Abstract—Distribution and demographics of the hogfish (*Lachnolaimus maximus*) were investigated by using a combined approach of *in situ* observations and life history analyses. Presence, density, size, age, and size and age at sex change all varied with depth in the eastern Gulf of Mexico. Hogfish (64–774 mm fork length and 0–19 years old) were observed year-round and were most common over complex, natural hard bottom habitat. As depth increased, the presence and density of hogfish decreased, but mean size and age increased. Size at age was smaller nearshore (<30 m). Length and age at sex change of nearshore hogfish were half those of offshore hogfish and were coincident with the minimum legal size limit. Fishing pressure is presumably greater nearshore and presents a confounding source of increased mortality; however, a strong red tide occurred the year before this study began and likely also affected nearshore demographics. Nevertheless, these data indicate ontogenetic migration and escapement of fast-growing fish to offshore habitat, both of which should reduce the likelihood of fishing-induced evolution. Data regarding the hogfish fishery are limited and regionally dependent, which has confounded previous stock assessments; however, the spatially explicit vital rates reported herein can be applied to future monitoring efforts.

Demographics by depth: spatially explicit life-history dynamics of a protogynous reef fish

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Protogynous species require special management considerations when fishing reduces the probability of survival to the male phase. Selective harvesting of males may skew the sex ratio and reduce the reproductive capacity of a population by increasing the probability of sperm limitation (Hamilton et al., 2007). Also, selective removal of a particular sex or size class over many generations can have evolutionary consequences, including slower growth rates, reduced size at maturation, and earlier sexual transformation (Harris and McGovern, 1997; Adams et al., 2000; Brulé et al., 2003; Heppell et al., 2006). However, protogyny does not automatically imply elevated vulnerability to fishing if the population is able to compensate for reduced male survival (e.g., by earlier transition to the male phase). This ability to compensate is most likely to occur in species in which sex change is socially or environmentally mediated rather than constrained to a certain size or age (Alonzo and Mangel, 2005). Therefore, to predict stock dynamics and a species' response to fishing pressure, it is important not only to establish whether sex change occurs, but also to quantify the mechanisms that influence sex change and characterize the related demographics.

We synthesized data from *in situ* observations and life history collections to evaluate factors that could potentially influence the presence, density, and demographics of a reef fish. The hogfish (Labridae: *Lachnolaimus maximus*), which occurs from temperate to tropical waters of the western North Atlantic Ocean, Gulf of Mexico, and Caribbean Sea, was chosen for this study for several reasons. It is an economically important reef fish (for a list of total U.S. fishery landings and their estimated values see: www.st.nmfs.noaa.gov/st1/commercial/index.html, accessed February 2011), and a better understanding of its ecology will assist managers in evaluating regulatory options. The principal fishing method for this species is spearfishing (McBride and Richardson, 2007), which presents an opportunity to evaluate the effect of a single fishery sector with fewer confounding effects from other fishery sectors (e.g., hook-and-line). Hogfish can exceed 800 mm fork length (FL), weigh more than 10 kg, and live as long as 23 years (McBride and Richardson, 2007). These life-history characteristics allow a wide latitude for measuring differences in size and age. Finally, they are monandric, protogynous hermaphrodites (all fish begin life as female and can eventually change sex to male) (McBride and Johnson, 2007) that form harems, with a single male controlling 2–15 females (Davis, 1976; Colin, 1982; Claro et al., 1989). This mating system allowed for investigation of the effects of fishing, habitat, and other environmental variables on sex change and social structure.

Fishery regulations for hogfish were first implemented in 1994. The minimum size limit (305 mm FL) corresponded with the minimum length at sex change (Davis, 1976) and was established to protect spawning fish. However, concerns about the effectiveness of this size limit emerged when further research demonstrated that median size at sex change was significantly larger (~380 mm FL; McBride et al., 2008). Continual removal of the dominant male can impact the reproductive capacity of a population (Bannerot et al., 1987; Sluka and Sullivan, 1998). Under heavy fishing pressure, constant disruption of hogfish spawning harems could be problematic because several months are required to complete sex change (McBride and Johnson, 2007) and new males have lower reproductive success (Muñoz et al., 2010). A stock assessment in 2003 (Ault et al.[1]) stated that hogfish were undergoing overfishing in the U.S., but these findings were disputed because of concerns that catch and effort data were inadequate (Kingsley[2]). Under such conditions, demographic data may provide the only basis for setting management reference points (Brooks et al., 2010) and evaluating future monitoring strategies.

Data were collected through cooperation with the spearfishing community, and revealed abrupt, cross-shelf patterns in hogfish demographics. These findings highlight interactions between fishing operations and the environment on reef fish populations, specifically demonstrating that sex change mechanisms can be spatially explicit and that refuges may exist for larger spawners that survive long enough to reach offshore habitats.

Figure 1

Study location in the central eastern Gulf of Mexico. Dive sites are indicated by dots (431 sites) and were surveyed for hogfish (*Lachnolaimus maximus*) between 2005 and 2007. Hogfish were harvested randomly from dive sites during scuba surveys. Bathymetry contours are isobaths and are labeled to 100 m; the 30-m isobath is bold and separates nearshore (<30 m) from offshore (≥30 m) sites.

Materials and methods

Sampling design

Visual observations and hogfish collections were made during scuba dives (to a depth of 69 m) in the central eastern Gulf of Mexico (Fig. 1). To investigate whether increasing depth and distance from shore affected hogfish distribution and demographics, scuba surveys were allocated to sample a range of depths and were categorized as nearshore (<30 m) or offshore (≥30 m). Thirty meters was chosen as the dividing point between the nearshore and offshore classification because many recreational divers do not exceed this depth on account of the reduced available bottom time and greater hazards associated with diving at deeper depths. Additionally, this 30-m depth corresponds roughly with a distance of 40–50 km from land, beyond which travel becomes more costly in terms of travel time, fuel expense, and risks associated with adverse weather. Sites were also examined by 10-m depth intervals to identify whether there were finer scale effects of depth on hogfish distribution.

