

MANGROVES AS ESSENTIAL NURSERY HABITAT FOR GOLIATH GROUPER (*EPINEPHELUS ITAJARA*)

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ABSTRACT

We evaluated goliath grouper's [*Epinephelus itajara* (Lichtenstein, 1822)] use of mangroves as essential nursery habitat by estimating absolute abundance, density, survival, age structure, home range, mangrove habitat association, habitat quality, and recruitment to the adult population. Densities (numbers km⁻¹ mangrove shoreline) were calculated using Jolly-Seber mark-recapture methods for mangrove-lined rivers and mangrove islands of the Ten Thousand Islands (TTI) and Everglades National Park, which includes Florida Bay, Florida, USA. Juveniles had smaller home ranges around islands (170 m) than in rivers (586 m), as determined from observations on telemetered fish. Goliath grouper remained in mangrove habitats for 5–6 yrs (validated ages from dorsal spine sections), then emigrated from mangroves at about 1.0 m total length. In the TTI, juvenile densities around mangrove islands were higher (mean = 25 km⁻¹, SE = 6.2, CV = 0.5) and less variable than those in rivers (mean = 11 km⁻¹, SE = 4.2, CV = 1.2). Density was negatively correlated with the frequency of dissolved oxygen and salinity minima. Mean growth rate of recaptured fish around mangrove islands (0.358 mm d⁻¹, 95% CL = 0.317–0.398) was significantly higher than that in rivers (0.289 mm d⁻¹, 95% CL = 0.269–0.308). The annual survival rate, as estimated by the Kaplan-Meier method on telemetered fish, was 0.947 (95% CL = 0.834–1.0). Very low densities in Florida Bay were probably related to other water-quality variables in this human-altered system. The offshore abundance of adults was largely explained by abundance of mangrove, but not seagrass habitat. Mangrove habitat with suitable water conditions, which appears essential to the recovery and sustainability of goliath-grouper populations, should be protected and/or restored.

Nearshore estuarine habitats are thought to provide “essential”¹ nursery habitat for many fish species (Kapetsky, 1985; Koenig and Coleman, 1998; Thorrold et al., 1998; Fitzhugh et al., 2005), but definitive tests of the nursery role rarely occur (Beck et al., 2001). Confirmation of the nursery role requires an understanding of the focal species' life history and a thorough evaluation that culminates in demonstration of the habitat's greater contribution per unit area to the production of the adult population (Beck, 1995; Beck et al., 2001; Laegdsgaard and Johnson, 2001; Nagelkerken et al., 2002; Halpern, 2004a,b). This confirmation is critical from a conservation perspective because it provides a distinction between source and sink habitats; source habitats are currently the primary focus of efforts to protect fishery production (Crowder et al., 2000).

In this study, we tested the hypothesis that mangroves are integral and essential to the early life stages of goliath grouper [*Epinephelus itajara* (Lichtenstein, 1822)] by pursuing four objectives: (1) estimating juvenile density, survival, growth, and move-

¹ Throughout the present paper, “essential” is used in the sense of the Sustainable Fisheries Act, wherein “essential fish habitat” is defined as “those waters and substrate necessary to fish for spawning, feeding, or growth to maturity” and “necessary” means “required to support a sustainable fishery and the managed species' contribution to a healthy ecosystem.”

ment patterns in the Ten Thousand Islands (TTI), southwest Florida; (2) comparing our estimates of density in the TTI with abundance estimates from published and unpublished sampling records from other estuarine and offshore habitats; (3) comparing the effects of water condition on densities in mangrove habitats of the TTI, in rivers of the Everglades National Park (ENP), and in Florida Bay (FB), a system altered by human activities; and (4) investigating the relative importance of juvenile habitat to adult production by correlating regional near-shore habitat coverage with offshore adult abundance.

STUDY ANIMAL

The goliath grouper is the largest grouper in the western North Atlantic. It matures in 5–7 yrs, is long-lived (surviving up to 37 yrs), and reaches sizes exceeding 400 kg and 3.0 m total length (TL) (Robins et al., 1986; Bullock et al., 1992). Its life cycle includes ontogenetic shifts in habitat use: larvae move from the pelagic environment to shallow coastal areas, benthic juveniles live in estuaries, and adults occur on offshore reefs (< 50 m deep) (Eklund and Schull, 2001).

Goliath grouper is considered by the World Conservation Union (IUCN) to be critically endangered throughout its range which extends from the west coast of Africa to the west coast of Central America including the Caribbean, and from Brazil to the southeastern U.S. (Heemstra and Randall, 1993; IUCN Red List, 2006, [<http://www.iucnredlist.org/search/search-basic>]). A fishing ban was put into effect in the southeastern U.S. in 1990 by the South Atlantic and the Gulf of Mexico fishery management councils and in the Caribbean in 1993 by Caribbean Fishery Management Council because it was considered to be severely overfished (GMFMC, 1990; Sadovy and Eklund, 1999). Although the National Marine Fisheries Service (NMFS) continues to list this species as overfished (NMFS, 2004), the actual status of the population remains unknown and difficult to assess (Porch and Eklund, 2004), as is often the case with fully protected species for which fisheries data collection has not been replaced with reliable population monitoring. This situation hinders development of management measures aimed at rebuilding the population, ending overfishing, or both, as required by the Sustainable Fisheries Act (Public Law 104-297).

STUDY SITES

Study sites in the TTI and ENP (Fig. 1A) occurred in red mangrove (*Rhizophora mangle* Linnaeus) habitat along the shorelines of islands, tidal rivers and passes, and shallow bays. The TTI system covers 1924 km² between latitudes 25°40'N and 26°00'N and longitudes 081°20'W and 081°40'W. The ENP covers the southern tip of the Florida peninsula and extends through FB, the largest (2072 km²) subtropical estuary in North America (Loftus, 2000).

