Protection of Grouper and Red Snapper Spawning in Shelf-Edge Marine Reserves of the Northeastern Gulf of Mexico: Demographics, Movements, Survival and Spillover Effects

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SEDAR33-DW02

30 April 2013

Please cite as:

Koenig, C.C. and F.C. Coleman. 2013. Protection of Grouper and Red Snapper Spawning in Shelf-Edge Marine Reserves of the Northeastern Gulf of Mexico: Demographics, Movements, Survival and Spillover Effects. SEDAR33-DW02. SEDAR, North Charleston, SC. 94 pp.

Protection of Grouper and Red Snapper Spawning in Shelf-Edge Marine Reserves of the Northeastern Gulf of Mexico: Demographics, Movements, Survival and Spillover Effects

MARFIN Project FINAL Report

Submitted: October 2011

by

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Project Number: NA07NMF4330120 (FSU Grant No. 022106)

October 2007 - September 2011

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BACKGROUND

The most economically important reef fish populations in the southeastern United States (SEUS)-- dominated by shallow-water groupers (Epinephelidae) and snappers (Lutjanidae)-- are considered either overexploited, in danger of being overexploited, or both, according to status reports from NOAA Fisheries (Turner *et al.* 2001, NMFS 2004). As of March 2011, NOAA Fisheries found that Gulf of Mexico (GOM) and US South Atlantic (SATL) populations of gag *Mycteroperca microlepis* and red snapper *Lutjanus campechanus,* and SATL populations of red grouper *Epinephelus morio* and snowy grouper *Hyporthodus niveatus* were both overfished and undergoing overfishing. They also found that SATL populations of speckled hind *E. drummondhayi* and Warsaw grouper *H. nigritus* were both as undergoing overfishing, but could not determine whether they were overfished or not, presumably because they are both rare and so few individuals are caught (Huntsman et al. 1999). Both these species are considered "species of concern" by NOAA Fisheries and "critically endangered" by the International Union for the Conservation of Nature and Natural Resources (IUCN).

Other grouper species in southeastern US waters, including the marbled grouper *Dermatolepis inermis* and goliath grouper *E. itajara,* are not assessed so their actual status in US waters is unknown. Marbled grouper lacks assessment because it is not included in any fishery management plans, despite catches in the northern GOM that peaked at 20 mt in 1993, declining to 1.7 mt by 2004 (IUCN 2010). It is currently heavily targeted by recreational fishermen on Geyer Bank, 52 km (32 mi) east southeast of East Flower Garden Banks National Marine Sanctuary (FGBNMS), the only known spawning aggregation site for this species (Emma Hickerson, research coordinator for FGBNMS, personal communication). Goliath grouper was recognized by both the South Atlantic and Gulf of Mexico Fishery Management Councils as heavily overfished in the late 1980s, and was given full protection by 1990. There are currently signs of recovery in the both the SATL and the US Gulf of Mexico (Koenig *et al.* 2011), while they remain critically endangered elsewhere throughout their range (IUCN 2010).

Groupers, like many other large reef-associated species, share a suite of life history characteristics and behaviors that make them particularly vulnerable to fishing pressure (Coleman *et al.* 2000). These include being long-lived, slow to mature, having a high degree of site fidelity, aggregating to spawn, and changing sex over the course of their lifetime. In addition, those species that use shallow inshore habitats as nursery grounds are perhaps even more vulnerable because these habitats are themselves vulnerable to a suite of climatological and anthropogenic impacts (fishing and land-based impacts) that can be quite severe that are more severe in shallow water (Koenig and Coleman 1998, Koenig *et al.* 2007, Coleman and Koenig 2010).

Traditional fishing and management practices have a synergy where reef fish are concerned that can result in high and unnecessary mortality and reduced reproductive capacity. Many of the snapper and grouper species, for instance, live at shelf-edge and slope depths, where their capture invariably results in their death because the rapid change in pressure when hauled to the surface causes severe gas bladder embolism and hemorrhage. This is not a problem if the fish is the one being targeted. However, for undersized fish or fish protected from capture, such as some of the deepwater species, it can result in a high incidence of mortality that is not sustainable.

There is also the tendency for fishing pressure to focus on large fish. Intensive fishing that targets large fish ultimately results in truncation of the size and age structure of the fished population and drives down the reproductive capacity of the population. Intensive fishing that specifically targets spawning aggregations takes this a step further by causing the extinction of historic aggregations (Domeier *et al.* 2002) and by distorting the sex ratio demographics (Coleman *et al.* 1996, Koenig *et al.* 1996, McGovern *et al.* 1998, Johannes *et al.* 1999, Nemeth 2005).

Studies by Berkeley et al. (Berkeley *et al.* 2004a, 2004b) and others suggest that protecting the size and age structure has significant population-level benefits for fished populations. He demonstrated for rockfish that the larger, older fish produce not only more offspring (the number increasing exponentially with length, as is true for most fish) but higher quality offspring with greater survival potential than those of their smaller, younger counterparts.

The goal of this project was to evaluate the effectiveness of marine reserves as a means of recovering and protecting the size and age structure of fished populations, as well their spawning aggregations and sex ratios, and in providing fishery benefits outside the reserve, such as spill-over (movement of some fish out of the reserve, and possible attraction to the reserve). Fishery scientists all over the world recognize the potential for marine reserves to supplement traditional fishery management practices to support sustainable fisheries (Coleman *et al.* 1999) and see *Bulletin of Marine Science*, March 2000 Special Issue, and *Ecological Applications* Special Feature, March 2003 for reviews). More recent articles have detailed the scientific justification for their use (Sale *et al.* 2005).

Our work focused on a suite of reef sites within a marine reserve in the northeastern Gulf of Mexico, the Madison Swanson Marine Reserve (MSMR) and similar sites outside of the reserve (**Figure 1**). We were particularly interested in evaluating a series of life history and behavioral traits for three significantly important and heavily exploited focal species – gag, red grouper, and red snapper – both within and outside of the reserve to determine if these species experienced any long-term benefits in the absence of fishing. Our objectives, therefore, were (1) to determine whether sex ratios of gag would approach historic levels (Hood and Schlieder 1992, Coleman *et al.* 1996) in the absence of fishing; (2) to evaluate changes in the size and age structure of populations of the focal species; (3) to estimate the home ranges of focal species and determine the rates, direction, and patterns of movement (because protection is afforded only if the fish have small home ranges relative to the size of the reserve); (4) to determine whether spill-over from the reserve presented a direct benefit to the fishery; and (5) to estimate mortality rates inside vs. outside the reserve (because protection is only afforded if their survival potential is high). The dominant fishing sectors operating in this area are the commercial reef fish fishery (both longline and hook and line) and the for-hire recreational fishery operating mainly out of Apalachicola, Port St. Joe, and Panama City, FL. Fishing is primarily concentrated on shelf-edge reefs in water depths of 40 to 120 m (131 to 394 feet). There is also a recreational pelagic trolling fishery outside and inside the reserve (May through October) that typically targets scombrid species.

INTRODUCTION

Researchers have long recognized the dangers of fishing on reef fish spawning aggregations (Domeier *et al.* 2002). Such fishing, if intense enough, eventually leads to aggregation extinction. The loss of spawning aggregations of Nassau grouper (*Epinephelus striatus*), goliath grouper (*E. itajara*) and red hind (*E. guttatus*) has been reported many times (Sadovy and Domeier 2005). Researchers also warned that chronic aggregation fishing could disrupt the social system at aggregation time and affect a reduced reproductive output (Shapiro 1979, Shapiro *et al.* 1994, Petersen and Warner 2002). However, direct evidence of the chronic effects is difficult to obtain and there is often much contention about to what extent, if at all, such effects impact production.

Comparison of historical and contemporaneous populations of some grouper species have shown changes in sex ratio (Coleman *et al.* 1996, McGovern *et al.* 1998, Johannes *et al.* 1999), apparently resulting from fishing pressure on spawning sites. The strongest evidence for a fishing-induced change in the sex ratio has been observed in gag, *Mycteroperca microlepis*, of both the US Gulf of Mexico (Koenig *et al.* 1996) and the SATL (McGovern *et al.* 1998). The consequences to the species of a decline in the proportion of males likely include genetic effects (Chapman *et al.* 1999) and a constriction to reproductive output. Economic consequences include a loss of fishery production of one of the most important reef fishery species of the southeastern United States. Ecological consequences of a greatly decreased gag population density, including possible loss of biodiversity through trophic cascades, may be equally severe as gag is an important apex predator on warm temperate reefs. For many examples of the impact of apex predator loss on trophic cascades see Terborgh and Estes (2010).

Our overall goal was to evaluate the effectiveness of MSMR in protecting spawning populations of reef fish. We also addressed another issue, the Deep Horizon oil spill that took place off Louisiana in April 2010 and evaluated the degree of contamination of selected reef fish habitat in and around MSMR and SLMR. Our overall objectives were:

(1) To observe demographic patterns (size, age, and sex ratio [of gag]) of our focal species of reef fish (gag, scamp, red grouper, and red snapper) inside relative to outside MSMR.
(2) To determine movement patterns in and around MSMR and evaluate spillover benefits to regional fisheries,
(3) To estimate natural mortality within the reserve using acoustic telemetry methods. We also estimated the abundance of economically important reef fish inside and outside MSMR using catch per unit effort and of species of concern (Warsaw grouper, speckled hind, and snowy grouper).
(4) After the Deep Horizon oil spill the opportunity arose to evaluate whether or not oil from that spill was detectable in the vicinity of the shelf edge reserves, MSMR and SLMR. So we added this to our list of objectives and the results of that evaluation are presented in this report.

STUDY AREA

This study was conducted along a series of sites along the West Florida Shelf (WFS) representing unprotected sites, partially protected sites (e.g., the Florida Middle Grounds (FMG) HAPC, and two fully protected sites (e. g., the Madison Swanson Marine Reserve MSMR and the Steamboat Lumps Marine Reserve SLMR, each roughly 100 NM^2; **Figure 1**). The two marine reserve sites were established by the Gulf of Mexico Fishery Management Council (GMFMC) and the National Marine Fisheries Service (NMFS) in 2000 largely due to research showing extreme demographic changes in gag populations, including alarming changes in the sex ratio and in the size and age structure of fished populations (Coleman *et al.* 1996, Koenig *et al.* 2000). Initially closed to fishing only through 2004, the GMFMC extended the closure to 2010, and then again in perpetuity effective 18 May 2009, based on popular support from fishing interests (Final rule, Amendment 30B, Federal Register 74(72):17603).

Although the FMG, and SLMR were visited and surveyed, the bulk of the project took place within, around, and to the southeast of MSMR, an area of the shelf edge described by Gardner *et al.* (2005) as a "drowned delta." From a reef fish standpoint, this area provides excellent habitat at a depth that is relatively secure from storm surge[1]. The rocky reefs also provide extensive habitat for sessile invertebrates, primarily octocorals and sponges (Koenig and Coleman 2006), and for a diverse array of reef fish, as described by Weaver *et al.* (2002) from an area to the west of MSMR.

Aspects of the study areas have been described by us in previous work funded in part by the NOAA MARFIN Program and appear in the appendix here.

FOCAL SPECIES

Gag

Life cycle: The life cycle of gag is relatively complex. Spawning occurs exclusively on the shelf edge primarily during February and March (Coleman *et al.* 1996); aggregations are concentrated along the 40 fathom isobath in the northeastern GOM (Koenig *et al.* 1996). Males remain on shelf-edge reefs in association with spawning sites (Coleman et al. 2011) while females migrate to shelf-edge aggregation sites after staging on mid-shelf 'pre-spawning' aggregation sites during December and January. Mature females form pre-spawning aggregations just prior to moving out to the shelf-edge spawning sites in late January and February. The function of these pre-spawning aggregations is unknown, but ephemeral color changes approximating that of male 'copperbelly' patterns observed on videos of these aggregations suggests that they may involve dominance hierarchies among females. Females are thought to return to home sites on the shelf when spawning ends in April, but this has not been verified through tagging. Pelagic juveniles settle in seagrass in April and May, then migrate to shallow reef systems in the early fall (Koenig and Coleman 1998). Juveniles reach sexual maturity between ages 3 and 5 (Fitzhugh et al 2006); length at 50% maturity is about 59 cm TL (Appendix 1).

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[1] Although note that hurricanes can produce quantifiable effects at depths of 900 – 950 m in the Gulf of Mexico

Fishery: The gag population of the southeastern US is overfished and is undergoing overfishing (http://www.nmfs.noaa.gov/sfa/statusoffisheries/SOSmain.htm). The population has also undergone significant declines in the size and age structure as well as changes in sex ratio over the past 35 years in the southeastern US (Coleman *et al.* 1996, Koenig *et al.* 1996, McGovern *et al.* 1998). These effects are correlated with increased fishing pressure overall and on increased targeting of spawning aggregations. Potential consequences of a low proportion of males in the gag population include a decline in reproductive output and inbreeding (Chapman et al. 1999).

Our major interest in the gag spawning population is the extremely low percentage of males (~ 2%) in the present fished population (Koenig et al. 1996, Coleman et al. 1996, and this study) relative to the historical population (~ 20%; Hood and Schlieder 1992). Gag, as well as other protogynous[2] reef fish, likely undergo facultative sex change (Warner 1988) which requires social cues at times when the fish are aggregated. There is no evidence that sex change is obligate at age or size thresholds. Therefore we expected that the sex ratio would return to normal if the spawning population, regardless of size or age, was protected from fishing. Indeed, results of our earlier demographic work have shown a significant increase in the proportion of males in 2003 within MSMR, but when the US Coast Guard (USCG) operations were redirected from reserve-surveillance and enforcement duties towards hurricane assistance for victims of hurricanes Ivan (2004) and Katrina and Rita (2005), the reserves were left unprotected. Poaching became intense, confirmed by our observations and those of other fishers. The Coast Guard Base Commander (Mobile Air Training Group) admitted to Koenig that surveillance was almost completely absent at that time (personal communication). The proportion of male gag again declined to that of areas outside the reserve (NOAA MARFIN final report NA17FF2876). With the 2007 requirement that commercial reef fish fishers operate Vessel Monitoring Systems (VMS) on all licensed vessels (Federal Register, vol. 72, no. 150, p.42583), enforcement of the reserves became easier, but poaching, albeit at a lower level than that of 2004 and 2005, continued, as we will show below.

Red grouper

Life cycle-- Red grouper are protogynous hermaphrodites (Moe 1969) and pair spawn on the shelf and shelf edge primarily during the spring, with peak spawning in April and May (Coleman *et al.* 1996). They do not form spawning aggregations, but instead spawn on low-relief rocky bottom in and around holes or pits they excavate (Coleman *et al.* 2010, Nelson *et al.* 2011). Juveniles settle in a variety of habitats including hardbottom areas (Coleman and Koenig 2010) and seagrass and shallow reefs (Colin *et al.* 1996; Koenig, personal observation). All benthic stages enhance their habitat via excavation activity (Coleman *et al.* 2010).

Fishery.—The red grouper fishery is the most productive grouper fishery in the southeastern US, where it is concentrated on the West Florida Shelf (WFS). Red grouper have accounted for nearly two-thirds of the total commercial grouper catch since 1986, primarily from the bottom long-line fishery (Schirripa *et al.* 1999). The species is not only important economically; it is important ecologically and may even serve in the capacity of a 'keystone' species because of its habitat-constructing behavior (Coleman and Williams 2002). This species, because of its very limited home range and tremendous investment in habitat structuring, is readily protected by areal closures.

[2] Sequential hermaphroditism in which individuals change from female to male over their lifetime.

Red grouper sex ratios have not changed significantly over the last 40 years (Coleman *et al.* 1996), but the effect of fishing on reproductive output is unknown. It is possible that if males are lost from haremic groups through fishing, the remaining females forego spawning that season. Evidence for this comes from the observation of masses of eggs in the process of resorption in the ovaries of many red grouper females (Fitzhugh, NMFS Panama City, personal communication).

Scamp

Life cycle.--The scamp spawning season broadly overlaps that of gag but is more protracted, extending into May (Coleman *et al.* 1996). Locations of scamp spawning are also similar to those of gag, but they use a broader variety of habitat types (Coleman *et al.* 2011). Similarities between gag and scamp extend to the mating system; both species are protogynous and form female-biased spawning groups. Although courtship behavior in gag has not been observed, it may be similar to the pattern displayed by scamp, wherein males patrol among females, occasionally chasing a female while displaying an ephemeral color pattern ("gray head" as described by Gilmore and Jones 1992). Scamp juveniles occur on shallow (15 to 25m) reefs and rarely enter estuaries.

Fishery.--The scamp fishery of the Gulf of Mexico is much less productive than the red grouper and gag fisheries, so stock assessments are not done. As stated above, scamp reproduction is similar to that of gag and they have experienced a similar decline in male to female sex ratio (Coleman *et al.* 1996).

Red snapper

Life cycle.--The gonochoristic[3] red snapper spawns on shelf and shelf edge rocky reefs. Juveniles occupy relatively shallow low-relief hard bottom and move to deeper sites as they grow (Workman et al. 2002). Adults in the Gulf of Mexico commonly occur on natural and artificial reefs including gas and oil rigs.

Fishery-- Red snapper supports the most important reef fish fishery in the Gulf of Mexico; the fish are taken primarily by recreational fishers (Coleman *et al.* 2004). The stock has been recognized as overfished since the 1980s. Fishing records and anecdotal information (Schirripa and Legault 1999) suggest that large reproductive "sows" (males and females) are caught in deeper waters including shelf-edge areas by the long-line fishery. We documented the spawning of red snapper within MSMR in the late spring and summer on the same sites as gag spawn in the winter and early spring. Acoustic data indicate strong site fidelity in both males and females (Koenig and Coleman 2006) suggesting protection by closed areas.

[3] Separate sexes

MATERIAL AND METHODS

Location of spawning sites

Commercial grouper fishermen are perhaps the most knowledgeable individuals about the location of spawning and aggregation sites for the species they pursue. Thus, we sought their help in locating reef fish spawning sites within and around the MSMR during the first years of our studies. Fishermen agreeing to work with us provided vessels in charter and their expertise throughout this study[4]. We plotted spawning sites identified by the fishermen on the habitat maps we developed with colleagues at the USGS to define our study area. Fishermen told us and we verified that gag spawning in the MSMR was confined to Madison Ridge, a 7 NM ridge in the southern part of the reserve. We estimated that there could be as many as 18 gag spawning sites along that ridge, but we could verify 12.

While we could not certify that sites outside of the reserves were historical aggregation sites because they were so heavily fished, we assumed that those sites identified by fishermen outside of the MSMR were in fact historical aggregation and male-occupied sites based on three pieces of information: (1) the fishermen had been completely accurate in identifying sites within the reserves; (2) they had knowledge of aggregation sites and presence of males at those sites outside of the reserves from having fished them; and (3) our own knowledge of male behavior that indicated that males remain on spawning sites (Koenig and Coleman 2006).

Our initial intent had been to couple spawning sites inside the MSMR with spawning sites outside the MSMR, but this proved futile because of the severe depletion of fish on outside sites. According to the fishermen, prior to the closure of MSMR, gag abundance was so low overall, that many of the fishermen had stopped fishing on these sites. This was a major reason why commercial fishers agreed to allow the Madison Swanson area to become a reserve. Our alternate plan put into action was to use all the gag caught on the shelf edge outside of the reserve for comparison with all caught inside the MSMR.

Geomorphology and Sediment Characterization

Geomorphological features of the sites were described from a combination of side-scan sonar images, multi-beam images, and ground-truthing operations using sediment sampling and videography (described in Coleman *et al.* 2011 and attached here as Appendix III). We collected sediment samples from a series of sites along the WFS to characterize bottom composition. Technical divers (see http://oceanexplorer.noaa.gov/technology/diving/technical/technical.html) were used for these collections as they are able to extend the range of depths surveyed much greater than conventional scuba, often from 170 ft to 350 ft. They made the collections in May 2008 onboard a research cruise funded for us by the National Undersea Research Center (NURC). The intent was to determine the composition of the sediments around the red grouper-excavated pits within the SLMR to determine if they differed within and outside of the pits. All samples were frozen from the time of collection to the time of analysis.

[4] Funds for the participation of commercial fishermen were obtained from the National Fish and Wildlife Federation.

We also collected sediments samples in red grouper-excavated pits in the SLMR in July 2010 as part of the Deepwater Horizon oil discharge work, funded by the BP Gulf of Mexico Research Initiative through the NOAA Cooperative, the Northern Gulf Institute. The vessel of opportunity here was the R/V Seward Johnson and the manned submersible, Johnson-Sea-Link II (JSL II) operated by Harbor Branch Oceanographic Institute-Florida Atlantic University (HBOI-FAU). Sediment samples were retrieved from four such pits at bottom depths of ~70 m using a grab sampler. Collections were taken from the middle and rim of each pit, and from a control site about 100 m away from the pit. Both pre- (2008) and post- (2010) spill sediments samples were analyzed for total petroleum hydrocarbon, volatile and semi-volatile hydrocarbons, and for a spectrum of poly-aromatic hydrocarbons (PAHs). Also, as an indicator for prior oil contamination, nickel and vanadium were analyzed as these metals occur in relatively high concentrations in crude oil.

Collecting biological information

We used all resources available to us to conduct surveys and obtain samples from shelf-edge[5] spawning sites in the MSMR and elsewhere along the northern WFS. For routine sampling, we chartered commercial and for-hire fishing vessels and crew. We also sampled on vessels-of opportunity made available to us by invitation from charter-boat captains and by the Florida Fish and Wildlife Conservation Commission scientists conducting MARFIN-funded research in and around MSMR. In July 2010, we were invited by the HBOI-FAU scientists to participate in a cruise along the WFS, the official purpose of which was to make submersible dives using the JSL II to investigate the effects of the Deepwater Horizon oil discharge of April 2010 on fish and invertebrate communities. We used the opportunity to dive on well-known fishing sites, record data on reef fish diversity and abundance, and collect sediment samples for evaluation of hydrocarbon contamination (see section below on the Deepwater Horizon oil discharge).

Capture and Tagging: We are not aware of any other tagging studies of reef fish on the shelf edge. Because the high mortality rates due to gas bladder embolism by fish brought up from depths of 50 to 100 m researchers only sample destructively. The physiological problems associated with swim bladder embolism when fish are hauled to the surface from such depths results in death in a high proportion of captured fish. However, we developed methods to dramatically increase survival using captures from both trapping and from hook and line captures.

We captured fish with chevron fish traps (2 m x 1.5 m x 0.7 m; mesh = 2.5 x 5 cm; modeled after those used in the MARMAP sampling program; Collins 1990) and with hook and line (for comparison of CPUE inside and out). Baited (cut mackerel) traps were set on spawning sites at depths of 50-100 m and left soaking on sites for 4 to 6 hours. Hook and line fishing was conducted with commercial electric reels fixed to the gunnel (60 lb test nylon monofilament line and single 5/0 circle hooks). To minimize capture release mortality, we raised fish from the bottom to a depth that allowed the swim bladder to increase up to, but not exceeding 2.5 times its volume on the bottom. This is equivalent to bringing a fish to the surface from about a 15 m capture depth. For example, fish caught in 100 meters of water were raised to 35 meters and held there while a diver descended to vent the swim bladder with a specially designed pole spear with a point (= 1 cm diameter, 3 cm long) that penetrated no deeper than 3 cm into the fish just behind the pectoral fin and below the midline. The trapped fish were then raised to the surface slowly, brought onboard the vessel, and released into a large (1000 l) tank constantly refreshed with running seawater. This capture method ensured that fish were not subjected to the often-lethal effects of swim bladder expansion and hemorrhage.

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[5] We define shelf-edge as bottom depths between 50 and 120 m

All biological sampling occurred onboard the vessel. Using non-consumptive methods for those fish we tagged and released, we obtained biopsies of gonads using a small (2 mm) diameter tube inserted into the gonoduct and using a manual vacuum pump we extracted gonad tissue. Gonad biopsies allowed us to determine sex and reproductive condition. We also took total length, excised dorsal fin rays for aging and took fin clips for DNA samples to use in a study on genetic relatedness[6].

Aging: We used dorsal fin rays for aging the fish. Although otoliths are typically used for aging, otolith removal is lethal and therefore not acceptable for tag-release studies. Spines and rays are like otoliths in laying down annuli. Unlike otoliths, in which the opaque zone is considered an annulus, in rays the translucent zones are counted (Chilton and Beamish 1982). We validated spine and ray ages by comparison with otolith ages (validated in other studies).Our method of preparing and scoring spines and rays closely followed that of Debicelli (2005). Two rays were snipped from the bases of the anterior portions of the second dorsal fin of gag, red grouper, scamp, and red snapper using diagonal cutters. Samples were put into labeled envelopes and kept on ice until returning to the laboratory. In the laboratory the samples were boiled for one minute to loosen the skin and muscle tissue which was then washed off while scrubbing with a stiff brush. The rays were then dried at room temperature overnight and imbedded in epoxy resin (Clear Cote Corp., St. Petersburg, FL).

We modified a Graves lapidary trim saw to cut cross-sections of the rays. The saw was outfitted with a plastic fence that was arranged parallel to two parallel diamond blades (9 cm diameter) separated by 1.0 mm. A chuck was used to hold the fin ray in an epoxy-filled tube. The chuck could be slid along the fence at the proper distance from the blades to cut sections at 0.5 to 0.8 mm thick. After each completed section, a 2.2 mm spacer was inserted between the guide and the chuck, advancing the chuck closer to the blade allowing an additional cut which produced two additional sections. Three cuts yielded five sections, which were removed with forceps, rinsed in distilled water, and placed on a labeled microscope slide. Sections were allowed to dry then were covered with Flotexx clear mounting medium. Mounted sections were viewed under a compound microscope at 40x power. Ray ages were validated by comparison with otolith ages in a regression model. Regressions of otolith age against fin ray age are given in our final report on demographics in Koenig and Coleman (2006).

