*Caribbean Journal of Science*, Vol. 40, No. 2, 232-244, 2004

# Degree of Fragmentation Affects Fish Assemblage Structure in Andros Island (Bahamas) Estuaries

CRAIG A. LAYMAN[1]*, D. ALBREY ARRINGTON[2], R. BRIAN LANGERHANS[3], AND BRIAN REED SILLIMAN[4]

[1]*Department of Wildlife and Fisheries Sciences, Texas A & M University, College Station, Texas 77843-2258*
[2]*Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487*
[3]*Department of Biology, Campus Box 1137, Washington University, St. Louis, Missouri 63130-4899*
[4]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912.*
[1]*Corresponding author: cal1634@yahoo.com*
*Current address: Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520-8106*

**ABSTRACT.—We used underwater visual census (UVC) to characterize fish assemblages among estuaries with different degrees of fragmentation on Andros Island, Bahamas. Estuaries were classified *a priori* into four fragmentation categories: totally fragmented (no surface water connectivity to the ocean), partially fragmented, minimally fragmented, and unfragmented (unimpeded surface water connectivity through the estuary to the ocean). Visual surveys (n = 159) were conducted in thirty estuarine systems using snorkeling gear in four habitat types: flat, mangrove, rock, and seagrass. Fish species density differed significantly among habitat types and among estuaries with different degrees of fragmentation. Highest species density occurred in rock habitats in unfragmented or minimally fragmented estuaries; lowest species density was in totally fragmented estuaries. Assemblages in unfragmented and minimally fragmented estuaries were characterized by presence of reef-associated (e.g., damselfish and parrotfish) and transient marine (e.g., jacks) taxa. In completely fragmented sites, assemblages were dominated by species tolerant of temperature and salinity extremes (e.g., sheepshead minnow). Multi-dimensional scaling suggested fish assemblages in mangrove and rock habitats experienced the greatest impact of estuary fragmentation (i.e., the most differentiation among surveys in estuaries with different fragmentation status). Fish assemblages were especially variable among partially fragmented estuaries (i.e., estuaries where hydrologic connectivity was maintained by a culvert), suggesting hydrologic connectivity through culverts may not be sufficient to maintain habitat quality, recruitment dynamics, or upstream movements by vagile organisms. These data reveal effects fragmentation has on faunal assemblages, and demonstrates that faunal presence/absence may guide initiatives to conserve and restore sub-tropical estuaries.**

**KEYWORDS.—connectivity, estuary, fish, fragmentation, hydrology, mangrove recruitment**

## INTRODUCTION

Estuaries are a critical component of Caribbean island coastal zones that serve as important nursery habitat for commercially important species such as Nassau grouper *Epinephalus striatus* (Dahlgren and Eggleston 2001) and spiny lobster *Panulirus argus* (Acosta and Butler 1997). Greater than 75% of commercially caught fish in The Bahamas, and 80-90% of fish caught recreationally, may inhabit estuarine mangrove habitat at some point in their life (Sullivan-Sealey et al. 2002). Dependence on estuaries is obligate for many species, and populations of these species would be substantially reduced or extirpated without access to estuaries (Lindeman et al. 2000). Further, estuarine mangrove habitats are often net exporters of carbon (e.g., in the form of organisms), which may provide a spatial energy subsidy to coral reefs and other marine food webs (Odum 1971; Deegan 1993; Lee 1995). For most estuaries to function naturally, hydrologic connectivity, in particular tidal exchange, is essential (Pringle 2001).

One threat to estuarine function is fragmentation, i.e., reducing the connectivity between marine and inland ecosystems. Many Caribbean island estuaries were fragmented by the construction of roads, which affects sedimentation processes (Burdick et al. 1997; Portnoy and Giblin 1997; Anisfeld et al. 1999), nutrient cycling (Anisfeld and Benoit 1997; Portnoy and Giblin 1997; Portnoy 1999), vegetation patterns (Roman et al. 1984; Sinicrope et al. 1990; Roman et al. 2002) and assemblages of resident and transient organisms (Peck et al. 1994; Burdick et al. 1997; Dionne et al. 1999; Roman et al. 2002). There remain little quantitative data characterizing ecological aspects of low-gradient tropical estuaries with different degrees of fragmentation, information that is critical to guide conservation and restoration initiatives. Our objectives were to describe the composition of fish assemblages using underwater visual census in estuaries along the eastern shore of Andros Island, Bahamas, and to evaluate the effects of ecosystem fragmentation on these assemblages. Specifically, we asked: (1) What effect does estuary fragmentation have on fish species density?, and (2) How do fish assemblages differ in estuaries with different degrees of fragmentation?

## MATERIALS AND METHODS

### *Study site*

Andros Island (Fig. 1) is a low-lying island in the Bahamas archipelago, dominated geologically by karst formations. Estuaries, including tidal creeks and wetlands, are found throughout the island. We conducted surveys in every accessible estuary on the eastern side of Andros Island (n = 30). Study systems varied from estuaries thousands of hectares in area (Northern Bight) to sites that were encroached by mangroves so that no open water habitat remains (Man-of-War Sound). Average depths in the latter systems are <0.5 m, whereas channels in larger estuaries have maximum depths >10 m (Stafford Creek). Some creek channels are <10 m wide throughout their length (White Bight); others have widths >250 m (Deep Creek). A detailed description of an Andros Island estuary is provided by Newell et al. (1951).

Following Dynesius and Nilsson (1994), we identified four categories of estuarine fragmentation (listed from highest degree of fragmentation to the least): (1) totally fragmented systems in which surface water connectivity from the ocean does not extend throughout the estuary, resulting in an isolated wetland (*sensu* Leibowitz 2003) upstream of the blockage (e.g., a road crossing an estuary), (2) partially fragmented systems in which some surface water connectivity remains (i.e., through culverts) throughout the estuary, (3) minimally fragmented systems in which the majority of surface water connectivity remains (i.e., through bridges), and (4) unfragmented systems which have unimpeded surface water connectivity throughout the estuary. Totally fragmented estuaries result from road construction without culverts or bridges to permit surface water (i.e., tidal) exchange. In partially fragmented systems, the placement of culverts, ranging from <0.25 m to >2.0 m in diameter, permit different degrees of tidal flow upstream of the blockage. Bridges allow more tidal flow than culverts and, therefore, the presence of a bridge results in minimal fragmentation (i.e., loss of hydrologic connectivity).

