WETLANDS, Vol. 27, No. 3, September 2007, pp. 702–718

FLORAL AND FAUNAL DIFFERENCES BETWEEN FRAGMENTED AND UNFRAGMENTED BAHAMIAN TIDAL CREEKS

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Abstract: We characterized biota in two unfragmented and two fragmented mangrove-lined tidal creeks on Andros Island, Bahamas, in May 2003, to examine particular effects of tidal creek fragmentation by road blockage. Total number of plant and fish species was significantly different between fragmented and unfragmented creeks, and species composition was significantly different both between unfragmented and fragmented creeks, and between downstream and upstream areas within fragmented creeks. More reef-associated, economically important and ecologically critical plant, macroinvertebrate, and fish species were observed in unfragmented tidal creeks, while fragmented creeks contained: 1) plant species typical of higher elevation estuarine habitat, 2) terrestrial and aquatic macroinvertebrate species typical of upland habitats, 3) macroinvertebrate species adapted to low flow, and 4) temperature-and saline-tolerant macroinvertebrate and fish species. Furthermore, fragmented tidal creeks had different size distributions of common organisms, e.g., smaller sizes of two economically important fish species (Lutjanidae). This study suggests that fragmentation of tidal creeks and the subsequent loss of hydrologic connectivity influences the diversity and composition of aquatic flora and fauna, and may considerably inhibit nursery function and other ecosystem services provided by these coastal systems. These data also provide a baseline with which community- and ecosystem-level responses to restoration of hydrologic connectivity in fragmented tidal creeks will be assessed.

Key Words: back reef, community structure, estuary fragmentation, hydrologic connectivity, mangrove, nursery, road-crossing, tidal flow, underwater visual census

INTRODUCTION

Ecosystem fragmentation and subsequent loss of ecosystem services is of growing concern worldwide. For example, obstructions of connectivity in coastal ecosystems can have substantial effects on the structure and function of these ecosystems, as well as the flora and fauna in them (Ray 2005). Tidal flow is the primary factor organizing estuarine communities, and restricting this flow alters physiochemical parameters as well as vegetative, macroinvertebrate, and fish community structure (Roman et al. 1984, Warren et al. 2002). Such changes are of particular concern because estuaries are critical nursery habitats for juvenile reef species and for sustainability of off-shore fisheries (Boesch and Turner 1984, Marx and Herrnkind 1986, Stoner 1988, Sasekumar et al. 1992, Acosta and Butler 1997, Edgar et al. 1999, Stoner 2003).

Back reef systems (i.e., interconnected shallow-water coastal habitats including lagoons, patch reefs, mangroves, seagrass macroalgal beds, as well as tidal creeks; Dahlgren and Marr 2004), have been identified as important nursery areas for many juvenile marine macroinvertebrate and fish species (Stoner et al. 1998, Nagelkerken et al. 2001, Adams and Ebersole 2002, Layman and Silliman 2002, Adams et al. 2006, Dahlgren et al. 2006). Certain fish species are mangrove and/or seagrass dependent at some point in their life cycle (Nagelkerken et al. 2002, Mumby et al. 2004), and thus tidal creeks (which contain large areas of mangrove and seagrass) may be essential for ecosystem function in the coastal zone. However, sub-tropical and tropical tidal creek community structure and function, as well as response to anthropogenic disturbance, remain poorly understood (but see Layman et al. 2004a, b, Mallin and Lewitus 2004).

Throughout the Caribbean, hydrologic connectivity (*sensu* Pringle 2001) in tidal creeks is often fragmented by road construction. On Andros Island, the largest Bahamian island with dozens of creek systems, more than 80% of major tidal creek systems have been partially or completely fragmented by roads or footpaths (Layman et al. 2004a) disrupting tidal flow and altering fish assemblage structure (Layman et al. 2004b). Yet only fish community structure has been examined in the context of fragmentation effects. To more fully document faunal differences between 1) unfragmented and fragmented tidal creeks, and 2) downstream and upstream areas within fragmented tidal creeks, we characterized plant, macroinvertebrate, as well as fish community characteristics, in two unfragmented and two fragmented mangrove tidal creeks on Andros Island, Bahamas in May 2003.

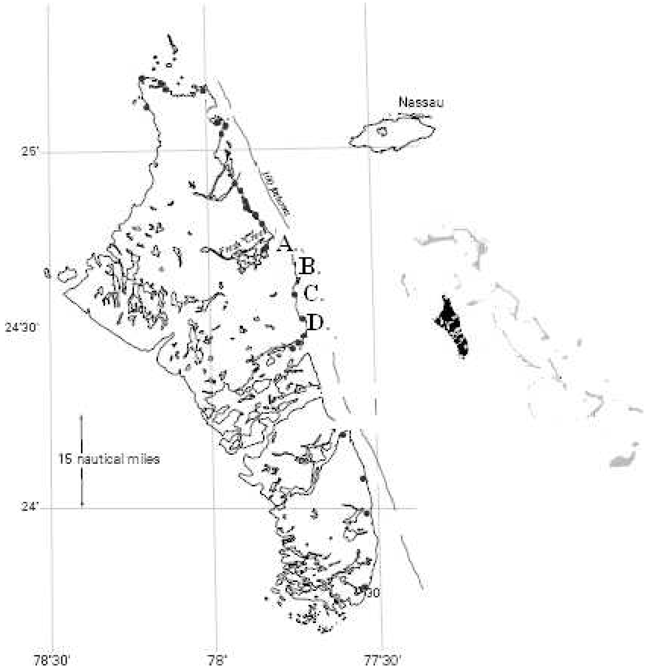

Figure 1. Line drawing of Andros Island, Bahamas. Surveyed creeks are A) Somerset, B) Bowen, C) Man-o-War, and D) White Bight.

METHODS

Study Sites

Field sampling was conducted from May 13–22, 2003, in four mangrove tidal creeks on the eastern coast Andros Island (Figure 1), the largest island in the Bahamas archipelago (see Layman et al. 2004b). Two tidal creeks, Somerset and White Bight, were classified *a priori* as unfragmented (e.g., Figure 2a), and two, Man-o-War and Bowen, as fragmented (e.g., Figure 2b) (Layman et al. 2004b). For the purposes of this study, the term "upstream" refers to fragmented areas isolated from tidal flow (i.e., upstream of roads or footpaths) in fragmented tidal creeks, or farthest from the ocean (i.e., the most upstream sites) in unfragmented tidal creeks. "Downstream" refers to areas that remain hydrologically connected to the ocean (i.e., downstream of roads) in fragmented tidal creeks, or "closest to" the ocean in unfragmented tidal creeks (for a conceptualization of these descriptions, see Figure 3). In the Bahamas, tidal creeks are clear water, mangrove-lined, low lying ecosystems formed from scouring of calcareous rock substrate, and are dominated by tidal exchange and receive little freshwater input (Buchan 2000).