In both systems, we haphazardly chose widely dispersed study locations primarily on the basis of accessibility (sites were often accessible only at high tides). In the TTI, we sampled seven rivers (Littlewood, Palm, Blackwater, Pumpkin, Wood, Whitney, and Ferguson), three man-made canals (92 Canal East, 92 Canal West, and Faka Union Canal), and four mangrove-island systems (Remuda Ranch, Russell Key, Fakahatchee, and Rabbit Key) (Fig. 1B). Water depths averaged < 0.1 to 2.0 m (MLW), reaching 5 m in passes. Mixed diurnal tides range from 2.9 ft at Naples to 4.5 ft

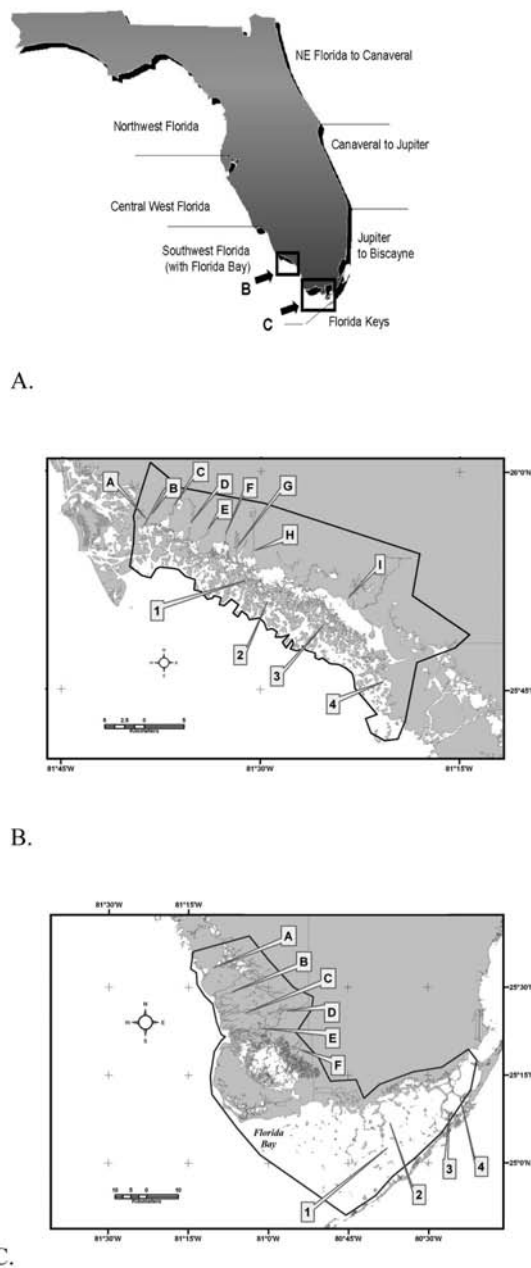


Figure 1. Study sites in southwest Florida, USA. **A.** Areas covered by the present study and Florida coastal regions as delimited for Reef Environmental Education Foundation surveys. **B.** Ten Thousand Islands system, showing sites used in the present study (those marked with asterisks are man-made). River and canal sites: (A) 92 Canal West,* (B) 92 Canal East,* (C) Palm River, (D) Blackwater River, (E) Whitney River, (F) Pumpkin River, (G) Little Wood River, (H) Faka Union Canal,* (I) Ferguson River. Passes: (1) Remuda Ranch Channel, (2) Fakahatchee Pass, (3) Russell Pass, (4) Rabbit Key Pass. **C.** Everglades National Park system. Rivers: (A) Lostmans River, (B) Broad River, (C) Harney River, (D) North Prong River, (E) Shark River, (F) Roberts River. Bay sites: (1) Bob Allen Key, (2) Black Betsey Key, (3) Little Buttonwood, (4) Blackwater Sound. Gray = land; white = water.

at the Shark River (NOAA tide tables). Undercuts (= scoured shorelines) formed a structurally complex habitat in sampled areas, especially around mangrove islands where mangrove roots formed "curtains" and submerged dead trees provided additional habitat structure. The ENP study sites included six rivers (Harney, Broad, Shark, Roberts, Lostman's, and North Prong) entering the Gulf of Mexico and four mangrove-island sites (Blackwater Sound, Little Buttonwood Sound, E. Bob Allen Key, and Black Betsy Key) in FB (Fig. 1C). The river sites in the TTI and ENP differed little in appearance, whereas the TTI mangrove island sites differed from those in the ENP in being shallower and more widely spaced and having fewer undercuts.

MATERIALS AND METHODS

JUVENILES

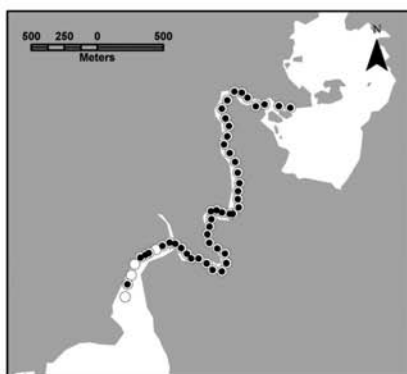
Capture.— In the rivers, we captured fish using blue-crab traps and commercial grouper fish traps baited with dead striped mullet (*Mugil cephalus* Linnaeus, 1758). Blue-crab traps were 61 cm wide by 61 cm long by 46 cm high and made of 3.8-cm, 17.5-gauge plastic-coated wire mesh; two funnels, each 13 cm long (proximal opening 19×12.7 cm; distal opening, 18×7.6 cm), led from the outside into a lower chamber, and two funnels, each 10 cm long (proximal and distal openings, 18×7.6 -cm) led from the lower chamber into an upper chamber. The fish traps were 61 cm wide by 107 cm long by 46 cm high. The top and bottom panels were 3.8-cm, 12.5-gauge plastic-coated wire mesh, and the side panels 2.5×5.2 -cm, 14-gauge wire mesh. The single entry funnel was 53 cm long (proximal opening, 45.7×30.5 cm; distal opening, 30.5×10.2 cm).

We deployed 50 traps in each river at 93-m (0.05 NM) intervals in a linear sequence 4.6 km (2.5 NM) long (Figs. 2A,B). The line of traps extended up each river from the mouth, except in rivers shorter than 4.6 km, such as the Pumpkin, Little Wood (Fig. 2B), and Whitney, where it extended past the river mouth into the bay. Trap spacing was arbitrary, but small enough to maximize catch and large enough to sample most of the river or canal. Each deployment lasted 21 d (sampled at 7 d intervals), with inter-deployment intervals about 42 d. Capture-efficiency studies during the first year identified the peak capture period for subsequent sampling: captures per set from June through November ($105/1365 = 0.077$) were significantly greater (binomial test, $P < 0.0001$) than those from January through May ($6/460 = 0.013$).

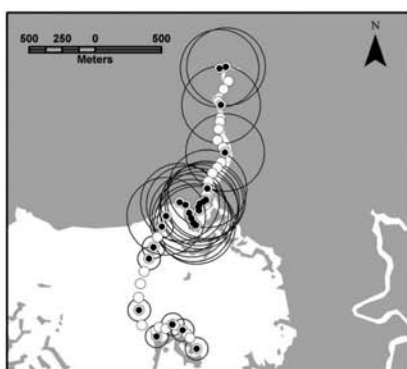
We sampled mangrove-island shorelines monthly during the summer and fall, mostly at neap tides, using setlines (Fig. 2C). Each setline was composed of a baited 14-0 circle hook attached by a 10-cm piece of 600-lb. test monofilament (which minimized hook electrolysis) to a 500-lb. test stainless steel cable attached to a 4-cm long section of 20 cm diam PVC pipe (as a reel and an aid in relocating the setlines), which was attached to a mangrove limb. At least three setlines were used per site (24–27 lines per sampling area). Each sampling event included at least two bait-and-sample rounds, each 4–12 hrs in duration.