Habitat was characterized into one of three major categories according to bottom type and relief: 1) natural habitat of rugose hard bottom with a maximum vertical relief >0.5 m, typically limestone outcroppings

[1] Ault, J. S., S. G. Smith, G. A. Diaz, and E. Franklin. 2003. Florida hogfish fishery stock assessment. Final report to Florida Fish & Wildlife Conservation Commission, 89 p. [Available from NOAA Southeast Fisheries Science Center, www.sefsc.noaa.gov/sedar/download/SEDAR6_RW4.pdf?id=DOCUMENT, accessed February 2011.]

[2] Kingsley, M. C. S., ed. 2004. The hogfish in Florida: Assessment review and advisory report. Southeast data and assessment review, 15 p. Prepared for the South Atlantic Fishery Management Council, the Gulf of Mexico Fishery Management Council, and the National Marine Fisheries Service. [Available at: http://www.sefsc.noaa.gov/sedar/download/SEDAR6_SAR2_hogfishall.pdf?id=DOCUMENT, accessed February 2011.]
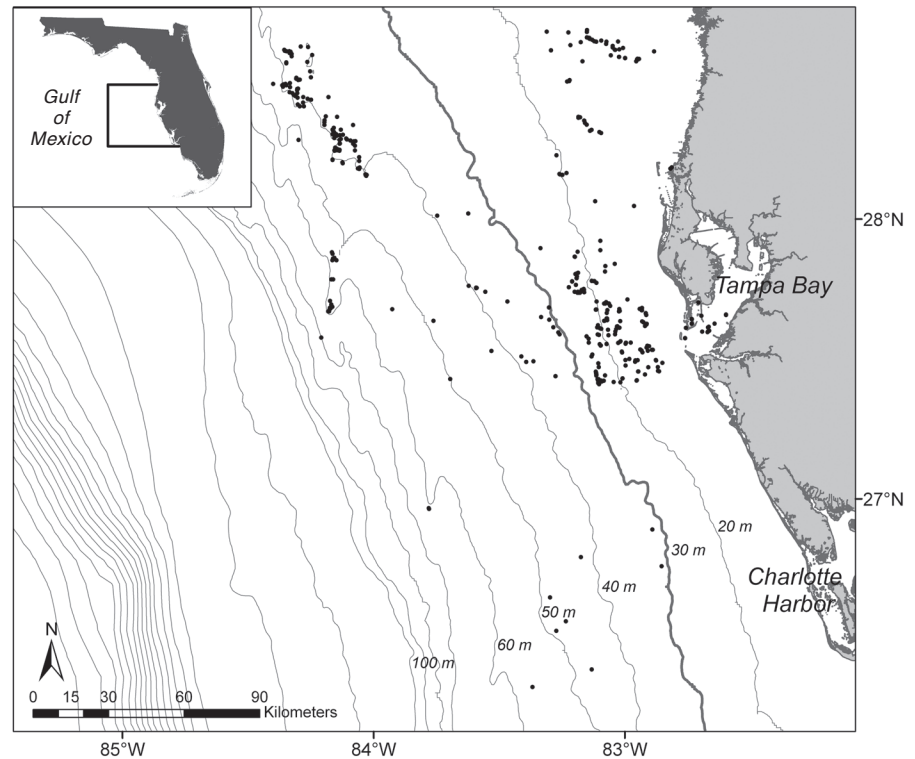
or ledges; 2) natural habitat of flat hard bottom with low-relief (<0.5 m), typically limestone outcroppings and shallow potholes; or 3) artificial habitat, which was primarily shipwrecks but also included other non-natural structures (e.g., bridge pilings, building debris). Other habitats (seagrass, plain sand, or mud bottom) were uncommon and were grouped together.

Three to nine research trips were conducted monthly through all seasons: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Sampling effort was focused on rugose hard bottom as recommended by veteran divers with knowledge of hogfish distribution in the study area, and as indicated in published reports regarding hogfish ecology (Davis, 1976; Colin, 1982). Remaining habitats were systematically surveyed less often, mainly to confirm the expectations that hogfish occurred there less frequently or in lower abundance. Attempts were made to visit sites representative of each combination of habitat type and depth category at least quarterly.

Research dives

Hogfish are in general unwary of divers (Davis, 1976; Colin, 1982) and typically remain in an area when divers are present (senior author, personal observ.)—a characteristic that makes this species a good candidate for visual survey techniques (Jennings et al., 2001). Underwater observations using scuba were performed to record the presence, density, size distribution, and sex ratio of hogfish.

During each dive, a single observer (A. Collins) swam the length of a straight line 50-m transect three consecutive times. Transects were placed at the observer's discretion to maximize the length of the transect over the targeted habitat type (typically rugose hard bottom, where transects were laid in a straight line on top of the ledge). The observer waited at least one minute between setting the transect line and beginning the survey. Additionally, the observer waited one minute between the end of one replicate and the beginning of the next. During each replicate, the total number, size, and sex of hogfish observed within 3 m of the line were recorded (survey band=6×50 m, or 300 m^2). The greatest number of fish recorded during a single replicate was used to calculate hogfish density in the transect area.

Hogfish are dichromatic and dimorphic (McBride and Johnson, 2007). This attribute typically allowed visual identification of the sex of each fish. Fish were categorized as male, female, or, if sex was not obvious, sex unknown. Sex ratio (number of males divided by number of females) was calculated for each transect. The four cases in which a fish was designated as unknown were not included in the calculation of sex ratio. Maximum, minimum, and mean sizes of hogfish observed during each site visit were based on visual survey data (estimated FL, cm) as well as on harvested hogfish (measured FL, mm). Hogfish harvested from the survey area were identified during the survey and were measured only once.

Horizontal visibility was assessed by the observer during the survey. If visibility was less than 3 m, or if the site was too deep (>45 m) to allow for transect replicates, only data on fish presence were considered in further analyses (i.e., sex ratio and density were not calculated for these dives).