The unfragmented tidal creeks in this study were characterized by rocky or sandy substrate at the creek mouths, channels 0.5–1.5 m deep and 2–5 m

Figure 2. Photographs of A) a typical fragmented tidal creek (Bowen Sound) downstream (left image) and upstream above the road blockage (right image) in which the road transects the down- and upstream areas of creek, and B) an unfragmented tidal creek (Somerset) downstream (left image) and upstream (right image). Downstream images are taken from the mouth at the creek-ocean interface looking upstream into the creek.

wide with a rocky substrate, and edges fringed with red mangroves (*Rhizophora mangle*). Channels in the fragmented tidal creeks contained more organic matter and sediment, and upstream areas were considerably shallower (< 0.5 m). Creek lengths from the mouth to the upstream terminus (i.e., an approximate location where the main-channel fades into shallow intertidal flats that have no distinct sub-tidal channels) were ~400 m in Man-o-War and Bowen, ~90 m in White Bight, and ~1,140 m in Somerset. Each road blocking the creeks was built in the 1960s. Bowen was completely blocked by a solid road structure that completely fragments downstream and upstream reaches, while Man-o-War was blocked by a footpath made of rocks allowing water seepage into and out of upstream areas.

Preliminary water quality analysis was performed concurrently with biotic sampling in each of the four tidal creeks using a Hydrolab MiniSonde 4a multiprobe (Hach Environmental, Loveland, Colorado) capable of recording salinity, temperature, dissolved oxygen, and pH. Samples were taken on two separate days in the morning and afternoon in each tidal creek, providing a "snapshot" of water quality conditions (Figure 4). Maximum salinities were higher in fragmented sites (39.0 and 43.0 in Man-o-War and Bowen, respectively) than in unfragmented (38.2 and 38.8 in Somerset and White Bight, respectively), presumably due to evaporation of standing water above the blockages. Likewise, temperature tended to be higher, and to have larger ranges, between morning and afternoon samples in the upstream portions of the fragmented sites (29.43–37.1°C and 28.28–37.7°C in Man-o-War and Bowen, respectively) compared to unfragmented sites (27.4–30.8°C and 27.7–33.3°C in Somerset and White Bight, respectively) on the sampling dates. Fragmented systems also tended to have greater differences between dissolved oxygen concentrations in the morning and afternoon. Bowen sound, for example, had the lowest recorded morning (~9:00) dissolved oxygen concentrations (3.18 mg/L), but had afternoon concentrations (~7–8 mg/L) that were equivalent to, or higher than other sites. No trends were detected for pH, which ranged from 7.5–8 in all creek areas.

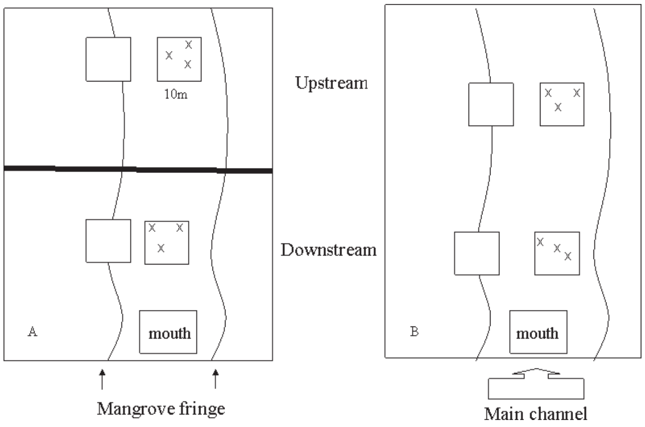

Figure 3. Schematic of transects and sampling plots upstream and downstream sites for A) fragmented and B) unfragmented tidal creeks. Plants, macroinvertebrates, and fish were surveyed in channel plots, while only fish were surveyed in mouth and side mangrove plots. Plots were 100 m^2. Repeated plant quadrats, represented by "x", within each plot were 1 m^2, while repeated macroinvertebrate quadrats within each plot were 0.0625 m^2.

Macrophytes and Macroalgae

Two 100 m^2 plots were randomly chosen within the main channel of each of the four tidal creeks, one in the upstream reach and one in the downstream reach of the tidal creek (Figure 3). Within these plots, the relative abundance of plant and macroalgal taxa based on aerial percent cover was estimated in 25 randomly-selected, non-overlapping 1 m^2 quadrats. Concentrating effort within these 100 m^2 plots ensured that we could best associate plant, macroinvertebrate, and fish composition in the same general area (see below). Recognizing this method may underestimate species richness within

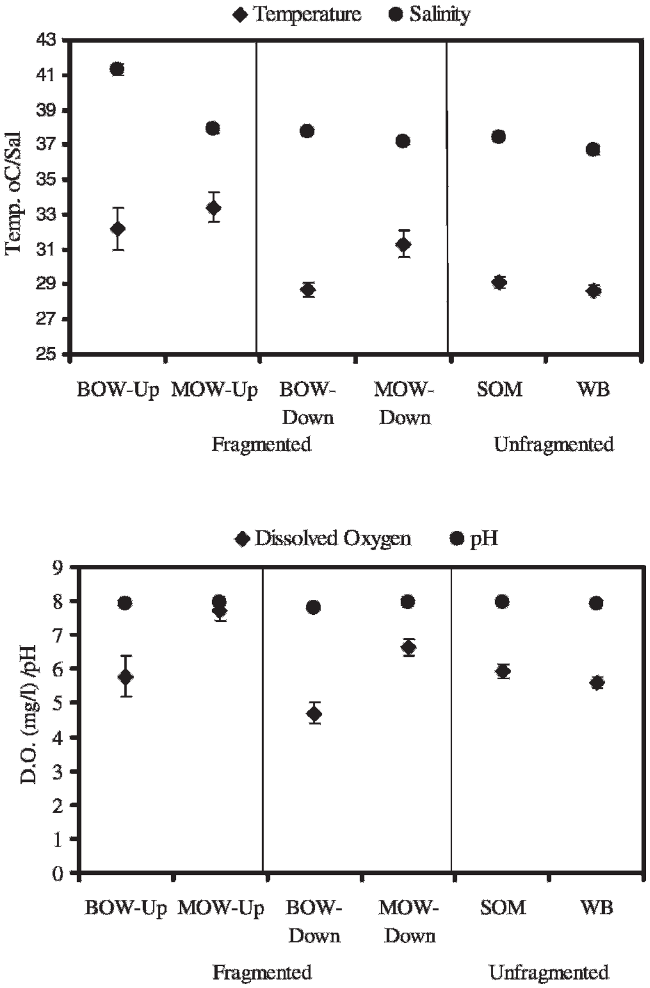

Figure 4. Means and standard deviations for A) temperature (°C), B) salinity, C) dissolved oxygen (mg/L), and D) pH. Mean values are reported for upstream (Up) and downstream (Down) areas in fragmented creeks. Tidal creek abbreviations: MOW = Man-o-War; BOW = Bowen, SOM = Somerset, WB = White Bight.

an entire creek, 20–25 additional 1 m^2 quadrats were randomly chosen and sampled for percent cover of macrophytes and macroalgae. Plants and algae were identified to the lowest taxonomic level possible using Correll and Correll (1982) and Littler et al. (1989).