We tagged each newly captured fish ventrally with an individually numbered stainless-steel-core internal-anchor tag (Floy Tag Company) and removed the third dorsal-fin spine and second and third dorsal-fin rays for age determination (Fig. 3). Records for each fish captured or recaptured included the time, date, tag number, weight (g), size (mm total length, TL), capture location (Trimble GeoExplorer GPS receiver in Arcview 8 GIS), and evidence of previous spine and ray removal. We recaptured fish ourselves, but we included a toll-free telephone number on each tag so that others could also report captures.

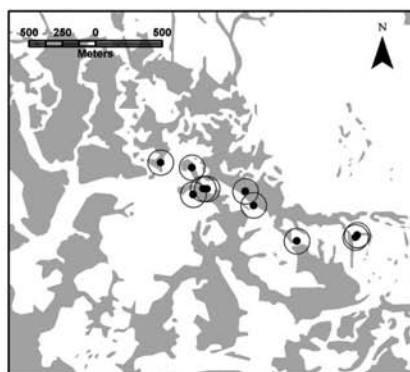
Age, Growth, and Tag Loss.—Collected spines were cleaned and dried, and several transverse 0.5 mm sections were cut from each (Beuhler low speed isomet saw) 5–10 mm above the spine base. The sections were mounted on slides, and two readers independently determined age by counting translucent bands (= annuli) under compound dissecting microscopes. The spine-aging method was validated by comparison with ages determined from otoliths and by determination of incremental change over time from additional spines collected from re-



A.



B.



C.

Figure 2. Examples of capture sites for juvenile goliath grouper, *Epinephelus itajara* in the Ten Thousand Islands. (A) trap sampling in the Palm River. (B) trap sampling in the Little Wood River. (C) setline sampling in Russell Pass. Traps were set at 0.093-km intervals. Sites of capture (small closed circles) and no capture (small open circles) are indicated along with home range (larger open circles) around capture sites. Gray = land; white = water.



Figure 3. Juvenile goliath grouper *Epinephelus itajara* (38 cm TL) caught by fish trap in the Ten Thousand Islands. Note tag on abdomen. Photograph by M. Finn.

captured fish that were either marked with oxytetracycline (50 IU kg^{-1}) or not (Brusher and Schull, unpubl. data). Growth rates (average daily increase in length, mm day^{-1}) were estimated from recaptured fish. To minimize the effects of measurement error on growth rate we used only recaptured fish at liberty for $> 30 \text{ d}$ ($n = 259$). Growth was assumed to be linear over the size range of juveniles captured in the study (following Bullock et al., 1992). Growth rate differences among sites were tested for significance with the Kruskal-Wallis non-parametric test (no normalizing transformation was found). Where data were normal (Shapiro-Wilk test), ANOVA was used to test for differences. Tag loss was indicated by evidence of previous spine and ray removal in untagged fish.

Absolute Abundance and Survival.—To estimate juvenile absolute abundance and survival, we used Jolly-Seber (J-S) mark-recapture methods (Krebs, 1999), the assumptions of which are (1) that every individual in the sampled population has the same capture probability (equal catchability); (2) that every marked individual has the same probability of surviving between sampling times; (3) that no tag loss occurs during the sampling period. It also requires that sampling time be short relative to intervals between samples (a feature built into our sampling design), that at least three sampling times occur for each site, and that a relatively high proportion (~ 0.50) of fish be marked.

We knew a priori that satisfying the equal catchability assumption would be difficult because no single gear type uniformly sampled the entire juvenile size range (20–1000 mm TL). (We collected newly settled juvenile goliath grouper at about 20 mm TL in multiple locations in mangrove leaf litter, but could not include them in the J-S abundance estimate due to collection gear limitations. However, they were included in the estimates of overall absolute abundance and density.) Traps worked in rivers but not around mangrove island undercuts, where they were dislodged by swift currents and rapidly fouled. Despite this bias and the potential difficulty of distinguishing habitat-specific size (or age) distributions from gear selectivity, we pursued multigear sampling to ensure capture of a greater size range (and therefore age spectrum) of fish.

We tested for equal catchability within the selection limits of the gear with the zero-truncated Poisson test and then compared the observed and expected frequency distributions using a chi-squared goodness-of-fit test (Krebs, 1999).

We estimated absolute abundance for all sizes, 20–1000 mm TL and for all ages, 0–6, present in the mangroves (N_A) (1) for trap sampling, by determining site-specific abundances of 2-yr-olds, the age most often selected by traps (= mean proportion of 2-yr-olds caught $\times N_{j,s}$ in each river), and (2) for setline sampling, by determining the site-specific abundances of 4-yr-olds, the age most often selected by setlines (= mean proportion of 4-yr-olds caught $\times N_{j,s}$ at each mangrove island site). We calculated the number in each age group by reconstructing all age groups (ages 0–5) based on $M = 0.05$, our Kaplan-Meier estimate of survival (see below), then summing to obtain the absolute abundance of all age groups at each sampling site during the sampling period. We did not include age 6 in the calculation because most fish appeared to leave the mangroves in their fifth year (Table 1).

To ensure equal probability of survival from one sampling time to the next we made sure that all released fish were in good condition. We estimated survival in two ways: (1) with mark-recapture and the J-S method, and (2) with telemetry and the Kaplan-Meier method (Krebs, 1999). J-S survival estimates, which depend only on the marked population, can be confounded by many factors related to the behavior of the fish and/or the sampling design. For example, if marked individuals emigrate, or for some reason cannot be recaptured (e.g., they outgrow the sampling gear or actively avoid recapture), they are assumed by the model to have died. The Kaplan-Meier survival estimate does not have such limitations and makes use of all the relocation data until the fish either dies or is lost from the sample.

Density, Habitat Association, and Home Range.—We estimated home range by tagging 22 juveniles (size range 430–940 mm TL) intraperitoneally with individually coded transmitters (Sonotronics; battery life 48 mo) and relocating them during our normal sampling activities over the period of the study. We assumed that tracking fish telemetrically left them relatively undisturbed and therefore provided more reliable information on movement patterns and home ranges than recaptures with traps or setlines, which could affect their behavior.

So that telemetered fish could be recognized externally, a numbered internal-anchor tag with external streamer was placed on either side of the incision, which was closed with stainless steel medical staples and covered with antibiotic salve before the fish was released.