The binary relationship between hogfish presence (vs. absence) and habitat, depth, and season were investigated by using a general linear mixed model (GLIMMIX, SAS, vers. 9.1, SAS Inst., Cary, NC), and presence was modeled by using a binary distribution. General linear models (GLM and GLIMMIX) were also used to test for the effects of habitat, depth, and season upon each of the following variables: hogfish density, size, and sex ratio. Density was modeled with a Poisson distribution.

Life history

Hogfish were typically harvested from dive sites in accordance with fishing regulations; therefore most speared fish were greater than 305 mm FL. However, an effort was made to sample a number of small, sublegal-size fish during each season of the year. Harvested fish were otherwise randomly chosen throughout the dive. Length (FL, mm) and whole body weight (BW, to the nearest 0.25 kg) were measured for all harvested fish. Gonads were excised immediately after the diver surfaced, were wrapped in plastic, and stored on ice until they could be returned to the laboratory. Within 24 hours, gonads were weighed to the nearest 0.01 g, and a section of tissue approximately 1 cm long was removed from the middle of each gonad and placed in formalin. Histological processing followed the procedures described in McBride and Johnson (2007). Slides were examined (100–200× magnification) at least twice by an individual reader to identify reproductive class.

Reproductive class was assigned according to the method of McBride and Johnson (2007). Briefly, the most advanced oocyte stage or evidence of previous spawning (i.e., atretic advanced stage oocytes) were used to designate females as immature, mature resting, mature active, or postspawning (classes 1–4, respectively). Transitional-stage fish (class 5) were identified by the presence of seminiferous crypts along the boundary of the tunica. Males were classified by the dominant stage of spermatogenesis, the nature of the germinal epithelium, and the connection and size of sperm ducts and were designated as immature, mature inactive, ripening mature, ripe mature, or postspawning (classes 6–10, respectively).

Fish were aged by examining sectioned otoliths (sagittae). Age was independently assessed by two individual readers following the methods and criteria outlined in McBride and Richardson (2007). Growth was modeled with the von Bertalanffy growth equation:

$$FL = L_\infty (1 - e^{(-K[t - t_0])}),$$

where L_∞ = asymptotic fork length
  K = the Brody growth coefficient; and
  t_0 = the predicted age at which fish length is equal to zero.

Growth was modeled for the entire sample, as well as independently by depth category (nearshore vs. offshore).

To test for effects of fish age and depth on fish size, a 2-way analysis of variance (ANOVA) was used to compare size at age for age classes common to both depth categories (ages 3–6 yr). Size and age at female maturity and sex change were calculated with the logistic curve (binary logit model):

$$PM_t = e^{a\,+\,bX}/1\,+\,e^{a\,+\,bX}.$$

where PM_t is the probability of maturity at a particular age or length class;
  a and b = constants; and
    X is either length or age.

Size or age at 50% maturity = |a/b|. Model structure and fitting followed Allison (1999). Size and age at first maturity (i.e., class 1 vs. classes 2–4) and at sex change (i.e, classes 1–4 vs. classes 5–10) were modeled for each depth category, as well as for the aggregate sample.

Additional otoliths and gonads were collected opportunistically through spearfishing tournaments, trawl research cruises (Fisheries-Independent Monitoring Program of the Fish and Wildlife Research Institute), and independent diver donations. Fish were used for life history analyses only if the location and depth at capture within the central eastern Gulf of Mexico could be verified.

Results

Research dives

Hogfish presence was significantly related to habitat and depth. Fish were recorded most often and in highest densities nearshore over rugose hard bottom (Fig. 2A). Hogfish were present during 74% of all surveys (318/431) and were observed during all months of the year throughout the sampled depths and major habitat types (Tables 1 and 2). Hogfish density was greater nearshore (range 0–25; mean=5.4) than offshore (range 0–15; mean=1.3) during all seasons, and highest densities were recorded during summer (Fig. 2B). No significant relationship between presence and season was detected, nor was there a significant interaction between habitat and depth or season and depth (Table 2).

Hogfish observed during research dives nearshore were half the size of those offshore (nearshore mean=24 cm FL [range: 6–56 cm, n=1352]; offshore mean=51 cm FL [range: 18–77 cm, n=296]). Nearshore hogfish were larger in summer than in winter (P=0.0029), and offshore hogfish were larger in spring than in fall
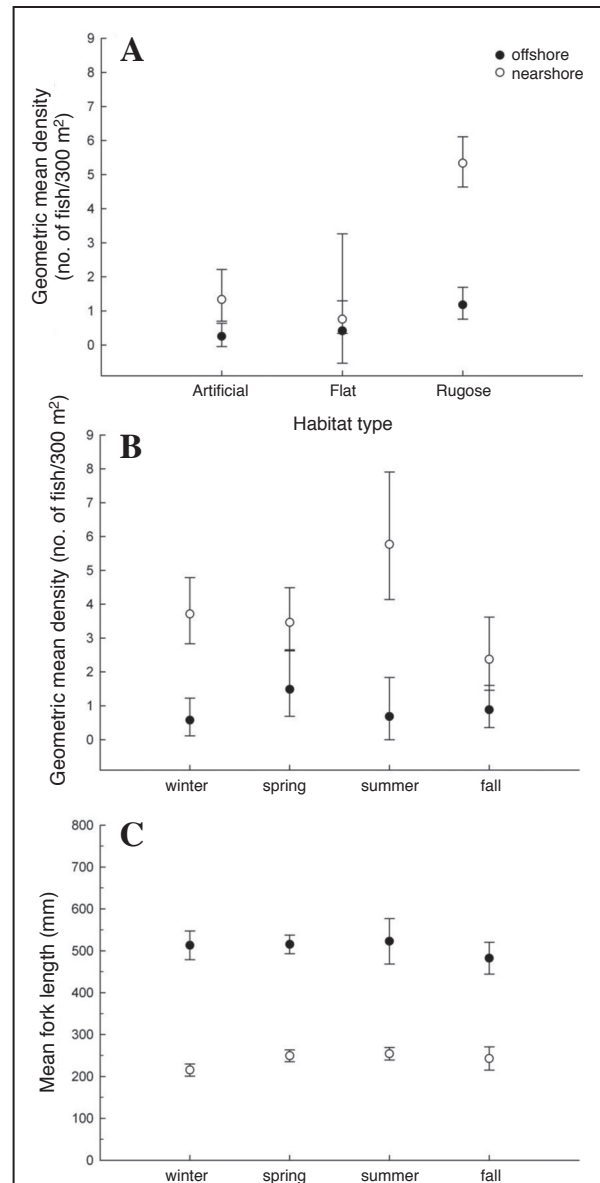