Macroinvertebrates

The presence and abundance of live macroinvertebrates was documented in three 0.0625 m^2 quadrat samples taken in each of the 100 m^2 plots. Fewer macroinvertebrate quadrats were sampled because macroinvertebrate abundance tended to be much higher than plant areal coverage, thus less effort was needed to document relative abundance of the most common individuals in the 100 m^2 plot. All live macroinvertebrates observed by snorkeling within quadrats were collected by hand for identification and recorded. In plots with emergent vegetation (e.g., *Rhizophora* spp.), all macroinvertebrates in the 0.0625 m^2 quadrat area, including that area above the waterline, were collected. Macroinvertebrates that could not be removed (e.g., corals) were documented and left in place. All macroinvertebrates were sorted, identified to the lowest taxonomic level possible, and counted. In addition to samples taken from 100 m^2 plots, visual surveys were conducted by snorkeling throughout all obvious microhabitats for a total of ~10 person-hours per tidal creek. These additional visual surveys were intended to describe the abundance and distribution of rare species, and species with more restricted distributions. Reference samples of all species were taken for identification and vouchers. Voucher specimens of each species were preserved in 95% ethanol and deposited in the Alabama Museum of Natural History. Samples were identified using Wiedenmayer (1977), Kaplan (1988), and Redfern (2001).

Fish

The presence/absence of fish were documented in main-channel 100 m^2 plots, and in additional plots established in adjacent mangrove habitat and at the creek mouths (n = 5 per creek) (for conceptualization, see Figure 3). 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 30 minutes while the snorkler moved slowly throughout the 100 m^2 plot, noting every fish species present. Surveys within each plot were repeated three to four times on two different days in each tidal creek. Fish were identified based on Robins and Ray (1986) and Human and Deloach (2002). Juvenile *Sparisoma* spp. were identified to generic level, and likely included bucktooth parrotfish (*S. radians*) (Valenciennes, 1840), redband parrotfish (*S. aurofrenatum*) (Valenciennes, 1840), and stoplight parrotfish (*S. viride*) (Bonnaterre, 1788). All mojarra (*Eucinostomus* spp.) also were grouped at the generic level and likely included slender mojarra (*E. jonesi*) (Gunther, 1879), mottled mojarra (*E. lefroyi*) (Goode, 1874), and silver jenny (*E. gula*) (Quoy and Gaimard, 1824), see Nagelkerken (2000) and Layman et al. (2004).

The size structure of two economically important fish species, schoolmaster (*Lutjanus apodus*) and gray snapper (*L. griseus*), also was assessed in each tidal creek. Survey quadrats (25 m^2) were located in mangrove prop-root habitat every 15 m from the mouth to the upstream terminus of the defined channel. Each quadrat was surveyed for approximately five minutes, and all surveys were conducted within two hours of high tide to minimize tide effects on size structure (Morrison et al. 2002, Greenwood and Hill 2003, Jaafar et al. 2004). Snapper in each plot were identified and enumerated by one author (JJC) based on four standard length (SL) size categories: 1) 0–75 mm, 2) 76–150 mm, 3) 151–225 mm, and 4) > 225 mm. Each tidal creek was surveyed on two separate days, with separate, random plot locations each day.

The main goals of this study were to obtain comparisons 1) between unfragmented and fragmented tidal creeks, and 2) between downstream and upstream areas within fragmented tidal creeks. We recognize that all data presented here provide a limited assessment of the characteristics in these tidal creeks, and that these variables undergo substantial tidal, diel, and annual variation. However, despite these fluctuations, the general comparisons (e.g., relative species richness, overall community composition) revealed by our data should be reasonably robust to temporal variability, and indicative of the longer-term environment of the tidal creeks.

Statistical Analyses

When examining biotic community assemblage composition, we used non-metric multidimensional scaling (NMDS) of plot-based presence/absence data to test if biotic assemblages varied 1) between unfragmented and fragmented tidal creeks and/or 2) between downstream and upstream areas within tidal creeks. NMDS graphically represents, in two dimensions, relationships between objects in multidimensional space using the Bray-Curtis similarity index (Bray and Curtis 1957). In ordination plots, as the distance between points (i.e., species presence recorded in a single census) increases, similarity of biotic species composition between the two surveys decreases. Analysis of Similarities (ANOSIM), a multivariate analog to MANOVA, was used to test for significant differences in assemblage composition among and within (i.e., upstream vs. downstream) tidal creeks. If ANOSIM revealed significant ($p < 0.05$) effects, then similarity percentage analysis (SIMPER, Clarke and 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, UK). Student t-tests were used to determine differences in total number of species between unfragmented and fragmented creeks, and paired t-tests were used to determine differences in total number of species between downstream and upstream areas within tidal creeks based on the quadrat samples. Each quadrat served as a replicate ($n = 50$ for plants, 6 for macroinvertebrates, and 8 for fish). Species lists for each taxonomic group (i.e., macrophytes and macroalgae, macroinvertebrates, fish) were made by synthesizing all relevant taxa observed to be present in each study creek, combining data from both plot-based and roving diver techniques. A MANOVA (performed in SPSS version 15) was performed to examine differences in relative abundance of snapper (*L. griseus* and *L. apodus*) size distributions among unfragmented and fragmented tidal creeks. Multiple comparisons within size groups were made with a Bonferroni correction. Data were arc sin transformed to meet distribution and variance assumptions.

RESULTS

Macrophytes and Macroalgae

A total of 40 species of macroalgae and vascular plants were observed within the four tidal creeks. Quadrats, random surveys, and transects resulted in 19 and 28 species in fragmented tidal creeks (Man-o-War and Bowen, respectively), and 25 and 29 species in unfragmented tidal creeks (Somerset and White Bight, respectively) (Appendix A). Twelve species were unique to unfragmented tidal creeks, and five were unique to fragmented tidal creeks. There were significantly fewer species 1) in quadrats in fragmented creeks compared to unfragmented creeks ($t = 3.586$, $df = 96$, $p < 0.001$) and 2) in upstream areas compared to the corresponding downstream areas within fragmented tidal creeks ($t = 5.734$, $df = 48$, $p < 0.001$) (Appendix A).

Multidimensional scaling indicated that plant assemblage structure (i.e., presence of constituent species) in unfragmented tidal creeks was significantly different from fragmented tidal creeks ($R = 0.77$, $p < 0.001$), and assemblages in upstream areas of fragmented tidal creeks were significantly different than those in corresponding downstream areas ($R = 0.73$, $p < 0.001$) (Figure 5A). In fragmented tidal creeks, common species included green algae (e.g., *Bataphora oerstedii* and *Penicillus capitatus*), the red alga, *Bostrychia montagnei*, and several species of vascular plants, some of which are characteristic of higher elevation marsh or semi-terrestrial zones (e.g., *Concocarpus erectus*, and *Rhachicallus americana*). Unfragmented tidal creeks