Gag sex ratio: In all captures, we noted the presence or absence of gray-black blotchy coloration on the ventral side (fishermen call these fish "copperbellies', **Figure 2**). Presence of the coloration is a reliable means of determining if a fish is male (Collins *et al.* 1998, Fitzhugh *et al.* 2006), but its absence is unreliable as a means of determining if a fish is female because not all males have this coloration. Thus, gonad biopsies were taken from fish being tagged and released, and gonad samples when feasible to evaluate for the presence of transitionals. In all cases, sampling methodology was consistent across all sample sites, although biopsy quality varied with the size of the fish and the time of the year.
The temporal pattern of female movements – from mid-shelf reefs to the shelf edge to spawn, then returning to the mid-shelf reefs – alters the apparent sex ratio on the shelf edge seasonally. To account for this alteration and to provide a better basis for comparison, we arranged the sex-ratio data into three biologically-relevant periods: the aggregation period (December to March), the post-aggregation period (April to July), and the pre-aggregation period (August to November).

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6 Analysis of genetic samples was subsequently funded by the NOAA Cooperative Research Program (NA04NMF4540213), "Investigating Gag Recruitment Processes Using Otolith Chemical and Genetic Markers"

Movement patterns and spillover

After capture and sampling, all fish were tagged with dart tags in the dorsal musculature just below the first dorsal fin. Some subset of these was also tagged with individually coded ultrasonic transmitter tags (Vemco Company, eight-year battery life). Ultrasonic tags (Vemco, VR16s with an output signal at 69 kHz) were surgically implanted intraperitoneally in selected fish, typically males and large females of gag and red snapper. Fish receiving ultrasonic transmitters were also tagged with dart tags so that they could be easily identified if resighted or recaptured. After tagging, fish were immediately released at the capture site. If sharks were abundant in the area we used a release cage that was designed to open when reaching the bottom, thus releasing the fish directly onto the reef.

Fish movements were monitored intermittently while we were offshore using a surface receiver (Vemco VR60) from the vessel with its attached hydrophone and continuously with *in situ* archiving receivers (VR2s, 15 month battery lives) moored on the spawning sites in MSMR; moorings had subsurface floats so that they were not easily visible from the surface. We experimentally estimated the radius of detection of the VR2 receivers to be about 0.5 km. VR2s continuously monitor the presence of ultrasonic tags which were programmed to emit signals at 2 min intervals. Data records were downloaded at about 6 month intervals and batteries were changed annually.

We tagged fish with ultrasonic transmitters for two reasons:

(1) To determine movement patterns which could be used to estimate home ranges; and

(2) To estimate natural mortality if it could be shown that fishing mortality was zero.

One of the objectives of our study was to calculate natural mortality of gag and red snapper using the Kaplan-Meier statistical method (Pollock et al. 1989 and Pollock et al. 2004) to analyze acoustic telemetry data (using Vemco tags and VR2 receivers moored on the spawning sites). Of course, if fishing mortality occurred in MSMR without our knowledge, our estimates of natural mortality would be erroneously high. So, to confirm no fishing on Madison Ridge, in 2008 we deployed two DSG archiving receivers (loaned by David Mann, University of South Florida) on two gag spawning sites, # 1 and #5 (**Figure 3**) to determine whether there was any near-field (within 1 km) boat traffic.

We assessed populations for a 'spillover effect' occurring around MSMR in several ways:
(1) By determining relative abundance of key species along the shelf edge (making a series of commercial trips from MSMR to SLMR employing fishermen who have fished the area for over 30 years)
(2) By evaluating movement patterns of focal species around MSMR,
(3) By mapping Vessel Monitoring System (VMS) patterns (Federal Register 72(150):49583) from MSMR to SLMR for 2008 to provide insight into areas where commercial fishers focused their effort. Patrick O'Shaughnessy (director VMS program in the southeastern US) provided anonymous VMS data for this study.

The advantage to using commercial fishers for estimating abundance is that they remain on each fishing site until the 'bite' ends rather than leaving while fish are still biting. To make sure they fished the entire shelf edge from MSMR to SLMR while we were aboard, we paid for their fuel. That is, travel distance was eliminated as an issue in their site selection and we made it clear that we wanted to travel down the shelf edge. For-hire fishers were not acceptable for this kind of work because, in contrast to commercial fishers, they do not want to deplete sites, so will move on before the 'bite' ends because they know that they must consistently provide good fishing spots for their clients throughout the fishing season.

Abundance

Patterns of relative abundance inside and outside MSMR were measured in two ways: through CPUE comparisons and by direct observation from the JSLII manned submersible. When we fished with hook-and-line inside and outside MSMR, we recorded the number of hooks (always one per reel) being fished over time at each site. These data were then averaged for each species inside and outside MSMR.

Surveys conducted onboard the JSLII in July 2010 included visual and videographic components. Videos were analyzed by making two count estimates for each species observed, a maximum count and a minimum count. A maximum count is the total number of individuals of a species seen entering the video field; this worked well for sedentary fishes. A minimum count is defined as the maximum number of individuals of a species seen in one video field. It was necessary to use the minimum count on species such as amberjack which tended to circle the submersible so that an individual would be seen multiple times.

Oil contamination in red grouper pits: We include here results from our oil spill work funded by the BP Gulf of Mexico Research Initiative through the NOAA Cooperative Northern Gulf Institute because it directly pertains to the reserves and the surrounding fisheries. Our intent was to determine if dispersed or particulate crude oil from the Deepwater Horizon oil discharge reached red grouper habitat, which we hypothesized presented the possibility of concentrating such particles because they act as natural sediment traps (see Coleman et al. 2010). The continuous excavating activities of the grouper would mix the oil that accumulates in the pit into the sediments and onto the rim of the pit where the grouper deposits them during their excavating activity, potentially having some effect on infaunal assemblages.

RESULTS

Geomorphology and Site Characterization

The seafloor in MSMR is dominated by a gently sloping central sandy region at depths of 80 – 120 m that drops abruptly (~8^{o} slope) to 160 m near the western and southern regions of the reserve (**Figures 3 & 4**). The sandy region is rimmed by rocky ridges across the northeastern corner and along the southern edge of the reserve. The northeastern ridge (Stu's Ridge; **Figures 3 & 4**) consists of several massive beds composed, at least in part, of oolitic packstone. The southern ridge (Madison Ridge; **Figures 3 & 4**) has as a main feature relict delta and barrier island complexes formed 58,000 and 28,000 years ago when slow sea level regression from 55 m to 85 m below present occurred (McKeown *et al.* 2004, Gardner *et al.* 2005). This region consists of a series of rugose carbonate pinnacles rising as high as 8 m above the surrounding seafloor. Some isolated rocky pinnacles occur within the relatively flat sandy central region whereas low-relief rock covered by a thin (<1 m) layer of sand occurs over a large expanse of the seafloor north and east of Stu's Ridge.

The sediments sampled in areas shallower than 120 m are predominantly carbonate sand or gravel, with greater than 90% $CaCO^3$ content, whereas those deeper than 120 m are predominantly sandy silty clay, with 65% to 80% $CaCO^3$ content.

The four most distinct geomorphologic features in the MSMR considered candidate grouper-snapper spawning sites were: (1) the high-relief ridge (Stu's Ridge) within the shelf terrace, (2) the high-relief ridge (Madison Ridge) along the relict delta shelf-edge drop-off, (3) the isolated rocky pinnacles, and (4) low-relief hardbottom covered with a veneer of sand.

High-relief ridge within the shelf terrace ("Stu's Ridge")

Geomorphologic features. -- This single arching feature within the shelf terrace crosses the northeastern boundary of the reserve and consists of tabular carbonate packstone slabs at a depth of ~70 m (**Figure 4**). The ridge extends about 5.6 km (3 NM) within the reserve and an approximate equal extent northwest of the reserve boundary; it is not associated with the delta-edge margin. The ridge face rises ~10 to 20 m, sloping almost vertically to the west and southwest where it is bordered by a mote (depth, 3 m). To the east and northeast, it grades into low-relief hardbottom covered with a veneer of carbonate sand and occasional boulders jutting through the sand. The base of the ridge has an accumulation of large boulders that broke off the top of the ridge, giving it the appearance of a talus slope (Scanlon *et al.* 2003).

Spawning observations.—Fishers did not report gag in this ridge area. In our survey of this area, few gag appeared on Stu's Ridge. When they did appear, they were not aggregated and showed no signs of spawning. Scamp occurred commonly, and exhibited spawning activity from the top of the ridge down to the talus slope. Females dispersed over an area of several hundred square meters while males patrolled among them, occasionally displaying to a female in the gray-head phase, similar to observations of Gilmore and Jones (1992).

High-relief ridge along the relict delta shelf-edge drop-off ("Madison Ridge").

Geomorphologic features.--This 12.9 km (7 NM) ridge occurs along a steep relict delta shelf-edge drop-off (**Figures 3A & 3B**), running northeast to southwest in the southern part of MSMR, gradually slopes from ~80 m at the eastern end to ~110 m at the western end. The drop-off south of the ridge extends to a depth of 150 m. Along the ridge, the rock structure has variable relief, with the eastern end of higher relief (up to 8 m) than the western (typically less than 2 m).

Spawning observations.--Six spawning sites surveyed along Madison Ridge had numerous gag and scamp, but few red grouper. The greatest density of gag spawning aggregations was found along this rocky ridge at the southern edge of the relict delta formation drop-offs (known to fishers as "breaks") (**Figures 3A & 3B**) and near other moderate-relief shelf-edge features. Gag spawning sites averaged about two sites per linear 1.8 km (1 NM). Gag in spawning aggregations occurred at heights up to 10 m above the seafloor, and appeared less tightly associated with structure than were the smaller scamp (Gilmore and Jones 1992, and this study).

Isolated rocky pinnacles

Isolated pinnacles appear as 5 to 10 m relief structures (depth, 70-80 m) surrounded mostly by sand and mud, occurring near the center of the MSMR (**Figure 4).** Neither grouper spawning aggregations nor courtship behaviors were observed in this region of MSMR.

Low-relief hardbottom covered by a thin veneer of sand

Geomorphologic features.--This area is located in the northeastern corner of the reserve, east of Stu's Ridge (**Figure 4**), and is littered with exposed rocks or boulders.

Spawning observations.--Fishers identified two gag spawning sites in this region associated with large exposed rocks of about 2 m relief. We observed no gag or scamp spawning aggregations on these sites, although both species occurred there.

Red grouper, however, were abundant in this area (Coleman *et al.* 2011, Nelson *et al.* 2011); they appear to prefer low-relief hardbottom. Red grouper exhibited courtship behavior and putative courtship sounds on the rocky flats to the east and northeast (**Figure 4**). This behavior entailed a single female approaching a male as she developed a distinctive barred color pattern. The male's color pattern also changed so that his back was intensely black, and white lines radiated from the eyes backward onto the black back. The male would invariably follow the female which would end in a spiraling spawning ascent (Nelson *et al.* 2011).

Size and Age structure

Except for scamp, the sizes of economically important reef fish captured inside MSMR were statistically significantly larger than those captured outside (T-tests, $p < 0.001$) (**Figure 5**). Size frequency distributions of gag (**Figure 6**), red snapper (**Figure 7**), and red grouper (**Figure** 8**)** show a clear and statistically significant shift in size distribution to the right for fish captured inside the MSMR relative to those outside. Ages (as determined from dorsal fin rays) were significantly greater ($p < 0.01$) inside MSMR for gag, red grouper and red snapper, but not for scamp (**Figure 9**, Table 1).

Gag sex ratio

Because only part of our samples were analyzed histologically, we standardized our sample to fish sizes 75 cm TL or greater based on the gag maturity ogive by Fitzhugh et al. 2006 (Appendix 1) for GOM gag to be certain that comparisons were only with mature fish. All juveniles are female, so including them would artificially lower the proportion of males in the sample. Considering that males smaller than 75 cm would be rare, we felt that this size cut-off produced the best comparison among samples: inside MSMR, outside MSMR and historical samples collected between 1977 and 1980 (Hood and Schlieder 1992).

Overall, the percentage of gag males (plus transitionals, the presumptive males) within MSMR increased significantly ($p < 0.0001$) over that outside of the reserve during our 3-year sampling period from December 2007 to December 2010 (**Tables 2 and 3**). Comparison of the historical proportion of males (**Table 4**, Hood and Schlieder 1992) with the present proportion within the reserve was also significantly different ($p < 0.0001$). These comparisons indicate that the percentage of males within the reserve has increased over that outside, but has not yet reached the historical level.

Seasonal comparisons of the percentage of males (**Tables 2 and 3**) also showed that the percentage of males within the reserve increased significantly over that outside with the exception of the aggregation period, where differences were not significant ($p > 0.05$). Comparison of the seasonal percentage of males inside MSMR with historical data (**Table 4**) showed a significant difference ($p < 0.05$) for all seasons except the post-aggregation period ($P > 0.05$). The lack of significance for this period is due in large part to low power of the test (power = 0.39) resulting from our small sample size. So, although the recent post-aggregation percent males for MSMR is relatively high (15.6%, **Table 2**), it is not correct to interpret the lack of significant difference from historical (24.8%, **Table 4**) as the two values being indistinguishable, but rather, low test power did not allow us to discern a difference.

The gag population has suffered a dramatic truncation of the size distribution (**Figure 10**). This was demonstrated in the early 1990s (Koenig *et al.* 1996) and persists today to a greater degree. Size truncation presented a problem when we standardized our samples for sex ratio. Outside of MSMR we sampled 630 gag, but only 205 of those fish (32.5%) were 75 cm or greater in total length. Thus, most of the gag we sampled on the outside were juveniles or recently matured adults. Inside MSMR, we sampled 290 gag and 183 (63.1%) were 75 cm TL or greater. Thus, even with a very large sample size on the shelf edge outside MSMR, we were left with very few mature gag with which to make our sex ratio comparisons.

Catch per unit effort (CPUE) for economically important species (gag, red grouper, red snapper, scamp, vermilion snapper, greater amberjack, and almaco jack) inside MSMR was significantly higher than CPUE for these species outside the reserve (Mann-Whitney test, $P<0.0001$) (**Figure 11**). Commercial and charter boat captains, whose boats we chartered to do our work, also commented on the relatively high abundance of fish inside MSMR. They would say that the abundance inside the reserve was similar to what they observed many years ago for the whole shelf-edge area.

We used catch from six commercial reef fishing trips to estimate patterns of reef fish abundance from MSMR to SLMR. Commercial catches provide a better estimate of site abundance than for-hire catches because commercial fishers fish a site until the "bite" stops, while for-hire fishers leave a site before the "bite" stops because they do not want to deplete a site that will be fished again with new clients in the following days. Abundance patterns from these commercial reef fishing trips suggest 'spillover' abundance around the reserve for gag and red snapper, but not for other species (**Figure 12**).
Gag abundance was clearly higher around MSMR than in other fished locations along the shelf edge (**Figure 13)**. Regression of catch abundance to distance from MSMR was significantly negative ($P = 0.002$; **Figure 14**) indicating a higher abundance around the reserve relative to distant from the reserve along the shelf edge. Red snapper also showed an affinity for the region around the reserve, albeit a weaker one (linear regression, $P = 0.058$; **Figure 15**).

Spillover around MSMR is implied by the relative abundance patterns of gag and red snapper (**Figures 14 and 15**), and by anecdotal evidence provided by several fishermen operating in and around MSMR for over 30 years. Commercial and for-hire fishermen stated to Koenig that they now catch a "better class of fish" when they fish around the reserve relative to the time prior the installation of MSMR. When pressed as to what "better class" meant, they stated that the fish were more abundant and larger than they had been before the closure or MSMR. Many fishermen who consistently fished around MSMR and have before the reserve was in place signed a support letter ("Fishermen Amendment 30B Action 11 Support Letter," available on the web) acknowledging the spillover benefits of the reserve and their desire to have other shelf-edge reserves put in place.

We also determined where commercial fishermen are spending their time offshore (in 2008) as an indication of places where the fishing was relatively good. In our plot of VMS (**Figure 16**) data, each point indicates the hourly position of a commercial vessel. The denser the dots, the more often a commercial vessel was present. In some areas the dots are so thick that they are seen as black areas rather than as discrete dots. These black areas along the shelf edge represent locations where commercial fishers spend most of their time while offshore, indicating these areas can be assumed to be important fishing areas. Fishing effort appears to be most intense to the immediate north and east of MSMR, and to the south of the reserve along the 40 fathom (70 m) isobath. Fishing is also concentrated to the east of the 'Edges' (due N of SLMR). These VMS data corroborate the relative abundance data collected from commercial fishing trips in that they show a relatively high fishing effort around MSMR.

A plot of the number of position records km^2 (**Figure 17**) shows a high density within 10 NM of MSMR, with a uniform decline with distance from the reserve until about 50 NM from the reserve where more inshore areas are included in the data and red grouper become more important in the catch (**Figure 12**).

Abundance, Movement, and Spillover (economically important species)

_Relative Abundance Patterns (Threatened and Endangered Species).—_Data from our hook-and-line catches from 2008 to 2010 and from submersible dives made aboard the JSLII suggest that populations of threatened species like Warsaw grouper (**Figure 18),** speckled hind, and snowy grouper are more common in MSMR than in any other reef sites along the shelf edge of northeastern Gulf of Mexico, including SLMR (a marine reserve), The Florida Middle Grounds (an HAPC, protected only from trawling and collection of coral), and several other sites that lack any form of protection (**Figure 19**). Warsaw grouper captures made by hook-and-line are indicated in **Figure 20** and from video surveys on the JSLII in **Figure 21.** Speckled hind captures made by hook-and-line are indicated in Fig**ure 22** and from video surveys on the JSLII in **Figure 23.** Snowy grouper captures made by hook-and-line are indicated in **Figure 24** and from video surveys on the JSLII in **Figure 25.**

It is clear that endangered (IUCN designation) Warsaw grouper and speckled hind are strongly associated with MSMR. These shelf-edge and slope species were only found in and immediately around the MSMR and nowhere else along the shelf edge (**Figures 20-23**). Snowy grouper were also only found in the vicinity of the reserve (**Figures 24 & 25**). These data provide strong evidence that no-take zones protect these deep-water species which are highly vulnerable to capture-release mortality.

Snowy grouper were observed (two independent observations) in association with excavations in the southern portion of MSMR (**Figure 26**). The excavations were on clay bottom with a slope of about 8 degrees. We have documented that red grouper dig pits throughout their lives (Coleman *et al.* 2010), but no such activity has been reported for snowy grouper, so we do not know if this is a typical behavior and habitat for this species. If snowy grouper do excavate these habitats—which would not be surprising given similar activities noted among their congeners—we would expect that they would also be sedentary and that many other species might derive refuge as a result of their excavating activities.

_Movement patterns.--_Movement patterns for tagged (dart tags) and recaptured economically important reef fish in this study are depicted in **Figure 27.** Most of the species tagged were red snapper and they typically moved very little with few exceptions. One gag tagged inside MSMR moved outside of the reserve and another moved from the southern end to the northern end of the reserve. Overall, movement does not appear to be directional for any species.

Illegal fishing in MSMR.-- We found intense fishing being conducted at night along Madison Ridge in 2008 and 2009 (Table 6, **Figure 28**), often in the early morning hours. We also recorded many boat sounds in the daytime (**Figure 29**), but had to discount them because illegal fishing activity was indistinguishable from that of vessels conducting research (the NMFS-Pascagoula Lab and our project vessels) and recreational vessel conducting legal trolling. The recreational trolling fishery[7] is allowed to operate within the reserve from May to October, just outside of the time frame we monitored (with the exception of early May).

We identified poaching occurring within the reserve, despite the fact that such activity is illegal and despite that fact that all licensed commercial vessels (including commercial and for-hire reef fish vessels) are required to have VMS since 6 May 2007 (Federal Register, vol. 72, no. 150, p. 43583). Apparently, poaching was done onboard vessels that either lacked VMS systems or had them turned off.
Koenig reported to the USCG several incidents of apparent poaching. For one incident, he provided the USCG with copies of the data presented here. The USCG subsequently apprehended three poachers fishing at night along Madison Ridge (USCG personal communication with Koenig), but would not provide any details of the arrests. Because of the continuous poaching, our objective to estimate natural mortality was abandoned since the illegal fishing effort would have biased the estimates high.

Koenig reported another apparent poaching incident to the USCG on 7 May 2008 that involved a commercial fishing vessel stern anchored in SLMR right in our research area where dense concentrations of red grouper occurred. According to USCG officials, the vessel had VMS onboard, but it was not operating at the time of our observations, and had not been operating for 5 days prior to our arrival (see letter to NMFS SE Regional Office for details, Appendix II).

Experienced commercial and for-hire fishermen working with us expressed how impressive they found the abundance and size of economically-important fish within the reserve. They told us that a poacher could easily catch 454 kg (~1000 pounds) per night on Madison Ridge. We contend that fishing of that intensity would present a serious impact to the 15 aggregation sites we monitored, and certainly could hinder recovery of the distribution of sexes in the population. Such fishing intensity may explain the rather slow recovery of sex ratio in this population.

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[7] We (Koenig, vessel captain, and crew) have repeatedly observed vessels trolling at less than 4 kts along Madison Ridge. When fishing at these speeds, trolling fishermen using downriggers could easily access the reef fish at 250 to 300 ft. depths.

DISCUSSION

Size and age structure and illegal fishing

Increases in mean size and age of species protected in no-fishing zones support the assumption of limited movement (small home range relative to the size of the reserve) and effective enforcement of the reserves. Limited movement has been observed many times in Marine Protected Areas. However, MSMR has been closed to fishing for a decade, so size-age differences would be expected to be greater than observed in this study. Undoubtedly, continued poaching on Madison Ridge, including night-time poaching and recreational fisher slow-troll poaching reported here and pre-VMS commercial poaching in the past explains at least in part the limited differences in size-age structure (and gag sex ratio recovery) between inside and outside. Clearly, the effectiveness of MSMR, and any other reserve, requires continued enforcement, day and night, and stiff penalties for illegal fishing.

The recreational pelagic trolling fishery is permitted to operate in MSMR from May to October each year (Federal Register 71(190):58168). Researchers at the NMFS Panama City Lab (lead by Andrew David) demonstrated clearly that an observer, such as a USCG agent, could not discern fishing depth of a trolling vessel, regardless of the speed of the vessel. They also demonstrated that a trolling vessel could catch reef fish at the depth of Madison Ridge--which is about 75 to 91 m (250 to 300 ft)-- if they trolled at 4 knots or less. Despite the fact that the federal law prohibits deep trolling, prohibits possession of reef fish, and requires that trolling vessels operate at speeds faster than 4 knots when trolling within MSMR or SLMR, circumventing these requirements is simple. Someone trolling can easily speed up to escape detection or dispose of any catch they've caught via deep-trolling before being boarded. The law appears to be difficult if not impossible to enforce.

To increase the efficiency of surveillance of marine reserves, better technology and techniques are required by the USGS. The VMS method appears to work well and should be continued, but its weakness lies in the fact that it is limited to commercial vessels. Thus, recreational vessels go undetected and unlicensed commercial vessels can fish at night in the reserve and then transfer their catch to a licensed vessel outside of the reserve.

We demonstrated in this study that simple acoustic receivers can be used to monitor boat traffic in marine reserves. In fact, we found that the quality of the recordings was sufficient to allow an acoustic analyst to identify individual vessels. The technology to transfer the surveillance information to a shore-based facility via satellite also exists, using receivers that are programmed to surface and descend once the information is transmitted. Such receivers could also incorporate radar for real-time surveillance. If the USCG would use similar devices strategically placed throughout the reserve, they could effectively monitor these sites year-round with significantly reduced effort and likely reduced cost. Such monitoring devices, whether they be based on acoustics or radar or both, add to the initial cost of the reserve, but may reduce cost in the long run. Nevertheless, surveillance devices add to the initial cost of the reserve, so should be considered in the early planning stages.

The primary impetus for our trying this acoustic method of surveillance was the lack of support from the USCG for conducting investigations and the reticence with which we were met by officials, who were unwilling to release any surveillance data, all of which they considered classified. Based on a simple calculation of the timing of poaching events coupled with opportunities for the USCG to make random surveillance flights, we determined that the USGS had a 95% chance of encountering poachers if they made seven night time surveillance flights per year during the time between midnight and dawn. We have no actual data on the number of surveillance flights made nor on the time at which they may have occurred. The USCGs reluctance to provide data to researchers may be warranted if there are real security risks. However, they do have a real obligation to NOAA – who provides them with funds for enforcement of fishery regulations—to provide a full assessment of how those funds are being used and to what end.

Gag sex ratio

Several questions are relevant to the analysis of a loss of the proportion of males in the population since the time when Hood and Schlieder (1992) collected gag for their study in the late 1970s:

(1) Has the sex ratio of gag changed from the 1970s to now?
(2) If the sex ratio has changed, what mechanisms are likely responsible for that change?
(3) What consequences would likely result from a low sex ratio?
(4) What are the appropriate management options?

The first question can be addressed by comparing historical and present catch data. Temporal comparisons must be made in the same areas and with the same sampling gears. In the GOM, Hood and Schlieder (1992) collected gag samples from November 1977 to May 1980 around the Florida Middle Grounds (R. Schlieder personal communication) from commercial vessels. Commercial vessels targeting gag use hook-and-line, typically with electric reels, although gag are sometimes taken with bottom long-line gear—long-line collections are not included. Koenig et al. (1996) collected samples in 1992 from commercial vessels along the shelf edge extending from the area south of MSMR to the area west of the Middle Grounds, so historical and recent areas of capture overlap.

Gag samples from the South Atlantic region were collected off South Carolina in the late 1970's (Collins et al. 1987) and from North Carolina to Florida in the mid 1990's (McGovern et al. 1998). Samples from the catch of a single commercial fisherman in the 1990's operating off southern Georgia at shelf-edge depths contained a proportion of males in the catch that approximated that of the late 1970's (McGovern personal communication). All the rest of the catch samples were similar to the recent samples from the Gulf, that is, with a low percentage of males ranging from 1 to 5%.

Estimating the sex ratio of gag requires that both spatial and temporal factors are taken into account. Males remain on shelf-edge reefs year-round (Koenig et al. 1996, Coleman et al. 1996) in close proximity to their spawning sites (Koenig and Coleman 2006) and most females migrate seasonally between the shelf-edge spawning sites and home sites on the shelf. So, sex ratio patterns on the shelf edge change seasonally. Arranging the data into three biologically relevant seasons, December to March (aggregation period—including pre-spawning aggregation), April to July (post-aggregation period), and August to November (pre-aggregation period) provides a better basis for comparison because most females migrate to and from spawning sites on the shelf edge while males remain on those sites year round. Thus, the proportion of males on the shelf edge changes seasonally.