Figure 2
Geometric mean density of hogfish (*Lachnolaimus maximus*) recorded during visual transects (50×6 m bands with replication) by (**A**) habitat type and (**B**) season. (**C**) Mean fork length for hogfish observed over all seasons during all research dives. Depth categories were classified as nearshore (<30 m depth; open circles) or offshore (≥30 m depth; filled circles), and error bars represent 95% confidence limits.

(P=0.0141), but otherwise, no significant relationship was detected between fish size and season (Fig. 2C). Although density decreased with depth (P<0.0001; Fig. 3A), FL exhibited a positive relationship with depth (P<0.0001; Fig. 3B). Males were larger than females within each depth category (P<0.0001), but both sexes were larger offshore than nearshore (P<0.0001; Fig. 3B). Within depth categories, further analysis by

Table 1

Number of dives, visual transects, and hogfish (*Lachnolaimus maximus*) sampled (August 2005–August 2007) at nearshore (<30 m) and offshore (≥30 m) sites. Visual transects (research dives where replicates could be completed and visibility was ≥3 m) are indicated by habitat type as artificial (A), flat hard bottom (F), rugose hard bottom (R). The number of transects (No. of transects) during which at least one hogfish was observed (present) and the total number of transects performed (total) are listed for each month. Only seven dives were performed over other habitat (O); therefore this category was excluded from further analyses. Survey samples were harvested during research dives. Additional fish (included in the number of total fish sampled) were collected during spearfishing tournaments, trawl cruises or through private donations. *n* = number of fish sampled.

Month	No. of dives (near/offshore)	No. of transects (present/total)					*n* (survey)	Total *n* (near/offshore)
		Total	A	F	R	O		
Jan	38 (25/13)	29	2/2	3/5	19/20	0/2	46	46 (25/21)
Feb	32 (16/16)	23	0/1	0/1	10/18	0/3	28	28 (11/17)
Mar	56 (55/1)	47	7/11	2/5	28/31	0	31	36 (32/4)
Apr	63 (30/33)	32	0/2	2/5	22/25	0	65	110 (52/57)
May	34 (30/4)	26	0/2	1/3	21/21	0	26	75 (34/41)
Jun	37 (23/14)	22	2/3	0/1	17/18	0	25	33 (6/14)
Jul	27 (10/17)	14	2/3	0/1	10/10	0	25	29 (5/24)
Aug	21 (8/13)	10	0	1/2	7/8	0	21	115 (14/63)
Sep	20 (16/4)	18	0	1/2	14/16	0	16	38 (13/25)
Oct	31 (16/15)	17	2/4	3/5	8/8	0	44	80 (47/33)
Nov	31 (23/8)	22	3/9	0/3	8/8	0/2	24	27 (11/16)
Dec	41 (12/29)	23	3/7	1/2	11/14	0	35	36 (14/22)
Total	431(264/167)	283	21/44	14/35	175/197	0/7	386	653 (264/337)

Table 2

Relationship of hogfish (*Lachnolaimus maximus*) presence and density to habitat type, depth zone, and season (main effects), as well as the interaction effects between habitat type and depth zone. Hogfish were considered present if at least one individual was observed. Surveys where hogfish were present and the total survey number are indicated in parentheses (no. of surveys present/no. of surveys performed). Hogfish presence and density were significantly related to habitat and depth, and they were most common and abundant on shallow, rugose habitat. There were no significant seasonal effects on hogfish presence or density, or interactions between depth and habitat or season. LSM indicates least squares means.

	Hogfish presence				Hogfish density			
	P>F	*F*	LSM	*P>|t|*	*P>F*	*F*	LSM	*P>|t|*
Habitat	<0.0001*	32.38			<0.0001*	13.40		
Artificial (23/55)			0.3943	0.1797			0.9641	0.9003
Flat (16/43)			0.3248	0.0606			0.9847	0.9682
Rugose (278/324)			0.8734	<0.0001			3.5074	<0.0001
Depth zone	<0.0001*	8.7			<0.0001*	18.46		
Deep (112/166)			0.4284	0.3376			0.7591	0.3607
Shallow (205/256)			0.6904	<0.0001			2.9395	<0.0001
Season	0.6439	0.56			0.2998	1.23		
Fall (66/101)			0.5285	0.671			1.5843	0.0125
Spring (106/133)			0.5741	0.2902			1.2634	0.2131
Summer (53/68)			0.6387	0.1101			1.7192	0.0084
Winter (92/120)			0.5111	0.8787			1.4467	0.0424
Depth zone×habitat	0.4968	0.7			0.3469	1.06		
Depth zone×season	0.1488	1.79			0.0659	2.44		

10-m intervals did not reveal significant differences for density or size distribution (Fig. 3, A and B).