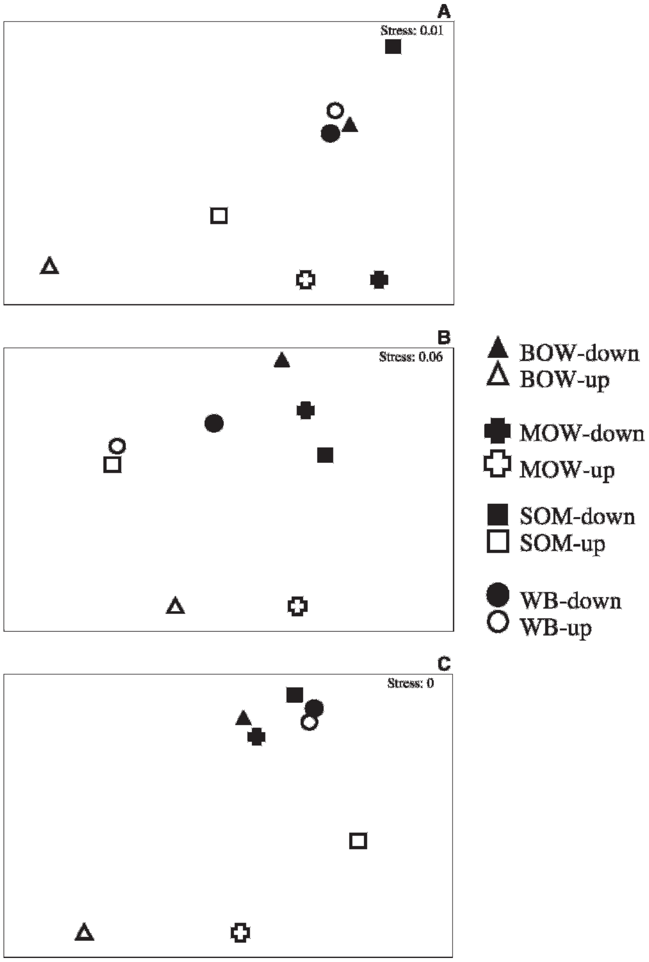

Figure 5. Non-metric Multi Dimensional Scaling results of A) Macrophytes and macroalgae, B) Macroinvertebrates, and C) Fish, presence/absence surveys in fragmented (Man-o-War and Bowen) and unfragmented (Somerset and White Bight) tidal creeks. Tidal creek abbreviations: MOW = Man-o-War; BOW = Bowen, SOM = Somerset, WB = White Bight. All quadrat data were analyzed as presence/absence in upstream and downstream locations in each tidal creek.

included similar common species, but additional green (e.g., *Halimeda* spp.), brown (*Sargassum* spp.), and red (e.g., *Centroceras clavatum*, *Ceramium nitens*, *Digenia simplex*, and *Laurencia* sp.) macroalgae were also common, as were the vascular plants, *Halodule bequdettei* and *Thalassia testudinum*. Fragmented and unfragmented creeks also differed in the composition of the mangrove community. Unfragmented creek surveys included only red mangroves (*Rhizophora mangle*), while in fragmented creeks, black and white mangroves (*Avincennia germinans* and *Laguncularia racemosa*, respectively) were also present.

Plants and macroalgae covered a greater amount of the substrate in unfragmented tidal creeks than in fragmented creeks. In unfragmented tidal creeks, $>$ 48% of the surveyed area in quadrats in downstream reaches was covered by vegetation, and $>$ 73% of the surveyed area in upstream reaches was vegetated, primarily by *Thalassia testudinum* in Somerset, and diverse assemblages of macroalgae fringed by *Rhizophora mangle* in White Bight (Appendix A). Downstream, in fragmented tidal creeks, $<$ 42% and $<$ 68% of the surveyed area was vegetated in Man-o-War and Bowen, respectively. Upstream, $<$ 36% was vegetated in both. Unfragmented tidal creeks exhibited a high number of species throughout, while fragmented tidal creeks were dominated by the green alga *Batophora oerstedii* in both upstream and downstream areas.

Macroinvertebrates

A total of 71 macroinvertebrate species were observed within the four tidal creeks (Appendix B). Quadrats, random surveys, and transects resulted in 18 and 25 species identified in fragmented tidal creeks (Man-o-War and Bowen, respectively), and 39 and 15 species in unfragmented tidal creeks (Somerset and White Bight, respectively) (Appendix B). Thirty-one species were unique to unfragmented tidal creeks, and 21 were unique to fragmented tidal creeks. The mean number of total species observed in quadrats per creek did not differ significantly 1) among fragmented and unfragmented tidal creeks ($t = 0.506$, $df = 10$, $p = 0.50$) or 2) between upstream and downstream areas within fragmented tidal creeks ($t = 0.807$, $df = 5$, $p = 0.28$), although there was a trend of fewer species upstream than downstream in fragmented tidal creeks (Appendix B).

Macroinvertebrate species composition was significantly different between unfragmented and fragmented tidal creeks ($R = 0.70$, $p = 0.03$), and between upstream and downstream areas of fragmented tidal creeks ($R = 0.34$, $p = 0.03$) (Figure 5B). Unfragmented tidal creeks had more species typically found in marine environments (e.g., *Aplysia dactylomela*, *Strombus gigas*, *Holothuria* spp., *Panilurus argus*, and *Penaeus* spp.) than downstream areas of fragmented tidal creeks. Within fragmented tidal creeks, the only aquatic species found above blockages were those with high tolerance of a broad range of salinity and temperature conditions (e.g., *Neritina virginea*, *Batillaria minima*) (Metcalf 1904, Andrews 1940).

Fragmented tidal creeks show a pattern of lower macroinvertebrate species richness (fragmented mean = 23 spp. per creek; unfragmented mean = 34.5 spp. per creek), yet high abundance (fragmen-

Table 1. Mean densities (m^{-2}) of *Lutjanus apodus* and *L. griseus* (± SD) in four size classes in mangrove habitat among two fragmented (Man-o-War [MOW] and Bowen [BOW]) and two unfragmented (Somerset [SOM] and White Bight [WB]) tidal creeks.

	Creek	0–75 mm	76–150 mm	151–225 mm	> 225 mm
L. apodus	MOW	0.80 (1.01)	2.80 (1.86)	0	0
	BOW	0.20 (0.63)	0.80 (0.92)	0.30 (0.48)	0.10 (0.32)
	SOM	0.72 (1.24)	2.90 (2.52)	3.05 (2.79)	0.02 (0.55)
	WB	0.56 (1.01)	1.38 (0.87)	0.67 (0.87)	0
L. griseus	MOW	1.40 (1.84)	5.13 (3.67)	0.40 (0.74)	0
	BOW	0.10 (0.32)	0.02 (0.63)	0.01 (0.32)	0
	SOM	0.82 (1.26)	2.23 (1.88)	1.50 (2.46)	0.20 (0.59)
	WB	0.89 (0.93)	1.67 (1.22)	1.11 (1.36)	0.06 (0.24)

ted mean = 82 individuals per species per creek; unfragmented mean = 43.2 individuals per species per creek). Surveys in upstream channels of fragmented tidal creeks were dominated by *Neritina virginea* and *Batillaria minima* individuals (89% of individuals). In contrast, upstream and downstream reaches of unfragmented tidal creeks exhibited a greater number of relatively rare species. For example, Somerset had 45 species that were less abundant (Appendix B).

Fish

A total of 33 fish species (Appendix C) were observed among all four tidal creeks. Surveys documented 21 and 23 species identified in fragmented tidal creeks (Man-o-War and Bowen, respectively), and 30 and 22 species in unfragmented tidal creeks (Somerset and White Bight, respectively). Nine species were unique to unfragmented tidal creeks, and two were unique to fragmented tidal creeks. There were significantly fewer species 1) in quadrats in fragmented creeks compared to unfragmented creeks ($t = -3.17$, $df = 12$, $p = 0.004$) and 2) in upstream areas compared to the corresponding downstream areas within fragmented tidal creeks ($t = -8.47$, $df = 14$, $p < 0.001$) (Appendix C).