As seen in **Tables 4 and 5,** seasonal comparisons of the percentage of male gag in the commercial catches of the late 1970's relative to the early 1990's show significant differences in both the Gulf of Mexico and in the US South Atlantic. Our recent data from the Gulf indicate that the sex ratio has remained low up to present times (**Table 1).** So, question 1 can be answered unequivocally: yes, the proportion of males in the gag population of the US South Atlantic and the Gulf of Mexico has declined and has remained low to the present.
<u>What mechanisms are involved</u>*?* At the root of this question of mechanisms involved in the decline in the proportion of males is the mechanism of sex change itself. Is the sex change mechanism endogenous, based on a trigger at a certain size or age, or exogenous, based on a socially mediated trigger? If one postulates an age- or size- related sex change, then truncation of the size distribution, which was shown by Koenig et al. (1996) for the Gulf population, could explain the decline in the proportion of males. In this case, increasing the size and age distribution would increase the proportion of males. However, if this is the mechanism it would be an exception to the general mechanism of sex change in the vast majority of species studied, including groupers (Warner 1988).

Behaviorally induced sex change is clearly the most parsimonious explanation for sex change in gag, as deduced from the many other studies of sex change in fishes (Shapiro 1979, Warner 1988, Ross 1990). It is far less likely to be under some endogenous control triggered at some age or size. To directly infer social control in gag, certain criteria must be met:

- Protogyny must be demonstrated, which it has been (McErlean and Smith 1964, Hood and Schlieder 1992, Coleman *et al.* 1996)
- Reproduction in gag must occur predominantly within aggregations that are consistent in time and space. This has been demonstrated repeatedly in the Gulf and in the Atlantic (Koenig et al. 1996, Coleman et al. 1996, Collins et al. 1998, McGovern et al. 1998, Gilmore and Jones 1992), and is well-known by fishermen in both regions.
- Relevant information, such as mating sex ratio or size ratio, is available to gag at the time of aggregation when the fish are together in mating groups, and not at other times.
- Gag aggregations are consistent in space and time. Most females disperse in April from the shelf-edge to the shelf environment while males stay at shelf-edge depths where they remain year round associated with their spawning sites (Coleman, Scanlon, and Koenig 2011, NOAA MARFIN final report NA17FF2876).
- Sex change occurs in temporal proximity to the aggregation period. The relative proportion of transitionals to males is significantly ($P < 0.001$) higher immediately post-spawning than it is either during the spawning season (Dec – Mar) or just prior (Aug-Nov) to spawning (Table 6).

In all protogynous species of fish that have been studied, the mating system consists of large males that monopolize the matings of females (Warner 1988). That the larger fish in a population become male is exactly what the size-advantage model for sex changing species predicts (Ghiselin 1969, Warner 1988). The model predicts that the circumstances required for sex change are largely related to the mating system. The reproductive success of these large males surpasses that of large females because it includes not only the fecundity of the female (which is the size advantage to females) but also the number of females with which he mates. In other words, he can contribute his genes to many more offspring than she can. He also monopolizes the matings of those females by being large. It has been suggested that the size at transition is determined by the size of the largest females in the social group, as Shapiro observed with the serranid bass, *Pronotogrammus (ex-Anthias) squamipinnis* (Shapiro 1979). Of course, it is also possible that there is some genetic predisposition to change sex at sizes above a certain threshold minimum size. It would be difficult to select between these two possibilities, but the former is most likely based on **Figure 30 and Figure 31**. That is, the youngest males found were at the approximate age of maturity, 3 to 5 years old—they only had to be mature for transition to occur.

So, the answer to the second question is that the main mechanism of sex change is highly likely to be based on social interactions at the time of aggregation. The mechanism of fishing-induced loss of males is directly related to the mechanism of sex change and is discussed below.

<u>Proposed mechanism of loss of males</u>: The data suggest an exogenous (facultative) sex change in gag (as with virtually all other protogynous species). We suggest the following conceptual model to explain loss of males in the gag population of the Gulf and US South Atlantic regions:

- Sex change is induced in females during the spawning period when males and females are in a social group. Thus, information relevant to sex change (e.g., sex ratio, size ratio, dominance hierarchy, etc.) is available only during the aggregation period. Sex change induction at the aggregation time (i.e., the timing of sex change) is supported by the occurrence of a high proportion of transitionals in the post-spawning period and not in other times of the year. (However, a very low number of transitionals were observed after the pre-spawning aggregations which suggest that a limited level of sex change can be induced in the all-female pre-spawning aggregations as well.)
- Males remain in association with spawning sites year round as demonstrated by acoustic tagging by Coleman and Koenig (2006, NOAA MARFIN final report NA17FF2876).
- Most females leave the spawning sites at the end of the aggregation period leaving a higher proportion of males and transitionals on spawning sites. This increase in the proportion of males (and transitionals) in the post-aggregation period can be seen in tables 2, 4, and 5.
- Fishermen continue to target the spawning sites after the spawning season. This is because other fishery species besides gag, such as red snapper (spawn on the gag sites during spring and summer), greater amberjack, almaco jack, red porgy, and scamp, are associated with gag spawning sites (see data in this report and in Coleman and Koenig (2006), NOAA MARFIN final report NA17FF2876).

Although there is a decline in the catch per unit effort during the post-aggregation period (Koenig et al. 1996) there is an increase in the absolute catch of males. Two data sets show this general pattern, one is from a commercial fisherman's log book (**Figure 32**) and the other is from Collins et al. (1998; **Figure 33**). In the logbook study a single commercial fishermen, after changing professions, presented his logbook data on gag to the NMFS Panama City Lab. In the Collins et al. (1998) study fish houses were requested to report all 'copperbellies' to the NMFS Panama City office. It is clear that the absolute catch of males is high during the post-aggregation period relative to the aggregation and pre-aggregation periods. This loss of males after the aggregation period short circuits sex change compensation, so the following spawning season there is again a paucity of males in the spawning aggregations. In effect, the gag population is constantly compensating for a low proportion of males but never attaining an equilibrium proportion of males on the spawning sites.

Because males are caught after the spawning season, the only meaningful protection would come from year-round closures of the spawning sites by setting aside marine protected areas or no-fishing zones. Seasonal closures do virtually nothing to protect the male component of the gag population and therefore do little to nothing to protect spawning. This is especially true in the areas such as the "Edges" and "Snyder Ridge" that once contained numerous gag spawning aggregations, but are now severely depleted according to our field sampling data.

Movement Patterns and spillover

To evaluate spillover conclusively, it is necessary to set up a before-after-control-impact (BACI) experimental scenario. Such a field experiment would be a luxury in fishery science where politics and science intermingle. Thus, we do not have regional abundance data from before the MSMR was put in place and we have only one MSMR, so we are left with the task of evaluating patterns and abundances post-closure. Our approach, then, was to collect as much information as possible on fish movements, fishing patterns, fish abundance patterns inside and outside of the MSMR, and the opinions of fishermen who had fished the area for over 30 years to provide evidence for or against spillover.

VMS data for 2008 imply that commercial fishing is heavy around MSMR, which, in turn, implies that fish abundance is high in that area. In other words, fishers concentrate their effort in locations where fish abundance is high. Relatively high commercial catches, especially of gag and red snapper, around MSMR and anecdotal comments from local fishers provide additional evidence for high abundance around the reserve. One dominant commercial and for-hire fisherman of the region, Captain Danny Tankersley of Port St Joe, who was initially opposed to the MSMR, stated that the reserve is the "best form of fishery management that he has seen yet". He also stated that he would like to see more shelf-edge reserves in the region. Other regional fishermen have made similar statements. Such statements strongly imply that fishing has improved in the vicinity of MSMR since its establishment in 2000.

Because juvenile habitat for our focal species is distant from MSMR, there is no build-up of populations within the reserve based on juvenile recruitment to the reserve. Thus, on shelf-edge reserves, spillover must come from movements of fish to and from the reserves. Data from our shelf-edge commercial fishing trip surveys show a clear association of gag with MSMR. Such a pattern is likely the result of females going to and from viable spawning sites in the MSMR. That is, females become susceptible to fishing while en route to and from spawning sites. Evidence supporting this mechanism comes from the movements of two gag, one moving to the east out of the reserve and the other moving to the northern border of the reserve. In a strict sense, this is not spillover, but attraction of gag to MSMR spawning sites. If spawning sites are not functional (i.e., fished out) in other areas of the shelf edge between MSMR and SLMR, and only functional in MSMR, then movement, and catch, of female gag would be most prominent around MSMR, which is what we observed.

Gag catches on commercial fishing trips were sparse in shelf-edge locations distant from MSMR. Areas to the south, the “Edges” and “Snyder Ridge”, where gag spawning aggregations were once abundant (Koenig and Coleman 2006) were virtually devoid of gag in this study. Does this mean that the shelf-edge gag aggregations of the NE Gulf of Mexico are all depleted and non-functional, except for those in MSMR? We don’t know, but if this is the case, then management measures that purport to protect spawning of the entire population by implementing seasonal closures of the shelf-edge areas south of MSMR in reality do nothing to support long-term sustainability.

In MSMR, red snapper spawn on gag spawning sites during the spring and summer (Koenig and Coleman 2006). If movement around these spawning sites is similar to that of gag, then that would explain the increased abundance of red snapper around MSMR. However, movements of tagged red snapper were limited and non-directional, similar to patterns observed by Patterson et al. (2001) for the northern Gulf of Mexico.

<u>VMS data as corroborative evidence for spillover effect</u>: ‘Spillover effect’, or the increase in fish around a reserve, likely combines both movement of fish out of the reserve and attraction of fish to the reserve. Clearly, for many species including gag, red grouper, red snapper, and scamp, juveniles settle and grow to maturity in relatively shallow areas remote from the shelf edge. After reaching maturity, they migrate, sometimes great distances (e.g., McGovern et al. 2005), to deeper waters. Thus, increased fishing success around the MSMR, which has been claimed by fishers with a long history of fishing in that area (e.g., Danny Tankersley of Port St Joe, FL and Chuck Guilford of Mexico Beach, FL) likely combines both movement of fish over the reserve boundaries and migrations related to spawning.

VMS data provides an indication of where commercial vessels concentrated their fishing effort in 2008. Effort, as indicated by hourly logging of the position of commercial fishing vessels on the shelf edge, is concentrated to the north and east of MSMR and down the shelf edge to Steamboat Lumps. Other areas of concentration are inshore, especially in the SE portion. Commercial vessel positions (detections per km^2) relative to distance from MSMR are most commonly recorded within 10 NM of the reserve, but records decline precipitously between 15 and 40 NM, then increase again. Increases distant from MSMR are due in large part to fishing areas inshore of the shelf edge. It is possible that closures in the areas south of MSMR, such as the Edges and Snyder Ridge would increase fish abundance around those closed areas similar in the way they increased them around MSMR. If they do, then several benefits may result, as they apparently did in and around MSMR—protection of the spawning of gag, scamp, red snapper and other species, protection of the gag sex ratio and improvement of the fishing around the closed area.

A large-scale experiment could be devised using a BACI (Before-After-Control-Impact) experimental design (e.g., Underwood 1994) to test the hypothesis that installing shelf-edge reserves in the US Gulf and SATL would result in not only protection of the reproductive output of shelf-edge spawners, but also provide a direct benefit to fishermen in terms of an increased abundance of fishery species around the reserve, as implied by the data presented in this report. We know that gag and probably scamp spawn exclusively on the shelf edge and that red snapper, red grouper, scamp, vermilion snapper and many other species also spawn on the shelf edge (Sedberry et al. 2006) as well as on the shelf. Thus, if the experimental results support the hypothesis, then the spawning of dominant reef fishery species would be protected with only temporary impact on the shelf-edge fishery.

An experiment could consist of initial 3-year monitoring of the fish abundance (e.g. ROV transects) and catches on fished reefs in 6 selected shelf-edge areas of the US Gulf and SATL. All 6 areas would be large enough to contain a 100 NM^2 reserve (like MSMR) and an area surrounding the reserve by at least 10 NM radius. After the 3 years of monitoring, three randomly selected reserves would be closed to fishing and three would serve as controls and left open to fishing. Researchers would continue to monitor fish abundance in all areas, open and closed, and fishery catches in all open areas for 10 years after closure to determine if fish abundance and catches increase outside the closed areas and to compare before and after closure catches in both control and test areas. Sites for these experiments must be high quality fishing areas, such as the Edges in the northeastern Gulf and multiple sites in the SATL (see Sedberry et al. 2006). Of course, surveillance and enforcement would be key elements of this study.

Threatened and Endangered species:

We observed threatened and endangered (IUCN) species (Warsaw grouper, speckled hind, and snowy grouper) on the shelf edge only in association with MSMR. Data came from both our fishing records and from direct observation with the JSL II submersible in July 2010. The most plausible explanation for this pattern is that these fish are being lost outside the reserve via incidental catch. Fish caught at shelf-edge depths or deeper frequently die from gas bladder embolism and hemorrhage (Burns, Koenig and Coleman NOAA MARFIN NA87FF0421; Koenig, personal observation). Because these species are nearly always associated with the shelf edge and slope, they are especially vulnerable to catch-release mortality. Because the population levels of these species are considered very low, it is important to protect the remaining component so that population recovery can take place. At present the only protection is catch limits, but this form of management does little to protect the species because fishermen catch them inadvertently, and if they are caught, they die, regardless of whether or not they are released.

Potential benefits of shelf edge closures: Multiple benefits would likely result from the permanent closure of large areas of the shelf edge of the northeastern Gulf to all fishing.

1. *Regain the evolutionary equilibrium sex ratio for gag*. The male gag population will be protected with the likely result of increased reproductive output. The data presented in this report provides strong evidence for a year-round closed area regaining the natural sex ratio of about 1:5 males to females in gag and therefore future insurance against declines in reproductive output.

2. *Increase in size and age of females*. We've observed an increase in the size of gag females. Large females produce exponentially larger numbers of eggs, so the output of fertilized eggs will likely be much greater in spawning areas protected year-round. It has been shown that larger and older females produce eggs of higher quality which gives them a better survival potential (Berkeley *et al.* 2004b, Birkeland and Dayton 2005).
3. *Stabilize recruitment*. Recruitment of gag as evidenced from annual relative abundance estimates of juveniles in the seagrass and in the age structure of the adult population has been extremely variable annually since we first started our seagrass monitoring in the early 1990s (Ingram and McEachran 2009). If the reproductive population of gag along the shelf edge could recover to some historical size, age and sex ratio, it is likely recruitment will be much less variable. This is because survival potential of offspring from gag spawns is expected to vary annually with spawning location, so a higher recruitment potential overall would result when spawning areas are protected over a wide geographical distribution (Berkeley *et al.* 2004b).
4. *Protection of reef fish spawning and nursery habitat*. We and other researchers (e.g., Sedberry *et al.* 2006) observed that many economically important reef fish spawn on shelf-edge reefs, some such as scamp and red snapper spawn directly on or near gag spawning sites and maintain populations in the vicinity of those sites year round. Other species would benefit from shelf-edge protection, including red grouper, vermilion snapper, red porgy, creolefish and a host of smaller species also spawn on the shelf edge, but not on gag spawning habitat. The shelf edge also appears to provide nursery habitat for threatened species such as Warsaw grouper and speckled hind. Protection of this habitat would protect both spawning and nursery habitat for a variety of species (Koenig *et al.* 2000).
5. *Spillover benefits*: Reef areas surrounding the closed area will be more productive. There is strong evidence from our studies that spillover benefits are occurring around MSMR, so the same benefits could be expected from other areas around the shelf edge. The evidence of spillover comes from VMS data, our own catch and submersible observational data, and anecdotal information from fishermen who have fished around the reserve for over 30 years. The most pronounced effect can be seen in gag and red snapper, and effect that most likely results from fish moving to and from functional spawning sites within MSMR.
6. *Protection of endangered (IUCN) and threatened shelf slope species*. Several deep water species, including Warsaw grouper, speckled hind, and snowy grouper were once abundant (Huntsman et al. 1999), but are now seriously depleted. We've observed and caught numerous juveniles of these three species in MSMR and some adults over the years of our studies in MSMR. But, the evidence is strong that they are being lost outside the reserve in large numbers via incidental catch (reef fish caught at shelf-edge depths or deeper die from gas bladder embolism and hemorrhage). The results of our work in MSMR strongly suggest that protection of shelf-edge habitat through year-round closure would also protect these highly threatened species.
7. *Biodiversity will be protected*. Many researchers have demonstrated both terrestrial and aquatic trophic cascades when top predators such as groupers are lost from an ecosystem (see Terborgh and Estes 2010 for numerous examples). Such trophic cascades threaten in an unpredictable way various members of the ecosystem and could lead to an altered functional state which undermines production (see Pauly and Maclean 2003 for examples from the North Atlantic) Year-round closures over a large spatial area of the shelf-edge would protect these highly diverse reef areas (Sedberry et al. 2004).

8. Provide a reference with which to compare the effects of fishing and other anthropogenic influences on the shelf-edge reef environment. MSMR and SLMR proved very useful in evaluating the potential effects of the DWH oil spill. We had characterized these reserves over the last decade (see background information) so they provided a solid baseline for comparison of the before and after spill condition. Red grouper pits in SLMR were especially useful in evaluating the accumulation of oil and effects on resident fishes and invertebrates. Such areas will also provide a baseline for comparison of fishing effects. For example, a recent multibeam sonar survey in SLMR in the area where red grouper habitat was quantified soon after closure of the reserve (Scanlon et al. 2005) showed a 40% increase in the number of red grouper excavations over the 1 km2 area surveyed (Carrie Wall, USF Marine Science Center). This observation suggests that in the absence of fishing red grouper habitat and red grouper density increases.

Our conceptual model, based on all available data, offers substantial understanding of the mechanism of gag male loss on the shelf edge. According to this model males are not caught up during the spawning season as suggested by others, but after it, during the time sex changing individuals are becoming males, but have not yet spawned as males. The data indicate that during this post-aggregation period both males and transitionals are abundant in the catch. The data also show that the proportion of males has increased in the reserve, even in the face of near constant poaching (see section on illegal fishing) over the entire 10 years of closure. Therefore, to manage sex ratio in this species it is clearly necessary to protect the spawning sites year round. Spawning sites are where the males and transitionals reside, so to protect spawning, the sites must be protected. Koenig et al. (1996) defined the shelf edge area of dominant gag spawning sites as an area on the shelf edge centered on the 40 fathom isobath and extending from the northern border of MSMR down to SLMR. This area includes the 'Edges' (**Figure 34**). Clearly, a major positive management initiative would be to close the 'Edges' to all fishing (including surface trolling) year round. Because the Edges is a well-known gag spawning area, and because it appears to be depleted (submersible and fishing surveys of this report), we expect that the benefits that accrued to MSMR over the last decade will also accrue to the Edges. That is, all the benefits described above will be realized and spillover will benefit the fishery displaced by the closure.

A large-scale experiment could be devised using a BACI (Before-After-Control-Impact) experimental design (e.g., Underwood 1994) to test the hypothesis that installing shelf-edge reserves in the US Gulf and SATL would result in not only protection of the reproductive output of shelf-edge spawners, but also provide a direct benefit to fishermen in terms of an increased abundance of fishery species around the reserve, as implied by the data presented in this report. We know that gag and probably scamp spawn exclusively on the shelf edge and that red snapper, red grouper, scamp, vermilion snapper and many other species also spawn on the shelf edge (Sedberry et al. 2006) as well as on the shelf. Thus, if the experimental results support the hypothesis, then the spawning of dominant reef fishery species would be protected with only temporary impact on the shelf-edge fishery.

An effective BACI experimental design of an experiment designed to evaluate benefits of shelf-edge reserves would consist of an initial 3-year monitoring of the fish abundance (e.g. ROV transects) and catches on fished reefs in 6 selected shelf-edge areas of the US Gulf and SATL, preferably areas where gag are known to spawn. All 6 areas would be large enough to contain a 100 NM^2 reserve (like MSMR) and an area surrounding the reserve by at least 10 NM radius. After the 3 years of monitoring to establish variability in reef fish abundance and catch, three randomly selected reserves would be closed to fishing and three would serve as controls and left open to fishing. Researchers would continue to monitor reef fish abundance in all areas, open and closed, after closure for 10 years; fishery catches in all open areas would also be monitored for spillover effects. Sites for these experiments must be high quality reef fish fishing areas, such as the Edges in the northeastern Gulf and multiple sites in the SATL (see Sedberry et al. 2006). Of course, surveillance and enforcement by the US Coast Guard would be key elements of this study.

Deepwater Horizon Oil Spill

The northeastern GOM shelf edge is an important fishing area for the commercial reef fish fishery. When the Deepwater Horizon Oil discharge occurred in April 2010 we worked with other research scientists to estimate the impact to the reef fish populations of the area. The two marine reserves provided useful areas for the study of the subsurface transport of oil. Deposition of oil and dispersants on the sea floor could have significant environmental and economic consequences.

Red grouper construct large (2 m deep x 5 m across) pits on the seafloor of the WFS (Scanlon *et al.* 2005, Coleman and Koenig 2010, Coleman *et al.* 2010). Red grouper pits represent natural sediment traps at about 70 to 100 m water depths, are biodiversity hot spots, and are thus have the potential to be sensitive to oil contamination. Oil mixed with fine sediment would be expected to move along the seafloor until encountering red grouper pits, then collect in the pits. Red grouper routinely dig out the pits with their mouths, so the contamination would be transported from the bottom of the pits to the rims surrounding the pits, and would directly contaminate the red grouper through their gills and perhaps contribute to declines of infaunal communities.

In July 2010 aboard the JSL II, we sampled surface sediments (about 10 cm deep) from the bottom of the red grouper pits in SLMR, from the rim, and from distant areas surrounding the pits (controls). We also had temporal controls—sediment samples collected from the same area in 2008 and kept frozen until analysis. Samples collected in 2008 were collected to determine the composition of sediments in and around red grouper pits (Coleman et al. 2010).

None of the sediment sampled from the grouper pits had significantly elevated total petroleum hydrocarbon (poly-aromatic hydrocarbon concentrations and concentrations of volatile and semi-volatile hydrocarbons) concentrations. In one of the pits, small amounts (3-4 mg/kg) of petroleum hydrocarbons were detected in the center of the pit and at the edges, where red grouper deposit excavated material. In another pit, small amounts of oil (3-5 mg/kg) were detected in the sediments at the rim of the pit and trace amounts of polyaromatic hydrocarbons (PAHs) were detected in the center of the pit. All oil concentrations were close to the detection limit (2.5 mg/kg) so a fingerprinting to determine the origin of the oil was not possible.

The metals, nickel and vanadium, are components of crude oil and therefore can be used as indicators of prior contamination. We found that concentrations of nickel and vanadium were higher than background in the center of the pits with increasing concentrations toward the rim in the 2010 samples, but not in the 2008 samples, suggesting that petroleum hydrocarbons may have been collected by the pits prior to our sampling in 2010 and after our sampling in 2008.

The data suggest that the grouper pits function as traps for petroleum hydrocarbons and the concentration distributions of nickel and Vanadium support this conclusion. As V and Ni are indicators for crude oil and remain in the environment after the oil has been degraded, these results suggest that the grouper pits accumulated some oil in the past. Thus, it may be possible that small particles of dispersed DWH oil from one of the subsurface plumes reached that area depositing some of these particles in the pits. As these particles were small and biological activity in the pits is relatively high due to concentrated animal activities, these oil particles may have degraded relatively quickly leaving only V and Ni. However, other oil sources of natural or anthropogenic origin cannot be discounted.

As in all samples retrieved from the grouper pits, total petroleum hydrocarbons were low, close to the detection limit. Nonetheless these samples showed an interesting trend: While in all eleven samples collected in 2008, total petroleum hydrocarbons could not be detected except in one sample (2.4 mg/kg), 8 of the 10 samples collected in October 2010, after the oil spill, contained measurable amounts of total petroleum hydrocarbons. Although fingerprinting could not be conducted due to the small amounts of oil present, this change between 2008 and 2010 and the presence of Ni and V in the 2010 samples suggests that some oil from the DWH accident reached the WFS. However, there were no clear signs of impact, and red grouper pits had a similar suite of dominant species (Table 1) as we observed prior to the oil spill (see Coleman et al. 2010).

ACKNOWLEDGEMENTS

We thank the following colleagues for their tremendous contributions to this project: David Mann, Misty Montie, David Naar, and Jim Locascio from the University of South Florida; Kathy Scanlon from United States Geological Survey, Woods Hole; Chris Gardner and Bob Allman from the National Marine Fisheries Service, Panama City; Shirley Pomponi and John Reed from the Harbor Branch Oceanographic Institute at Florida Atlantic University. We thank the following fishermen for their support throughout this study for their sincere interest in the conservation of fishery resources: David Sauls and the late Wendell Sauls, the late John "Big John" Roberts, Danny and Jacob Tankersley, and Chuck Guilford. Finally, we thank the following students and technicians in our lab for their dedication and support: Alicia Brown, Nate Jue, Kelly Kingon, Justin Lewis, Jimmy Nelson, Christopher Peters. Funding was provided primarily through NOAA's MARFIN Program in the form of a grant to us (NA07NMF4330120). Components were funded by the recent BP Gulf of Mexico Research Initiative to the Northern Gulf Institute (a NOAA Cooperative). Other aspects were funded previously by an earlier NOAA MARFIN Project (Koenig and Coleman 2006), the Pew Charitable Trust (Coleman 2006), the National Sea Grant (Project Number: R/LR-B-51), and The National Fish and Wildlife Federation. Additional funding for the red grouper habitat engineer work was obtained from the Marine Conservation Biology Institute and The National Undersea Research Center at the University of North Carolina, Wilmington (NOAA Grant #03OAR4300088).

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Tables

Table 1. Differences in mean age of dominant reef fish fishery species between inside and outside MSMR. GA = gag, RG = red grouper, RS = red snapper, SC = scamp.