Because fish assemblages typically differ among habitats in tropical estuarine systems (Robertson and Duke 1987; Sedberry and Carter 1993; Laegdsgaard and Johnson 1995; Gray et al. 1996; Gray et al. 1998; Jenkins and Wheatley 1998; Guidetti 2000), we conducted fish surveys in each of four common habitats: flats, mangrove, rock structure, and seagrass. These habitat designations are based on earlier work in estuaries on Andros Island (Layman and Silliman 2002), and are similar to those used by Nagelkerken et al. (2000) in a Caribbean estuarine bay. Flat was the most common habitat type in estuaries, and represented unvegetated substrate consisting of sand and mollusk shell fragments, for example, *Battillarium* spp. and *Cerithium* spp. (ceriths), *Neritina virginea* (virgin nerite), and *Brachidontes exustus* (scorched mussel). In some estuaries (usually those partially or completely fragmented), flat was composed of fine mud and organic debris. Mangrove habitat was characterized by monodominant stands of red mangrove. We combined "fossil reef rock" and "fossil reef boulders" used by Nagelkerken et al.

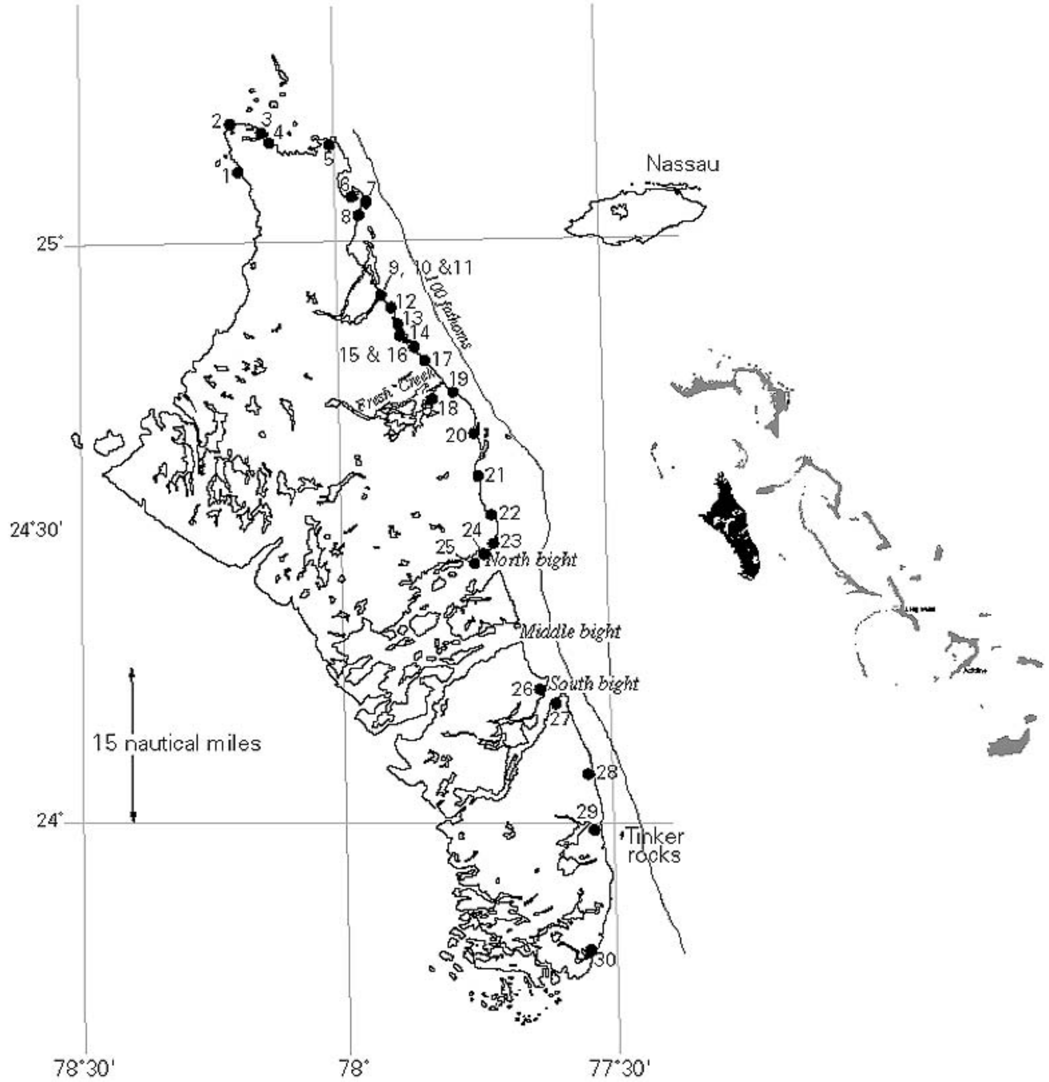

FIG. 1. Map of Andros Island with the location of sampled estuaries indicated. Site names are given in Table 1. Map courtesy of Robert L. Smith.

(2000a), as well as karst formations, into a single rock structure designation. We designated seagrass habitat has substrate with >50% cover of *Thallasia testudinum* (turtle grass).

### *Survey methods*

Fishes represent multiple trophic levels, are affected by large-scale influences, and can be relatively long-lived (providing temporal integration of aquatic system influences); therefore, they can be excellent indicators of the health of ecosystems (Karr 1981). Fish often are collected using destructive techniques (Murphy and Willis 1996), however, in tropical and subtropical estuarine systems water clarity allows aquatic fauna assessment in a non-destructive manner using underwater visual census (UVC). This technique, first developed by Brock (1954), has become standard methodology for assessing fish populations in tropical estuarine and marine habitats. UVC may result in an underestimate of cryptic species (Brock 1982; Ackerman and Bellwood 2000; Willis 2001), highly mobile species (Thresher and Gunn 1986), and other large piscivores (Kulbicki 1998; Willis et al. 2000), but has been used extensively because it is non-destructive, rapid, and simple. UVC is an especially useful method to assess fauna in aquatic systems where destructive sampling techniques are not desirable.