Hogfish aggregations varied in number and sex ratio. Females were most common and were recorded during 206 out of 283 transects (mean $n=6$), whereas males were recorded during only 103 out of 283 transects (mean $n=1.5$). As many as 25 individuals were recorded during a single transect. The maximum number of females observed during a transect was 23, and the maximum number of males observed was 4. Occasionally, more than four males were noted at a site beyond the boundaries of the transect, but typically, if males were observed, it was more common to see only one or two during the survey. When both sexes were present ($n=94$ transects), the largest fish observed were always males. Sex ratio (males:females) ranged from 0.0 to 1.0 (Fig. 4), with a mean of 0.14 (overall), 0.14 (nearshore), and 0.20 (offshore). Sex ratio showed no relationship to depth ($P=0.90$) or season ($P=0.99$).
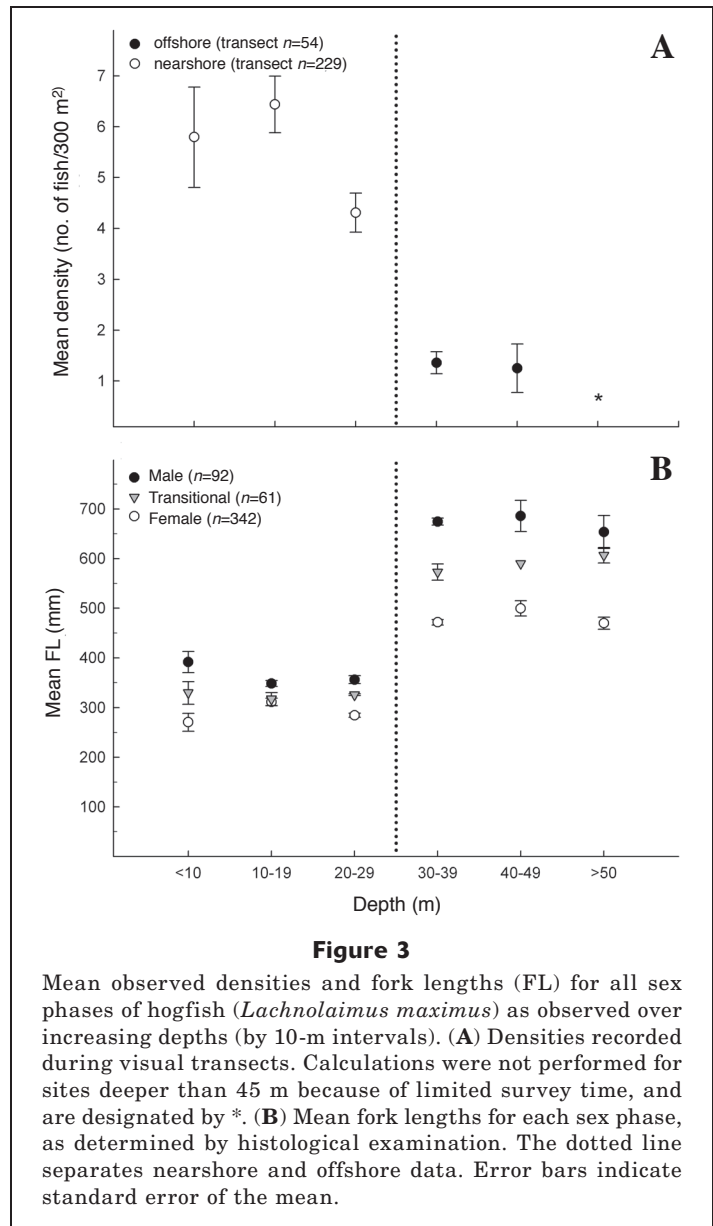
Visual surveys were completed between November 2005 and June 2007, when bottom temperature, dissolved oxygen, and salinity were measured within the following ranges: 15.7–31.2°C, 6.0–9.6 mg/L, and 29–36 PSU, respectively.

Life history

Life history analyses supported visual survey observations, with hogfish size and age positively related to depth. Ages were assigned to 622/653 fish (95%), and ranged from 0 to 19 years old. Collection depth data were available for 92% of all harvested hogfish (601/653). Hogfish collected nearshore ($n=264$) ranged from 102 to 492 mm FL and from 0 to 8 years old; those from offshore ($n=337$) ranged from 319 to 774 mm FL and from 2 to 19 years old (Fig. 5). Fish at a common age were larger offshore, indicating that faster growing fish occur in deeper water (Fig. 6).

Reproductive classes were assigned to 472 aged individuals. As expected for a protogynous hermaphrodite, the majority of hogfish were female (classes 1–4; $n=342$). The remaining individuals were classified as transitional or immature males (class 5 or 6, respectively; $n=61$) or mature males (classes 7–10; $n=92$). Size and age at 50% maturity for females were 151.6 mm FL and 0.9 years. It is assumed that females completed maturation nearshore because immature females were not observed at depths >22 m.

Females were smaller and younger nearshore (means: 246 mm FL, 2.3 yr; $n=159$) than offshore (means: 479 mm FL, 6.7 yr; $n=161$) ($P<0.0001$). Sex change occurred across a wide range of sizes (197–727 mm FL) and ages (1–11 yr) and was observed both nearshore and offshore. Median size and age at sex change were significantly less nearshore (327 mm FL; 2.8 yr; $n=15$) than offshore (592 mm FL; 7.8 yr; $n=18$) ($P<0.0001$)

Figure 3

Mean observed densities and fork lengths (FL) for all sex phases of hogfish (*Lachnolaimus maximus*) as observed over increasing depths (by 10-m intervals). (**A**) Densities recorded during visual transects. Calculations were not performed for sites deeper than 45 m because of limited survey time, and are designated by *. (**B**) Mean fork lengths for each sex phase, as determined by histological examination. The dotted line separates nearshore and offshore data. Error bars indicate standard error of the mean.

(Fig. 7). The smallest transitional fish collected offshore was 449 mm FL. All fish >685 mm FL or older than 10.5 years were in the process of sex change or were already male.

Discussion

We identified distinct cross-shelf patterns in the presence and density of hogfish; both were greater nearshore. Hogfish were distributed widely, but not randomly. Across all depths sampled, their presence and density were greatest over complex, natural hard bottom habitats. In the Florida Keys, hogfish actively select habitat, preferring sandy rubble and gorgonian microhabitats (Muñoz et al., 2010).

The spatially explicit demographic patterns evident within this study were not detected in previous research in the eastern Gulf of Mexico, probably because the data were analyzed in aggregate from collections over a broad geographic area (McBride and Richardson, 2007; McBride et al. 2008). These new results reveal distinct demographic structure across the shelf. Nearshore, hogfish occurred in higher densities and were younger, smaller, and slower growing than those offshore. Moreover, fish changed sex at a smaller size and younger age nearshore—perhaps as a response to social cues that maintain harem structure and increase spawning success. Given these facts, the potential would be great for fishing-induced genetic shifts, except for the existence of larger, faster growing fish offshore. Potential mechanisms are evaluated in the following sections to synthesize these ecological findings and elucidate the resilience of these reef fishes to fishing and environmental factors.