We relocated telemetered fish with a directional hydrophone (Sonotronics), recorded positions, and confirmed that detected fish were still alive by direct observation using SCUBA or by prodding. We then estimated home range (= distance traversed by an individual during the sampling period) by averaging the greatest straight-line distances between relocation sites (White and Garrott, 1990). Half of the home range was equivalent to the radius of a circle centered on the sampling site (Seber, 1982). Home ranges were estimated separately for rivers and islands. Densities (D) were determined from

$$D = n_A H^{-1} \quad (1)$$

Table 1. Size and age distribution of juvenile goliath grouper, *Epinephelus itajara*, in mangrove-lined rivers and mangrove islands of the Ten Thousand Islands, southwest Florida, USA, 1998–2000. All fish caught in rivers were taken in traps; those caught near mangrove islands were taken with setlines. Data are numbers of individuals; TL = total length.

TL (mm)	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Total
101–200	1	8	3	25				37
201–300	3	90	107	108	3			311
301–400		52	239	100	9			400
401–500		1	81	48	17	2		149
501–600			8	21	36	3		68
601–700			4	8	34	11	1	58
701–800				3	22	17	2	44
801–900					15	17	2	34
901–1,000					6	7	2	15
Total n	4	151	442	313	142	57	7	1,116

where n_A = estimated absolute abundance for all size classes (20–1000 mm TL) and H = kilometers of mangrove shoreline within the home range about each sampling area.

Patterns of dispersion were estimated by use of the coefficient of dispersion (CD, variance to mean ratio), where means and variances were calculated from the number of fish captured at each sampling site over the 2 yr sampling period.

Water Condition.—We evaluated the relationship between dissolved oxygen (DO, mg L⁻¹) and salinity and fish density using 5 yrs of water quality data (1997–2001) collected monthly near or at our sampling sites from the surface and bottom (total samples = 116–120 per site) by the South Florida Water Management District and archived on websites [<http://www.sfwmd.gov/org/ema/envmon/wqm/coastal/tti.html> and <http://www.sfwmd.gov/org/ema/envmon/wqm/flab/flabindex.html>]. We assumed that salinity and DO were among the most important variables affecting fish distribution in these systems. We did not include temperature minima in this analysis—even though goliath grouper are sensitive to low temperatures (Sadovy and Eklund, 1999)—because any cold fronts moving through the area would affect the entire SW Florida system, not just individual sites within the system. The State of Florida minimum DO water quality standard for marine waters is 4 mg L⁻¹, but we used 3 mg L⁻¹ to reflect the dynamic diurnal and seasonal conditions in estuarine habitats. The State of Florida has no salinity standards for estuaries, so we used lower (salinity of 5) and upper (salinity of 40) limits known for other serranid fishes found in estuaries (e.g., gag, black sea bass, and red grouper) (Koenig and Coleman, 1998; Atwood et al., 2001).

ADULTS

Abundance.—We used goliath grouper sighting frequency data as a proxy for adult population abundance rather than population-density data to minimize the effects of feeding or reproductive aggregations on regional estimates. We determined sighting frequency based on dive surveys conducted by The Reef Environmental Education Foundation (REEF) on Florida reefs from 1993 to 2004 (REEF database = <http://www.reef.org/data/twa/index.htm>). REEF surveyors use a standardized “roving diver method” in which divers swim freely through sites, recording every observed fish species that can be positively identified. Because adult goliath grouper are distinct in terms of size, shape, and color pattern, we are confident that both novice and expert surveyors made correct identifications.

We compared goliath grouper sighting frequency off Florida with the abundance of two major estuarine habitat types in coastal Florida, mangrove habitat (data from the Florida Natural Areas Inventory, available at <http://www.fnai.org/about.cfm>) and seagrass habitat (data from Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute), using a logistic regression model to determine the significance ($P < 0.05$), direction, and strength of the relationship (R^2) between the variables.

RESULTS

AGE, GROWTH, AND TAG LOSS.—Juvenile goliath grouper ($n = 1116$) were found in mangrove habitat up to age 6 and 1000 mm TL (Table 1). The overall mean growth rate for all recaptured fish was 0.300 mm d⁻¹ (95% CL = 0.282–0.318, $n = 259$). In the TTL, growth rates were not significantly different among rivers (Kruskal-Wallis, $P > 0.05$) nor among mangrove-island sites (Kruskal-Wallis, $P > 0.05$), but growth rates around islands (mean = 0.358 mm d⁻¹, 95% CL = 0.317–0.398, $n = 41$) were significantly greater (Kruskal-Wallis, $P < 0.01$) than growth rates in rivers (mean = 0.289 mm d⁻¹, 95% CL = 0.269–0.308, $n = 218$). We found no significant (Kruskal-Wallis, $P > 0.05$) relationship between growth rate and population density among rivers, nor among island sites.

Tag loss was negligible ($n = 1$), all fish were released in good condition, and recaptured fish did not have infected tagging wounds.

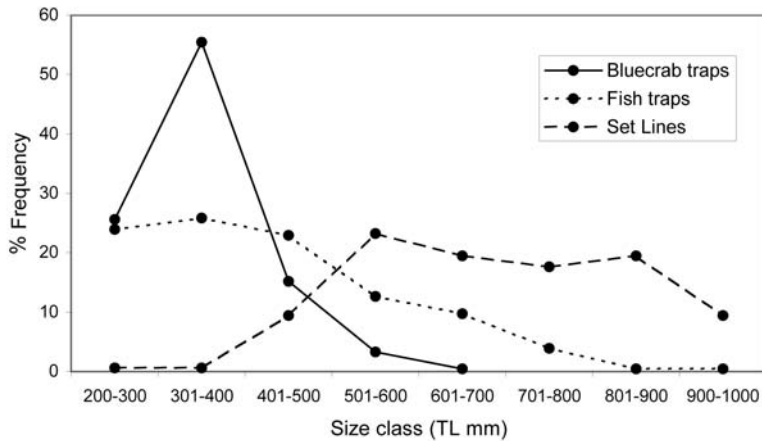


Figure 4. Percent frequency of size classes of juvenile goliath grouper *Epinephelus itajara* captured by each of the three gear types in the Ten Thousand Islands. TL = total length.

ABSOLUTE ABUNDANCE AND SURVIVAL

Equal Catchability.—Although TTI goliath grouper met the general assumption of equal catchability (within the selective limits of the gear; zero-truncated Poisson test; χ^2 , $P > 0.05$), all three gears showed some size (= age) selectivity (ANOVA, $P < 0.05$; Fig. 4). Crab traps selected primarily fish 300–400 mm TL because the funnel opening excluded larger individuals and the mesh size allowed smaller ones to escape during trap retrieval. Fish traps were less selective at the upper size range but also allowed fish < 200 mm TL to escape. Setlines captured primarily fish 500–1000 mm TL and appeared to exclude fish < 400 mm TL.