Significant differences in fish assemblage composition was found in unfragmented and fragmented tidal creeks ($R = 0.48$, $p < 0.002$), and between upstream and downstream areas in fragmented tidal creeks ($R = 0.42$, $p < 0.001$) (Figure 5C). Unfragmented tidal creeks had more reef associated species (e.g., Labridae, Chaetodontidae, Haemulidae, and Scaridae). Some species (e.g., *Lutjanus griseus*, *L. apodus*, *Gerres cinereus*, and *Eucinostomus* spp.) were observed in every downstream or unfragmented tidal creek survey. The dominant species observed upstream of blockages in fragmented tidal creeks (and the only species observed upstream in Bowen) were *Cyprinodon variegates* and *Gambusia hubsii*, species highly tolerant of a broad range of environmental conditions. Fish assemblages differed significantly in an unfragmented creek (Somerset) between up- and downstream areas ($R = 0.72$, $p < 0.001$). Fish assemblages in up and downstream areas did not differ significantly ($R = 0.04$, $p = 0.62$) in the other unfragmented tidal creek (White Bight).

More large snapper (*L. griseus* and *L. apodus*) were found in unfragmented creeks (Table 1, Table 2, Figure 6). Snapper in the largest size class (> 225 mm) were only found in unfragmented creeks. In upstream areas of fragmented creeks, snapper were either restricted to the two smaller size classes (0–75 mm and 75–150 mm) (Man-o-War) or not found at all (Bowen).

DISCUSSION

Fragmentation of hydrologic connectivity in tidal creeks alters the total number of species and community composition of biota, as well as the size structure of economically important fish species (Lutjanidae). Total number of plant and fish species was lower in fragmented creeks than unfragmented creeks. Within fragmented creeks, there were fewer plant and fish species upstream of blockages than downstream, as was expected. However, given the *a priori* categorization of tidal connectivity, this study did not fully support the expectation that total species number would be lower in fragmented creeks than unfragmented creeks, or in upstream areas of fragmented creeks compared to downstream areas, as all creek areas often had a similar number (but different composition-see below) of macroinvertebrate species. As such, these data suggest that the assemblage composition, not the total number, may be a better criterion for distinguishing between unfragmented and fragmented tidal creeks.

Biotic communities in unfragmented tidal creeks were comprised of more diverse assemblages of

Table 2. Summary of MANOVA results for comparisons of *Lutjanus apodus* and *L. griseus* size class distributions in mangrove habitat among two fragmented (Man-o-War [MOW] and Bowen [BOW]) and two unfragmented (Somerset [SOM] and White Bight [WB]) tidal creeks. Significance (standard error) at $p < 0.05$ is noted with an asterisk (*).

	Creek comparison		0–75 mm Significance	76–150 mm Significance	151–225 mm Significance	> 225 mm Significance
L. apodus	SOM	WB	1 (.014)	0.157 (0.17)	0.043* (0.07)	0.009* (0.02)
	SOM	MOW	0.103 (0.12)	1 (0.14)	0.000* (0.06)	0.002* (0.01)
	SOM	BOW	0.032* (0.14)	1 (0.17)	0.001* (0.07)	0.009* (0.01)
	WB	MOW	0.498 (0.15)	1 (0.18)	0.013* (0.08)	1 (0.02)
	WB	BOW	0.166 (0.17)	1 (0.20)	1	1 (0.02)
	MOW	BOW	0.166 (0.17)	1 (0.20)	1	1 (0.02)
L. griseus	SOM	WB	1 (0.07)	1 (0.13)	1	0.118 (0.03)
	SOM	MOW	1 (0.06)	0.016* (0.12)	0.000* (0.06)	0.003* (0.03)
	SOM	BOW	1 (0.07)	0.000* (0.14)	0.002* (0.07)	0.018* (0.03)
	WB	MOW	1 (0.07)	0.165 (0.14)	0.001* (0.07)	1 (0.04)
	WB	BOW	1 (0.08)	0.001* (0.16)	0.007* (0.08)	1 (0.04)
	MOW	BOW	1 (0.07)	1 (0.13)	1 (0.07)	0.118 (0.03)

marine biota, important food and refugia sources (e.g., *Thalassia* spp., *Laurencia* spp., *Penaeus* spp; Dahlgren and Eggleston 2000) for other biota, and economically important species (e.g., *Strombus gigas*, *Panilurus argus*, Serranidae, Haemulidae, Lutjanidae; Buchan 2000). In contrast, biotic communities in upstream areas of fragmented tidal creeks were characteristic of higher elevation intertidal areas (e.g., *Avicennia germinans*, *Laguncularia racemosa*, and *Ligia* spp.) and included species tolerant of broad ranges of temperature and salinity conditions (e.g., *Neritina virginea*, *Batillaria minima*, *Cyprinodon variegates*, and *Gambusia hubsii*) (Metcalf 1904, Andrews 1940, Abbott 1954). Presence of these species is typical of low tidal connectivity, and indicates a shift from a marine to a more upland or higher elevation community when hydrologic connectivity and the associated ebb and flood tidal cycles are eliminated or severely curtailed.

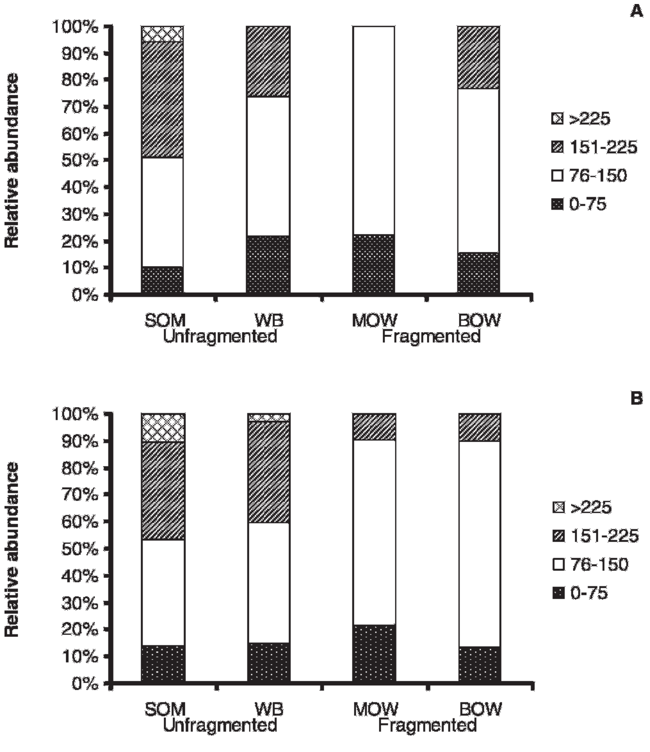

Figure 6. Relative abundance of A) schoolmaster snapper (*Lutjanus apodus*) and B) gray snapper (*L. griseus*) from four tidal creeks. Tidal creek abbreviations: MOW = Man-o-War; BOW = Bowen, SOM = Somerset, WB = White Bight. Data were obtained by determining the mean densities of each size class from all survey plots in each creek (Table 1). Significance values for MANOVA comparisons among creeks are found in Table 2.