All estuaries were surveyed in either August 2001 or August 2002 (Table 1). Surveys were conducted during daylight hours using one of two techniques. In the majority of cases, UVC, using snorkeling gear, was completed by one of the authors. A 100 $m^2$ area was chosen haphazardly, and all fish species observed within the area were recorded. Each individual survey lasted for 30 minutes and was conducted within approximately 2 hours of high tide. These surveys provide a "snapshot" of fishes at a given site, not fully incorporating the diel, tidal, and seasonal changes of fauna (Weinstein and Heck 1979; Robblee and Zieman 1984; Rooker and Dennis 1991; Nagelkerken et al. 2000c), but were sufficient to document common species in habitats surveyed. Surveys were conducted in water less than 2 m deep, and water clarity was excellent (>10 m) for every census. The second survey protocol was necessary in

TABLE 1. Site numbers (from Fig. 1), names, status, and the number of surveys in each habitat type.

| Site number | Name | Status | Habitat<br>Sand flat | Seagrass | Mangrove | Rock |
|---|---|---|---|---|---|---|
| 1 | Red Bays Pond | TF | 1 | - | 1 | - |
| 2 | Money Point | U | 2 | 4 | 4 | - |
| 3 | Miller Creek | U PF | 3 | 1 | 3 | 1 |
| 4 | Davy Creek | PF | 2 | 2 | 2 | 1 |
| 5 | Conch Sound | PF | - | - | 2 | 1 |
| 6 | Bird Pond | PF | 1 | - | 1 | 2 |
| 7 | Cemetery Pond | PF | 1 | - | 2 | 2 |
| 8 | Mastic Point Creek | PF | 3 | - | 2 | 3 |
| 9 | South Blanket Sound | TF | 1 | - | 1 | - |
| 10 | Thompson Creek | TF | 1 | - | 2 | - |
| 11 | Stafford Creek | U | 1 | - | 3 | 2 |
| 12 | Store Creek | TF | 2 | - | 2 | - |
| 13 | Staniard Creek | U MF | 4 | 2 | 5 | 3 |
| 14 | Sandy Creek | TF | 2 | - | 1 | - |
| 15 | Love Hill Creek | U PF | 4 | - | 4 | - |
| 16 | Middle Creek | PF | 1 | - | 1 | - |
| 17 | Davis Creek | U PF | 4 | 3 | 4 | 2 |
| 18 | Fresh Creek | MF | 2 | 2 | 2 | 2 |
| 19 | Sommerset Creek | U | - | 1 | 2 | 1 |
| 20 | Bowen Sound | TF | 1 | - | 1 | 1 |
| 21 | Man of War Sound | TF | 3 | - | 3 | 1 |
| 22 | White Bight | U | 1 | - | 3 | 1 |
| 23 | Cargill Creek | MF | 3 | 1 | 2 | 1 |
| 24 | Independence Park | TF | 1 | - | 1 | - |
| 25 | Northern Bight | U | 1 | - | - | 1 |
| 26 | Lisbon Creek | U | 1 | 1 | 3 | 1 |
| 27 | Harrey's Creek | U | 1 | - | - | - |
| 28 | Deep Creek | U | 1 | 2 | 1 | 2 |
| 29 | Little Creek | U | 1 | 1 | 1 | 1 |
| 30 | Grassy Creek | U | - | 1 | - | 1 |

Status refers to fragmentation category: TF = totally fragmented, PF = partially fragmented, MF = minimally fragmented, U = unfragmented). Multiple designations are given when parts of estuaries are characterized by a different degree of fragmentation.

TABLE 2. Frequency of occurrence of fish species in all surveys (Total %, n = 159), surveys in unfragmented estuaries (% U, n = 62), and surveys in totally fragmented estuaries (% TF, n = 27).

| Scientific name | Common name | Total % | % U | % TF | Habitat |
|---|---|---|---|---|---|
| *Gerres cinereus* | Yellowfin mojarra | 65 | 68 | 30 | F G M R |
| *Lutjanus griseus* | Gray snapper | 59 | 69 | 22 | F G M R |
| *Lutjanus apodus* | Schoolmaster | 57 | 69 | 15 | F G M R |
| *Eucinostomus* spp. | Mojarra spp. | 51 | 56 | 26 | F G M R |
| *Stegastes leucostictus* | Beaugregory | 48 | 73 | 0 | F G M R |
| *Sphyraena barracuda* | Barracuda | 40 | 52 | 11 | F G M R |
| *Lutjanus cyanopterus* | Cubera snapper | 33 | 34 | 4 | F G M R |
| *Abudefduf saxatilis* | Sergeant major | 31 | 45 | 0 | F M R |
| *Halichoeres bivittatus* | Slippery dick | 31 | 63 | 0 | F G M R |
| *Haemulon sciurus* | Bluestriped grunt | 28 | 40 | 0 | F G M R |
| *Sparisoma radians* | Bucktooth parrotfish | 28 | 52 | 0 | F G M R |
| *Engraulid/Atherinid* spp. | Anchovies and silversides | 25 | 37 | 0 | F G M R |
| *Sphoeroides testudineus* | Checkered puffer | 19 | 16 | 4 | F G M R |
| *Cyprinodon variegatus* | Sheepshead minnow | 18 | 0 | 78 | F M R |
| *Stegastes fuscus* | Dusky damselfish | 19 | 26 | 0 | F M R |
| *Haemulon flavolineatum* | French grunt | 19 | 32 | 0 | F G M R |
| *Scarus croicensis* | Striped parrotfish | 19 | 37 | 0 | F G M R |
| *Chaetodon capistratus* | Foureye butterflyfish | 18 | 31 | 0 | F M R |
| *Gambusia hubbsi* | Bahamas mosquitofish | 14 | 2 | 48 | F M R |
| *Ocyurus chrysurus* | Yellowtail snapper | 14 | 24 | 0 | F G M R |
| *Strongylura notata* | Redfin needlefish | 11 | 18 | 11 | F G M R |
| *Thalassoma bifasciatum* | Bluehead wrasse | 13 | 23 | 0 | F G M R |
| *Acanthurus chirurgus* | Doctorfish | 10 | 16 | 0 | F G M R |
| *Blenny* sp. 1 | Blenny sp. | 9 | 18 | 0 | F G R |
| *Strongylura marina* | Atlantic needlefish | 10 | 13 | 0 | F M R |
| *Epinephalus striatus* | Nassau grouper | 9 | 16 | 0 | F G M R |
| *Lophogobius cyprinoides* | Crested goby | 9 | 6 | 0 | F G M R |
| *Coryphopterus glaucofraenum* | Bridled goby | 8 | 16 | 0 | F G M R |
| *Gobidae* sp. 1 | Goby sp. | 8 | 8 | 0 | F G M R |
| *Sparisoma viride* | Stoplight parrotfish | 8 | 16 | 0 | G M R |
| *Caranx ruber* | Bar jack | 5 | 8 | 0 | F G R |
| *Pomacanthus paru* | French angelfish | 5 | 8 | 0 | F M R |
| *Halichoeres garnoti* | Yellowhead wrasse | 5 | 8 | 0 | G M R |
| *Halichoeres radiatus* | Puddingwife | 5 | 8 | 0 | F G M R |
| *Acanthurus bahianus* | Ocean surgeonfish | 5 | 13 | 0 | F G M R |
| *Holocentrus coruscus* | Reef squirrelfish | 4 | 5 | 0 | R |
| *Halichoeres poeyi* | Blackear wrasse | 4 | 10 | 0 | F G R |
| *Caranx latus* | Horse-eye jack | 3 | 5 | 0 | F G R |
| *Chaetodon ocellatus* | Spotfin butterflyfish | 4 | 10 | 0 | F G R |
| *Haemulon parra* | Sailors choice | 4 | 8 | 0 | M R |
| *Calamus* sp. 1 | Porgy sp. | 3 | 5 | 0 | F G M R |
| *Gymnothorax funebris* | Green moray | 3 | 2 | 0 | R |
| *Latjanus analis* | Mutton snapper | 3 | 3 | 0 | F G R |
| *Lutjanus synagris* | Lane snapper | 3 | 3 | 0 | F G M R |
| *Diodon holocanthus* | Spiny pufferfish | 3 | 2 | 0 | M R |
| *Gnatholepis thompsoni* | Goldspot goby | 3 | 2 | 0 | F R |
| *Labrisomus nuchipinnis* | Hairy blenny | 3 | 6 | 0 | M R |
| *Acanthurus coeruleus* | Blue tang | 3 | 5 | 0 | R |
| *Epinephelus guttatus* | Red hind | 2 | 3 | 0 | R |
| *Malacoctenus macropus* | Rosy blenny | 2 | 5 | 0 | G M R |
| *Pomacanthus arcuatus* | Gray angelfish | 2 | 2 | 0 | M R |
| *Scarus taeniopterus* | Princess Parrotfish | 2 | 3 | 0 | M R |
| *Stegastes planifrons* | Threespot damselfish | 2 | 2 | 0 | F R |