Species	Mean Age in (N; SE)	Mean Age out (N; SE)	Signif. (t-test)
GA	5.7 (227; 0.107)	5.1 (214; 0.105)	P < 0.001
RG	5.9 (83; 0.148)	5.3 (83; 0.141)	P < 0.01
RS	4.6 (297; 0.056)	4.1 (382; 0.041)	P < 0.001
SC	4.9 (63; 0.152)	5.1 (19;0.206)	P > 0.05

Table 2. Percent males and transitionals in the gag population inside MSMR. Fish collected from Dec. 2007 to Dec. 2010. Fish sizes standardized to 75 cm TL and larger. F=female, T=transitional, M=male.

Periods	F	T	M	total	% T	% M+T
Agg, Dec-May	19	0	1	20	0	5.0 [a]
Post agg, Apr-Jul	70	4	9	83	4.8	15.6 [b]
Pre agg, Aug-Nov	72	0	8	80	0	10 [c]
total	161	4	18	183	2.2	12.0 [b]

[a] Not significantly different between inside and outside MSMR (p>0.05)
[b] Significantly different between inside and outside MSMR (p<0.0001)
[c] Significantly different between inside and outside MSMR (p<0.003)

Table 3. Percent males and transitionals in the gag population outside MSMR. Fish collected from Dec. 2007 to Dec. 2010. Fish sizes standardized to 75 cm TL and larger. F=female, T=transitional, M=male.

Periods	F	T	M	total	% T	% M+T
Agg, Dec-May	172	0	2	174	0	1.1 [a]
Post agg, Apr-Jul	22	0	0	22	0	0 [b]
Pre agg, Aug-Nov	9	0	0	9	0	0 [c]
total	203	0	2	205	0	1.0 [b]

[a] Not significantly different between inside and outside MSMR ($p>0.05$)
[b] Significantly different between inside and outside MSMR ($p<0.0001$)
[c] Significantly different between inside and outside MSMR ($p<0.003$)

Table 4. Percent males and transitionals in the gag population from Hood and Schlieder (1992). Fish collected from 1977 to 1980. Fish sizes standardized to 75 cm TL and larger only. F=female, T=transitional, M=male.

Periods	F	T	M	total	% T	% M+T
Agg, Dec-Mar	249	1	50	300	0.33	17.0
Post agg, Apr-Jul	148	5	44	197	2.5	24.8
Pre agg, Aug-Nov	124	0	40	164	0	24.3
total	521	6	134	661	0.90	21.2

Table 5. Species composition of 8 red grouper pits in SLMR, observed on the JSL II cruise made in July 2010, 3 months after the Deepwater Horizon oil spill. Compare with data from Coleman et al. 2010.

Common Name	Species	Abundance
Yellowtail Reef fish	Chromis enchysura	388
Red Barbier	Hemanthisa vivanus	148
Yellowfin Bass	Anthias nicholsi	60
Striped Grunt	Haemulon striatum	48
Bank Butterflyfish	Chaetodon aya	37
Squirrelfish	Sarocenton bullisi	36
Bank Seabass	Centropristis ocyurus	33
Roughtongue Bass	Pronotogrammus martinicensis	29
Two-spot cardinalfish	Apagon pseudomaculatus	26
Tattler	Serranus phoebe	21
greenband wrasse	Halichoeres bathyphilus	19
Tomtate	Haemulon aurolineatum	13
Red Grouper	Epinephelus morio	8
Flame fish	Apogon maculatus	5
Scamp	Mycteroperca phenax	5
Reticulate moray	Muraena retifera	3

Table 6. Dates and times (only night time is presented) vessels were recorded in the vicinity of gag spawning sites on Madison Ridge in the Madison Swanson Marine Reserve on the northern West Florida Shelf.

Times vessel traffic recorded at # 5		Times vessel traffic recorded at # 1	
Date	Time (EST)	Date	Time (EST)
8/14/2008	0:50 to 4:10	**Receiver on # 1 malfunctioned in 2008**	
8/18/2008	2:50 to 4:35		
8/19/2008	1:15 to 5:10		
8/21/2008	5:20 to 5:55		
8/24/2008	3:25 to 4:55		
8/27/2008	21:00 to 22:25		
8/28/2008	22:35 to 23:30		
8/31/2008	3:45 to 4:05		
9/7/2008	1:30 to 2:20		
9/9/2008	2:25 to 2:55		
9/9/2008	4:45 to 6:00		
9/9/2008	23:20 to 0:15		
9/11/2008	21:50 to 22:50		
9/14/2008	3:35 to 4:15		
9/16/2008	2:15 to 2:45		
9/18/2008	23:15 to 0:00		
9/22/2008	23:55 to 2:40		
9/26/2008	1:30 to 3:05		
10/26/2008	3:45 to 4:10		
10/27/2008	4:40 to 5:10		
10/28/2008	23:35 to 6:10		
11/1/2008	19:15 to 20:00		
11/10/2008	4:35 to 5:15		
11/14/2008	5:35 to 7:05		

Table 6 (CONTINUED). Dates and times (only night time is presented) vessels were recorded in the vicinity of gag spawning sites on Madison Ridge in the Madison Swanson Marine Reserve on the northern West Florida Shelf

Times vessel traffic recorded at # 5		Times vessel traffic recorded at # 1	
Date	Time (EST)	Date	Time (EST)
	3:35 to 4:10		
11/22/2008			
Receiver malfunctioned during this time interval.		**A new receiver was deployed on site #1**	
3/18/2009	18:20 to 22:30	2/7/2009	2:40:00 to 3:20:00
3/22/2009	22:10 to 2:20	2/9/2009	0:05:00 to 0:40:00
3/26/2009	21:20 to 21:50	2/9/2009	5:35:00 to 5:55:00
3/30/2009	0:50 to 1:50	2/12/2009	6:15:00 to 6:55:00
4/8/2009	23:10 to 23:30	2/17/2009	3:50:00 to 5:15:00
4/10/2009	3:20 to 3:40	2/19/2009	22:55:00 to 23:50:00
4/11/2009	22:00 to 22:20	2/26/2009	23:15:00 to 23:30:00
4/13/2009	3:40 to 4:20	2/28/2009	3:25:00 to 4:20:00
4/18/2009	2:40 to 2:50	3/10/2009	21:50:00 to 22:25:00
4/21/2009	2:10 to 3:40	3/12/2009	4:55:00 to 5:20:00
4/26/2009	23:50 to 0:00	3/13/2009	2:25:00 to 2:55:00
4/27/2009	0:00 to 0:40	3/14/2009	4:50:00 to 7:30:00
4/29/2009	0:00 to 0:50	3/17/2009	4:40:00 to 5:30:00
4/30/2009	1:00 to 1:40	3/19/2009	19:10:00 to 19:30:00
5/5/2009	1:30 to 2:10	3/27/2009	3:30:00 to 4:25:00
5/10/2009	4:40 to 5:20	4/12/2009	2:05:00 to 2:35:00
5/13/2009	2:50 to 3:50	4/13/2009	3:40:00 to 5:20:00
		4/16/2009	1:15:00 to 1:50:00
		4/20/2009	1:10:00 to 1:50:00

Table 7. Gag sex ratio: Gulf of Mexico comparison of historical 1970s (Hood and Schleider 1992) with more recent data 1990s (Koenig et al. 1996). The numbers of females: males plus transitionals and the percentage of males plus transitionals (in parentheses) in the catch data are presented.

	Gulf of Mexico		
Period of Observation	1970s	1990s	p-value
Dec-Mar (Aggregation)	301:52 (15%)	311:6 (2%)	<0.001
Apr-Jul (Post-aggregation)	188:48 (20%)	119:6 (5%)	<0.001
Aug-Nov (Pre-aggregation)	163:39 (19%)	24:0 (0%)	<0.01

Table 8. Gag sex ratio: South Atlantic region comparison of historical 1970s (Collins et al. 1987) and more recent data mid-1990s (McGovern et al.1998). The numbers of females: males plus transitionals and the percentage of males plus transitionals (in parentheses) in the catch data are presented.

	South Atlantic Region		
	1970s	1990s	p-value
Dec-Mar (Aggregation)	189:24 (11%)	2392:131 (5%)	<0.001
Apr-Jul (Post-aggregation)	131:62 (32%)	1405:163 (10%)	<0.001
Aug-Nov (Pre-aggregation)	91:22 (19%)	131:7 (5%)	<0.001

Figures (Legends)

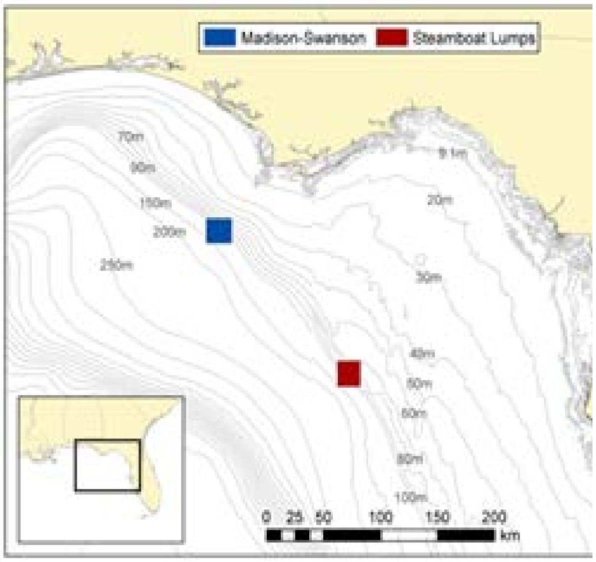
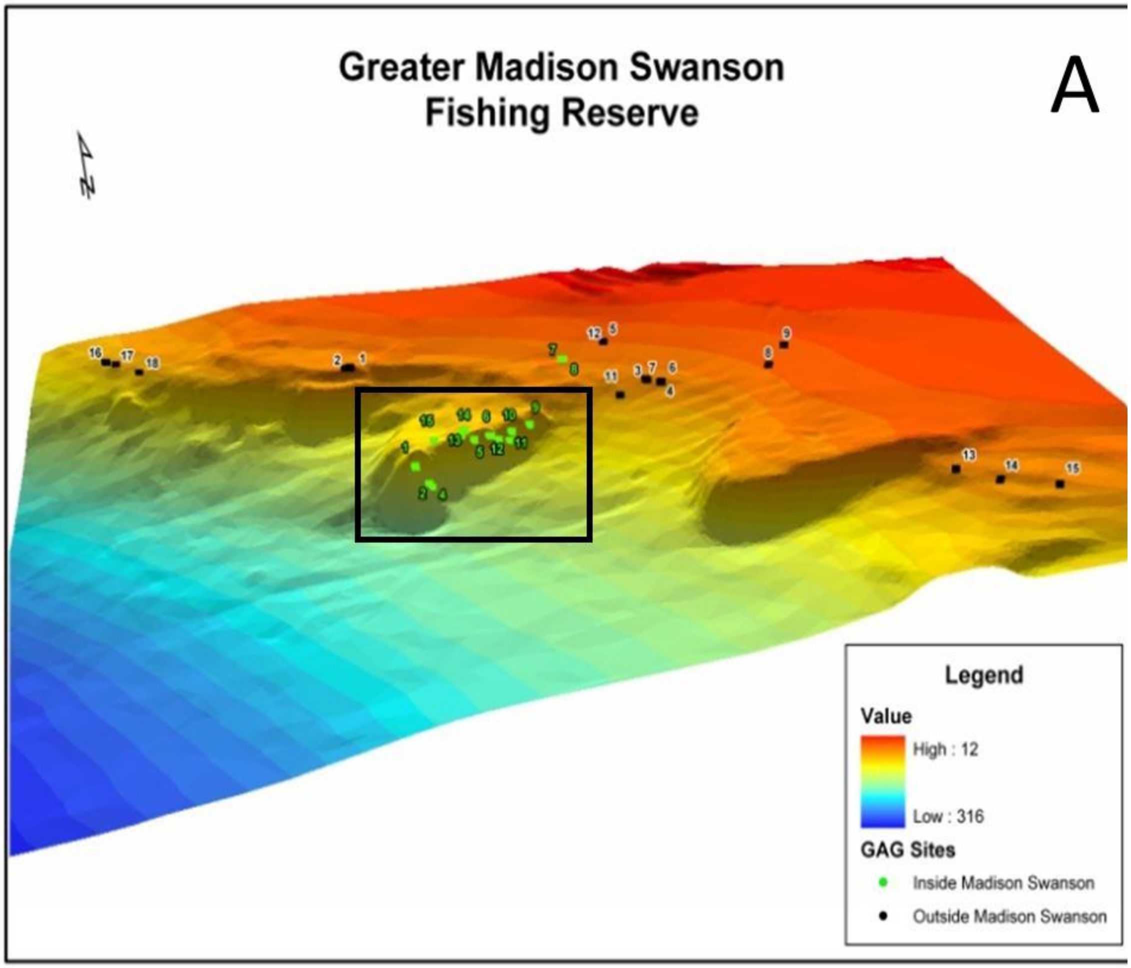


Figure 1. Marine reserves on the West Florida Shelf include Madison Swanson Marine Reserve (blue) and Steamboat Lumps Marine Reserve. These reserves were established in 2000 by the Gulf of Mexico Fishery Management Council.

Figure 2. Photograph of three gag (*Mycteroperca microlepis*) showing male coloration ('copperbelly') on bottom specimen. Image from Fitzhugh et al. (2006).


Greater Madison Swanson
Fishing Reserve
A
Legend
Value
High : 12
Low : 316
GAG Sites
Inside Madison Swanson
Outside Madison Swanson

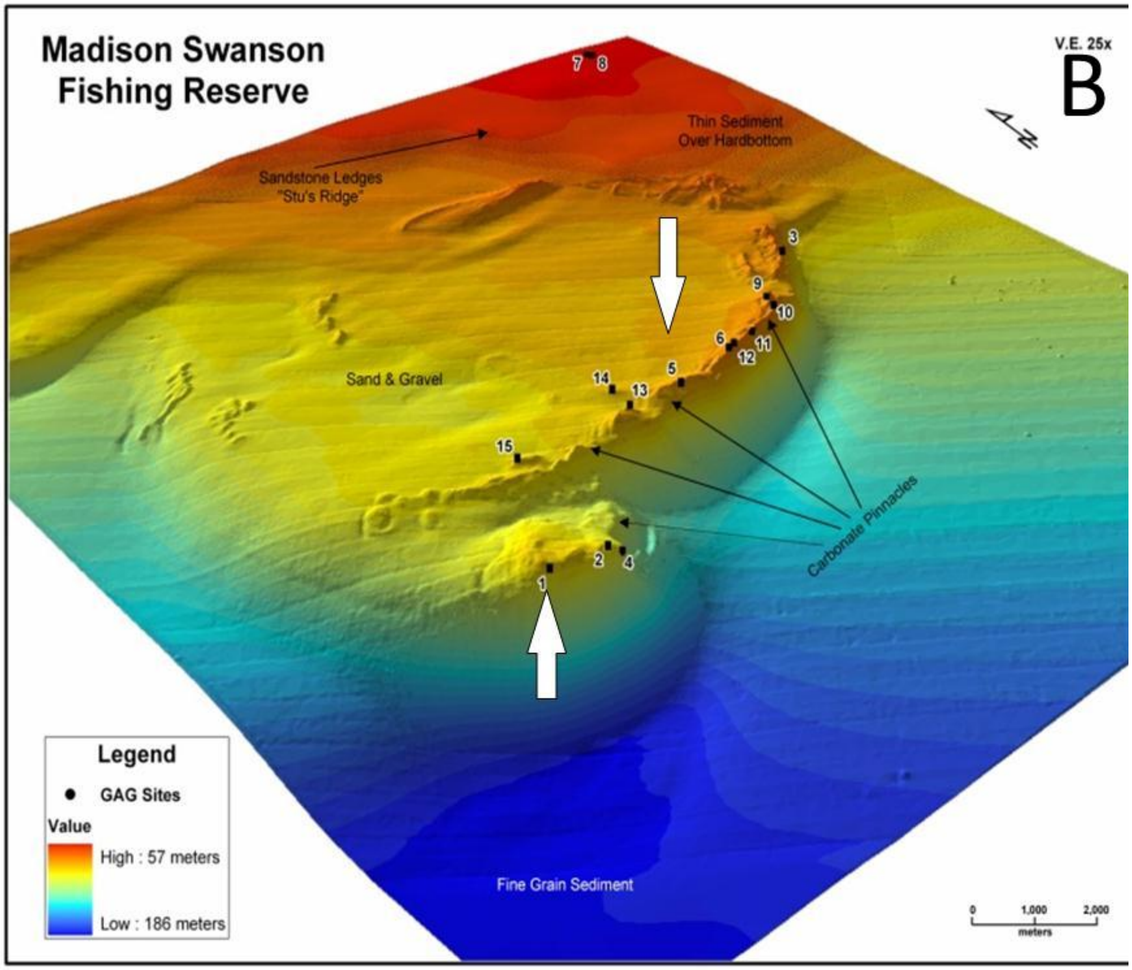


Figure 3. Multibeam images of the northern West Florida Shelf indicating spawning aggregation sites of gag *Mycteroperca microlepis*. (A) sites both outside and within the Madison Swanson Marine Reserve (MSMR, indicated by the black box). (B) expansion of the area within the black box, showing the entire MSMR. Indicates spawning sites 1 through 15 on the Madison Ridge and location of DSG receivers (white arrows) deployed to monitor boat traffic around spawning sites. All acoustic data on DSG receivers were blocked to sounds within 1 km radius of the receiver. Distance to the border of the reserve is 6 to 8 km.

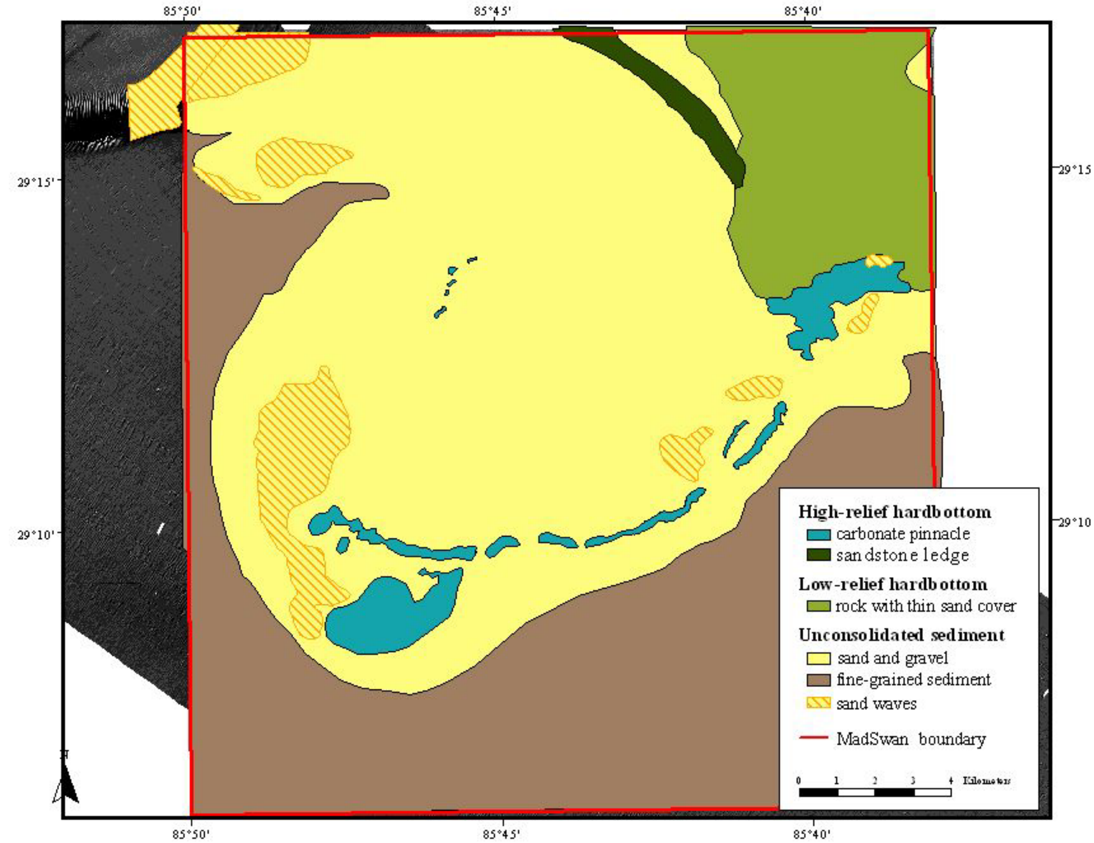


Figure 4. Surficial geology of MSMR. See text for explanation.

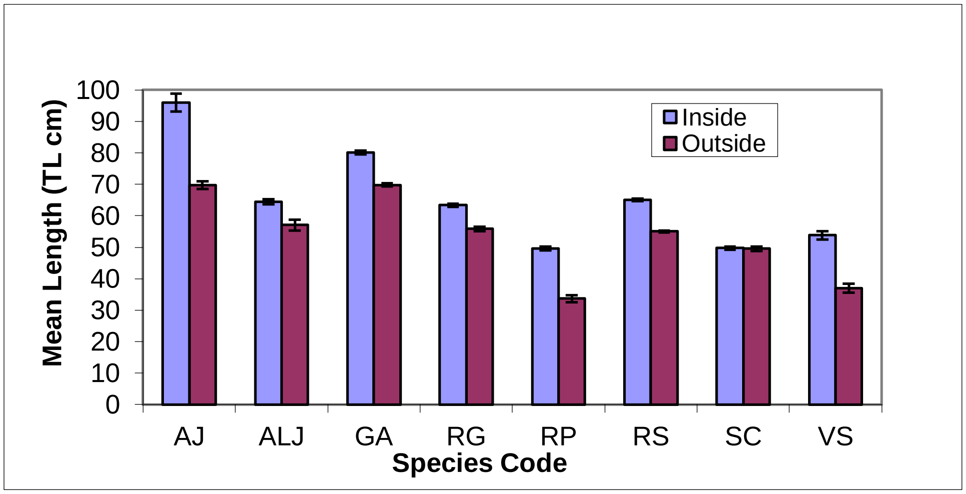


Figure 5. Mean length (TL cm) of reef fish captured inside vs. outside MSMR. All data from 2007 to 2010 combined. Abbreviations: AJ = greater amberjack, ALJ = almaco jack, GA = gag, RG = red grouper, RP = red porgy, RS = red snapper, SC = scamp, and VS = vermilion snapper. Error bars are SE.

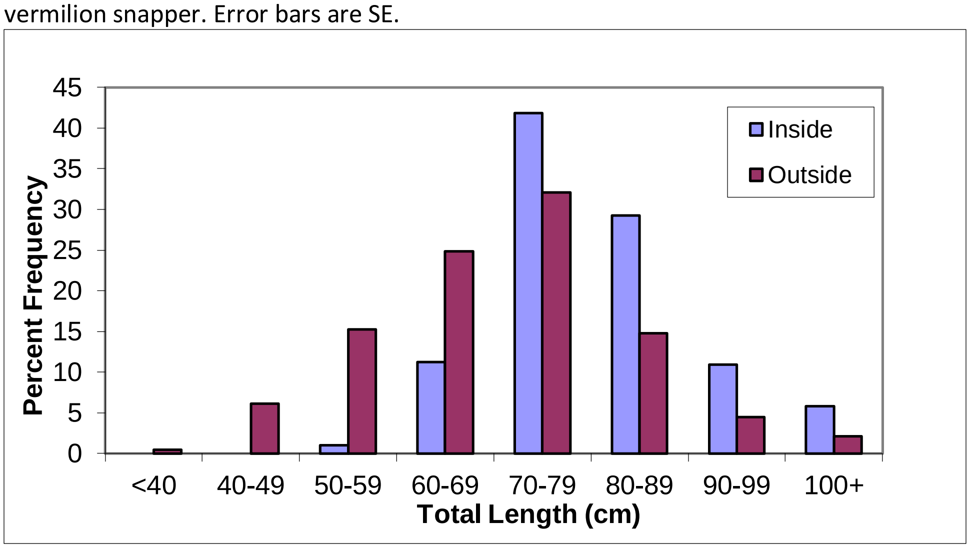


Figure 6. Percent size frequency distributions of gag captured inside MSMR relative to outside from 2008 to 2011.

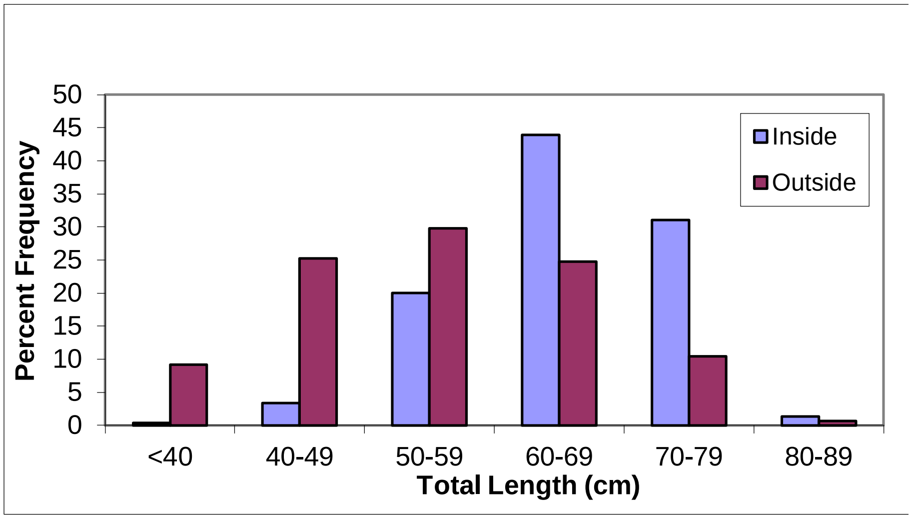


Figure 7. Percent size frequency distributions of red snapper captured inside MSMR relative to outside from 2008 to 2011.