Absolute Abundance.—Because of gear selectivity, the J-S method only estimated the absolute abundance of the selected sizes for each gear type. These were calculated directly by the J-S method and indirectly with a predictive model (Table 2; Fig. 5) based on catch per unit effort (CPUE; one unit of effort = one set of traps 4.6 km long), such that:

$$Y = -7.9 + 5.1X \quad (2)$$

where Y is the absolute abundance and X is the mean CPUE for the sampling site (Linear Regression, $P < 0.05$, $R^2 = 0.89$). The CPUE model was developed from annual J-S estimates of absolute abundance of trap catches for 1999 and 2000 for six rivers. [We did not include Little Wood River because the fish in that river were unusually abundant and highly clumped (Fig. 2B); such a situation produced a low CPUE relative to absolute abundance because traps saturated in high density areas around the river mouth]. The regression model provided an efficient means of estimating abundance outside of the TTI system and in areas where capture frequencies were too low for direct use of the J-S method.

Estimating the abundance over all sizes (and therefore all gears) required accepting three assumptions: (1) that all sizes were present in river and island systems, (2) that year-class strength was constant among sampling years, and (3) that mortality was uniform across all age groups. The first assumption is justified because in our collections, fish sizes ranged from 20 to 800 mm TL in rivers and 20 to 930 mm TL

Table 2. Mean estimates of absolute abundance (n), survival probability (PHI), and density (D) of juvenile goliath grouper, *Epinephelus itajara*, sampled in mangrove shoreline of the Ten Thousand Islands (TTI), Everglades National Park (ENP), and Florida Bay (FB), southwest Florida, USA, 1998–2001. Density estimates include all fish 20–1,000 mm SL (ages 0–5). S = number of sampling times. α = maximum proportion of population marked. $n_{J,S}$ = age-specific absolute abundance estimate based on Jolly-Seber model. PHI = finite probability of survival standardized to 30 d. n_A = absolute abundance based on all ages, with annual mortality (M) of 0.05. H = area sampled in kilometers of mangrove shoreline.

System	S	α	$n_{J,S}$ (95% CL)	PHI (95% CL)	n_A (M = 0.05)	H (km)	D (n km ⁻¹)
TTI rivers							
Little Wood River	6	0.39	202 (163–242)	0.84 (0.48–1.0)	571	13.1	44
Palm River	6	0.58	70 (58–81)	0.69 (0.42–0.93)	196	9.2	21
Blackwater River	6	0.67	42 (1–83)	0.64 (0.28–0.87)	118	9.2	13
92 Canal East	6	0.79	41 (28–55)	0.86 (0.60–1.0)	116	10.4	11
Pumpkin River	5	0.43	38 (14–62)	0.81 (0.52–1.0)	106	8.5	12
Faka Union Canal	5	0.26	12 (2–22)	0.32 (0.16–0.60)	24	10.6	2
92 Canal West	5	0.72	10 (8–36)	0.64 (0.23–0.88)	27	10.4	3
Wood River*	5	–	5 (0–20)	–	14	5.4	3
Whitney River*	6	–	3 (0–20)	–	8	8.2	1
Ferguson River*	3	–	3 (0–20)	–	8	10.7	1
ENP rivers							
Harney River*	2	–	26 (18–36)	–	74	15.9	5
Broad River*	2	–	18 (7–29)	–	52	15.8	3
Shark River*	2	–	3 (0–20)	–	8	12.2	1
Roberts River*	2	–	0	–	0	13.7	0
Lostmans River*	2	–	0	–	0	7.8	0
North Prong*	2	–	0	–	0	12.1	0
TTI mangrove islands							
Remuda Ranch Pass	4	0.42	31 (13–158)	1.0 (0.57–1.0)	82	2.0	41
Russell Key Pass	7	0.80	31 (15–117)	0.78 (0.32–1.0)	82	3.0	27
Fakahatchee Pass	5	0.75	18 (12–58)	0.61 (0.22–0.93)	49	3.2	15
Rabbit Key Pass	7	0.86	23 (13–70)	0.95 (0.53–0.97)	60	4.0	15
FB mangrove islands							
Blackwater Sound*	2	–	3 (0–20)	–	8	3.6	2
Little Buttonwood S*	2	–	0	–	0	4.3	0
E. Bob Allen Key*	2	–	0	–	0	2.3	0
Black Betsey Key*	2	–	0	–	0	5.3	0

*Absolute abundance estimate based on catch-per-unit-effort linear-regression model ($Y = -7.9 + 5.1X$).

around islands. That, combined with strong site fidelity (see below), suggests that juveniles remained near settlement sites in both systems. The second assumption is justified because between sampling years at each site, we observed similar J-S absolute abundances, suggesting a similar year-class size among years, especially in rivers where highly selective crab-trap gear was used. For rivers, the mean absolute abundances for 1999 and 2000 were: 217 and 193 for Littlewood; 64 and 73 for Palm; 33 and 42 for Blackwater; 37 and 39 for Pumpkin; and 48 and 37 for 92 Canal East. For island sites, the mean absolute abundances for 1998 and 1999 were: 28 and 33 for Remuda Ranch; 18 and 18 for Fakahatchee; 34 and 17 for Rabbit Key; and 36 and 28 for Russell Key. The third assumption is probably unjustified because young (small) fish likely experience higher mortality rates than older (larger) fish, which is a general

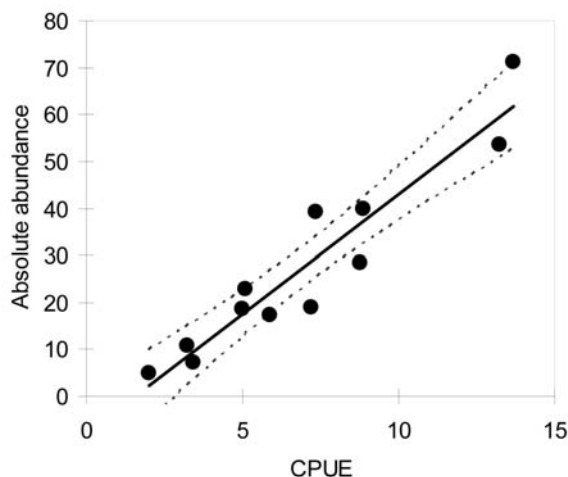


Figure 5. Linear regression of absolute abundance on catch per unit effort (CPUE; individuals per trap set) for trap-caught goliath grouper, *Epinephelus itajara*, in rivers of the Ten Thousand Islands: Blackwater River, Palm River, Pumpkin River, Faka Union Canal, 92 Canal West, and 92 Canal East. Mean values for 1999 and 2000. Regression model: $Y = -7.9 + 5.1X$ ($R^2 = 0.89$). Dashed lines represent 95% confidence boundaries.

pattern (Roff, 1992). Because we have no way of estimating size-specific mortality, we used the Kaplan-Meier estimate of annual mortality, $M = 0.05$, which was observed on telemetered fish from about 400 to 1000 mm TL.