Although downstream areas (i.e., in segments of the creek that remain tidally connected to the ocean) of unfragmented and fragmented creeks were similar in total species number and biotic community composition, effects of fragmentation were not limited to upstream (i.e., isolated) areas within fragmented tidal creeks. Effects of hydrologic fragmentation may continually alter the function of downstream areas in tidal creeks through increased sedimentation caused by lower water velocities. Such sedimentation covers exposed rock habitat and decreases overall channel depth, thereby decreasing the complexity, quantity, and quality of available aquatic habitat. Positive relationships between habitat complexity and species abundance suggest that complexity has an important role in structuring biotic assemblages in other marine communities, and loss of complexity may severely alter biotic communities and species interactions (Carr 1994, Beukers and Jones 1998, Gust 2002, Cocheret et al. 2003, Almany 2004, Grabowski 2004, Grabowski and Powers 2004, Nagelkerken 2004). For example, nearly 80% of commercially important fish species in the Bahamas inhabit mangrove habitat at some point in their life (Sullivan-Sealey et al. 2002), at least partially because of the mangroves' structural complexity (Nagelkerken et al. 2002, Mumby et al. 2004). Following fragmentation, other habitat types, especially rocky outcroppings, are rendered less hospitable for biota because of siltation. Loss of habitat complexity may have affected the presence of rare species in downstream areas of fragmented tidal creeks, as there were less rare plant, macroinvertebrate, and fish species in these areas. Despite their low abundance, rare species can contribute significantly to ecosystem function (Walker et al. 1999, Yachi and Loreau 1999, Lyons and Schwartz 2001, Lyons et al. 2005), and thus their loss can have important community- and ecosystem-scale consequences. Loss of alternative low-tide shelter habitat interrupts the "interconnected habitat mosaic" that is essential for species' survival within these tidally variable systems (Sheaves 2005).

Downstream areas of fragmented creeks also had fewer and smaller individuals of commercially important species (*Lutjanus griseus* and *L. apodus*). There are many plausible explanations for the change in snapper size structure in fragmented creeks. For example, recruitment of post-settlement snapper may have decreased due to reduction in larval supply rates (Gaines and Roughgarden 1985), and decreased quantity and quality of preferred habitat (Carr 1994, Jordan et al. 1998, Adams and Ebersole 2004, Mumby et al. 2004, Dorenbosch et al. 2005). Growth and survivorship rates may have decreased due to loss of preferential food sources (Fisher and Bellwood 2001, Booth and Beretta 2004, Kieckbusch et al. 2004, Nemerson and Able 2004), or inadequate refuge habitat (Valentine-Rose et al. 2007). Very little is known about how changes in mangrove habitat complexity affect the biodiversity and abundance of the associated fauna (Field et al. 1998, Manson et al. 2005), but here we show a trend between low mangrove structural complexity (i.e., dwarf mangroves) and low macroinvertebrate and fish diversity and abundance.

Decreased connectivity resulted in greater extremes in salinity, temperature, and dissolved oxygen in fragmented tidal creeks, which also likely contributed to biotic differences between unfragmented and fragmented tidal creeks. We recognize that coastal ecosystems experience daily and seasonal fluctuations in abiotic variables (e.g., Layman et al. 2000), and that we have a fairly limited snapshot view of these fluctuations; however, according to our preliminary data, fragmented tidal creeks seem to exhibit larger extremes in abiotic conditions than unfragmented creeks. Salinity and temperature were higher in upstream fragmented areas, likely due to high evaporation and rapid heating in shallow, stagnant water during the summer months. This trend in salinity is probably heavily influenced by recent rainfall; salinities would likely be much lower in stagnant upstream areas after a heavy rainfall. Also, an opposite trend for temperatures most likely occurs in winter months, when shallow areas cool more rapidly than deep areas. Extreme salinity and temperature decreases growth and productivity in juvenile fish species (Wuenschel et al. 2004, 2005). This may be one explanation of the presence of only smaller fish in upstream areas of Man-o-War, as juvenile fish might take much longer to reach large sizes under conditions of slow growth. Upper thermal tolerance limits of some intertidal species may be near the temperature maxima experienced in upstream areas of fragmented creeks. An increase in temperature of only 2°C higher than that common in favorable habitats can directly cause mortality in intertidal crab species (Stillman and Somero 2000, Stillman 2002).

Mangroves are thought to be present near their upper thermal and salinity tolerance limits, and higher water temperatures and salinities inhibit *Rhizophora mangle* growth and productivity (Koch 1997, McKee and Faulkner 2000). In the fragmented tidal creeks, especially in Bowen upstream areas, there was greater cover of dwarf *Avicennia germinans* and *Laguncularia racemosa*, which are adapted to higher salinities than *Rhizophora mangle* (Lugo and Snedaker 1974). Typically, mangrove forests throughout the Bahamas exhibit a zonation pattern in which creeks are fringed by tall *Rhizophora mangle* before transitioning into a dwarf *Rhizophora mangle* zone, and then a zone with more *Avicennia germinans* and *Laguncularia racemosa* (Lugo and Snedaker, 1974, Buchan 2000). The presence of *Avicennia germinans* and *Laguncularia racemosa* in the upstream sites of fragmented creeks suggests that fragmentation disrupts the natural zonation pattern. There are several potential explanations for the decline in *Rhizophora mangle* cover, and the subsequent encroachment of *Avicennia germinans* and *Laguncularia racemosa* into areas that would otherwise be dominated by *Rhizophora mangle*. Lack of tidal exchange and higher levels of stress associated with increased salinity and temperature likely limited growth of *Rhizophora mangle*, favoring the growth of more salt-tolerant species (Lugo and Snedaker 1974, Lugo 1990). Low ambient nitrogen and phosphorus levels may also have limited *Rhizophora mangle* growth, as other studies have demonstrated that tall fringing mangroves are nitrogen limited, while mixed stands of dwarf mangroves are often phosphorus limited (Boto and Wellington 1983, McKee 1993, Feller et al. 2002). Differences in other environmental variables, including flooding frequency, redox potential of sediments, and sulfide concentrations, between downstream and upstream areas of fragmented creeks have been associated with changes in production and tree stature in other mangrove forests (e.g., Lugo and Snedaker 1974, Pool et al. 1977, Jiménez and Sauter 1991, McKee 1993, 1995).

Recent studies have shown that re-establishment of tidal flow can restore estuarine biotic community structure and function, as well as abiotic and hydrogeomorphological characteristics (Burdick et al. 1997, Eertman et al. 2002, Raposa 2002, Roman et al. 2002, Tanner et al. 2002, Warren et al. 2002, Raposa and Roman 2003). In these studies, restoration of tidal flow was the force driving the successful restoration of overall community structure and function. Similarly, a recent restoration project (Layman et al. 2004a) showed signs of increased macroinvertebrate and fish species richness and biomass after only three months, and increased plant diversity after six months. Therefore, alleviation of hydrologic fragmentation (i.e., through the installation of bridges or culverts) in Caribbean tidal creeks may rapidly improve habitat quality to a level comparable to unfragmented creeks, result in restoration of biotic communities, and in turn, an improvement of commercial and cultural aspects of Bahamian society. Data from this study will be used as baseline conditions in efforts to monitor the success of future restoration projects in the Bahamas.