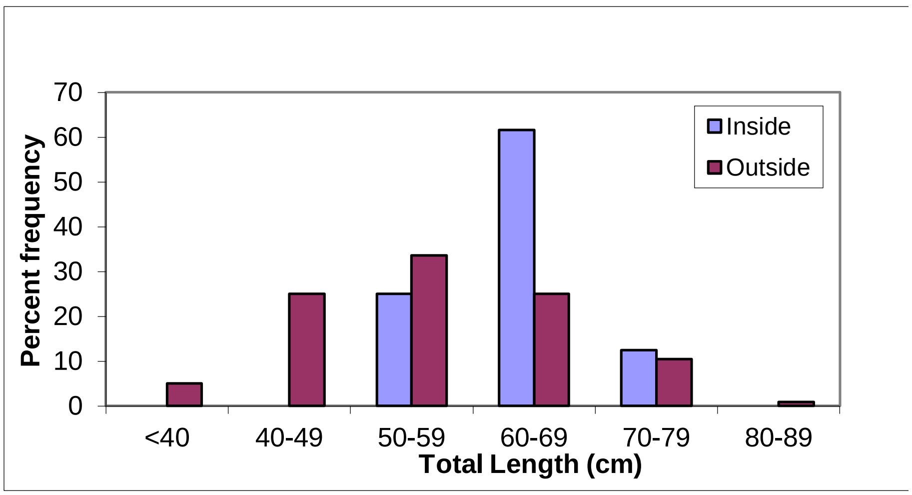


Figure 8. Percent size frequency distributions of red grouper captured inside MSMR relative to outside from 2008 to 2011.

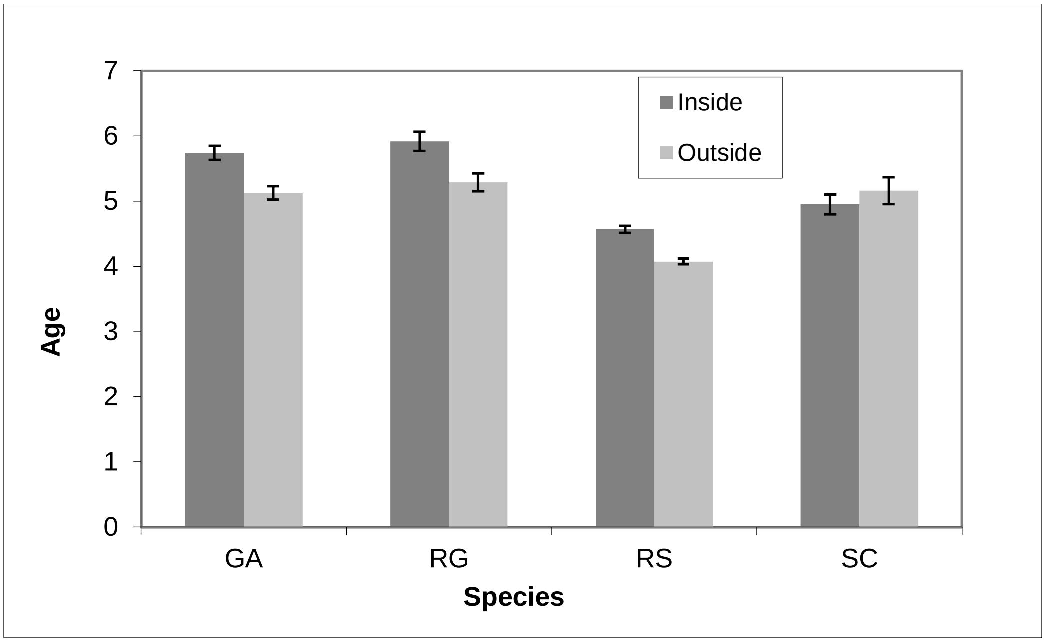


Figure 9. Mean ages of our focal species (2008 to 2010), GA = gag, RG = red grouper, RS = red snapper, and SC = scamp, showing age differences between inside and outside of MSMR. Error bars are SE.

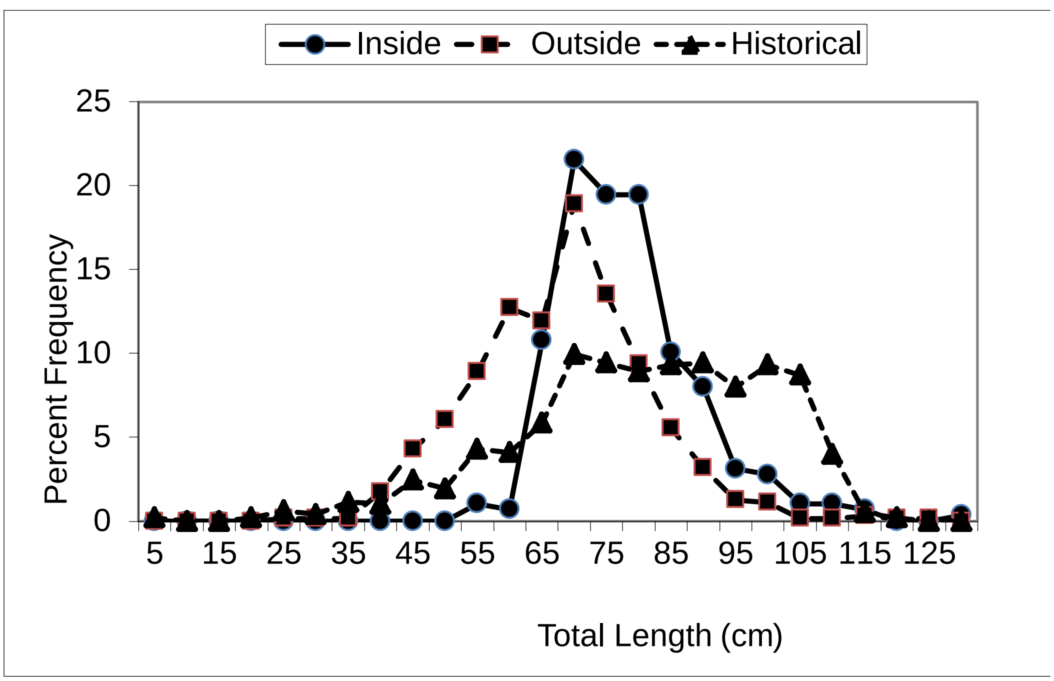


Figure 10. Percent size frequency distributions of gag comparing historical (1977 – 1980, N = 976, from Hood and Schlieder (1992)) compared to the present study (2008 – 2010) inside MSMR (N = 288) and outside (N = 629). Percent of catch > 75 cm TL (approximate size of 100% maturity).

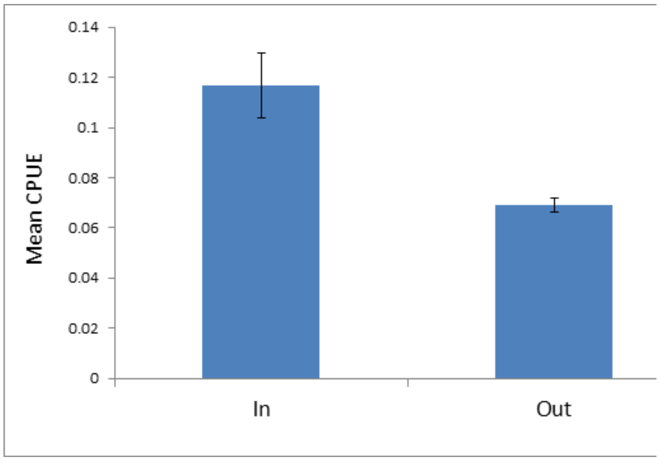


Figure 11. Catch per unit effort (CPUE, fish per minute per hook)) by hook-and-line of economically important reef fish inside vs. outside MSMR during 2008 to 2010. Species represented are gag, red grouper, scamp, red snapper, vermilion snapper, greater amberjack, and almaco jack. 'CPUE in' (N=20) is significantly higher than 'CPUE out' (N=220; Mann-Whitney test, p<0.0001). Error bars are SE.

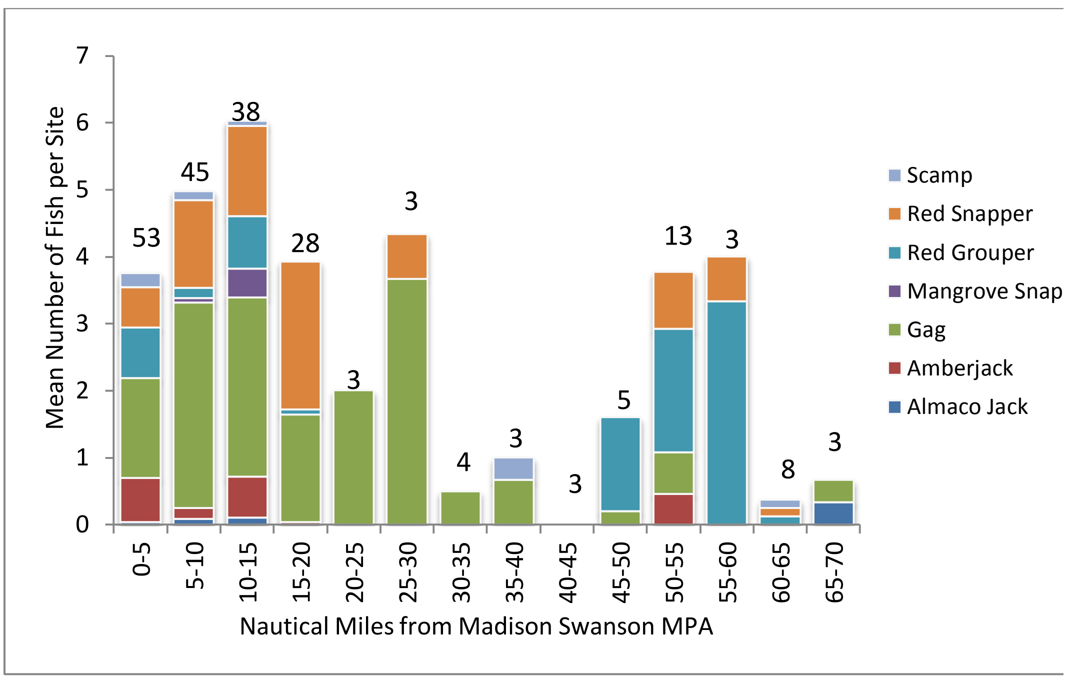


Figure 12. Mean number of economically important fish species captured per site on six commercial reef fish trips along the shelf edge of the northeastern Gulf of Mexico relative to distance from MSMR. Numbers above the bars indicate number of sites fished.

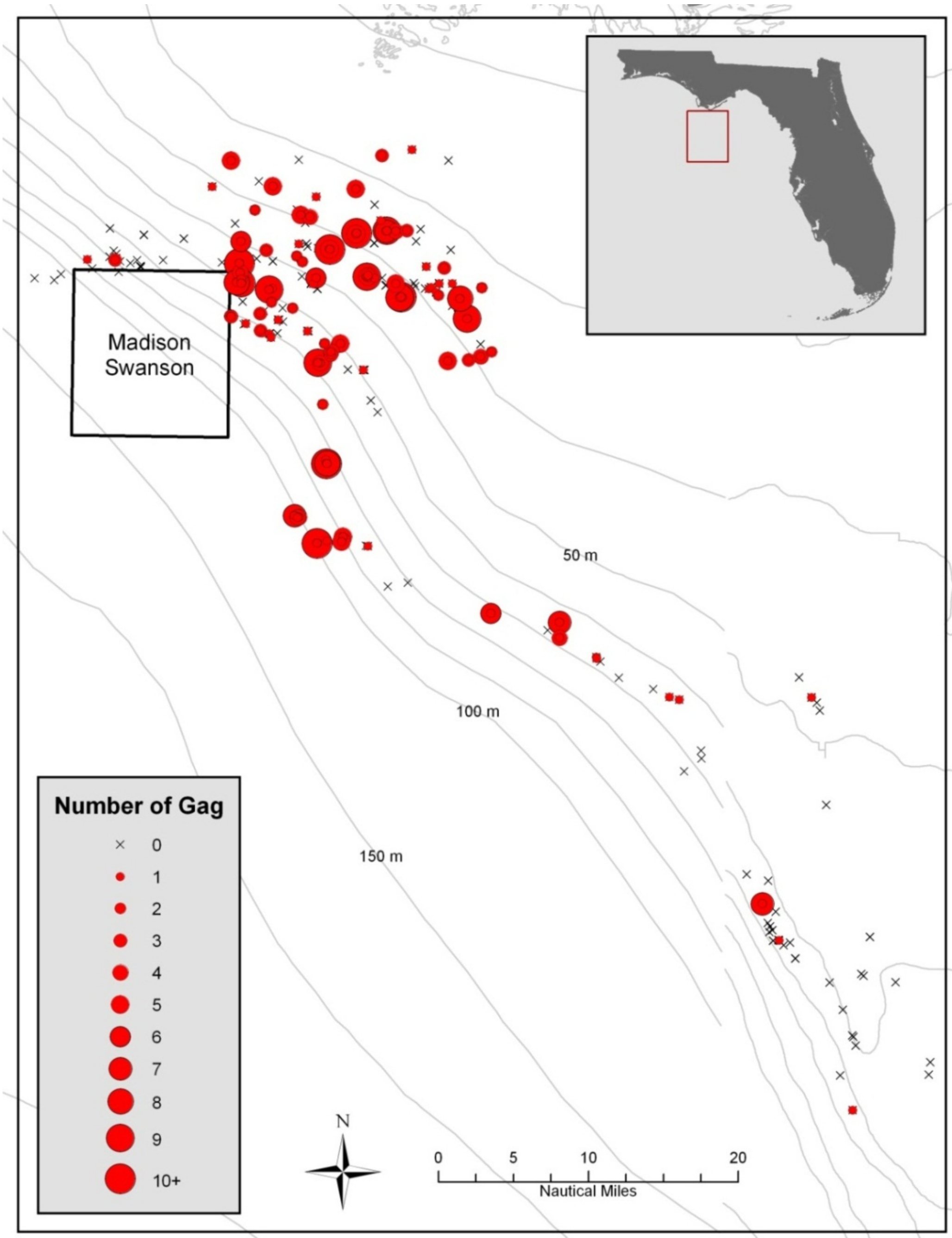


Figure 13. Total number of gag caught during six commercial reef fish trips at reef sites along the shelf edge of the northeastern Gulf of Mexico from 2008 to 2010. All fished sites are represented.

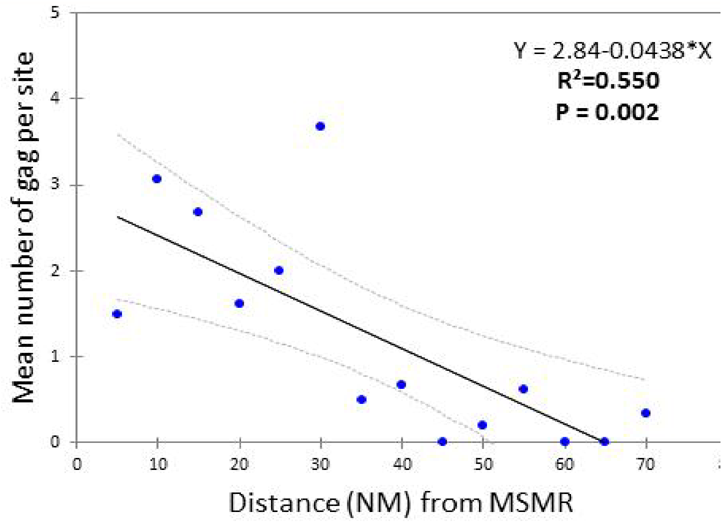


Figure 14. Mean number of gag captured on six commercial reef fish trips along the shelf edge of the NE Gulf of Mexico relative to distance (NM) from MSMR

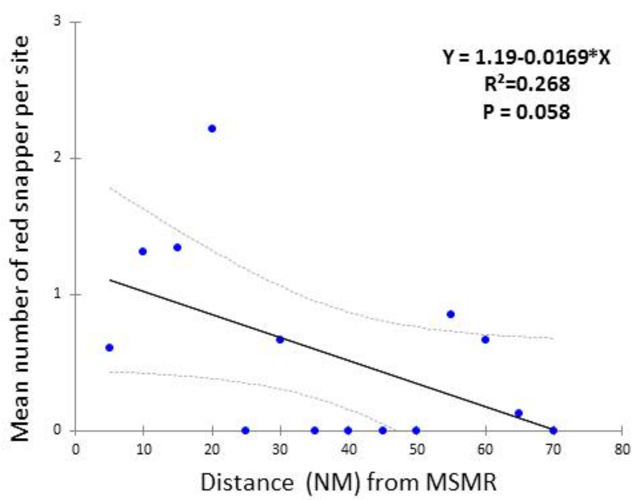


Figure 15. Mean number of red snapper captured on six commercial reef fish trips along the shelf edge of the NE Gulf of Mexico relative to the distance from MSMR.

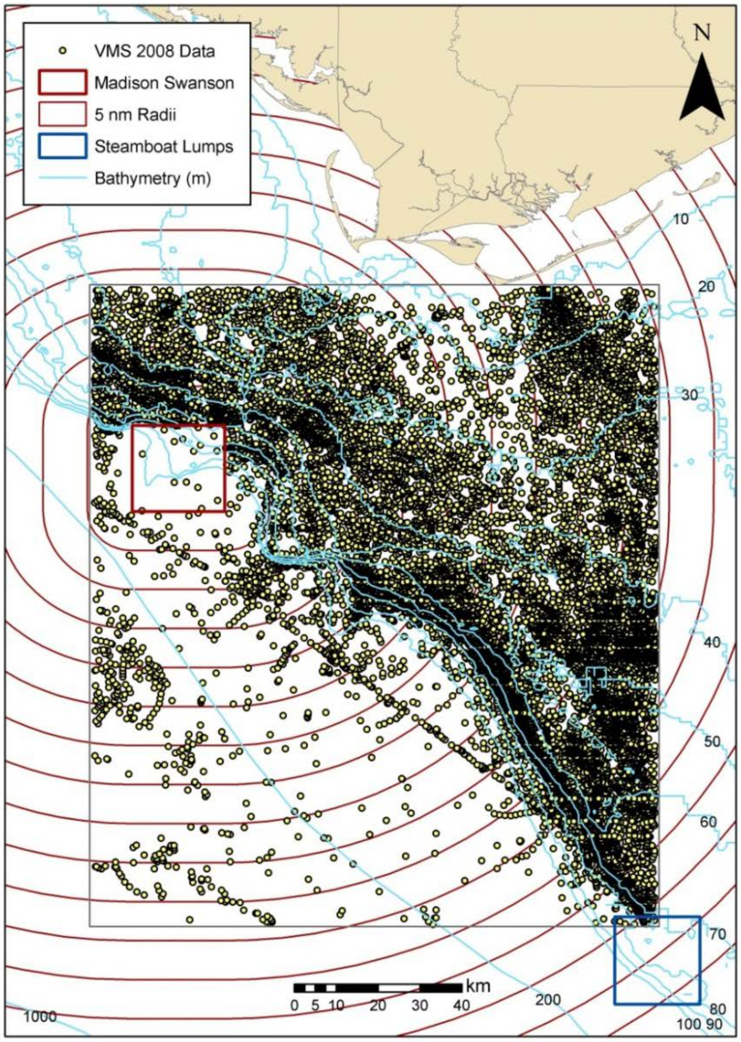


Figure 16. VMS data (position of commercial reef fishing vessels recorded every hour) for 2008 suggesting areas where commercial fishermen concentrate their effort (dark areas). Note significant effort around the eastern and northern boarders of MSMR and down the shelf edge to Steamboat Lumps.

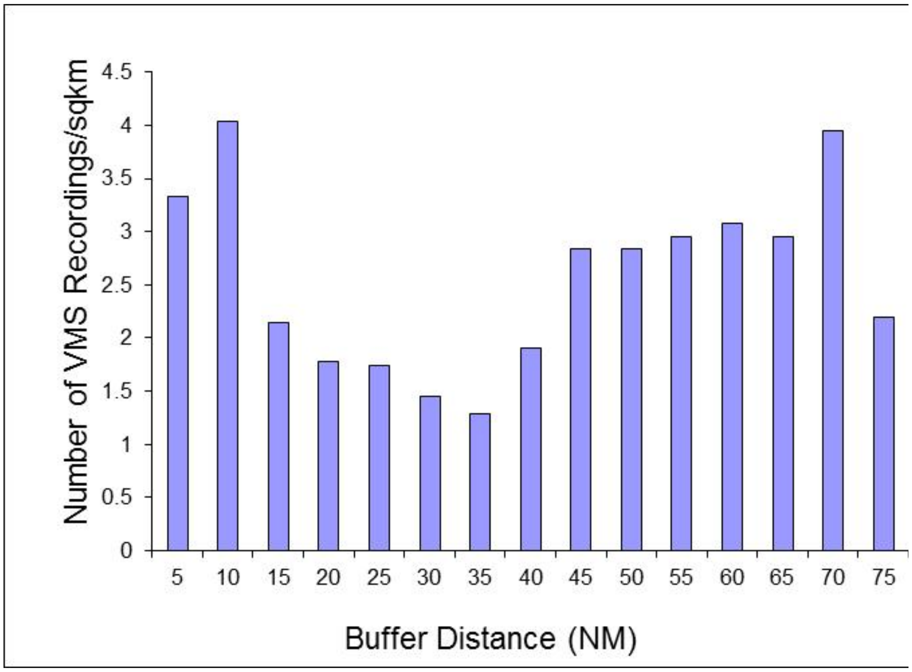


Figure 17. Number of records of the position of commercial reef fish vessels per km^2 relative to distance from MSMR in 5 NM increments. Position of commercial reef fishing vessels with active VMS transmitters was recorded every hour.

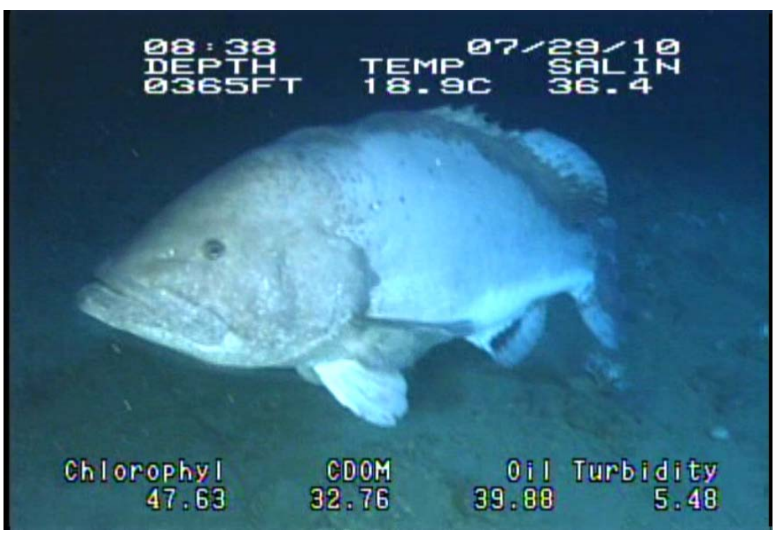


Figure 18. Photo of a large Warsaw grouper (estimated length, ~1.7 m) taken in MSMR on Madison Ridge from the JSL II submersible (Harbor Branch Oceanographic Institute—FAU) in July 2010. Photo credit: Shirley Pomponi.

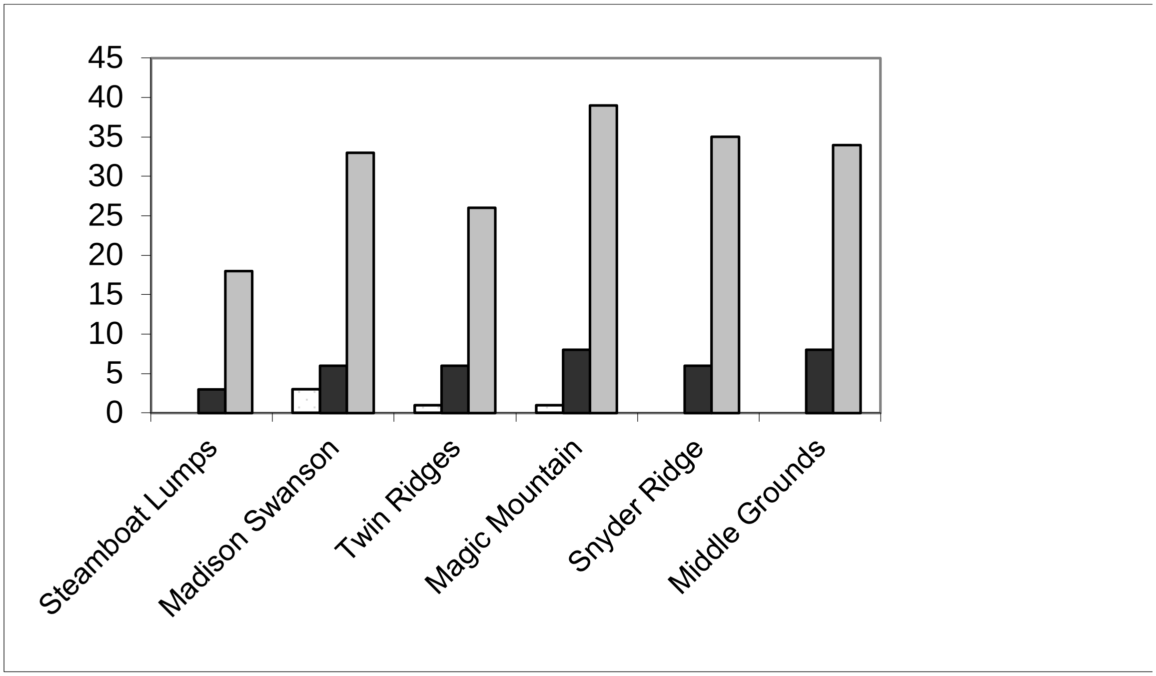


Figure 19. Mean number of species observed along the shelf edge of the northeastern Gulf of Mexico on Johnson Sea Link II dives, including "threatened species" (WHITE BAR: Warsaw grouper, speckled hind, snowy grouper), economically important species (BLACK BAR), and all species combined (GRAY BAR).