Survival.—The proportion (α) of marked juvenile goliath grouper increased over the course of the study to a maximum that usually exceeded 0.5 (Table 2), suggesting high survival of marked fish, which was further supported by monitoring telemetered fish. The survival probability of TTI mangrove island fish (mean = 0.835) and river fish (mean = 0.727) did not differ significantly in J-S 30-d survival probability (ANOVA, $P > 0.05$, Table 2).

Two of the transmitters implanted in fish malfunctioned (could not be detected upon release), and three others were never detected after the initial check. The remaining 17 fish were monitored for 34 mo, and Kaplan-Meier survival was estimated on those fish. The 30-d survival rate was 0.995 (95% CL = 0.985–1.00); annual survival rate was 0.947 (95% CL = 0.834–1.00).

Habitat Association, Home Range, and Density.—Observations of telemetered juveniles showed that they were strongly associated with structure (mangrove undercuts and root curtains, submerged mangrove branches or trees, and rocky outcrops). They also showed patchy distributions in both rivers and around islands (mean CD for islands = 5.3 and rivers = 3.0). Because structure is associated with shoreline, we used a linear measure (number km^{-1} shoreline) as the basis for density estimation.

Recaptured juveniles showed high site fidelity; over 90% moved no farther than 0.5 km during the entire sampling period. Straight-line home ranges for telemetered fish in rivers averaged 586 m (radius = 293 m) and those around mangrove islands, 170 m (radius = 85 m; Table 3). Home range estimates served as the basis for density estimation.

Mean densities around mangrove islands (25 km^{-1} , SE = 6.2, CV = 0.5) were significantly greater and less variable than those in rivers (11 km^{-1} , SE = 4.2, CV = 1.2) (Table 2).

Table 3. Home-range estimates of telemetered juvenile goliath grouper, *Epinephelus itajara*, in the Ten Thousand Islands rivers and mangrove islands, southwest Florida, USA. Ranges are measured linearly, in kilometers of mangrove shoreline.

Location	Fish size at tagging (mm TL)	Times observed	Observation period (months)	Maximum distance traversed (m)
Rivers				
Little Wood R.	555	22	20	259
	543	20	18	611
Palm R.	438	18	12	926
	620	10	19	315
	579	24	20	818
Mean home range				586
Mangrove islands				
Rabbitt Key	610	6	26	340
	640	9	16	350
Russell Key	909	4	10	197
	825	2	9	86
	580	4	16	100
Fakahatchee	695	9	25	50
	805	4	15	67
	580	5	25	86
Pumpkin Bay	508	8	13	100
	559	16	31	320
Mean home range				170

Water Condition.—Fish densities in all TTI rivers and mangrove islands were negatively correlated with low salinity (Correlation, $P < 0.05$) and with low salinity in concert with low DO (Correlation, $P < 0.01$) (Fig. 6), but not with low DO alone ($P = 0.07$). Low densities in FB were not correlated with low DO or salinity (Table 4).

Adult Abundance.—Offshore adult abundance (from REEF surveys) was positively correlated with the quantity of mangrove shoreline along the Florida coast (Logistic Regression, $P < 0.001$, $R^2 = 0.83$; Table 5, Fig. 7). A stronger relationship ($R^2 = 0.92$) resulted if the Florida Keys were excluded—exclusion was justified by the low proportion of goliath-grouper sightings (4% of 14,386 observations) and the poor water quality around the Keys (Kruczynski, 1999). Adult abundance was negatively related to seagrass abundance (Logistic Regression, $P < 0.001$, $R^2 = 0.75$).

DISCUSSION

Beck et al. (2001) refined the definition of nursery habitat in such a way that demonstrating nursery function for a particular species requires that researchers evaluate density, survival, growth, and above all, the contribution of the habitat to the production of the adult population. Other than this study, there are virtually no published studies that have unequivocally demonstrated a nursery function of mangroves for fishes according to this definition (Faunce and Serafy, 2006).

This study clearly demonstrates that mangroves can only provide important nursery habitat for juvenile goliath grouper when local environmental conditions are suitable. Rivers are more likely than mangrove islands to experience frequent hypoxic ($\text{DO} < 3 \text{ mg L}^{-1}$) or low-salinity (< 5) conditions because they drain upland ar-

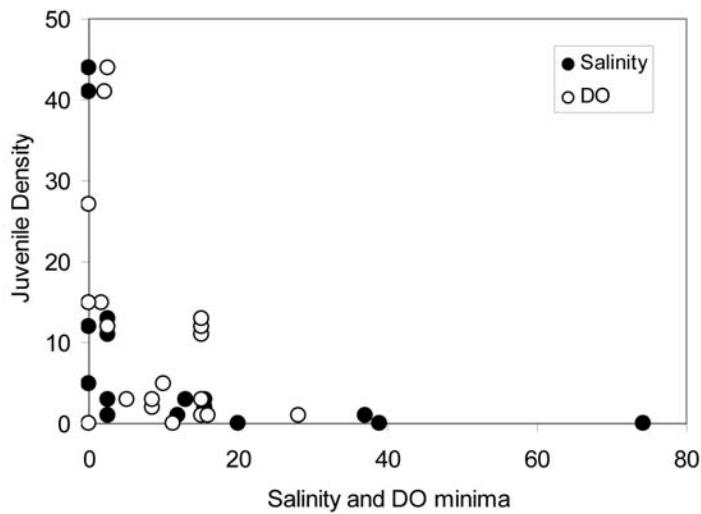


Figure 6. Relationship between density (number km^{-1} of mangrove shoreline) of juvenile goliath grouper, *Epinephelus itajara*, and dissolved oxygen and salinity minima (percent of monthly sampled dissolved oxygen and salinity measures collected top and bottom from 1997 to 2001, total of about 120 samples, below 3.0 mg L^{-1} and 5, respectively), in the Ten Thousand Islands and Everglades National Park rivers and mangrove islands. Negative correlations for dissolved oxygen and salinity minima are $P = 0.07$ and $P = 0.03$, respectively.

eas, include man-made canals, and are impacted more acutely by upland freshwater management projects that occur throughout this area (Ogden et al., 2005). Thus, it is not surprising to find in rivers that juveniles occur at lower densities, experience slower growth rates, and have greater home ranges than island fish—keeping in mind that density may be influenced by the availability of structure (Frias-Torres, 2006), and growth rates may be affected by food availability.