TABLE 2. Continued

| Scientific name | Common name | Total % | % U | % TF | Habitat |
|---|---|---|---|---|---|
| *Stegastes variabilis* | Cocoa damselfish | 2 | 3 | 0 | M R |
| *Apogon* sp. 1 | Cardinalfish sp. 1 | 1 | 2 | 0 | R |
| *Chaetodon striatus* | Banded butterflyfish | 1 | 2 | 0 | M R |
| *Coryphopterus dicrus* | Colon goby | 1 | 2 | 0 | M R |
| *Haemulon carbonarium* | Ceasar grunt | 1 | 2 | 0 | M |
| *Megalops atlanticus* | Tarpon | 1 | 0 | 4 | M |
| *Scarus* sp. 1 | Parrotfish sp. | 1 | 3 | 0 | G R |
| *Holocanthus ciliaris* | Queen angelfish | 1 | 3 | 0 | R |
| *Mulloidichthys martinicus* | Yellow goatfish | 1 | 3 | 0 | G M |
| *Scarus coeruleus* | Blue parrotfish | 1 | 3 | 0 | M R |
| *Diodon hystrix* | Porcupinefish | 1 | 3 | 0 | R |
| *Albula vulpes* | Bonefish | 1 | 0 | 0 | F |
| *Canthigaster rostrata* | Sharpnose puffer | 1 | 0 | 0 | R |
| *Lachnolaimus maximus* | Spanish hogfish | 1 | 2 | 0 | R |
| *Malacoctenus triangulatus* | Saddled blenny | 1 | 2 | 0 | F |
| *Muraenidae* sp. 1 | Moray eel | 1 | 2 | 0 | R |
| *Mycteroperca bonaci* | Black grouper | 1 | 0 | 0 | R |
| *Mycteroperca tigris* | Tiger grouper | 1 | 2 | 0 | R |
| *Scorpaena plumieri* | Spotted Scorpionfish | 1 | 2 | 0 | R |
| *Sparisoma chrysopterum* | Redtail parrotfish | 1 | 0 | 0 | F |
| *Sparisoma rubripinne* | Yellowtail parrotfish | 1 | 0 | 0 | R |
| *Stegastes partitus* | Bicolor damselfish | 1 | 0 | 0 | R |
| *Dasyatis americana* | Southern stingray | 1 | 2 | 0 | F |
| *Myrichthys ocellatus* | Goldspotted moray eel | 1 | 2 | 0 | G |
| *Gramma loreto* | Fairy basslet | 1 | 2 | 0 | R |
| *Halichoeres* sp. 1 | Wrasse sp. | 1 | 2 | 0 | R |
| *Serranidae* sp. 1 | Other grouper sp. | 1 | 2 | 0 | R |
| *Hypoplectrus unicolor* | Butter hamlet | 1 | 2 | 0 | R |
| *Lutjanus* sp. 1 | Snapper sp. | 1 | 2 | 0 | R |
| *Sphoeroides spengleri* | Bandtail puffer | 1 | 2 | 0 | G |
| *Holocentrus adscensionis* | Squirrelfish | 1 | 2 | 0 | R |
| *Hypleurochilus bermudensis* | Barred blenny | 1 | 2 | 0 | R |
| *Holacanthus bermudensis* | Blue angelfish | 1 | 2 | 0 | R |
| *Mycteroperca venenosa* | Yellowfin grouper | 1 | 0 | 0 | R |
| *Haemulon plumieri* | White grunt | 1 | 2 | 0 | R |

Habitats in which species were observed: F = sand flat, G = seagrass, M = mangrove, R = rocky

extremely shallow sites (depth < 30 cm), often in totally fragmented estuaries. For these samples, fish species presence was observed from above the water by one of the authors. Each survey was conducted for 30 minutes in a 100 $m^2$ area. All fishes observed in these sites, typically *Cyprinodon variegatus* (sheepshead minnow) and *Gambusia hubbsi* (Bahamas mosquitofish), were easily identified from above the water, though we collected some specimens to verify their identification. Survey areas were typically conducted in areas 10 × 10 m, except when habitat characteristics did not allow; for example, along mangrove fringes, surveys were conducted in a 25 × 4 m area.

Because of potential observer bias (Sale and Sharp 1983; Cheal and Thompson 1997), we conducted a pilot study to ensure that underwater species identifications were accurate (Layman and Silliman 2002). A few problematic taxa were identified to genus only, and most of these taxa were rare. We collected specimens of one abundant, yet problematic taxa, *Eucinostomus* spp., in August 2001 and in a previous study (Layman and Silliman 2002), and identified species most likely included in this grouping: *Eucinostomus jonesi* (slender mojarra), *Eucinostomus lefroyi* (mottled mojarra), and *Eucinostomus gula* (silver jenny). Similar lumping of *mojarra* species were made in other studies that employed UVC in the Caribbean (Nagelkerken et al. 2000a). Some taxa, often juveniles, were given code names (pseudo-species) to differentiate between distinct members of the same genus when the taxa could not be identified to species (e.g., Gobidae sp. 1).