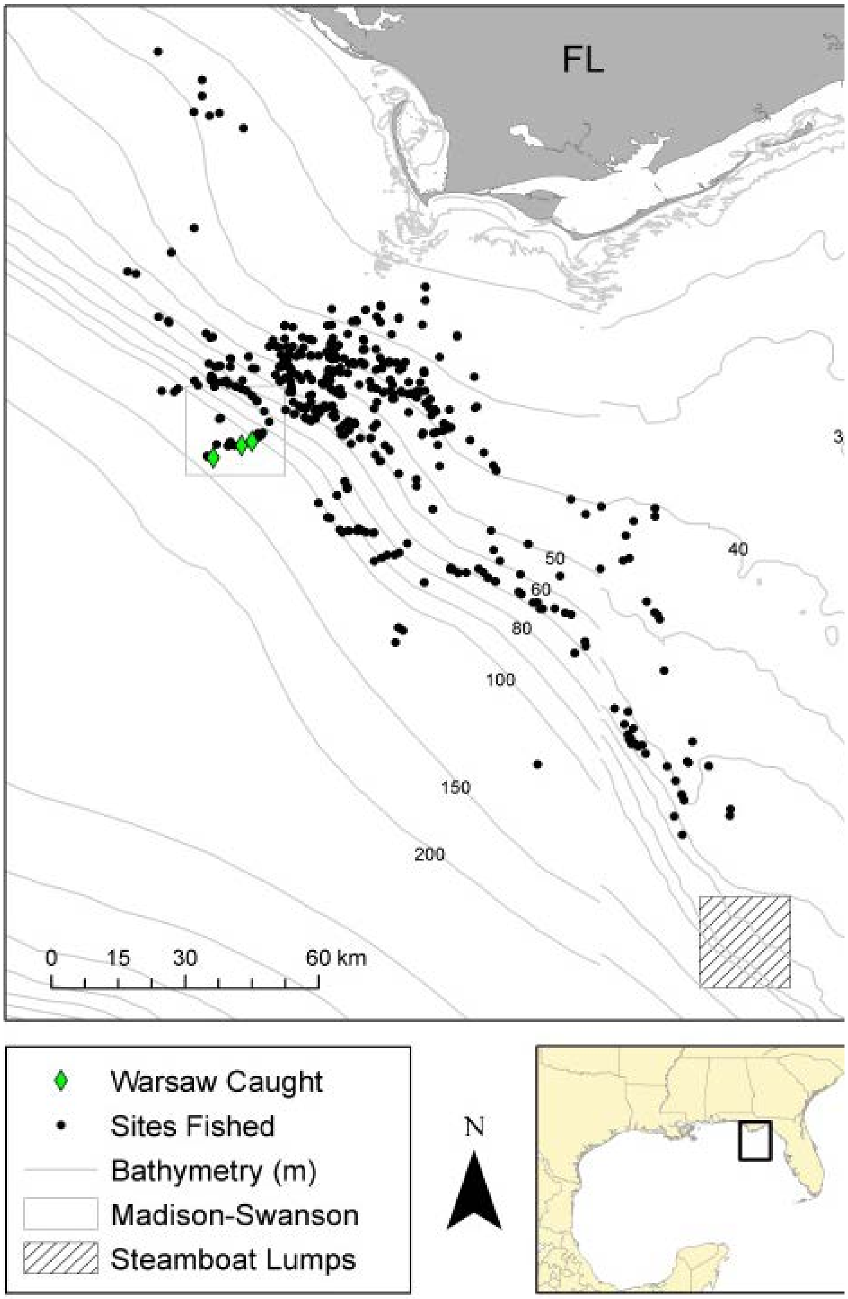


Figure 20. Location of Warsaw grouper (Hyporthodus nigritus) caught by hook-and-line along the shelf edge of the northeastern Gulf of Mexico. Dots represent all sites fished. Numbers beside dive sites indicate number seen

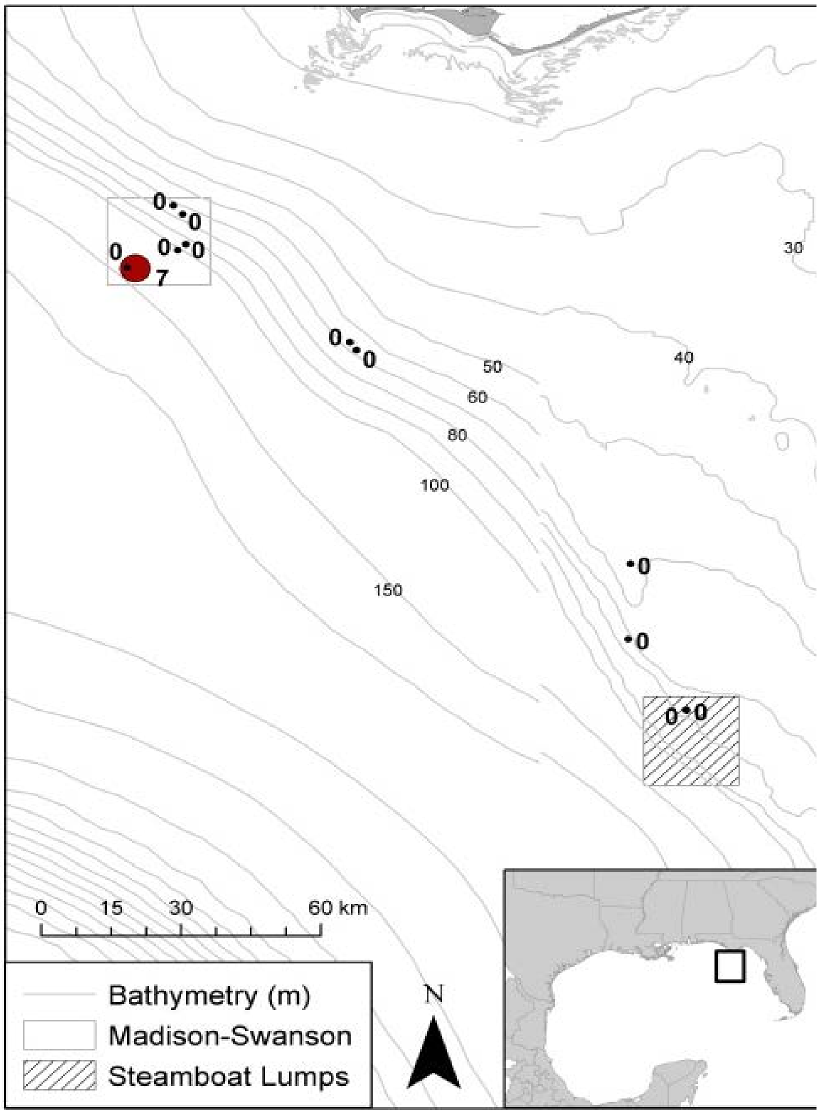


Figure 21. Location and number of Warsaw grouper (Hyporthodus nigritus) seen from submersible dives made onboard the Johnson Sea link II (Harbor Branch Oceanographic Institute—FAU) along the shelf edge of the northeastern Gulf of Mexico. Dots in figure represent dives sites. Number beside dive sites indicates number of Warsaw grouper seen.

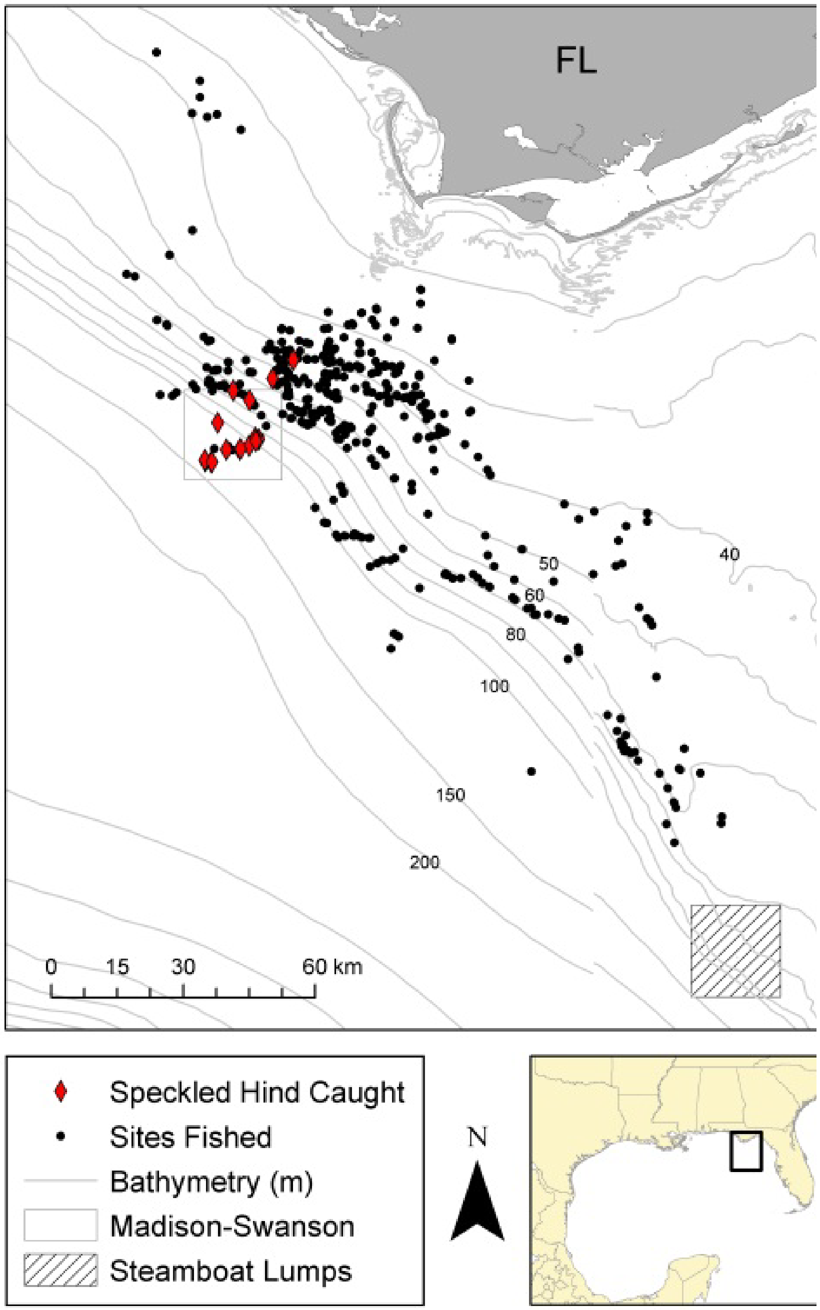


Figure 22. Location of speckled hind (Epinephelus drummondhayi) caught by hook-and-line along the shelf edge of the northeastern Gulf of Mexico. Dots in figure represent all sites fished during this project.

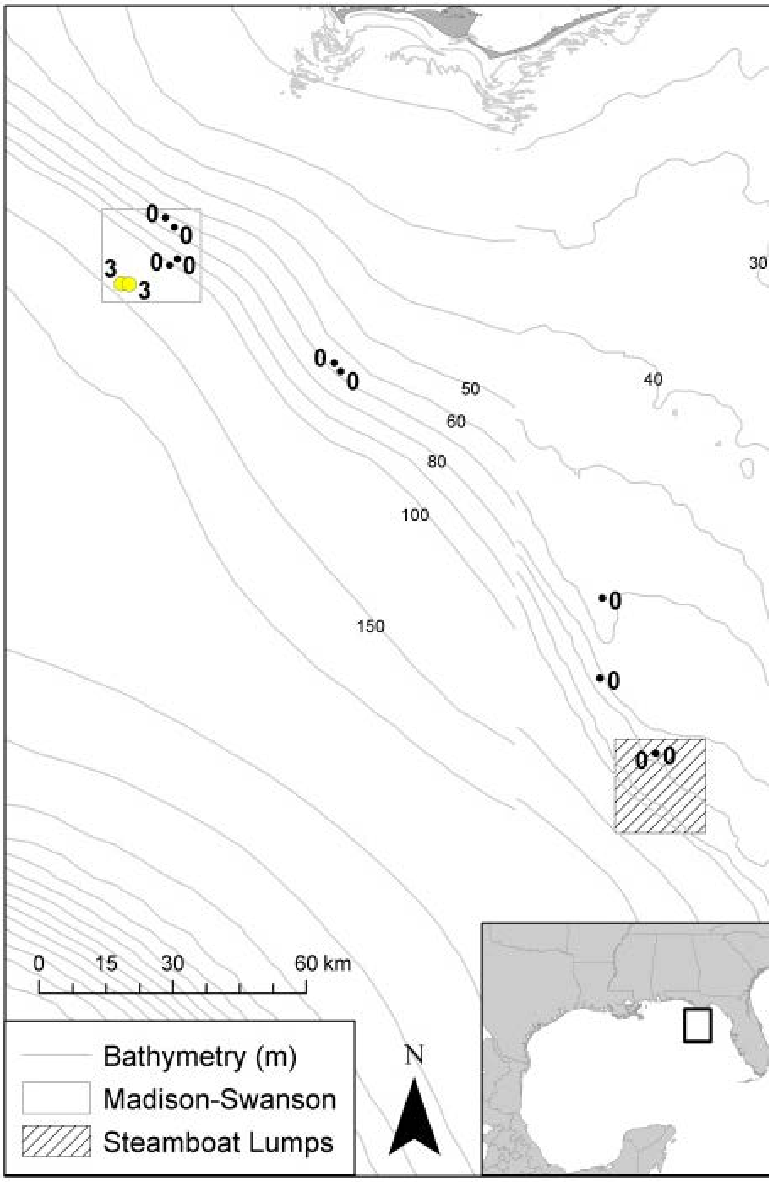


Figure 23. Location and number of speckled hind (Epinephelus drummondhayi) seen aboard the JSL II submersible along the shelf edge of the northeastern Gulf of Mexico. Dots in figure represent JSL II dive sites. Numbers beside dive sites indicate number of individuals seen.

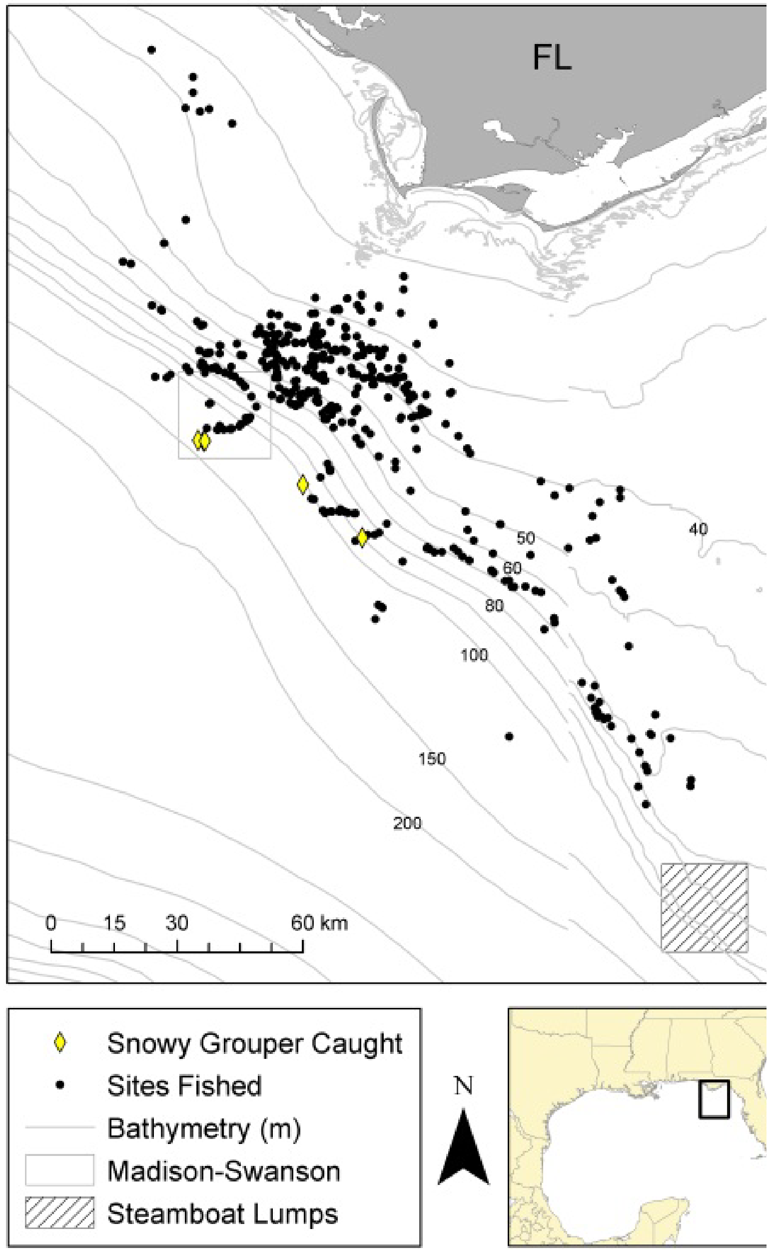


Figure 24. Location of snowy grouper (Hyporthodus niveatus) caught by hook and line along the shelf edge of the northeastern Gulf of Mexico. Dots in figure represent all sites fished.

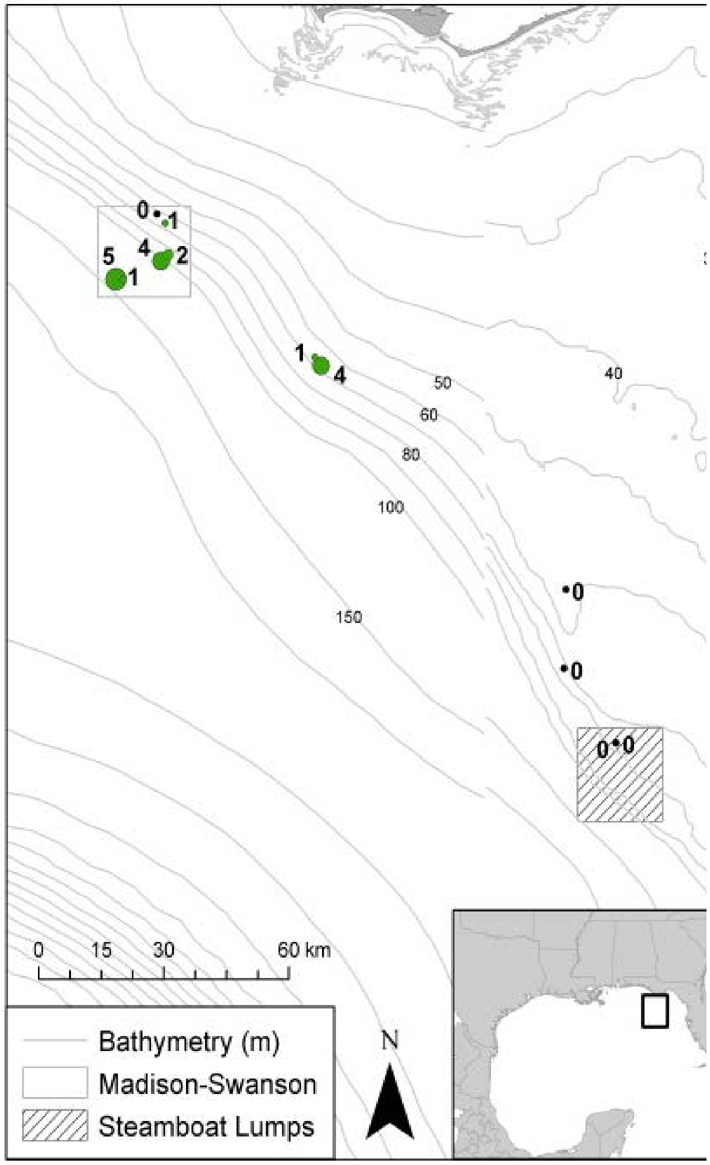


Figure 25. Location and number of snowy grouper (*Hyporthodus niveatus*) seen aboard the JSL II submersible along the shelf edge of the northeastern Gulf of Mexico. Dots in figure represent JSL II dive sites. Numbers beside dive sites indicate number s

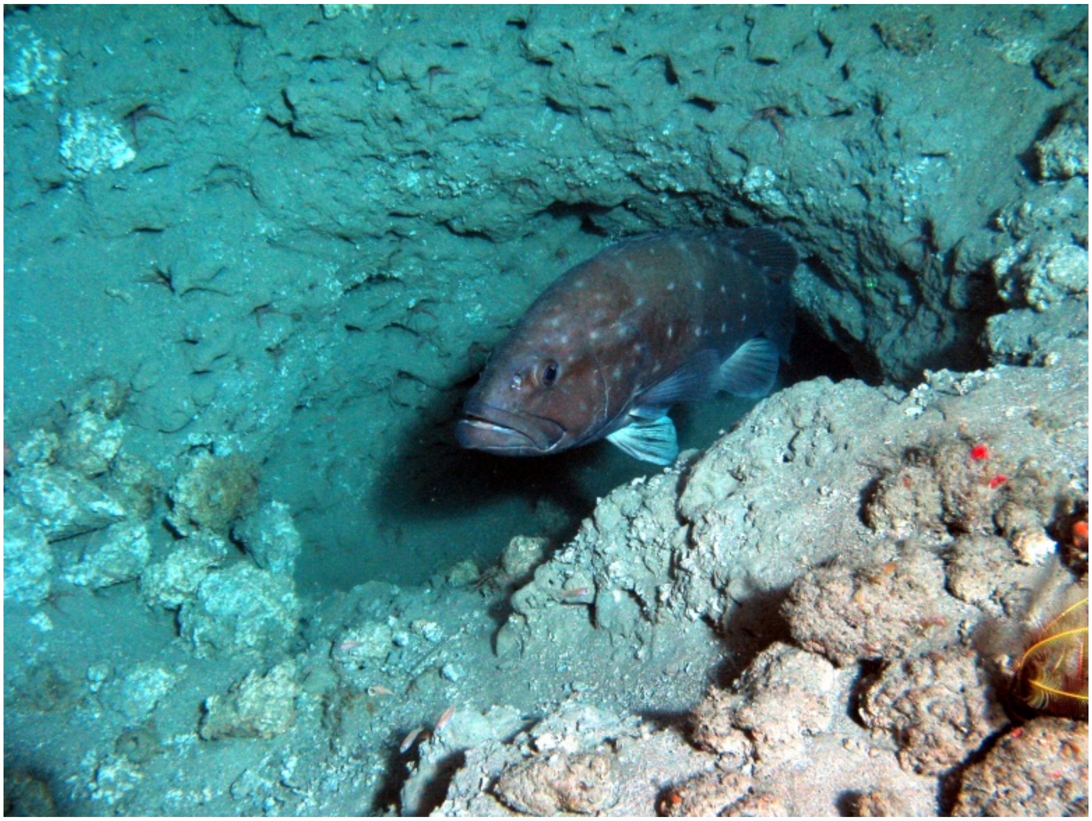


Figure 26. Snowy grouper (Hyporthodus niveatus) in a cave on the slope of Madison Ridge in MSMR. This fish was one of two observed along a single transect up the slope. It is unknown if the grouper excavated the cave, however such ecological engineering is known for red grouper (Coleman et al. 2010). Photo credit: C. C. Koenig.

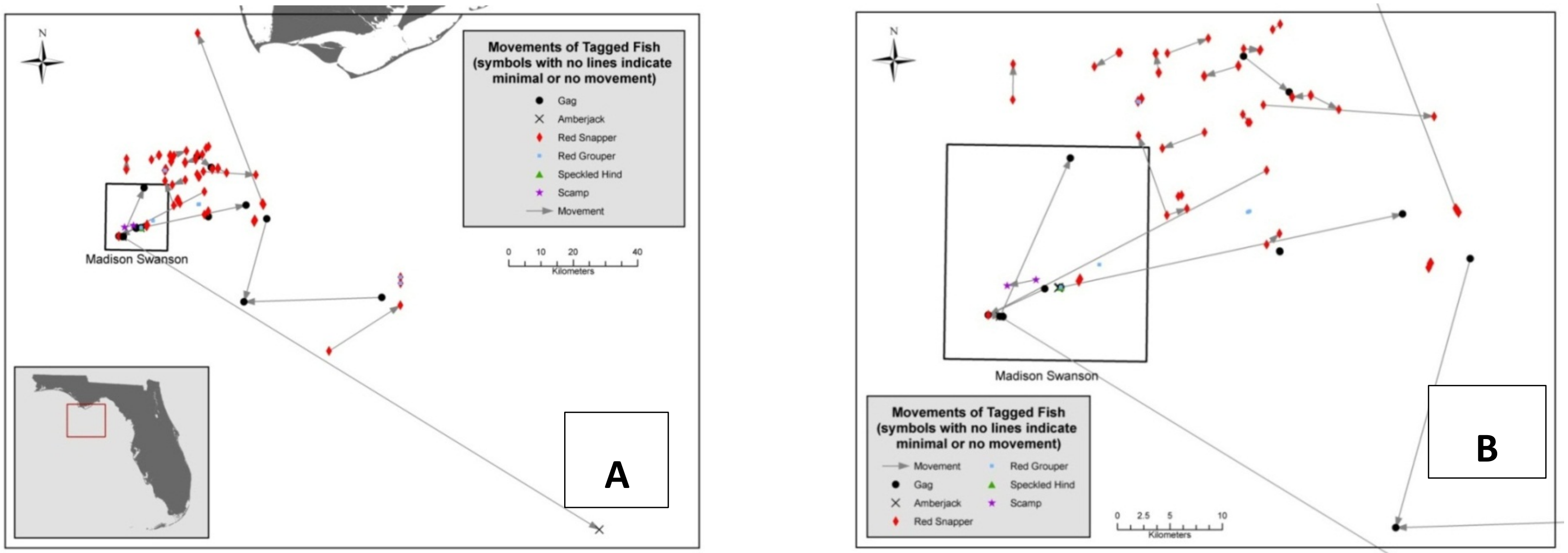


Figure 27. (A) Movement patterns of tagged and recaptured economically important reef fish in and around the Madison Swanson Marine Reserve (MSMR, 2008-2010). (B) Blow up of the same figure.