Cross-shelf dynamics

Spatial variation in demographic parameters is not unusual for widely distributed reef fishes (Gust, 2004; DeVries, 2006; Allman, 2007; Lombardi-Carlson et al., 2008). It is likely that the underlying cross-shelf gradients of density and life history parameters observed for hogfish reflect their bipartite life cycle. Hogfish are broadcast pair-spawners whose larvae are planktonic for 30–45 d (Colin, 1982) before settling in shallow inshore habitat such as seagrass beds (Roessler, 1965; Victor, 1986; Lindeman et al., 2000). Along the west coast of Florida, juvenile hogfish use as nursery areas Tampa Bay, Charlotte Harbor, and the shallow inshore waters off Tarpon Springs and the Big Bend region (McMichael, unpubl. data[3]).

Ontogenetic migration offshore is suspected but is difficult to verify without tagging studies. Our research provides strong support for this hypothesis. Immature females were not collected from depths >22 m, and the youngest fish collected offshore (>30 m) was 2 years old, indicating that it takes at least two years to migrate from inshore settlement areas to offshore habitat. Although many reef fish have limited home ranges after settlement (e.g., Williams et al., 1994), ontogenetic habitat shifts to deeper water are not uncommon (e.g., surgeonfish [*Acanthurus chirurgus*] and parrotfish [*Scarus* spp.], Nagelkerken et al., 2000; gag grouper [*Mycteroperca microlepis*], Brulé et al., 2003; gray snapper [*Lutjanus griseus*], Faunce and Serafy, 2007).

It is likely that nearshore and offshore differences in maximum fish size and age were also, at least partially, related to the persistent, severe red tide (*Karenia brevis*) that occurred off the west coast of Florida during
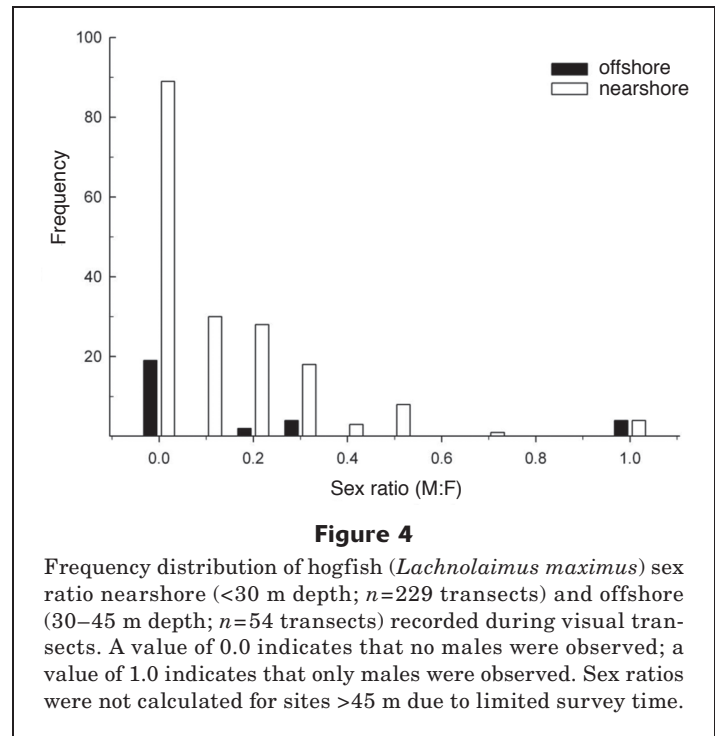

Figure 4

Frequency distribution of hogfish (*Lachnolaimus maximus*) sex ratio nearshore (<30 m depth; n=229 transects) and offshore (30–45 m depth; n=54 transects) recorded during visual transects. A value of 0.0 indicates that no males were observed; a value of 1.0 indicates that only males were observed. Sex ratios were not calculated for sites >45 m due to limited survey time.

2004–05, the year before this study began. Nearshore benthic communities in the study area suffered significant mortality during and following that red tide (Landsberg et al., 2009), when widespread fish kills and dead or reduced benthic fauna were reported in waters <30 m deep off Tampa Bay (Hu et al., 2006; Gannon et al., 2009).

During the last red tide outbreak of similar severity (in 1971), hogfish died or were displaced from many reefs in 13–30 m (Smith, 1975) but recolonized the affected areas within 4–10 months (Smith, 1979). Smith did not report length data, and therefore it was not possible to identify whether the source of recovery was new recruits or transient fish from unaffected reefs. Our findings regarding nearshore demographics may partially reflect the recovery of the population in that area after a major (but uncommon) toxic event.