To avoid bias associated with pseudoreplication (Hulbert 1984), no particular site was surveyed more than once, and no more than two surveys were conducted within a single habitat type in any estuary. If two surveys were conducted in the same habitat type in the same estuary, sites were separated by at least 50 m, and were taken in different years or in areas of the estuarine with a different fragmentation status (e.g., when there were multiple connections to marine waters). Species density was expressed as the number of species recorded in the 100 m$^2$ survey areas (following Gotelli and Colwell 2001).

### *Statistical analysis*

We tested for differences in fish species density due to degree of fragmentation and habitat type using a two-factor analysis of variance (ANOVA) model followed by Tukey's post-hoc tests. To compare assemblage similarity/dissimilarity we used Multi-dimensional scaling (MDS) to compare assemblage among samples. MDS constructs a 2-dimensional ordination in a manner that best represents relationships among samples in a similarity matrix (Field et al. 1982; Clarke and Warwick 2001). In ordination plots, the relative distance between points reflects the dissimilarity of species composition in those samples. We calculated similarity matrices using the Bray-Curtis similarity index (Bray and Curtis 1957). We conducted two types of MDS analysis. First, we used MDS to ordinate fish assemblages from all surveys simultaneously, and analyzed ordination patterns based on habitat type. Second, we carried out a MDS ordination within each habitat type, and analyzed ordination patterns according to *a priori*-designated fragmentation categories. To test for differences in species composition according to degree of estuary fragmentation, we used analysis of similarities (ANOSIM, Clarke and Warwick 1994), a non-parametric analog of MANOVA. When ANOSIM revealed significant differences, we performed similarity percentage analysis (SIMPER, Clarke and Warwick 1994) to identify species accounting for differences. We also performed a discriminant function analysis (DFA) to test for effects of *a priori* fragmentation categories on species composition. This procedure predicts the fragmentation category for each survey based on species composition, with the null hypothesis being 25% of sites correctly classified by chance.

## RESULTS

We conducted 159 UVCs in 30 estuaries on Andros Island and identified 89 fish taxa (Table 2). Four taxa were observed in more than half of the surveys: *Gerres cinereus,* (yellowfin mojarra, 65% of surveys), *Lutjanus griseus (*gray snapper, 59%), *Lutjanus apodus* (schoolmaster, 57%), and *Eucinostomus* spp. (mojarra spp., 51%). These taxa were found in all habitat types, and were common in most estuaries. The majority of snappers were juveniles, whereas both adult and juvenile mojarra were common. Other fishes included juveniles and adults of commercially or recreationally important reef-associated species, including *Epinephalus striatus* (Nassau grouper), *Scarus croicensis* (striped parrotfish), and *Chaetodon capistratus* (foureye butterflyfish). Fish species density was affected by both fragmentation category ($F_{3,152} = 40.9$, $p < 0.001$) and habitat type ($F_{3,152} = 24.5$, $p < 0.001$) (Fig. 2). Tukey's post-hoc analysis revealed species density was higher in UVC surveys conducted in unfragmented and minimally fragmented estuaries than partially or totally fragmented estuaries, and higher in partially than totally fragmented sites. There was significantly higher species density in rock habitats than mangroves, and significantly higher species density in both of these habitats than in flat and seagrass.

MDS analysis of all surveys indicated

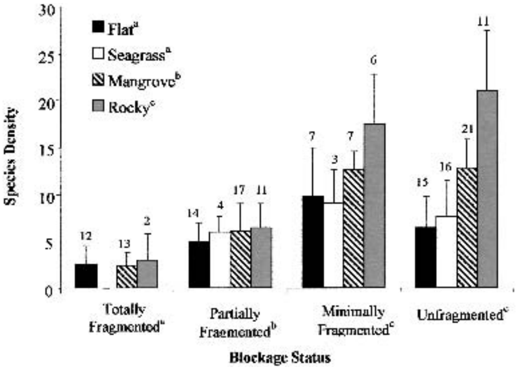

FIG. 2. Mean fish species density, based on UVC samples, among estuaries with different degrees of fragmentation and among habitat types. Error bars represent one standard deviation. We did not locate any seagrass habitats in totally fragmented estuaries. The number above each bar represents the number of surveys conducted in that particular habitat classification. Small subscripts represent results of Tukey's post-hoc tests for differences among habitat or fragmentation category.

overlap in fish assemblages among the four habitat types. Despite this overlap, ANOSIM revealed significant differences in assemblage composition among habitats ($R = 0.23$, $p < 0.001$). Pairwise comparisons revealed significant differences between all pairs of habitat types ($p < 0.001$), except between flat and seagrass ($R = 0.059$, $p = 0.15$). Since assemblages were found to differ among habitat types, we conducted a separate MDS ordination for each habitat (Fig. 3).

In three of the four habitats (seagrass the exception), MDS indicated a transition in assemblage composition from samples in totally fragmented estuaries to those collected in estuaries with minimal or no fragmentation. Similarity of assemblage composition varied depending on habitat type; ordination of samples taken from mangrove and rock habitats revealed the largest separation among fragmentation categories. This can be attributed to the relatively high proportion of species that remain within a relatively small area (e.g., within one 100 $m^2$ survey area) during daylight hours. In flat and seagrass habitats, by contrast, there was more overlap in assemblage composition because characteristic species typically were extremely motile and patchily distributed. There was high similarity in assemblage composition between surveys collected in minimally fragmented and unfragmented estuaries, with degree of similarity depending on habitat type. In mangrove, rock, and flat habitats, samples from partially fragmented estuaries were characterized by assemblages that were "intermediate" in composition between that of totally fragmented and unfragmented systems. Estuary location (i.e., latitudinal position on Andros) did not appear to influence differences in fish assemblage composition.

Since mangrove is a common habitat in estuarine systems, and assemblages in this habitat apparently provided the best indication of degree of fragmentation, we further analyzed mangrove survey data using a Discriminant Function Analysis (DFA). DFA correctly classified the degree of estuary fragmentation for 46 of 58 sites (79.3%, Wilks' $\Lambda = 0.045$, $p < 0.001$) based on the presence/absence of fish taxa. Some taxa were particularly good indicators of fragmentation in mangrove sites. *Cyprinodon variegatus* and *Gambusia hubbsi* were found only in totally fragmented estuaries, and these species occurred in 78% and 48%, respectively, of surveys conducted in totally fragmented systems (Table 2). The number of species within specific phylogenetic (e.g., grunts) or trophic (e.g., piscivores) groups frequently associated with marine coral reef environments also indicated relative degree of fragmentation (Table 3). For example, there were no damselfish species in samples from totally fragmented systems, 0.59 ± 0.21 species in samples from partially fragmented systems, 1.86 ± 0.34 in samples from minimally fragmented systems, and 2.14 ± 0.16 in samples from unfragmented estuaries.