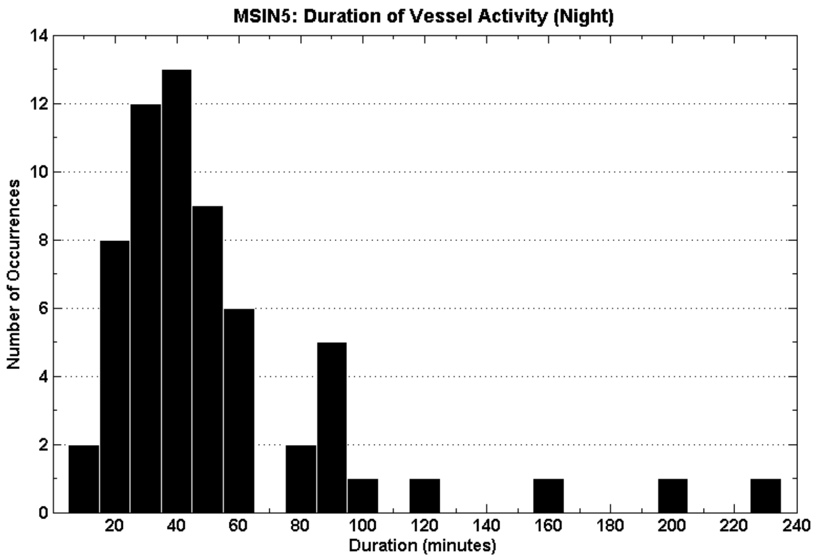


Figure 28. Acoustic monitoring (8/14/08 – 11/22/08 and 2/15/09 to 5/21/09) of station 5, located approximately in the center of our 12-receiver array along the southern ridge of MSMR (see Figure 3) showing duration of night-time activity within 1 km of the receiver (within the MSMR near the southern ridge over a 6 month period. Patterns at station 1 were similar.

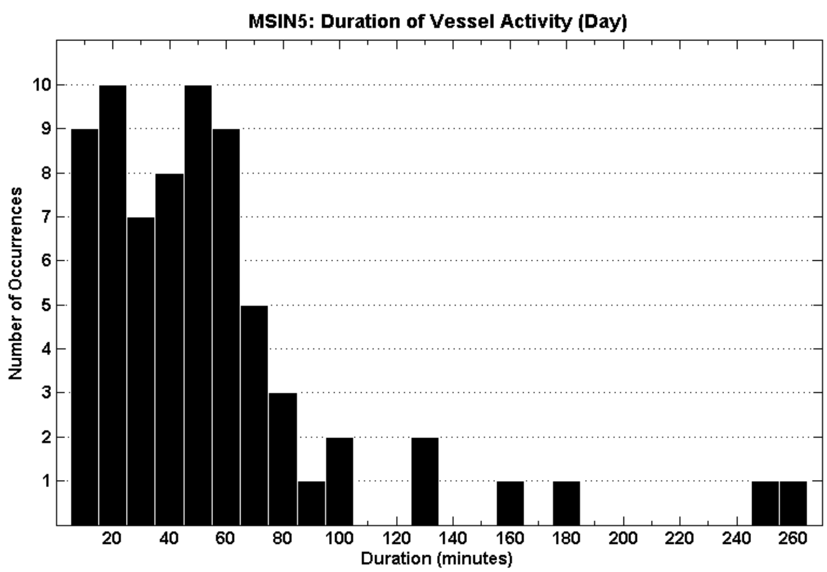


Figure 29. Duration and occurrence of vessel engine sounds heard in the day within 1 km of a gag spawning site #5 within MSMR. Sounds were recorded on a DSG hydrophone receiver over a 6-month period (8/14/08 – 11/22/0; 2/15/09 to 5/21/09). Patterns at station #1 were similar.

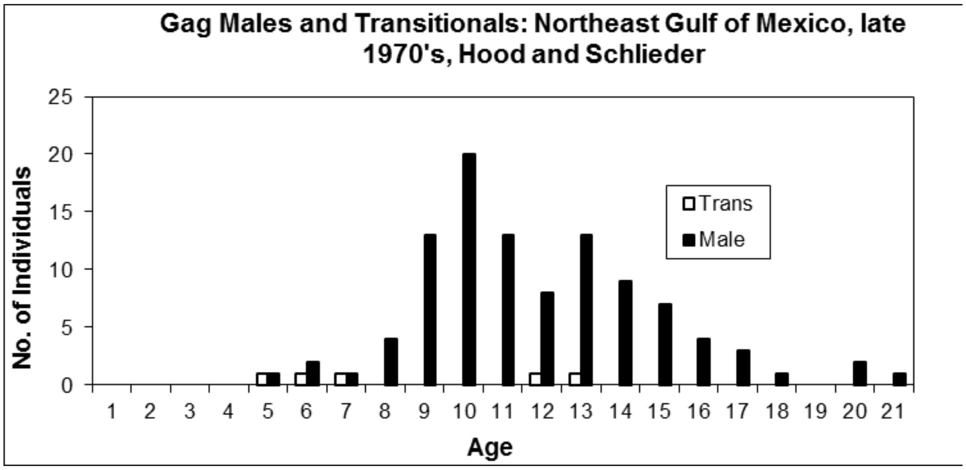


Figure 30. Age distribution of gag males and transitional in the northeastern Gulf of Mexico commercial hook and line fishery, 1976 to 1980. Data from Hood and Schlieder (1992).

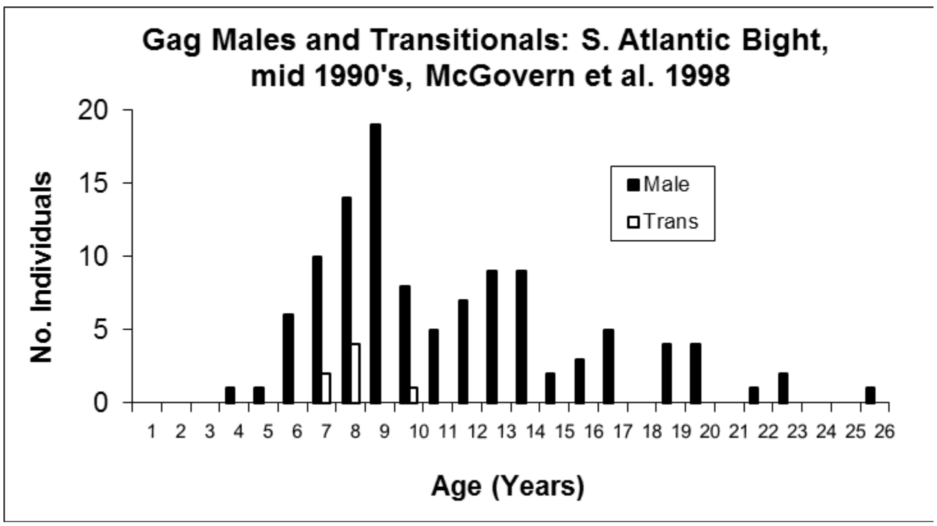


Figure 31. Age distribution of gag males and transitionals from the South Atlantic Bight commercial hook and line fishery, 1994 and 1995. Data from McGovern et al. 1998.

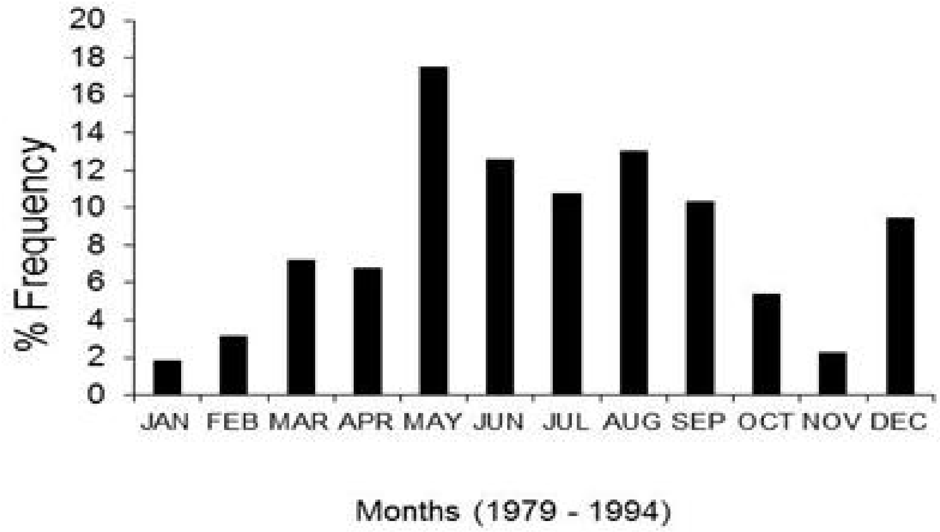


Figure 32. Logbook records of a commercial fisherman showing the absolute catch by month of male gag ('copperbellies') on the shelf edge in the NE Gulf of Mexico.

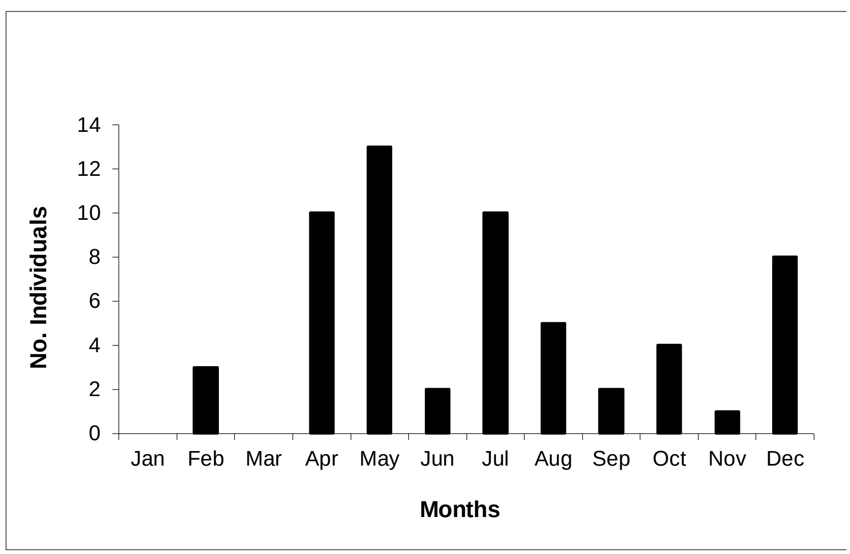


Figure 33. Record of absolute number of male gag ('copperbellies') landed in Panama City, FL. Data from Collins et al. (1998).

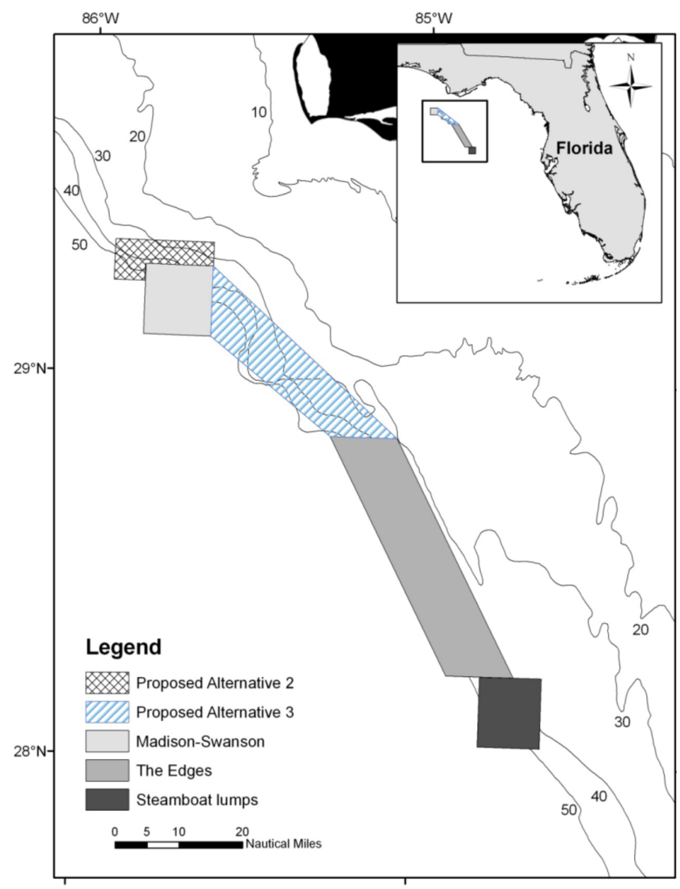
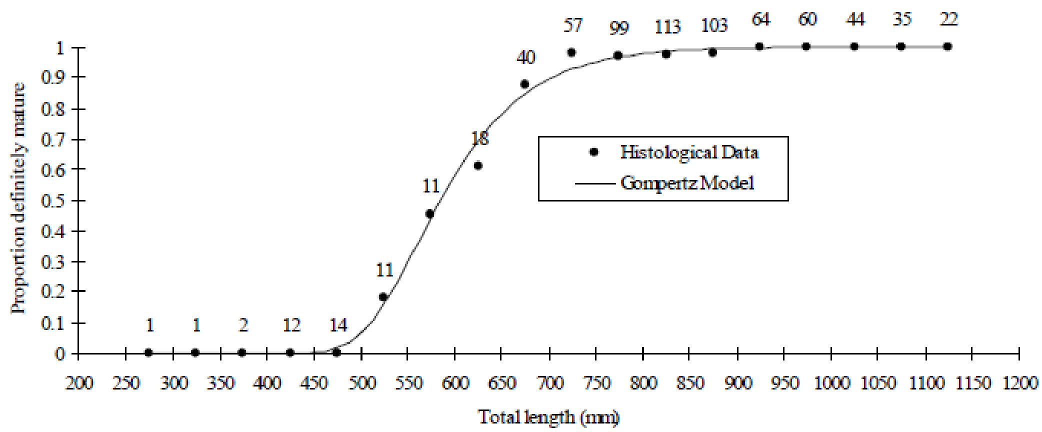


Figure 34. Map of the shelf edge of the northeastern Gulf of Mexico showing MSMR, SLMR and the "Edges" as well as two proposed alternative closed areas in Gulf Councils amendment 32.

APPENDIX I

Figure 4. Length at maturity based on definitely mature and immature female gag. Logistic regression function (Gompertz): Proportion = EXP(-EXP(-(-9.02 + 0.016*TL))), r^2 (McFadden) = 0.6, n = 707, L_{50} maturity = 585 mm TL.



From: Fitzhugh, GR, HM Lyon, LA Collins, WT Walling, and L Lombardi-Carlson. 2006. Update of gag (*Mycteroperca microlepis*) reproductive parameters: Eastern Gulf of Mexico, SEDAR 10 Data Workshop. SEDAR10-DW-03.

APPENDIX II

Florida State University
Coastal and Marine Laboratory

Memorandum

To: Dr. Roy Crabtree, Regional Administrator, NMFS Southeast Region
Patrick O'Shaughnessy, VMS Program Manager

Cc: Wayne Swingle, Gulf of Mexico Fishery Management Council

Subject: VMS and illegal fishing.

Date: 24 May 2008

I am writing this letter to state my position on a putative illegal fishing incident that occurred on 7 May 2008 within the Steamboat Lumps Marine Reserve. It was observed by me, by Dr. Felicia Coleman (FSU), and by Dr. David Mann (University of South Florida) during our studies of the reproductive biology, survival, and demographics of groupers in the northeastern Gulf of Mexico. It was also observed by Captain W. Bren Wade of the NASA M/V LIBERTY STAR, and members of his crew.

On May 7 2008, upon approaching our first research study site, ck1 (28 12.282'N / 084 43.016W), within the Steamboat Lumps Marine Reserve, we observed the commercial fishing vessel JUDY ANN, (Doc number 951560, home port Madeira Beach, FL) stern anchored directly on our study site within the reserve at ~0630 hrs. There was no one on deck or in the wheel house, although a bandit reel was clearly visible in fishing position on the gunwale. We approached the vessel closely and video taped it. After ~30 minutes, a person appeared in the wheel house and the fishing vessel left the area. Times, dates, positions, and observations were verified by Captain Wade in his log, recorded on DVD, and the information was subsequently handed over to NMFS SE region criminal investigator, Manny Antonaras. Also, I reported the incident to the US Coast Guard (USCG) Air Training Station, Mobile, AL, as soon as I observed it.

Poaching by commercial and recreational1 fishing vessels has been a serious problem in the northeastern Gulf of Mexico marine reserves since their inception in June 2000. In response to the problem, the Gulf of Mexico Fishery Management Council (GMFMC) in May 2007 passed a ruling requiring that all commercial fishing vessels in the Gulf purchase, install, and use vessel monitoring systems (VMS). The intent was to aid enforcement and ensure that the National Marine Fisheries Service (NMFS) and the USCG could monitor the movement patterns of these vessels 24/7 to eliminate further reserve fishing violations and to reduce the need for on-site boat surveillance.

According to USCG enforcement personnel, the F/V JUDY ANN's VMS had not functioning since 2 May 2008. That is, for five days, the vessel did not register on enforcement monitors. The evidence is very strong that the VMS was intentionally disabled for the purposes of illegal fishing because the vessel was not only in the reserve, it was anchored in an area of the reserve that has the highest abundance of red grouper. It would be interesting to see how often similar incidents of non-functioning VMS occurred with

1 We observed a recreational fishing vessel fishing within the Madison Swanson Marine Reserve on 10 May 2008. This incident was also reported to the Coast Guard and information turned over to agent Manny Antonaras.

3618 Highway 98• St. Teresa, FL 32358-2702•Telephone: 850.697.4139•Fax: 850.697.3822•Email: koenig@bio.fsu.edu

this vessel in the past, or any other vessel for that matter. I suggest that such a study be undertaken and reported to the Gulf of Mexico Fishery Management Council at its next meeting.

I have additional concerns about this incident, mainly because it went unnoticed or unreported by either NMFS or USCG enforcement until brought to their attention by my call. It suggests that at some level the person disabling the FV JUDY ANN's VMS knew that lack of detection equated with free reign in the reserves. Again, how widespread this perception is makes an interesting study. I realize that NMFS enforcement or the Coast Guard does not have the resources to track down every non-functioning VMS in the Gulf of Mexico, but there should be some mechanism in place to control this obvious weakness in the VMS enforcement system.

It is our job as research biologists to provide accurate information to the GMFMC and NMFS so they can make informed fishery management decisions. Providing accurate information is impossible if illegal fishing is not constrained. One commercial reef fish bandit boat has the capacity to catch over 1000 lbs of fish (e.g., gag, red snapper, red grouper) per day if the fish are available, as in the reserves (Koenig, personal observation). Thus, the possibility exists that the FV JUDY ANN could have removed 5000 lbs of groupers from the reserves during the time it was undetected. This level of catch may greatly alter the accuracy of our research within the reserves. It also allows the poachers to rob their fellow fishermen of their livelihoods, rob the managers of access to accurate scientific data for rulemaking, and ultimately rob all citizens of a sustainable resource. This should not happen with the present surveillance/enforcement system.

My colleagues and I, and the law biding fishermen we know and admire, are very disappointed with the present situation. There is an extremely effective mechanism in place to ensure that fishermen don't fish in marine reserves. It is the job of the enforcement agents to use it. Please look into this issue and determine where the weakness exists that allowed this F/V Judy Ann incident to occur. We consider this lack of enforcement unacceptable, as do all those interested in sustainable fishery resources.

Sincerely,

Chris Koenig

Dr. Chris Koenig
Marine Research Ecologist
FSU Coastal and Marine Laboratory

APPENDIX III

Groupers on the Edge: Shelf Edge Spawning Habitat in and Around Marine Reserves of the Northeastern Gulf of Mexico*

Felicia C. Coleman
Florida State University Coastal and Marine Laboratory

Kathryn M. Scanlon
United States Geological Survey

Christopher C. Koenig
Florida State University Coastal and Marine Laboratory

The northeastern Gulf of Mexico contains some of the most diverse and productive marine habitat in the United States. Much of this habitat, located on the shelf edge in depths of 50 to 120 m, supports spawning for many economically important species, including groupers. Here, we couple acoustic surveys with georeferenced videography to describe the primary spatial and geologic features of spawning aggregation sites for four economically important species: gag (*Mycteroperca microlepis*), scamp (*M. phenax*), red grouper (*Epinephelus morio*), and red snapper (*Lutjanus campechanus*), with notes on fish distribution and abundance and spawning activities. We provide information on movement patterns of reef fish determined using acoustic telemetry. Finally, we discuss the possible coupling of geomorphology with hydrographic features to influence the overall productivity of the region and the importance of spatial fishery management in sustaining that productivity. **Key Words: acoustic maps, gag, red grouper, reef fish, scamp, spatial management, spawning aggregations, spawning behavior.**

墨西哥湾东北部海域包含了一些在全美国最多样化和多产的海洋栖息地。这些深度为 50 至 120 米的陆架边缘的栖息地，为许多具有重要经济价值的物种，包括石斑鱼，提供了产卵区域。在这里，我们将有地理坐标参照的录像与声纳调查相结合，对四个重要经济鱼类聚集产卵的主要场所的空间和地质特点进行了描述：小鳞喙鲈（*Mycteroperca microlepis*），石斑鱼（*M. phenax*），红石斑鱼（*Epinephelusm orio*），红鲷鱼（*Lutjanus campechanus*），并附以鱼类分布、数量和产卵活动的说明。我们提供了珊瑚鱼群运动的模式信息，这是根据声学遥测的结果。最后，我们讨论了将地貌与水文特征相结合的可行性，以此影响该地区的整体生产力，以及维护这种生产力的空间渔业管理的重要性。**关键词：声纳地图，小鳞喙鲈，红石斑鱼，珊瑚鱼，石斑鱼，空间管理，聚集产卵，产卵行为。**

*For offshore field support, we thank S. Earle (National Geographic Society Explorer in Residence), G. P. Schmahl, E. Hickerson, D. Weaver (Flower Gardens National Marine Sanctuary), and the captains and crews of the R/V *Oregon II*, the R/V *Gordon Gunter*, the D/V *Spree*, the *Deepworker* (Nuytco Research Ltd.), the R/V *Liberty Star*, and the R/V *Bellows*. We acknowledge Steve Rash (Waterstreet Seafood, Apalachicola) and Bob Jones (Director, Southeastern Fisherman's Association, Tallahassee) for help engaging fishers in this study, including Clay Bailey (Apalachicola), Michael Laudacina (Key West, Florida), Danny Grizzard (Panama City), David and the late Wendell Sauls (Panama City), and Danny Tankersley (Port St. Joe). Financial support was provided by The Pew Conservation Fellows Program (fellowship to Felicia C. Coleman); National Sea Grant (project number: R/LR-B-51); the National Undersea Research Center (NURC) at the University of North Carolina, Wilmington (UNCW; NOAA Grant #030AR4300088); NOAA MARFIN Program (NA17FF2876), The National Fish and Wildlife Federation (2002–0073-000), the U.S. Geological Survey, and The National Oceanic and Atmospheric Administration. We thank Nuytco Research, Ltd., and the National Geographic Society's Sustainable Seas Expedition for use of video cameras offshore. The Florida State University Coastal and Marine Laboratory Academic Diving Program and NURC (UNCW) provided diving support. This research was conducted under the guidelines of the Florida State University Animal Care and Use Committee and under permits from the National Marine Fisheries Service. We thank three anonymous reviewers and K. Y. McMullen and J. Bratton (U.S. Geological Survey, Woods Hole) for their very helpful comments on the article.

The Professional Geographer, 63(4) 2011, pages 1–19
Initial submission, December 2008; revised submission, June 2010; final acceptance, September 2010.
Published by Taylor & Francis Group, LLC.

El nordeste del Golfo de México alberga algunos de los habitats marinos más diversos y productivos de los Estados Unidos. La mayor parte de este entorno, localizado en el borde de la plataforma continental, en profundidades de 50 a 120 m., sirve de lugar de desove para muchas especies económicamente importantes, incluyendo los meros. En este trabajo, juntamos observación acústica con videografía georeferenciada para describir los rasgos primarios espaciales y geológicos de sitios de concentración de desove para cuatro especies económicamente importantes: mero *gag* (*Mycteroperca microlepis*), pícaro (*M. phenax*), mero rojo (*Epinephelus morio*) y pargo rojo (*Lutjanus campechanus*), con anotaciones sobre distribución y abundancia de peces, y actividades de desove. Suministramos información sobre los patrones de movimiento de peces de arrecife, a partir del uso de telemetría acústica. Por último, discutimos sobre la unión de la geomorfología con rasgos hidrográficos para influir la productividad general de la región y la importancia del manejo espacial pesquero para sostener la productividad. **Palabras clave: mapas acústicos, gag, mero rojo, peces de arrecife, pícaro, manejo espacial, concentraciones de desove, comportamiento de desove.**

Taking fish in spawning time may be said to be against nature.

—Izaak Walton and Charles Cotton ([1653] 1998, 52)

The spatial scale of ecological function has gained importance concomitant with a declining natural resource base and the expanding capability of humans to find and exploit that base. Spatial management in marine systems, therefore, is a high priority as scientists and managers explore the scales at which ecosystems function and the scales at which humans operate (e.g., see papers in Coleman and Travis 2000; National Research Council [NRC] 2001; Lubchenco et al. 2003; Coleman and Thistle 2010).

The turning point for addressing spatial aspects of fishery management occurred with the 1996 reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act, which included a mandate to evaluate essential fish habitat (EFH)—its location, description, potential threats, and conservation and enhancement methods. Designation of essential areas for every managed species fell to the nation's nine fishery management councils, and the councils turned to geographers to provide the information in a visual context. Maps became essential tools for managers.

Most of the essential habitat supporting marine fisheries productivity occurs on the world's continental shelves. Globally, continental shelves represent only 7.6 percent of marine ecosystems. In the Gulf of Mexico, however, they represent 30 percent of the Gulf's total 1.5 million km^2 area (Rabalais, Carney, and Escobar-Briones 1999). Although most of the Gulf shelf consists of sediment-covered bottom (90 percent), some areas have significant three-dimensional structure. Among the latter are the Flower Garden Banks in the western Gulf of Mexico (see http://flowergarden.noaa.govscience/habitat.html), forming the northernmost coral reefs on the North American continental shelf (Rezak, Bright, and McGrail 1985) and the entire West Florida Shelf (WFS; Rabalais, Carney, and Escobar-Briones 1999), including the Florida Middle Grounds (Coleman, Dennis, et al. 2004), Pulley's Ridge (Halley et al. 2005), and the Tortugas (see http://floridakeys.noaa.gov/tortugas/).