The near lack of juveniles in FB is best explained by the bay's long-standing degraded state, characterized by periods of hypersaline and high-nutrient conditions; periodic toxic phytoplankton blooms; and significant seagrass, sponge, and mangrove die-offs (Boyer et al., 1999; Fourqurean and Robblee, 1999). These conditions and events probably affected nursery function (Butler et al., 1995), although other factors, such as limited larval delivery and lack of microhabitat features, cannot be ruled out.

Nursery habitat is expected to promote survival in part by providing refuge from predation. While mangrove habitat is rife with possible predators of juvenile goliath grouper—including gray snapper (*Lutjanus griseus* Linnaeus, 1758), snook [*Centropomus undecimalis* (Bloch, 1792)], red drum [*Sciaenops ocellatus* (Linnaeus, 1766)], and gag [*Mycteroperca microlepis* (Goode and Bean, 1879)], as well as bull sharks [*Carcharhinus leucas* (Müller and Henle, 1839)], and lemon sharks [*Negaprion brevirostris* (Poey, 1868)]—it also is structurally complex, providing significant refugia.

Measuring survival is problematic. We found that the J-S method routinely underestimated survival in goliath grouper because fish loss due to emigration or escapement was indistinguishable from fish loss due to mortality. The Kaplan-Meier method minimizes these biases, and therefore provides a more realistic estimate. Indeed, the Kaplan-Meier survival estimate is quite high (annual rate = 0.947, 95%

Table 4. Dissolved oxygen, salinity, and the density of juvenile goliath grouper, *Epinephelus itajara*, in mangroves at Ten Thousand Islands (TTI), Everglades National Park (ENP), and Florida Bay (FB) water-quality stations. Density estimated for all juveniles 20–1,000 mm TL (ages 0–5). DO min = percentage of monthly dissolved oxygen observations below 3 mg L⁻¹. Salinity min = percentage of monthly salinity observations below 5; max = percentage of monthly salinity observations above 40. Density was measured as individuals per km of shoreline.

Location	Station	DO min	Salinity		Density
			Minimum	Maximum	
Rivers					
Littlewood River	TTI 72	2.5	0.0	3.4	44
Palm River	TTI 75	15.0	2.6	0.0	21
Blackwater River	TTI 75	15.0	2.6	0.0	13
Pumpkin River	TTI 72	2.5	0.0	3.4	12
92 canal E	TTI 75	15.0	2.6	0.0	11
Harney River	FLAB 36	10.0	0.0	0.0	5
92 Canal W	TTI 75	15.0	2.6	0.0	3
Wood River	TTI 70	8.6	15.5	3.4	3
Faka Union Canal	TTI 70	8.6	15.5	3.4	3
Broad River	FLAB 35	5.1	13.0	0.0	3
Whitney River	TTI 75	15.0	2.6	0.0	1
Ferguson River	TTI 64	16.0	12.0	1.7	1
Shark River	FLAB 39	28.0	37.0	0.0	1
Lostmans River	FLAB 29	0.0	20.0	0.0	0
Roberts River	FLAB 47	0.0	39.0	0.0	0
North Prong River	FLAB 38	11.2	74.3	0.0	0
TTI mangrove islands					
Remuda Ranch	TTI 74	2.1	0.0	0.0	41
Russell Key	TTI 65	0.0	0.0	2.5	27
Fakahatchee	TTI 69	1.7	1.7	2.5	15
Rabbit Key	TTI 52	0.0	0.0	2.6	15
FB mangrove islands					
Blackwater Sound	FLAB 05	0.0	0.0	0.0	2
E. Bob Allen Keys	FLAB 21	0.0	0.0	17.1	0
Little Buttonwood Sound	FLAB 05	0.0	0.0	0.0	0
Black Betsey Key	FLAB 23	0.0	0.0	0.0	0

CL = 0.834–1.00), and thus strengthens confidence that the marked (= telemetered) population adequately represents the unmarked population, an important consideration in any mark-recapture study.

The most important criterion for determining the nursery status of a particular habitat is its contribution to the adult population relative to that of other juvenile habitats occupied by the particular species (Beck et al., 2001). The fact is that juvenile goliath grouper only rarely occur in any other habitats besides mangroves. No juveniles were collected in intensive inshore surveys of seagrass beds (> 2500 trawl tows and gillnet sets by Coleman et al., 1993, 1994; Thayer et al., 1999; Fitzhugh et al., 2005) and mud bottom (~500 trawl tows by Coleman et al., 1993, 1994) from the Florida panhandle to Florida Bay. Only three of 143 juvenile sightings reported to the FWC hotline occurred in habitat other than mangroves, including one offshore, one in seagrass about 100 m from a mangrove coastline, and one in concrete rubble near a river mouth. Further, anecdotal information from interviews with long-time local

Table 5. Distributions of adult goliath grouper *Epinephelus itajara* sightings offshore (1993–2004) and the extent of mangrove shoreline and seagrass area inshore in all Florida coastal regions, from Reef Environmental Education Foundation surveys. % = (no. sightings/no. surveys) $\times$ 100.

Location (as marked in Fig. 1A)	No. sightings	No. surveys	%	Mangrove shoreline (km)	Seagrass (km ²)
Gulf of Mexico Coast					
Northwest Florida	36	322	11	48	2,778
Central West Florida	105	332	32	2,778	307
Southwest Florida (with Florida Bay)	365	535	68	8,752	1,538
Florida Keys	640	14,386	4	2,584	2,862
Atlantic Coast					
NE Florida to Canaveral	33	170	19	1,065	217
Canaveral to Jupiter	61	765	8	545	71
Jupiter to Biscayne	170	4,498	4	532	2,018

fishermen revealed that mangrove-associated goliath grouper are exclusively juveniles (i.e., < 1000 mm TL) (L. Demere, Chokoloskee, FL fishing guide and third generation fisherman), and that offshore reef-associated goliath grouper are virtually all adults (i.e., > 1000 mm TL) (D. DeMaria, Key West, FL commercial spearfisher who targeted goliath grouper before 1990; Porch and Eklund, 2004). Indeed, the cover provided by habitat types other than mangroves is insufficient for a fish that reaches a meter in length.

Demonstrating connectivity between nursery and adult habitats for a protected species such as goliath grouper is more difficult in the absence of a regular monitoring program. In this study, we opted to compare regional abundance of adult goliath grouper offshore with the quantity of mangrove shoreline immediately inshore of sampled populations. (We assumed that the local population, still being in the recovery phase, had not reached the carrying capacity that would force population expansion to neighboring lower-density areas.) The relationship between adult abundance and quantity of mangrove shoreline is strongly positive and corroborates the contention that southwest Florida is the center of goliath grouper abundance in the southeastern United States (see Sadovy and Eklund, 1999; Porch and Eklund, 2004).