## DISCUSSION

Fish assemblages differed significantly among sites based on *a priori* defined categories of estuary fragmentation. We propose that estuary fragmentation influences aquatic organisms in the following manner: (1) reduced tidal exchange results in decreased habitat quality (e.g., greater salinity extremes), (2) reduced tidal exchange low-

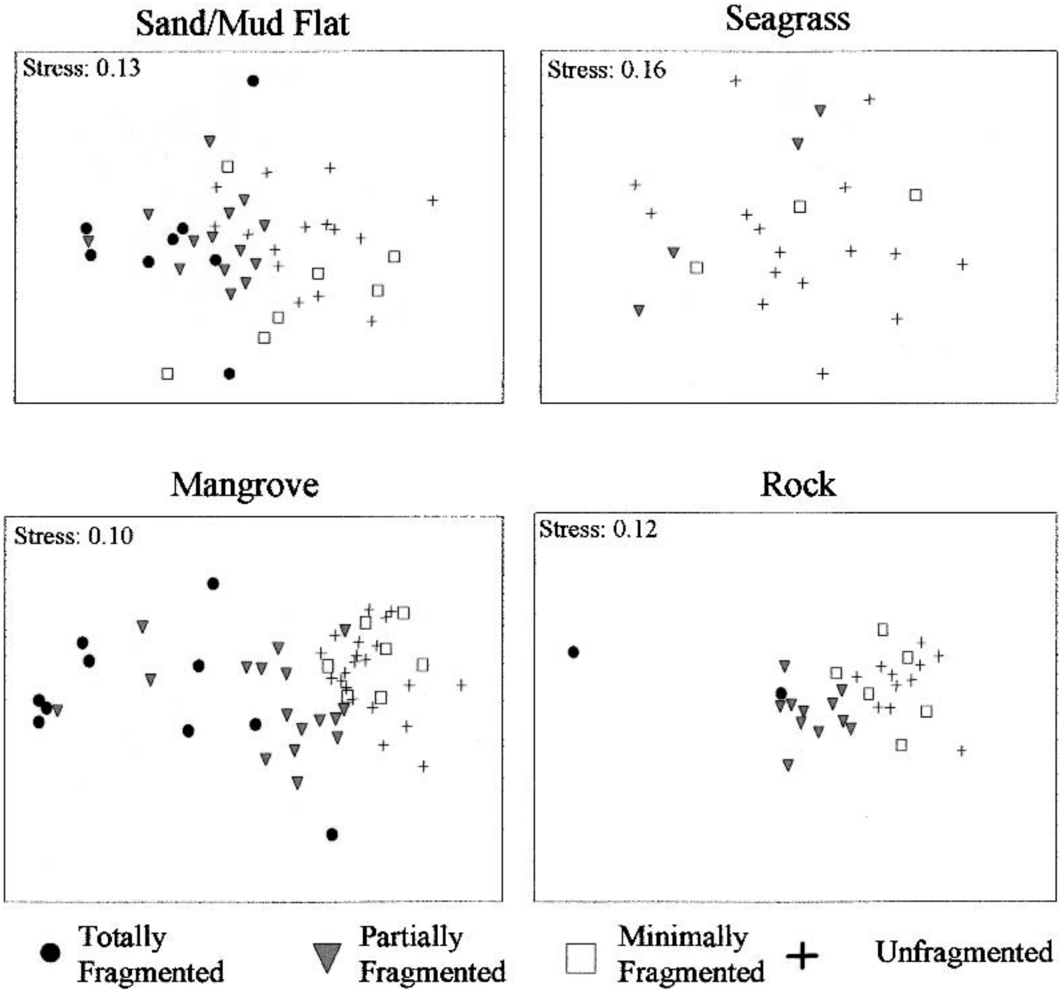

FIG. 3. MDS ordination of fish assemblages based on species presence/absence data. Labels are based on *a priori* defined categories of estuary fragmentation. MDS analysis was conducted separately for each of the four habitat types.

ers the influx of planktonic larvae and juveniles with subsequent reduction in the colonization rate of demersal marine species (e.g., Nassau grouper), and (3) nonpermeable landscape features (e.g., roads without culverts) halt upstream movements by transient marine species (e.g., bonefish). In fragmented Bahamian estuaries, partial or total obstruction of tidal flow leads to increased sediment accumulation. Sediment buildup facilitates *Rhizophora mangle* (red mangrove) encroachment into creek channels. Mangroves further slow water velocities, increasing sediment deposition, and leading to additional losses of aquatic habitat. This process results in shallower water depths, a decrease in available aquatic habitat, lower dissolved oxygen, and changes in other physiochemical parameters (Arrington et al. *unpublished manuscript*). Fragmentation creates a physical barrier to movement, but also initiates processes that render remaining aquatic habitat inhospitable for many marine species.

Fish observed in surveys on Andros Island were similar to those described from earlier studies in the Caribbean (e.g., Thayer et al. 1987; Sedberry and Carter 1993; Nagelkerken et al. 2000a, b, c). The

TABLE 3. Mean (± standard error) number of species of common taxa observed in UVC samples in mangrove habitats taken in estuaries of varying degrees of fragmentation.

| | Degree of fragmentation | | | |
|---|---|---|---|---|
| Fish group | Totally fragmented | Partially fragmented (culverts) | Minimally fragmented (bridges) | Unfragmented |
| Grunt (*Haemulidae* spp.) | 0.00 (±0.00) | 0.24 (±0.14) | 1.71 (±0.29) | 1.29 (±0.17) |
| Snappers (*Lutjanidae* spp.) | 0.38 (±0.2) | 1.71 (±0.25) | 3.00 (±0.22) | 2.90 (±0.18) |
| Damselfishes (*Pomacentridae* spp.) | 0.00 (±0.00) | 0.59 (0.21) | 1.86 (0.34) | 2.14 (0.16) |
| Piscivores | 0.23 (±0.12) | 0.65 (±0.19) | 0.57 (±0.20) | 1.43 (±0.21) |

The occurrences of these taxonomic and trophic groups correlate with the degree of estuary fragmentation. The "piscivore" category includes groupers, needlefish, barracuda, and tarpon.