Resiliency to localized environmental perturbations such as red tides is likely related to a species' distribution over a wide geographical range. The existence of large individuals in deep water offshore should provide a reservoir of spawning individuals to help replenish inshore areas (e.g., Simberloff, 1974). Although there were no reef-specific demographic data for the study area before the 2005 red tide, local divers recalled that the hogfish in shallow water were larger and more abundant before the toxic event. Additionally, greater numbers of relatively larger hogfish have been observed in shallow waters during research dives performed since the completion of this study (senior author, unpubl. data).
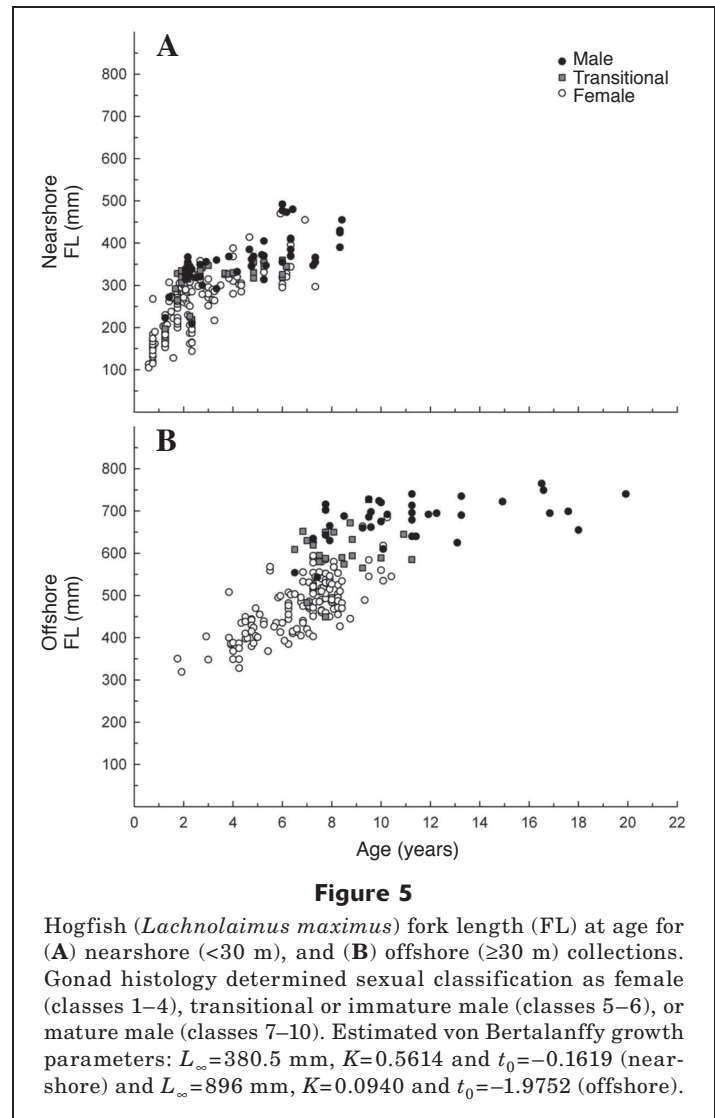
The pronounced size and age truncation observed nearshore is also likely related to greater fishing mor-

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[3] McMichael, Robert. 2011. Unpubl. data. Fish and Wildlife Research Institute, Fisheries-independent monitoring group, 100 8th Avenue SE, Saint Petersburg, Florida 33701.

tality associated with increased accessibility of fish to fishing vessels. Hogfish feed on slow moving, benthic invertebrates (Randall and Warmke, 1967) and are less vulnerable to hook-and-line fishing methods than most other reef species in the region. Consequently, they are harvested primarily by spearfishing. Most recreational diving is done at depths <130 ft (40 m; PADI, 1999); at greater depths a diver's bottom time is limited and restricted to divers with higher skill levels. Additionally, because deep sites are farther from shore, fuel expense and travel time are greater. Together, these factors potentially contribute to decreased fishing-induced mortality of hogfish offshore. Tupper and Rudd (2002) noted a similar pattern in the Caribbean, where larger hogfish were present in deeper and unfished areas. This pattern has also been observed for other species in the Gulf of Mexico. Gray triggerfish (*Balistes capriscus*) exhibit decreasing mortality with increasing distance from shore (Ingram, 2001), and vermillion snapper (*Rhomboplites aurorubens*) display a spatial size dichotomy that has been related to higher exploitation rates within waters closer to shore (Allman, 2007).

Notably different patterns of sex change were observed for nearshore and offshore regions. In aggregate, sex change occurred over a broad range of ages and sizes (1–11 years and 197–727 mm FL), indicating that it is likely to be under social control (e.g., removal of the dominant male initiates sex change in a large female). The size advantage model predicts that sexual transition will occur at an earlier age in populations experiencing higher mortality (Warner, 1988), and it has often been observed that the continued removal of males results in reduced size at sex change and that size and age at the onset of sex change are lower in areas of greater fishing pressure (Warner 1975; Hawkins and Roberts, 2003; Hamilton et al., 2007). The smaller size and younger age of hogfish at sex change indicates shorter life spans and greater mortality in nearshore waters.

In this study, median size at sex change nearshore (327 mm FL) just exceeded the legal minimum size (305 mm FL). These data indicate that many nearshore females are changing sex within one year after reaching legal size, since hogfish take about one year to complete sex change (McBride and Johnson, 2007). The probability of moving offshore may be related to an individual's growth rate because hogfish of the same age were larger offshore than nearshore. These faster-growing fish may have had greater energy reserves (perhaps by delaying sex change), allowing successful migration offshore. Alternately, resource (e.g., food, habitat) availability or another environmental factor may have allowed for faster growth within deeper habitat. The higher densities observed nearshore may result in an increased competition for food; however, a qualitative assessment of stomach fullness (stomach weight divided by total

Figure 5
Hogfish (*Lachnolaimus maximus*) fork length (FL) at age for (**A**) nearshore (<30 m), and (**B**) offshore (≥30 m) collections. Gonad histology determined sexual classification as female (classes 1–4), transitional or immature male (classes 5–6), or mature male (classes 7–10). Estimated von Bertalanffy growth parameters: L_∞=380.5 mm, K=0.5614 and t_0=−0.1619 (nearshore) and L_∞=896 mm, K=0.0940 and t_0=−1.9752 (offshore).

body weight) did not show any relationship with depth. A more quantitative assessment of prey availability and prey quality should be performed to address this question.

It is possible that differences in life history traits could reflect genetically distinct populations. Although this scenario was considered unlikely (because of the absence of immature hogfish offshore), DNA samples were collected from a subsample of individuals from both depth ranges (n=82; authors of this article, unpubl. data). Preliminary genetic analysis of microsatellite loci provided no evidence of separate stocks in our sampling area (Seyoum, unpubl. data[4]). The level of analysis available at this time cannot completely exclude the possibility, but it seems unlikely.

4 Seyoum, Seifu. 2011. Unpubl. data. Fish and Wildlife Research Institute, 100 8th Avenue SE, Saint Petersburg, Florida 33701.