Emigration of juvenile goliath grouper occurred in 5- to 6-yr-olds at about 1000 mm TL, just under the size of maturity estimated by Bullock et al. (1992): 1100–1150 mm TL for males; 1200–1350 mm TL for females. Emigration is more likely to be size rather than age dependent, given that size-at-age became increasingly more variable over time and that fish left the estuary at about one meter TL regardless of age (Table 1). A seasonal cue such as temperature is unlikely to trigger egress in goliath grouper as it appears to in gag (see, e.g., Koenig and Coleman, 1998) because juvenile goliath grouper remain in mangroves for years, whereas gag leave their nursery habitat during the first fall season of residency.

Mangrove habitat suitable as goliath grouper nursery in the South Florida Ecosystem was probably much more abundant and widespread a century ago than it is now, extending at least from Indian River Lagoon on the east coast to the Caloosahatchee estuary on the west coast, including Biscayne and Florida bays (Ogden et al., 2005). Human activity has had an enormous impact, including that caused by water management, agriculture, industrial and housing developments, roadways, and mosquito abatement, resulting in major changes in the timing, quantity, and quality of freshwater flows into the estuary. Goliath grouper is only one of a diverse array of species

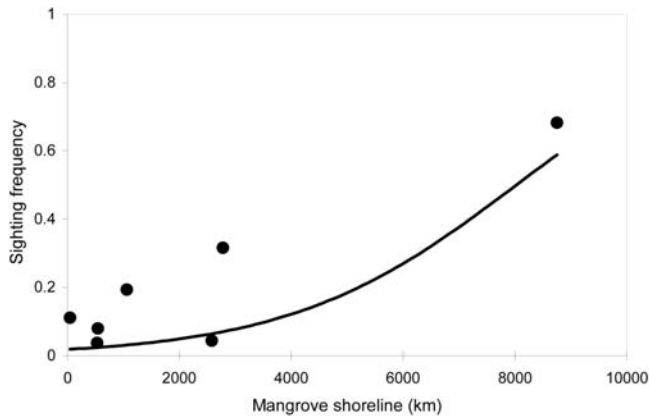


Figure 7. Logistic regression of proportion of REEF surveys with adult goliath grouper (proxy for offshore adult abundance) on kilometers of mangrove shoreline for coastal regions of Florida ($P < 0.001$, $R^2 = 0.83$).

affected by these hydrologic and water quality alterations (Sklar and Browder, 1998; Ogden et al., 2005).

In mangrove habitat, goliath grouper appear to be intolerant of large and/or highly variable flows of fresh water, but conditions of low DO, other water quality factors, and episodic events such as red tide, possibly stimulated by enhanced nutrient loads, undoubtedly affect the suitability of the mangrove nursery. Additional studies are needed to determine the productivity of other South Florida mangrove habitat for goliath grouper (and other species) and to define the various factors affecting density, growth, and home range including interactions of water quality, food availability, microhabitat features.

In addition to reduced mangrove habitat quality in the South Florida system, direct mangrove loss is occurring. Current mangrove coverage ($\sim 2174 \text{ km}^2$, based on FWRI data) represents a significant reduction from coverage that existed 100 yrs ago, before significant human-induced changes in the system (Johnson, 1974; Gilmore and Snedaker, 1993; Sklar and Browder, 1998; Ogden et al., 2005). The most recent losses (between 1986 and 1997) include 3.3% (from 366 to 354 km^2) for FB and 28% (from 259 km^2 to 186 km^2) for TTI (Fig. 8). Worldwide, mangrove ecosystems have declined by $\sim 35\%$ since the 1980s, primarily because of mariculture in third-world countries (Mendelssohn and Mckee, 2000; Valiela et al., 2001).

Our data suggest that availability of suitable mangrove habitat is the primary bottleneck to goliath grouper production, making suitable mangrove habitat not only essential, as defined by the Sustainable Fisheries Act, but critical in the sense defined by the U.S. Endangered Species Act (16 U.S.C. Section 1531 et seq.). Given that nearly 75% of Florida's human population lives in coastal counties, that the population is expected to increase by 9 million people in the next 25 yrs (Florida Office of Economic and Demographic Research, <http://edr.state.fl.us/population.htm>), and that mangrove losses of 20% are expected in the next 50 yrs (J.U., unpubl. data), we contend that to be effective, any recovery plan for this species should include protection and restoration of mangrove nursery habitat, which in turn depends in large part on restoration of "defining characteristics" (Ogden et al., 2005) of the South Florida ecosystem.

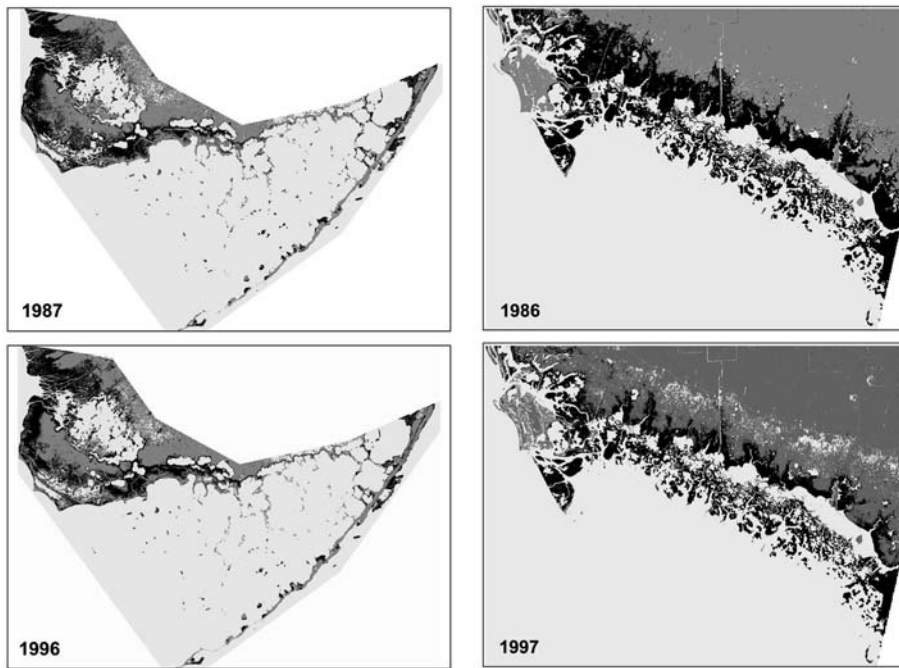


Figure 8. Satellite images of Florida Bay and Ten Thousand Islands mangrove coverage. Upper panels, before mangrove die-back; lower panels, after mangrove die-back. Black = mangrove, gray = land and other wetlands; white = water. Data are from Landsat TM imagery through an ISO data classification at 30-m resolution. Fish and Wildlife Research Institute (Florida Fish and Wildlife Conservation Commission), St. Petersburg, FL, USA.

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