most commonly observed fishes in estuaries were snappers (*Lutjanus* spp.) and mojarra spp. (*Gerres cinereus* and *Eucinostomus* spp.). Although there was much variability in assemblage structure among samples, there was a distinct continuum in species composition from unfragmented to totally fragmented estuaries. Unfragmented and minimally fragmented estuaries were characterized by significantly higher species density than partially and totally fragmented estuaries, suggesting when roads are constructed across estuaries, that bridges (or multiple culverts) should be installed to maintain fish species density. Sites with minimal anthropogenic fragmentation supported species with a variety of life histories. Some marine species periodically enter estuaries to feed (e.g., jacks), and juveniles of other species utilize estuaries as nursery grounds. For example, Nassau grouper enter estuaries as larvae and early juveniles (Eggleston et al. 1998), and they then undergo ontogenetic shifts in habitat occupancy until they emigrate from estuaries to patch reefs and ultimately deep offshore reefs (Dahlgren and Eggleston 2001). Both juvenile and adults of other reef-associated species, including damselfish, parrotfish, angelfish, and wrasses, are common in estuaries with a low degree of fragmentation. Juvenile snappers and grunts, abundant along mangrove fringes of minimally fragmented and unfragmented estuaries, either may move to marine habitats as adults or complete their life cycle in estuaries. Other species, such as the recreationally important bonefish (*Albula vulpes*), may enter estuaries to forage on a daily basis in association with tidal flux, and therefore are largely dependent on functional estuaries throughout their lives.

Assemblages in partially fragmented estuaries were the most variable among the four fragmentation categories, suggesting installation of culverts may be a potentially effective means to minimize fragmentation. Nonetheless, this variability also indicates the potential inadequacy of culverts in maintaining hydrologic connectivity, which influences habitat quality, recruitment dynamics, and migration potential by vagile species. In particular, the installation of a single culvert or small culverts (<0.5 m diameter) may limit hydrologic connectivity and result in estuary degradation. Fish assemblages in partially fragmented estuaries with a small culvert (or multiple collapsed culverts) were most similar to those in totally fragmented estuaries, with only small snapper, mosquitofish, and sheepshead minnow common. Those species can tolerate shallow water depths (<0.1 m), low salinities (<5 ppt), and high temperatures (>42 °C), which characterize highly fragmented estuaries. Field observations suggest the most effective design is the placement of multiple culverts arranged along an entire blockage (i.e. road) throughout the extent of the estuary, allowing a greater volume of water to pass per tidal cycle and more natural "sheet" flooding. Greater tidal exchange increases water depth upstream of the blockage, reclaiming additional aquatic habitats. Multiple culverts also allow more access points to upstream habitat, likely increasing overall recruitment of juvenile and adult organisms. For example, species density in partially fragmented estuaries with multiple culverts was within the range found in minimally fragmented and unfragmented estuaries, and reef-associated species were commonly observed in estuaries.

There is a need to further quantify criteria that can be used to evaluate ecosystem "health" (*sensu* Rapport et al. 1998) of estuaries. One approach is a faunal-based system similar to the Index of Biotic Integrity (see Whittier and Hughes 2001), in which presence or absence of specific taxa can be used as quantifiable metrics. We identified six potential metrics based on our extensive dataset: (1) total number of species, (2) number of species tolerant of extreme salinity (i.e. mosquitofish, sheepshead minnow), (3) number of grunt species, (4) number of snapper species, (5) number of damselfish species, and (6) number of piscivorous fish species (e.g., groupers, barracuda). Each of these metrics was shown to discriminate, to some degree, among assemblages in estuaries with different degrees of fragmentation. Data from other Caribbean islands are needed to further refine these metrics and identify other faunal indicators.

Critical to the design and implementation of estuarine conservation and restoration initiatives is a better understanding of the effect of fragmentation on ecosystem structure (e.g., species assemblages) and ecosystem function (e.g., energy flow). Data collected with UVC provide information that can be used to this end, and may provide be a primary tool for designing management strategies for estuaries throughout the Caribbean.

*Acknowledgments.*—This project was made possible by the assistance, guidance and support of G. Carleton Ray at the University of Virginia Department of Environmental Sciences. The Henry Foundation of Washington D.C. and Acorn Alcinda Foundation funded this research. Permits MAF/FIS 12 and MAF/FIS 17 provided by the Bahamas Department of Fisheries, and support by the Andros Conservancy and Trust, were essential to the completion of the project. Margo Blackwell (Bahamas Environmental Research Center), Jeff Birch (Small Hope Bay Lodge), Mike and Petegay Hartman (Tiamo Resort), and staff of the FORFAR research station provided logistical support. "Bonefish" Simon Bain, Jeff Cartwright, and Andy Bair helped us access remote parts of Andros. Jerry McCormick-Ray provided photographic and other field assistance. Kirk Winemiller provided support for the project in numerous ways. William Loftus, Jerry Lorenz, G. Carleton Ray, and Kirk Winemiller provided valuable comments that improved the quality of this manuscript.

## LITERATURE CITED

Ackerman, J. L., and D. R. Bellwood. 2000. Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar. Ecol-Prog. Ser.* 206:227-237.

Acosta, C. A., and M. J. Butler. 1997. Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. *Mar. Freshwater Res.* 48: 721-727.

Anisfeld, S. C., and G. Benoit. 1997. Impacts of flow restrictions on salt marshes: an instance of acidification. *Environ. Sci. Technol.* 31:1650-1657.

Anisfeld, S. C., M. J. Tobin, and G. Benoit. 1999. Sedimentation rates in flow-restricted and restored salt marshes in Long Island Sound. *Estuaries* 22:231-244.

Bray, J. R., and J. C. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27:325-349.

Brock, R. E. 1982. A critique of the visual census method for assessing coral reef fish populations. *B. Mar. Sci.* 32:269-276.

Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations. *J. Wildlife Manage.* 18:297-308.

Burdick, D. M., M. Dionne, R. M. Boumans, and F. T. Short. 1997. Ecological responses to tidal restorations of two northern New England salt marshes. *Wetlands Ecology Man.* 4:129-144.

Cheal, A. J., and A. A. Thompson. 1997. Comparing visual counts of coral reef fish: implications of transect width and species selection. *Mar. Ecol-Prog. Ser.* 158:241-248.

Clarke, K. R., and R. M. Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth, UK: PRIMER-E Ltd.

Clarke, K. R., and W. M. Warwick. 1994. Similarity-based testing for community pattern: the 2-way layout with no replication. *Mar. Biol.* 118:167-176.

Dahlgren, C. P., and D. B. Eggleston. 2001. Spatiotemporal variability in abundance, size, and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Mar. Ecol-Prog. Ser.* 217:145-156.

