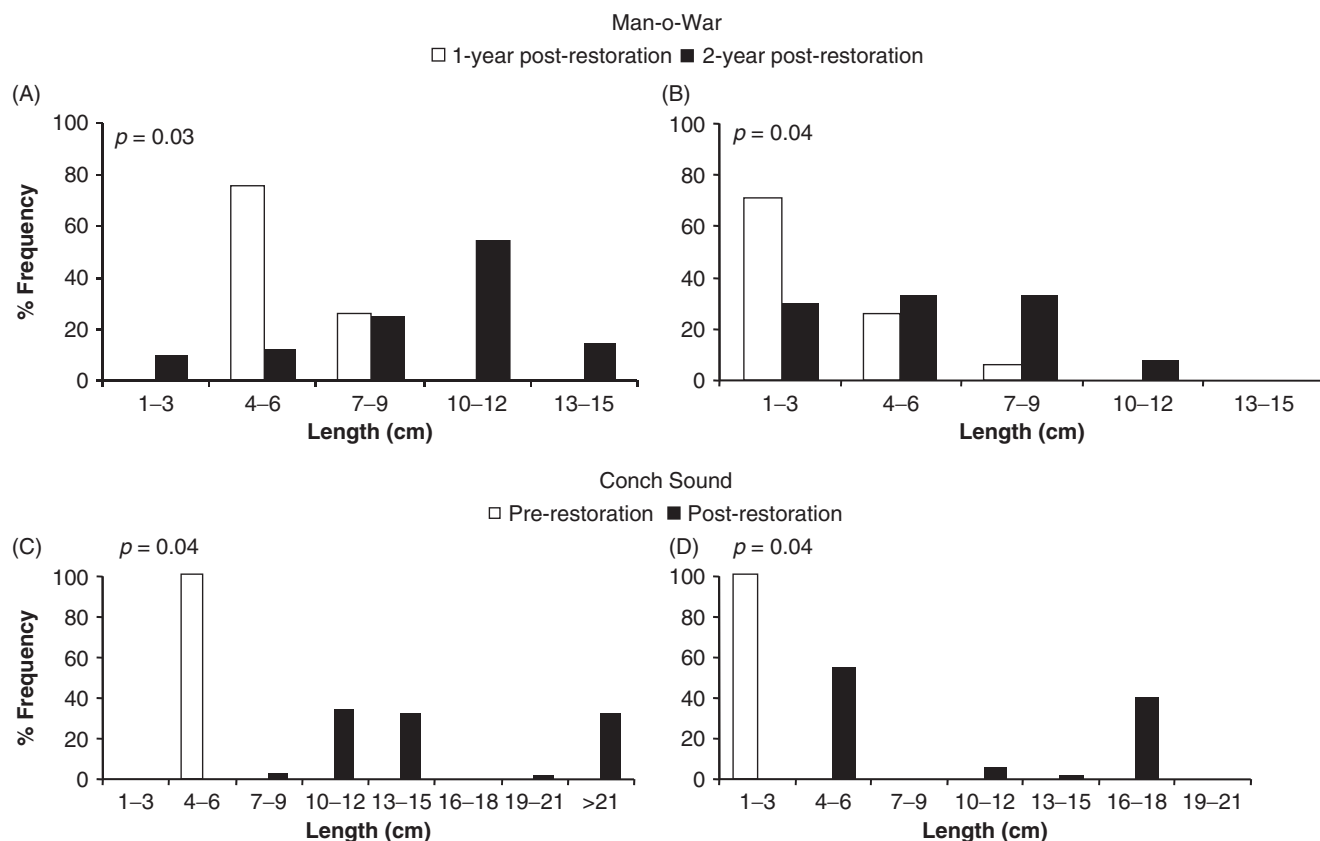


Figure 5. Length–frequency of *Gerres cinereus* (A and C) and *Eucinostomus* spp. (B and D) pre- and post-restoration in upstream MOW and CS.

more complex, and perhaps more stable (Rooney et al. 2006), after simple restoration efforts. Further, an economically and socially relevant result was the increased production of commercially important snapper and grunt species.