ACKNOWLEDGMENTS

This project was funded by the National Science Foundation through an IGERT training grant to Amy Ward, The University of Alabama (DGE 0319143). We owe sincere thanks to M. Blackwell, Bahamas Environmental Research Center, and the College of the Bahamas for providing research facilities, support, and help with logistics and planning. The support of the Andros Conservancy and Trust were essential to this project. We thank participants of the 2003 Summer Bahamas Field Course and all Androsians for help with field work, especially G. Bethel, N. Johnson, and "Big" Chris. We also thank all others on Andros Island who helped in any way during this research project.

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Manuscript received 7 March 2006; accepted 1 May 2007.

Appendix A. Percent cover of macrophyte and macroalgae taxa (± 1SD) in downstream (DS) and upstream (US) areas of four tidal creeks on Andros Island, Bahamas. Tidal creek abbreviations: MOW = Man-o-War, BOW = Bowen, SOM = Somerset, WB = White Bight. Total cover is for macroalgae and macrophytes only; remaining cover consisted of rock, sand, and/or coarse detrital matter. Species not present in 100 m^2 plots, but observed in additional surveys, are indicated by a "P" and are included in the count for total species observed. Species listed in alphabetical order by phylum for algae and by class for macrophytes.

	Fragmented				Unfragmented			
	MOW		BOW		SOM		WB	
	DS	US	DS	US	DS	US	DS	US
Chlorophyta								
Acetabularia calyculus J.V. Lamouroux	2.1 (1.9)	0.2 (0.4)	8.0 (9.8)	0	0	P	0	0.1 (0.2)
Batophora oerstedi J. Agardh	31.2 (18.9)	16.7 (18.6)	6.6 (8.1)	0	9.4 (4.3)	1.4 (2.4)	1.4 (2.1)	0.9 (2.4)
Bryopsis plumose (Hudson) C. Agardh	P	P	1.1 (2.1)	0	0.2 (0.5)	0	0.6 (1.4)	0.6 (1.0)
Caulerpa cupressoides var. *lycopodium* Weber-van Bosse	0	0	0	0	0	0	0.4 (1.6)	0.4 (1.6)
Caulerpa lanuginosa J. Agardh	0	0	0.1 (0.5)	0	0	0	0	0
Caulerpa sertularioides (S.G. Gmelin) M. Howe	0	0	0	0	0.4 (0.8)	0	0	0
Chaetomorpha aerea (Dillwyn) Kützing	0	0	0	0	0.2 (0.4)	0	0	0
Cladophoropsis macromeres W.R. Taylor	0	0	0	0	P	0	0	0
Dictyosphaeria cavernosa (Forsskål) Børgesen	0	0	0	0	P	0	0.1 (0.2)	0
Halimeda incrassata (J. Ellis) J.V.Lamouroux	0	0	0.1 (0.3)	0	0	0	0.1 (0.2)	0.6 (1.2)
Halimeda monile (J. Ellis and Solander) J.V. Lamouroux	0	0	0.6 (0.9)	0	3.2 (3.5)	0	1.3 (4.1)	4.2 (4.8)
Penicillus capitatus Lamarck	P	0	12.3 (17.5)	0	0.4 (1.3)	4.5 (4.2)	1.6 (2.3)	4.8 (4.9)
Udotea flabellum (J. Ellis and Solander) M.A. Howe	0	0	1.6 (2.7)	0	1.6 (1.8)	0	0	0.5 (0.7)
Ulva lactuca Linnaeus	P	0	1.1 (1.8)	0	0	0	0	0.1 (0.2)
Ventricaria ventricosa (J. Agardh) J.L. Olsen and J.A. West	0	0	0	0	0	0	0	P
Phaeophyta								
Chnoospora minima (K. Hering) Papenfuss	0	0	0.1 (0.2)	0	P	0	0	0
Dictyota divaricata J.V. Lamouroux	0.1 (0.2)	0	0	P	P	0	P	0
Padina sanctae-crucis Børgesen	0	0	0	0	0	0	0	0.1 (0.2)
Rosenvingea sp.	0.2 (0.4)	0	0.1 (0.2)	0	P	0	P	0
Sargassum fluitans (Børgesen) Børgesen	0	0	P	0	0	0	P	0
Sargassum natans (Linnaeus) Gaillon	P	0	0.3 (0.8)	0	P	0	0.1 (0.9)	0.4 (0.7)
Turbinaria turbinata (Linnaeus) Kuntze	0	0	0	0	0	0	P	0
Rhodophyta								
Bostrychia montagnei Harvey	0	3.5 (3.6)	3.8 (4.9)	0	P	P	1.8 (2.1)	2.4 (2.4)
Centroceras clavulatum (C. Agardh) Montagne	0	0	2.7 (6.7)	0	4.5 (4.0)	0	P	0
Ceramium nitens (C. Agardh) J. Agardh	0	0	P		P	0	0	7.3 (8.8)
Ceramium sp.	0	0	0	0	P	0	0	P
Coelothrix irregularis (Harvey) Børgesen	0	0	0	0	0.5 (2.0)	0	0	0
Digenea simplex (Wulfen) C. Agardh	P	0	P	0	17.2 (8.2)	0	4.3 (6.6)	0.1 (0.4)
Gracilaria sp.	0	0	3.2 (7.2)	0	0	0	0	0
Laurencia sp.	0.1 (0.5)	0	3.6 (6.0)	0	10.8 (6.1)	0	8.4 (13.9)	9.7 (11.7)
Monocotyledoneae								
Bromeliaceae sp.	0	0	P	0	0	0	0	0
Halodule wrightii Ascherson	7.0 (6.1)	0.2 (0.4)	P	0	P	0	4.13 (10.6)	0
Thalassia testudinum Banks ex K.D. König	0.5 (1.2)	0	2.5 (6.1)	0	P	55.1 (25.7)	4.2 (6.9)	0.6 (1.2)
Dicotyledoneae								
Avicennia germinans Linnaeus	0	P	P	6 (11.2)	P	0	0	0
Conocarpus erectus Linnaeus	0	P	P	0	0	0	0	0
Cuscuta sp.	0	P	0	P	0	0	0	0
Laguncularia racemosa (L.) Gaertn. f.	0	P	1.1 (4.1)	P	0	0	0	P
Rhachicallis americana (Jacq.) Ktze.	0	P	P	P	0	0	0	P
Rhizophora mangle Linnaeus	P	14.5 (17.9)	18.2 (25.5)	0.6 (1.4)	P	12.8 (23.3)	33.8 (40.5)	44.0 (41.2)
Salicornia bigelovii Torr.	0	0	P	0	0	0	0	P
TOTAL SPECIES OBSERVED	13	11	28	6	24	6	19	22
PERCENT COVER IN MAIN CHANNEL	41.1 (29.2)	35.2 (41.0)	67.6 (105.4)	7 (12.6)	48.4 (32.8)	73.8 (55.6)	62.7 (94.2)	76.8 (84.3)

Appendix B. Average abundance of macroinvertebrate taxa (± SD) in quadrats in downstream (DS) and upstream (US) areas of four tidal creeks on Andros Island, Bahamas. Tidal creek abbreviations: MOW = Man-o-War, BOW = Bowen, SOM = Somerset, WB = White Bight. Species not present in 100 m^2 plots, but observed in additional surveys, are indicated by a "P" and are included in the count for total species observed. Species listed in alphabetical order, grouped by class.