Deegan, L. A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Can. J. Fish. Aquat. Sci.* 50:74-79.

Dionne, M., F. T. Short, and D. M. Burdick. 1999. Fish utilization of restored, created, and reference salt-marsh habitat in the Gulf of Maine. *American Fisheries Society Symposium* 22:384-404.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266:753-762.

Eggleston, D. B., J. J. Grover, and R. N. Lipicuis. 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *B. Mar. Sci.* 63:111-126.

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analyzing multi-species distribution patterns. *Mar. Ecol-Prog. Ser.* 8:37-53.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4:379-391.

Gray, C. A., R. C. Chick, and D. J. McElligott. 1998. Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. *Estuar. Coast. Shelf.* 46:849-859.

Gray, C. A., D. J. McElligott, and R. C. Chick. 1996. Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Mar. Freshwater Res.* 47:723-735.

Guidetti, P. 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuar. Coast. Shelf.* 50: 515-529.

Hulbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187-211.

Jenkins, G. P., and M. J. Wheatley. 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal, and unvegetated sand habitats, with emphasis on their importance to recruitment. *J. Exp. Mar. Biol. Ecol.* 221:147-172.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* 6:21-27.

Kulbicki, M. 1998. How the acquired behavior of commercial reef fishes may influence the results obtained from visual census. *J. Exp. Mar. Biol. Ecol.* 222:11-30.

Laegdsgaard, P., and C. R. Johnson. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Mar. Ecol-Prog. Ser.* 126:67-81.

Layman, C. A., and B. R. Silliman. 2002. Preliminary survey and diet analysis of juvenile fishes of an estuarine creek on Andros Island, Bahamas. *B. Mar. Sci.* 70:199-210.

Lee, S. Y. 1995. Mangrove Outwelling—a Review. *Hydrobiologia* 295:203-212.

Leibowitz, S. G. 2003. Isolated wetlands and their functions: an ecological perspective. *Wetlands* 23: 517-531.

Lindeman, K. C., R. Pugliese, G. T. Waugh, and J. S. Ault. 2000. Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. *B. Mar. Sci.* 66:929-956.

Murphy, B. R., and D. W. Willis (editors). 1996. *Fisheries Techniques, Second Edition*. Bethesda, Maryland, USA: American Fisheries Society.

Nagelkerken, I., M. Dorenbosch, W. C. E. P. Verbeck, E. Cocheret de la Morinière, and G. van der Velde. 2000a. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Mar. Ecol. Prog. Ser.* 202: 175-192.

Nagelkerken, I., M. Dorenbosch, W. C. E. P. Verberk, E. Cocheret de la Morinière and G. van der Velde. 2000b. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar. Ecol. Prog. Ser.* 194:55-64.

Nagelkerken, I., G. van der Velde, M. W. Gorissen, G. J. Meijer, T. van't Hof and C. den Hartog. 2000c. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar. Coast. Shelf Sci.* 51:31-44.

Newell, N. D., J. K. Rigby, A. J. Whiteman, and J. S. Bradley. 1951. Shoal-water geology and environments, eastern Andros Island, Bahamas. *Bull. Am. Mus. Nat. Hist.* 97.

Odum, W. E. 1971. Pathways of energy flow in a South Florida estuary. *University of Miami Program Sea Grant Technological Bulletin* 7:1-162.

Peck, M. A., P. E. Fell, E. A. Allen, J. A. Gieg, C. R. Guthke, and M. D. Newkirk. 1994. Evaluation of tidal marsh restoration: comparison of selected macroinvertebrate populations on a restored impounded valley marsh and an unimpounded valley marsh within the same salt marsh system in Connecticut, USA. *Environ. Manage.* 18:283-293.

Portnoy, J. W. 1999. Salt marsh diking and restoration: biogeochemical implications of altered wetland hydrology *Environ. Manage.* 24:111-120.

Portnoy, J. W., and A. E. Giblin. 1997. Effects of historic tidal restrictions on salt marsh sediment chemistry. *Biogeochemistry* 36:275-303.

Pringle, C. M. 2001. Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecol. App.* 11:981-998.

Rapport, D. J., R. Costanza, and A. J. McMicheal. 1998. Assessing ecosystem health. *Trends Ecol. Evol.* 13: 397-402.

Robblee, M. B., and J. C. Zieman. 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. *B. Mar. Sci.* 34:335-345.

Robertson, A. I., and N. C. Duke. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* 96:193-205.

Roman, C. T., W. A. Niering, and R. S. Warren. 1984. Salt marsh vegetation change in response to tidal restriction. *Environ. Manage.* 8:141-150.

Roman, C. T., K. B. Raposa, S. C. Adamowicz, M.-J. James-Pirri, and J. G. Catena. 2002. Quantifying vegetation and nekton response to tidal restoration of a New England salt marsh. *Rest. Ecol.* 10:450-460.

Rooker, J. R., and J. D. Dennis. 1991. Diel, lunar, and seasonal changes in a mangrove fish assemblage off Southwestern Puerto Rico. *B. Mar. Sci.* 9:684-698.

Sale, P. F., and B. J. Sharp. 1983. Correction for bias in visual transects of coral reef fishes. *Coral Reefs* 2: 37-42.

Sedberry, G. R., and J. Carter. 1993. The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries* 16:198-215.

Sinicrope, T. L., P. G. Hine, R. S. Warren, and W. A. Niering. 1990. Restoration of an impounded salt marsh in New England. *Estuaries* 13:25-60.

Sullivan-Sealey, K., B. Brunnick, S. Harzen, C. Luton, V. Nero, and L. Flowers. 2002. *An Ecoregional Plan for the Bahamian Archipelago.*—Jupiter, Florida: Taras Oceanographic Foundation.

Thayer, G. W., D. R. Colby, and W. F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. *Mar. Ecol-Prog. Ser.* 35: 25-38.

Thresher, R. E., and J. S. Gunn. 1986. Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). *Environ. Biol. Fish.* 17:93-116.

Weinstein, M. P., and K. L. Heck, Jr. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure, and community ecology. *Mar. Biol.* 50:97-107.

Whittier, T. R., and R. M. Hughes. 2001. Comment: test of an index of biotic integrity. *Trans. Am. Fish. Soc.* 130:169-172.

Willis, T. J. 2001. Visual census methods underestimate density and diversity of cryptic reef fishes. *J. Fish Biol.* 59:1408-1411.

Willis, T. J., R. B. Miller, and R. C. Babcock. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Mar. Ecol. Prog. Ser.* 198: 249-260.