Conversely, there was little response in resident fish diversity and production to the restoration in the MOW system. This suggests a need to manipulate more factors in addition to hydrologic connectivity (i.e., water depth sensu), or cross more than one threshold (i.e., both abiotic and biotic sensu Whisenant et al. 1995) to achieve a more successful restoration of ecosystem structure and function. Three site-specific factors may explain differing results in the two projects: recruitment source, seascape characteristics, and upstream bathymetry. First, CS showed greater increases in resident biodiversity and biomass following restoration, possibly a function of its proximity to structurally complex nearshore habitats (e.g., subtidal rocky outcroppings, seagrass, macroalgal beds), which are good sources for recruitment (Grabowski et al. 2005; Cowen et al. 2006). Second, other aspects of the surrounding seascape (sensu Pittman et al. 2007) likely affected responses. MOW is dominated by a rather homogenous calcium carbonate rock substrate that presented little probability for reestablishment of structurally complex habitat types (e.g., seagrass). Conversely, CS was characterized by a heterogeneous habitat template, with abundant fringe mangrove, seagrass, and patch

reefs. Faunce and Serafy (2008) show that snapper, grunt, and Barracuda choose mangrove habitat based not only on total mangrove prop root area but also on proximity to nearby seagrass and coral habitats.

Third, upstream water depths may also account for the substantial increases in production at CS (Boesch & Turner 1984; Ruiz et al. 1993; Paterson & Whitfield 2000; Linehan et al. 2001). Attention was focused on creating deep channel pools in CS restoration, which provide low-tide refugia for small resident fishes in intertidal systems. When deep channel pools are absent, as in MOW, most fishes are forced to leave creek channels at low tide. That is, most fishes utilize the upstream habitat only during high tide when there is sufficient water depth. MOW may have historically been a shallow hard bottom creek, and perhaps never supported higher levels of fish production (similar to results in Vose & Bell 1994; McKee & Faulkner 2000). Choosing sites with relatively deep upstream refugia, or artificial creation of these deep pools, is necessary to maximize the resident fish production in these shallow systems.

Despite the lack of response in MOW resident assemblage characteristics, there was an increase in the utilization of previously blocked upstream habitat by transient fishes. Transient fishes take advantage of natural flood cycles to utilize upstream areas for shelter and food resources (Pringle 2003; Ray 2005;

Rypel et al. 2007). As a result, the area of intertidal wetland available to fishes has been linked to the quantities of offshore catches (Boesch & Turner 1984). Transient fishes are also an important mechanism of nutrient, biomass, and energy transport from inshore tidal creek habitat to the nearshore marine environment (Deegan et al. 2000; Kneib 2000). Therefore, although augmentation of resident production was unsuccessful in MOW, the restoration still reestablished a more natural daily flood cycle and accompanying fish movement dynamic in both restored creeks. Several studies in which tidal flow has been restored in marine habitats also found a rapid return of transient species to restored areas while resident species richness and biomass were slow to respond, if at all (Gilmore et al. 1982; Bell & Vose 1993; Burdick et al. 1997; Raposa 2002).

Conclusion

These small-scale projects provide an example of how rapid and low-cost efforts can result in significant ecosystem benefit. We provide a unique example of how small-scale restoration of hydrologic connectivity (i.e., tidal flow) enhances resident fish production as well as provides habitat for transient fishes. Because of the extent to which creeks have been fragmented in the Bahamas and the Caribbean (Layman et al. 2004a, 2004b), there are many opportunities for community-based restoration initiatives that can significantly improve the ecosystem function to coastal mangrove wetlands. Further, the significant results in these small-scale projects suggest that restoration of larger fragmented systems may have enormous benefit. Future studies linking food web dynamics with changes in production before and after restoration may provide insightful information regarding the dynamics of tidal creek communities. We suggest future conservation efforts should be directed toward preserving the integrity of tidal creeks with natural tidal flow as well as efforts that focus on restoration of tidal flow following the framework outlined here.

Implications for Practice

- Combining both structural (e.g., species richness) and functional (e.g., secondary production) monitoring metrics will help restoration ecologists use results from ecological restoration projects to build upon scientific theories and improve restoration strategies. We suggest designing restoration projects that employ both structural and functional monitoring metrics.
- If small, rapid, low-cost restoration is the goal, then ensuring proper characteristics are in place for autogenic restoration is essential. For tidal creeks similar to those in this study, adequate water depths, mature mangrove fringe, and a nearshore colonization source (e.g., seagrass or reef) are ideal. If these characteristics are not in place, then additional time and money may be required to artificially create necessary habitat to reestablish the function of the system.

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