	Fragmented				Unfragmented			
	MOW		BOW		SOM		WB	
Species	DS	US	DS	US	DS	US	DS	US
Phylum Mollusca								
Class Bivalvia								
Asaphis deflorata (Linnaeus)	P							
Barbatia cancellaria (Lamarck)	P							
Brachidontes exustus (Linnaeus)			P					
Codakia orbiculata (Montagu)	P		P		P		P	
Codakia orbicularis (Linnaeus)		16 (28)						
Isognomon alatus (Gmelin)	P		187 (323)					
Lucina pennsylvania (Linnaeus)	P							
Modulus modulus (Linnaeus)			P					
Pinctada imbricata Roding					P			
Tellina aequistriata Say				P				
Tellina laevigata Linnaeus		5 (9)			P			
Class Gastropoda								
Aplysia dactylomela Rang					P			
Batillaria minima (Gmelin)	117 (203)	P		P			P	
Bulla striata (Bruguiere)	P							
Cerithidea costata (da Costa)			P					
Cerithium eburneum Bruguiere	P		P				P	
Cerithium litteratum (Born)	P		P		5 (9)			
Epitonium sp.			P					
Fasciolaria tulipa (Linnaeus)					P			
Fissurella nodosa (Born)					P			
Littorina angulifera (Lamarck)	27 (46)		21 (37)	P	P	37 (65)	P	5 (9)
Natica sp.	P							
Neritina virginea (Linne)	16 (28)	171 (149)		P				
Polinices lacteus (Guilding)	P							
Prunum apicinum (Menke)	P		P					
Strombus gigas Linnaeus					P		P	
Thais rustica (Lamarck)					P			
Vermicularia spirata (Philippe, RA)			P					
Class Polyplacophora								
Acanthopleura granulata (Gmelin)							P	
Phylum Arthropoda								
Subphylum Crustacea								
Order Decapoda								
Alpheus sp.			P		P		P	
Callinectes sapidus Rathbun	5 (9)	P			P			
Pariclemes sp.					P			
Panulirus argus Latreille					P			
Clibanarius tricolor (Gibbes)			P		59 (65)			
Calcinus tibicen (Herbst)					11 (9)			
Dardanus fucosus Biffar and Provenzano					P			
Paguristes grayi Benedict					P			
Mithrax sculptus (Lamarck)			P		P			
Panopeus sp.					P		P	
Aratus pisonii Edwards							P	
Order Cirripedia								

Appendix B. Continued.

	Fragmented				Unfragmented			
	MOW		BOW		SOM		WB	
Species	DS	US	DS	US	DS	US	DS	US
Chthamalus fragilis Darwin	P	P			5 (9)			
Chthamalus angustitergum Pilsbry					P			
Order Stomatopoda								
Pseudosquilla ciliata (Fabricius)					P			
Order Isopoda								
Ligia sp.				P				
Phylum Annelida								
Class Polychaeta								
Polychaete			P					
Stabella melanostigma (Linnaeus)					P			
Arenicola sp.					P			
Onuphis sp.							P	
Phylum Chordata								
Subphylum Urochordata								
Ecteinascidia turbinata Herdman	P		P		P		P	P
Phylum Porifera								
Unidentified pink-colored encrusting sponge			P		P			
Iricinia sp.			5 (9)		P	P	P	P
Anthosiginella varians (Duchassaing and Michelotti)					P	5 (9)	P	
Amphimedon compressa (Duchassaing and Michelotti)					P			
Chondrilla nucula Scmhidt					P		P	
Phylum Echinodermata								
Class Holothuroidea								
Holothuria Mexicana (Ludgwig)			P					
Holothuria floridana Pourtales					P			
Holothuria grisea Selanka						P		
Echinometra lucunter (Linnaeus)					P			
Lytechinus variegatus (Lamarck)					P			
Phylum Cnidaria								
Cassiopea xamachana Bigelow			P			P		
Siderastrea radians Pallas					P		P	
Condylactis gigantea (Weinland)					P			
Bartholomea annulata (Le Sueur)					P			
TOTAL SPECIES OBSERVED	15	5	19	5	37	5	15	3

Appendix C. Presence/absence of fish taxa in quadrats in downstream (DS) and upstream (US) areas of four tidal creeks on Andros Island, Bahamas. Tidal creek abbreviations: MOW = Man-o-War, BOW = Bowen, SOM = Somerset, WB = White Bight. Presence of a species in at least one survey in the area is indicated with a "P". Species listed phylogenetically (Nelson 1994).

	Fragmented				Unfragmented			
	MOW		BOW		SOM		WB	
Species	DS	US	DS	US	DS	US	DS	US
Muraenidae								
Gymnothorax funebris Ranzani							P	P
Belonidae								
Strongylura notata (Poey)	P		P		P		P	P
Poeciliidae								
Gambusia hubbsi (Poey)		P	P	P	P	P		
Cyprinodontidae								
Cyprinodon variegates Lacepede	P	P	P	P				
Scorpaenidae								
Scorpaena plumieri Bloch					P			
Serranidae								
Epinephelus striatus (Bloch)	P		P		P			
Carangidae								
Caranx spp.			P					
Lutjanidae								
Lutjanus apodus (Walbaum)	P	P	P		P	P	P	P
Lutjanus cyanopterus (Cuvier)	P	P	P		P		P	P
Lutjanus griseus (Linnaeus)	P	P	P		P	P	P	P
Lutjanus synagris (Linnaeus)						P		
Ocyurus chrysurus (Bloch)					P			
Gerreidae								
Eucinostomus spp.	P	P	P	P	P	P	P	P
Gerres cinereus (Walbaum)	P	P	P	P	P	P	P	P
Haemulidae								
Haemulon flavolineatum (Desmarest)	P		P		P		P	P
Haemulon parra (Desmarest)	P		P		P		P	P
Haemulon sciurus (Shaw)	P		P		P	P	P	P
Chaetodontidae								
Chaetodon capistratus Linnaeus	P		P		P		P	P
Chaetodon striatus Linnaeus					P		P	
Pomacentridae								
Abudefduf saxatilis (Linnaeus)	P	P	P		P	P	P	P
Stegastes adustus (Troschel)	P		P		P	P	P	P
Stegastes leucostictus (Muller and Troschel)	P		P		P	P	P	P
Labridae								
Halichoeres bivittatus (Bloch)			P		P		P	P
Halichoeres garnoti (Valenciennes)					P			
Halichoeres poeyi (Steindachner)					P			
Halichoeres radiatus (Linnaeus)					P			
Thalassoma bifasciatum (Bloch)					P		P	P
Scaridae								
Scarus iserti (Bloch)	P		P		P	P	P	P
Sparisoma spp.	P		P		P	P	P	P
Gobiidae								
Malacoctenus macropus (Poey)	P				P		P	P
Acanthuridae								
Acanthurus chirurgus (Bloch)			P		P			

Appendix C. Continued.

	Fragmented				Unfragmented			
	MOW		BOW		SOM		WB	
Species	DS	US	DS	US	DS	US	DS	US
Sphyraenidae								
Sphyraena barracuda (Walbaum)	P		P		P	P		
Tetraodontidae								
Sphoeroide testudineus (Linnaeus)	P	P	P		P	P	P	P
TOTAL SPECIES OBSERVED	20	9	23	4	29	14	21	20