Spawning harems and management

Mature hogfish form harems; isolated males are sometimes observed but females tend to occur in pairs or groups (Davis, 1976; Colin, 1982; this study). Previous

Figure 6

Mean fork length (mm) at age of hogfish (*Lachnolaimus maximus*) collected from nearshore (<30 m) and offshore (≥30 m) depths for four age classes commonly collected from both depth categories. Error bars represent 95% confidence limits.

Figure 7

Maturity schedule for male hogfish (*Lachnolaimus maximus*) by fork length (top) and age (bottom). Nearshore (<30 m) hogfish are indicated by hollow squares and offshore (≥30 m) hogfish by filled squares. Lines indicate the predicted curve.

reports of hogfish sex ratios (0.1 M:F in Puerto Rico [Colin, 1982] and 0.2 M:F in Cuba [Claro et al., 1989]) coincided with the modal range that we observed (0.1–0.4 M:F). The variability in sex ratios reported herein was not related to season; therefore we conclude that harems are probably maintained throughout the year. Colin (1982) and Muñoz et al. (2010) reported high site fidelity and restricted home ranges for hogfish, at least during their spawning season (primarily winter–spring).

The wide range of sizes observed for transitional hogfish indicates the mechanism is under social (rather than genetic) control. Warner (1984) showed that female wrasse change sex at smaller sizes when densities are high because a single small male could not monopolize mating, increasing female incentive to change sex. However, large male size or low density discouraged competition, and sexual transition by females was postponed. Smaller sizes and higher densities of hogfish observed nearshore would indicate that social mechanisms were likely responsible for the cross shelf patterns of size and age at sex change for this protogynous fish.

Spawning success was much higher in a protected area of the Florida Keys than in an adjacent area open to fishing, even though the frequency of contact between sexes was the same in both areas (Muñoz et al., 2010). Muñoz et al. proposed that lower rates of mortality will create a familiar social order, facilitating courtship and increasing spawning rates. Higher levels of mortality in nearshore waters may thus potentially disrupt harem structure and reduce reproductive output in more heavily fished areas.

Conclusions

Although there is evidence of fishing effects in nearshore waters, the continued escapement of fast-growing fish to deeper waters reduces concerns about fishery-induced evolution of life history traits that could occur if fast growers were being harvested at such a rate that they could no longer spawn successfully. The maximum size and age of hogfish reported herein are similar to those reported for Cuban waters, where there is a relatively "unfished population" (Claro et al., 1989), and to those measured previously within the current study area (1995–2001; McBride and Richardson, 2007). The technical and logistic limits that prevent most spearfishing in offshore waters and the behavioral peculiarities that make hogfish less vulnerable to hook-and-line fisheries appear to support a *de facto* refuge for some of the faster growing and largest hogfish. Offshore females spawn for longer periods and produce larger batches of eggs than do nearshore females (authors of this article, unpubl. data), and therefore the persistent escape-
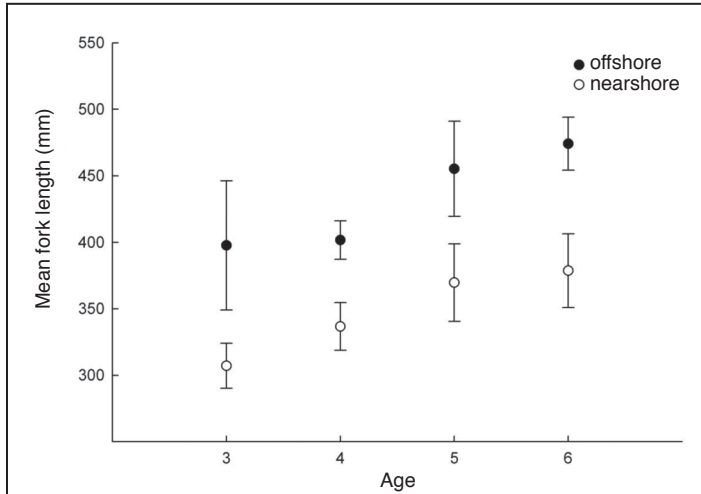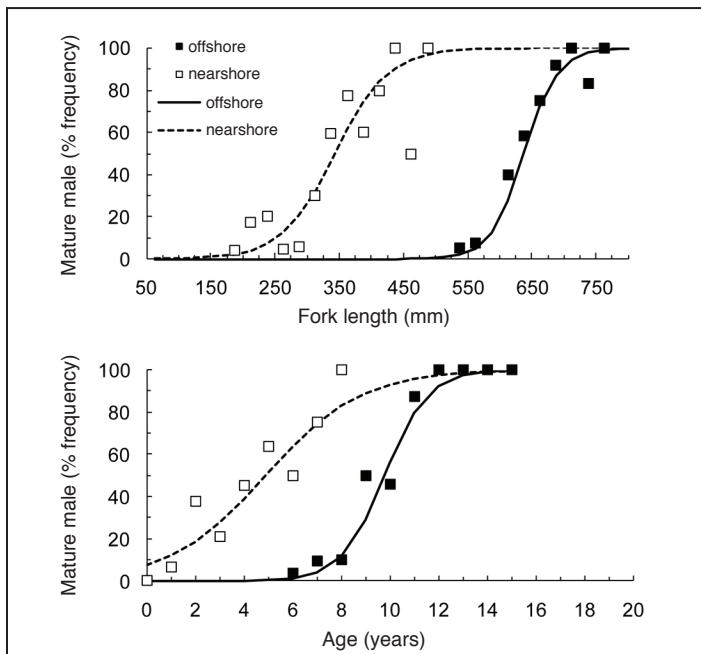
ment to offshore waters may contribute notably to the reproductive success of hogfish in the eastern Gulf of Mexico (Johannes, 1998; Birkeland and Dayton, 2005). Still, because the conspicuous nature and inquisitive behavior of hogfish make them very vulnerable to fishing, routine monitoring of fishing effort or fishing power by the spearfishing sector is warranted, as is periodic monitoring of spatially explicit densities, harem structure, and life history traits of this species.

Acknowledgments

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