The WFS, which extends along the length of the Florida panhandle and peninsula, represents 75 percent of the U.S. Gulf of Mexico shelf area and includes some of the most ecologically productive and biologically rich marine habitat in the United States. It also represents some of the most economically important regions, from the standpoint of both oil and gas and fisheries production. Indeed, the WFS, and more particularly the shelf edge, supports important fisheries that have been intensively fished for a century (Camber 1955; Coleman, Koenig, and Collins 1996; Koenig et al. 1996).

The practice of fishing on the shelf edge intensified in the Gulf of Mexico and elsewhere during the 1970s when fishers started targeting spawning aggregations to increase their catch-per-unit effort. This move was precipitated by the combined effects of depleted inshore fishery resources and changes in the regulatory milieu (e.g., increased size limits and gear restrictions) that forced fishermen into deeper water. Although fishery production increased in the short term, this practice inadvertently led to fishery declines because intensive fishing on spawning aggregations eroded aggregation size, reduced reproductive output, and, in some species, distorted sex ratios (Coleman, Koenig, and Collins 1996; Koenig et al. 1996; Domeier and Colin 1997; McGovern et al. 1998; Koenig et al. 2000; Heyman et al. 2005; Sadovy and Domeier 2005).

Despite the presumed importance of spawning aggregation sites on the WFS to fishery productivity and the impact of intensive fishing on that productivity, relatively little is known about where species aggregate to spawn, what geomorphologic characteristics define important spawning habitat, or how economically important species use that habitat. Indeed, few objective, systematic, and intuitively understandable habitat maps exist for these sites, and data on sea floor geology are limited (Madden, Grossman, and Goodin 2005). Yet these data coupled with data on the direct and indirect effects of fishing (Watling and Norse 1998; Coleman and Williams 2002; Dayton, Thrush, and Coleman 2002) and other disturbances on habitat and benthic communities (Hughes, Reed, and Boyle 1987; Hughes 1994; Waycott et al. 2009) are critical to the conservation and management of natural resources.

The primary purpose of this article is to describe the spawning habitat of four of the most economically important reef fish fishery species in the Gulf of Mexico: gag (*Mycteroperca microlepis*), scamp (*Mycteroperca phenax*), and red grouper (*Epinephelus morio*), a triad of winter–spring-spawning protogynous[1] grouper (Family Serranidae), and red snapper (*Lutjanus campechanus*), a single summer-spawning gonochoristic[2] species (Family Lutjanidae). The descriptions come from two marine reserves on the WFS and include geomorphologic characterizations and notes on spawning-related activity observed on those sites using a combination of acoustic sampling and georeferenced videography. We also briefly describe movement patterns of fish that were acoustically tagged on spawning sites. The discussion addresses the utility of these kinds of data for the development of spatial management for reef fish populations.

Study Sites and Species

The Madison–Swanson Marine Reserve (MSMR) and the Steamboat Lumps Marine Reserve (SLMR; each ~ 400 km^2; located on the 80 m isobath; Figure 1) serve as the main study sites. These reserves were closed to fishing in 2000 primarily to provide opportunities for grouper research. They represent areas on the WFS that are the least influenced by fishing impacts on habitat or demographic structure, at least in the recent past. Data herein are derived from studies conducted by the authors and others at these sites over the past six years.

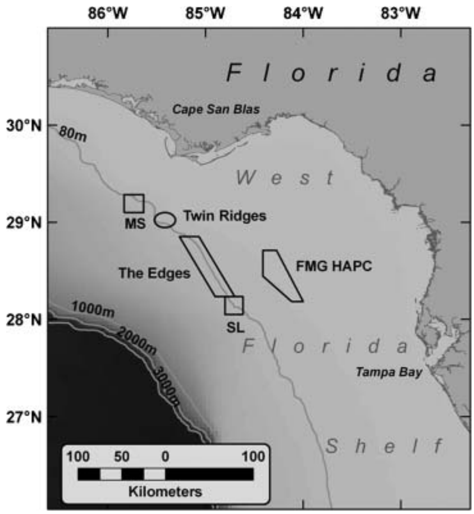


Figure 1 *Spawning habitats on the northern West Florida Shelf, Gulf of Mexico, including the Madison–Swanson Marine Reserve (MS), Steamboat Lumps Marine Reserve (SL), the Florida Middle Grounds HAPC (FMG HAPC), the Edges, and Twin Ridges.*

Although we include data from several species, our primary focus in this study is gag. Gag spawn exclusively on the shelf edge of the southeastern United States, most abundantly on the northern WFS (Koenig et al. 1996). Females typically form prespawning aggregations on shallow reefs in December and January, antecedent to offshore migrations for spawning events that peak in February and March. Gag form relatively small (<100 individuals) spawning aggregations (Gilmore and Jones 1992) that can occur great distances from their home sites. McGovern et al. (2005), for instance, recorded migrations exceeding 1,500 km between offshore waters of South Carolina and the northeastern Gulf of Mexico shelf edge. More typically, fish probably move from shallower to deeper reef sites to spawn, releasing eggs and sperm into the water column, where they are fertilized and hatch into larvae that have a six- to eight-week pelagic duration (Fitzhugh et al. 2005). Larvae are transported to estuaries, where they settle out as juveniles (Keener et al. 1988; Ross and Moser 1995) primarily in seagrass habitat (Koenig and Coleman 1998). Late juveniles egress in fall to shallow reefs and remain there for about three years before maturing as females. Some individuals eventually become males (Hood and Schlieder 1992; Coleman, Koenig, and Collins 1996). The mechanism of transition is unknown but likely results from social stimuli (Warner 1988). Gag populations of the southeastern United States exhibit a significantly female-biased sex ratio and a severely truncated size and age structure in response to intense fishing pressure (Coleman, Koenig, and Collins 1996; Koenig et al. 1996; McGovern et al. 1998; Heppell et al. 2006).

Scamp reproductive biology resembles that of gag in two respects: (1) scamp spawn on the shelf edge in relatively small (<100 individuals) aggregations, often in close proximity to and in concert with gag (Gilmore and Jones 1992; Coleman, Koenig, and Collins 1996; Sedberry et al. 2006); and (2) scamp exhibit a fishing-induced female bias in sex ratio (Coleman, Koenig, and Collins 1996). Scamp juveniles, rarely found in estuaries, inhabit reefs at depths of 20 to 30 m (C. Koenig, personal observation).

In spite of the fact that no observations of spawning have been reported for either scamp or gag, we have compiled significant indirect evidence for the timing and location of the spawning aggregations described herein. Specifically, sites were considered spawning aggregations when a majority of females captured at the sites during the spawning season contained hydrated eggs and when direct observations of courtship behaviors and spawning coloration changes were made for these species (Gilmore and Jones 1992; Coleman, Koenig, and Collins 1996).

Red grouper differ from gag and scamp in spawning somewhat later in the year (April and May) and by not forming spawning aggregations (Coleman, Koenig, and Collins 1996). They spawn on their home sites (Coleman et al., unpublished data), which consist of excavated sediment-covered rocks (Coleman and Williams 2002; Coleman et al. 2010). Juveniles occur primarily inshore over hardbottom throughout the WFS.

Red snapper spawn from April through October on the midshelf and shelf edge in the Gulf of Mexico and the South Atlantic Bight (Collins et al. 1998; Sedberry et al. 2006). Juveniles occur on the inner shelf on low-relief structured bottom (Workman and Foster 1994).

Materials and Methods

Spawning sites were identified by working offshore with commercial fishers, developing acoustic maps, and making observations using remotely operated vehicles (ROV) and manned submersibles. We developed long-term working relationships with several commercial fishers from northwest Florida who had years of experience on the water, extensive knowledge of fish behavior, and knowledge of the location of spawning aggregation sites. By targeting gag spawning sites during the spawning season, they historically landed between 1,000 and 3,000 pounds of mostly gravid gag per day (Stephenson 1993). Their interest in the long-term protection of this fishery resource led them to participate in this study and to provide locations of key gag spawning sites, identified by the presence of male gag, which they called *copperbellies* because of dark coloration that appeared on their abdomens, and females with hydrated eggs. We discovered red grouper spawning habitat by ground truthing previously unidentified features on side-scan images using ROVs and a manned submersible (described later).

Habitat Mapping

Side-scan sonar images of the MSMR and SLMR were produced using a EdgeTech DF1000[1] system, Isis topside acquisition system (Triton Elics, Inc.), and chirp-seismic-reflection profiles (Scanlon et al. 2003). Parallel adjacent transect images were made at 7.5 pings per second, yielding a 200-m (100 m to each side) swath. A median filtering routine allowed reduction of data to a 0.4-m pixel size and processing removed artifacts. We located specific habitat features of interest either within acoustic images or in the absence of such images, by using the vessel's echosounder.

For all sites, we used a two-step process to ground-truth and accurately interpret side-scan images. First we performed analysis of sediment samples collected by Van Veen grab sampler (Scanlon et al. 2003; Scanlon, Coleman, and Koenig 2005) using the Folk (1974) classification scheme. Second, we conducted analysis of video images of flat bottom areas made by towing a camera (Sony Hi8) in an Amphibico housing mounted on a camera sled. We developed acoustic maps by merging side-scan sonar data (100 kHz) from the MSMR produced by Scanlon et al. (2003)[3] with high-resolution (300 kHz) multibeam bathymetry from the MSMR produced by Gardner, Dartnell, and Sulak (2002).

Sea floor topographic features were surveyed using georeferenced videography obtained using underwater vehicles, including a manned submersible (Nuytco Research, Ltd.) and ROVs. Downward- and forward-looking (oblique) video cameras were mounted on the submersible (Sony Hi-8 in an Amphibico housing) and the Deep Ocean Engineering Phantom S2 ROV (Sony color video camera—DOE 12:1 optical zoom high-resolution, PAL/NTSC > 450 Lines—1/3″ CCD, Auto-iris, 780 wide-angle lens; and a Scorpio Plus Digital Nikon 99.5 Still TV Camera with ultrahigh definition, 2.048 × 1.536 megapixel still images with a zoom lens of 38 mm to 115 mm range in 35 mm format). Within spawning sites, ROVs were used to make a series of statistically haphazard transects, recording numbers of fish observed per minute of transect time to estimate relative fish abundance, and also recording basic habitat characteristics of the sites. The vehicles worked 0.5 to 1.0 m off the bottom at a speed range of 0.1 to 0.2 m/s (0.36 to 0.72 km/hr).

Movement Patterns of Aggregating Fishes

Fish capture and tagging occurred in 2003 and in 2004; the observation period extended through the summer of 2005. Reef fish were captured for tagging in chevron fish traps (2 m × 1.5 m × 0.7 m; mesh = 2.5 × 5 cm), modeled after those used by the Marine Resources Monitoring Assessment and Prediction Program. Baited traps were set on gag spawning sites for four to six hours, which proved to be sufficient to ensure capture. Traps with fish were subsequently raised partially off the bottom to allow divers to vent fish (i.e., to allow gas to escape from the swim bladder by puncturing the body wall to a depth of 2 cm with a 1.0 cm diameter point mounted on a pole spear). The depth at which venting occurred limited swim bladder gas expansion to 2.5 times that experienced on the bottom, equivalent to bringing a fish to the surface from about a 15-m capture depth. For example, fish caught at 100 m were raised to 35 m for venting. After venting, the trapped fish were hauled to the surface slowly, brought onboard the vessel, and released into a large (5001) tank with constantly running seawater. This method ensured that fish were not subjected to the often-lethal effects of swim bladder expansion, rupture, and hemorrhage.

Captured fish were measured (cm total length: TL) and tagged in the dorsal aspect with individual-identifier dart tags stamped with an 800-number for tag reporting. A subset of fish was selected—based on condition (appearing healthy), sex, size, and reproductive state—to receive individually coded ultrasonic transmitters (Vemco Company, four-year or two-year battery life, 69 kHz). The intent was to determine whether the large spawners remained within the reserves year-round or returned to spawning sites during the spawning season. These fish received both transmitters surgically implanted in the body cavity and an anchor tag to identify them as having transmitters when resighted or recaptured. After being tagged, fish were released immediately at the capture site.

The transmitters in tagged fish produce a consistent number of coded signals per day at random intervals to avoid constant signal collision. We used transmitters that produced signals at average intervals of either 2 or 5 minutes. VR2 receivers (Vemco Company) attached to moorings at eight spawning sites within the MSMR (Sites 46, 49, 50, 51, 53, 54, 55, and 57) detected and recorded the signals. We evaluated the detection radius of each VR2 receiver by lowering a transmitter tied to a weighted fishing line to within several meters of the bottom adjacent to the receiver and then drifting downstream to simulate fish movement away from the receiver. To determine detection distance, we synchronized start time on the receiver with the on-board clock and recorded both time and Global Positioning System position every few minutes from our start position to an end position 1.0 km (0.54 nautical miles [NM]) away. Divers retrieved VR2s every three to six months to download data and once a year to replace batteries. For a live fish, the proportion of the maximum number of detections per day indicates the proportion of the day the tagged fish remained within range of the receiver. To determine a "dead fish" pattern, we deployed a control transmitter 0.1 km from a moored receiver at station 54 (depth, 85 m).

Results

Potential spawning habitats were surveyed inside the MSMR and the SLMR during the spawning season (Table 1). Geomorphologic features of the habitat are described in relation to observations of courtship and potential spawning behavior.

Geomorphology and Spawning Sites Within the Madison–Swanson Marine Reserve

The sea floor in the MSMR is dominated by a gently sloping central sandy region (depth, 80–120 m) that drops abruptly (~8-degree slope) to 160 m near the western and southern regions of the reserve. The sediments sampled in areas shallower than 120 m are predominantly carbonate sand or gravel, with greater than 90 percent $CaCO_3$ content, whereas those deeper than 120 m are predominantly sandy silty clay, with 65 percent to 80 percent $CaCO_3$ content. Rocky ridges rim the sandy region across the northeastern corner and along the southern edge of the reserve (Figure 2).

The four most distinct geomorphologic features in the MSMR considered candidate grouper spawning sites were (1) the high-relief ridge (Stu's Ridge) within the shelf terrace, (2)

Table 1 *Grouper spawning-site characteristics on the West Florida Shelf, Gulf of Mexico, in the Madison–Swanson Marine Reserve (MSMR) and the Steamboat Lumps Marine Reserve (SLMR)*

Site	Grouper abundance	Geomorphology (water depth)
Madison–Swanson Marine Reserve		
Stu's Ridge	Gag (R) Scamp (A) Red grouper (A)	Carbonate packstone ridge on northern boundary with a talus slope ~10–20 m high and boulder fields at base (70 m)
46	Gag (A) Scamp (A) Red grouper (F)	Madison Ridge near terrace drop-off; scattered low-relief rock and sand with low ledges and boulders (100 m)
53	Gag (A) Scamp (A) Red grouper (N)	Madison Ridge near terrace drop-off; high-relief rocks, large caves, holes, and overhangs (80 m)
57	Gag (A) Scamp (A) Red grouper (N)	Madison Ridge near terrace drop-off; high- (large pinnacles with caves) and low-relief rocks and sand (85 m)
55	Gag (A) Scamp (A) Red grouper (F)	Madison Ridge near terrace drop-off; high- (large pinnacles with caves) and low-relief rocks and sand (90 m)
54	Gag (A) Scamp (A) Red grouper (F)	Madison Ridge near terrace drop-off; mostly sand waves with few rocks that provide the only structure (90 m)
49	Gag (A) Scamp (A) Red grouper (F)	Madison Ridge near terrace drop-off; high-relief rock with many holes and caves (90 m)
38	Gag (R) Scamp (N) Red grouper (A)	Northeast MSMR on flats away from drop-off; low-relief ledges under flat rocks and sandy areas with pits (60 m)
Steamboat Lumps Marine Reserve		
Multiple sites	Gag (N) Scamp (N) Red grouper (A)	North-central area, on edge of low-relief delta terrace; sandy pits with rocks and small caves mostly at bottom of each pit (73 m)

Note: Data were collected during the spawning seasons for gag (*Mycteroperca microlepis*), scamp (*M. phenax*), and red grouper (*Epinephelus morio*; 21–29 March 2005). Number of individuals observed by remotely operated vehicle within each site during thirty-minute transects: A = abundant; F = few; R = rare; N = none observed. A $\geq$ 10; 9 $\leq$ F $\geq$3; R $\leq$ 2. Sites denoted on maps in Figure 3.

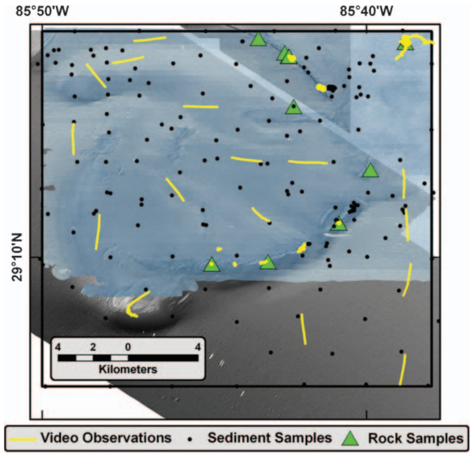


Figure 2 *Data collection sites within the Madison–Swanson Marine Reserve, including video transects conducted with remotely operated vehicles (ROVs), towed cameras, and stationary drop cameras; sediment samples collected using a van Veen grab, and rock samples collected by divers or with ROV manipulator arm. Sites overlay merged multibeam bathymetry data (Gardner, Dartnell, and Sulak 2002; D. Naar, University of South Florida) and side-scan sonar data (this study). (Color figure available online.)*

the high-relief ridge (Madison Ridge) along the relict delta shelf edge drop-off, (3) the isolated rocky pinnacles, and (4) low-relief hardbottom covered with a veneer of sand.

High-Relief Ridge (Stu's Ridge) Within the Shelf Terrace. This single arching feature within the shelf terrace crosses the northeastern boundary of the reserve and consists of tabular carbonate (some oolitic) packstone slabs at a depth of ~70 m. The ridge extends about 5.6 km within the reserve and an approximately equal extent northwest of the reserve boundary; it is not associated with the delta-edge margin. The ridge face rises ~10 m to 20 m, sloping almost vertically to the west and southwest where it is bordered by a moat (depth, 3 m). To the east and northeast, it grades into low-relief hardbottom (described later) covered with a veneer of carbonate sand and occasional boulders jutting through the sand. The base of the ridge has an accumulation of large boulders that broke off the top of the ridge, giving it the appearance of a talus slope (Scanlon et al. 2003).

Fishers did not report gag in this ridge area. In this study, few gag appeared on Stu's Ridge during the spawning season. When they did appear, they were not aggregating and showed no signs of spawning. Scamp occurred commonly and exhibited courtship behavior from the top of the ridge down to the talus slope. Females dispersed over an area of several hundred square meters and males patrolled among them, occasionally displaying to a female in the grayhead phase, similar to observations of Gilmore and Jones (1992).

High-Relief Ridge (Madison Ridge) Along the Relict Delta Shelf Edge Drop-Off. Madison Ridge is dominated by relict delta and barrier island complexes formed 58,000 and 28,000 years ago when slow sea level regression from 55 m to 85 m below present occurred (McKeown, Bart, and Anderson 2004; Gardner et al. 2005). This 12.9-km ridge occurs along a steep relict delta shelf edge drop-off, running northeast to southwest in the southern part of MSMR, and gradually slopes from ~80 m at the eastern end to ~110 m at the western end. The drop-off south of the ridge extends to a depth of 150 m. The rock structure along the ridge has variable relief, up to 8 m at the eastern end down to typically less than 2 m at the western end.

The greatest density of gag spawning aggregations was found along this rocky ridge at the southern edge of the relict delta formation drop-offs (known to fishers as *breaks*; Figure 3) and near other moderate-relief shelf edge features. Gag spawning sites averaged about two sites per linear 1.8 km. Six spawning sites were surveyed carefully along Madison Ridge and had numerous gags and scamps but few red groupers. Larger individual gags in spawning aggregations occurred up to 10 m above the sea floor and appeared less tightly associated with structure than were the smaller scamp (Gilmore and Jones 1992; this study). A scamp spawning aggregation occurred in close association with a gag aggregation at Site 53.

Isolated Rocky Pinnacles. Isolated pinnacles appear as 5- to 10-m relief structures (depth, 70–80 m) surrounded mostly by sand and mud, occurring near the center of the MSMR. Neither grouper spawning

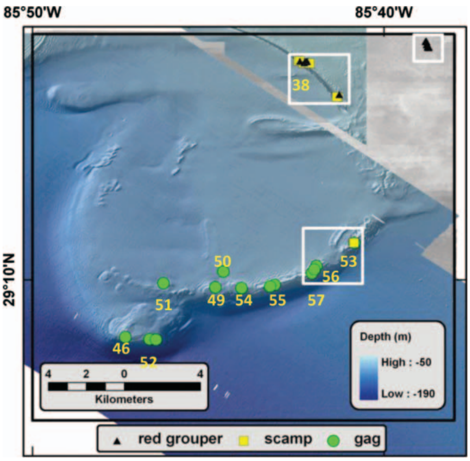


Figure 3 *Spawning sites in the Madison–Swanson Marine Reserve, West Florida Shelf, Gulf of Mexico. Sites overlay merged multibeam bathymetry data (Gardner, Dartnell, and Sulak 2002; D. Naar, University of South Florida) and side-scan sonar data (this study). Upper box: Red grouper spawning sites; middle box: Scamp and red grouper spawning sites on Stu's Ridge; lower box: gag and scamp spawning sites on Madison Ridge. Image courtesy of J. Gardener, U.S. Geological Survey, modified by J. Ueland, Bemidji State University, MN. (Color figure available online.)*

aggregations nor courtship behaviors were observed in this region of MSMR.

Low-Relief Hardbottom Covered by a Thin Veneer of Sand. This area is located in the northeastern corner of the reserve, east of Stu's Ridge, and is littered with exposed rocks or boulders. The southern ridge (Madison Ridge) is dominated by relict delta and barrier island complexes formed 58,000 and 28,000 years ago when slow sea level regression from 55 m to 85 m below present occurred (McKeown, Bart, and Anderson 2004; Gardner et al. 2005). This region consists of a series of highly rugose carbonate pinnacles rising up to 8 m above the surrounding sea floor.

Fishers identified two gag spawning sites in this region associated with large exposed rocks of about 2-m relief. We observed no gag or scamp spawning aggregations in this site, although both species occurred. Red grouper, however, were abundant here (Coleman et al. 2010) in upper box of Figure 3. In fact, this area serves as the primary red grouper habitat in the MSMR. Red grouper exhibited courtship behavior on the rocky flats to the east and northeast, especially in association with exposed boulders. This behavior entailed a single female approaching a male as she developed a distinctive barred color pattern. The male's color pattern also changed so that his back was intensely black, and white lines radiated from the eyes backward onto the black back. The male would invariably follow the female, which would end in a spiraling spawning ascent (Coleman et al. unpublished data).

Geomorphology and Spawning Sites Within the Steamboat Lumps Marine Reserve

Bottom features of the SLMR consist of a series of northeast-to-southwest trending terraces, the shallowest (depth, 71–73 m) of which occupy the northeast corner and resembles the delta formation of the MSMR in sloping (2.5 degree slope) toward the next terrace (depth, 80 m; Gardner et al. 2005) but with considerably lower relief than the MSMR. There are no major rocky outcrops or ridges evident in the SLMR side-scan data, but some of the terraces contain carbonate cobbles and boulders up to 1 m in diameter strewn over large areas. The sea floor in this area is composed of biogenic carbonate sand (>95 percent carbonate; Scanlon, Coleman, and Koenig 2005) interspersed with low-relief carbonate rock covered by sessile macroinvertebrates, including sponges, sea fans, corkscrew sea whips, and occasionally small clusters of the stony coral, *Oculina* sp., and crustose coralline algae. Side-scan images revealed conical depressions averaging 5.0 to 6.8 m wide and 2 m deep (range: <1 m to >25 m wide, 1.0–3.0 m deep) with clusters of carbonate rocks flanking their sides and bottom. The depressions occur in a clumped distribution at densities of ~250 km^{-2} (Scanlon, Coleman, and Koenig 2005). There were very few other rocky features within the SLMR and the relief was very low (Figure 4).

We found no gag spawning aggregations within the SLMR and none were reported by fishers. However, red grouper were abundant and are responsible for excavating the large conical pits (Scanlon, Coleman, and Koenig 2005; Coleman et al. 2010) averaging 6 m across

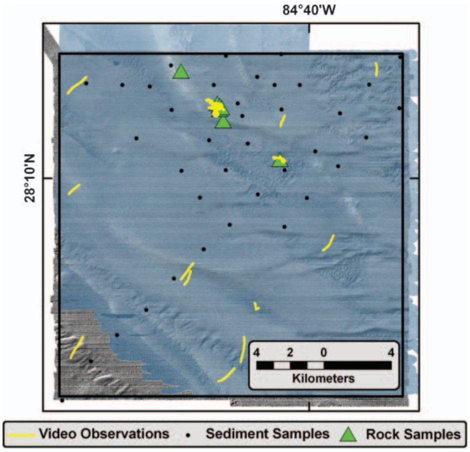


Figure 4 *Data collection sites within the Steamboat Lumps Marine Reserve, including video transects conducted with remotely operated vehicles (ROVs), towed cameras, and stationary drop cameras; sediment samples collected using a van Veen grab, and rock samples collected by ROV manipulator arm. Sites overlay merged multibeam bathymetry data (Gardener et al. 2002) and more extensive side scan sonar data (this study). (Color figure available online.)*

and 2 m deep. Females make short excursions to a male's excavation, where courtship and mating ensue (Coleman and Koenig unpublished data) accompanied by specific courtship sounds (Nelson et al. 2011). Both male and female red grouper remain at excavation sites year-round. In fact, our tagging studies on the shelf edge indicated a sedentary pattern with little to no movement. Red grouper exhibited exceedingly strong fidelity to these sites (Coleman et al. 2010), which was likely related to the investment involved in excavation (Figure 5).

Movement Patterns of Aggregating Fishes

All fish tagged with transmitters were from aggregation sites on Madison Ridge, including eleven gag males, eleven gag females, one scamp male, and seven red snapper (Table 2). We did not implant transmitters in red grouper because they were so sedentary that we could not easily determine if the signals received were from live or dead fish.

Gag. We found sexually distinct movement patterns among gag (Figures 6A, B, C). Males

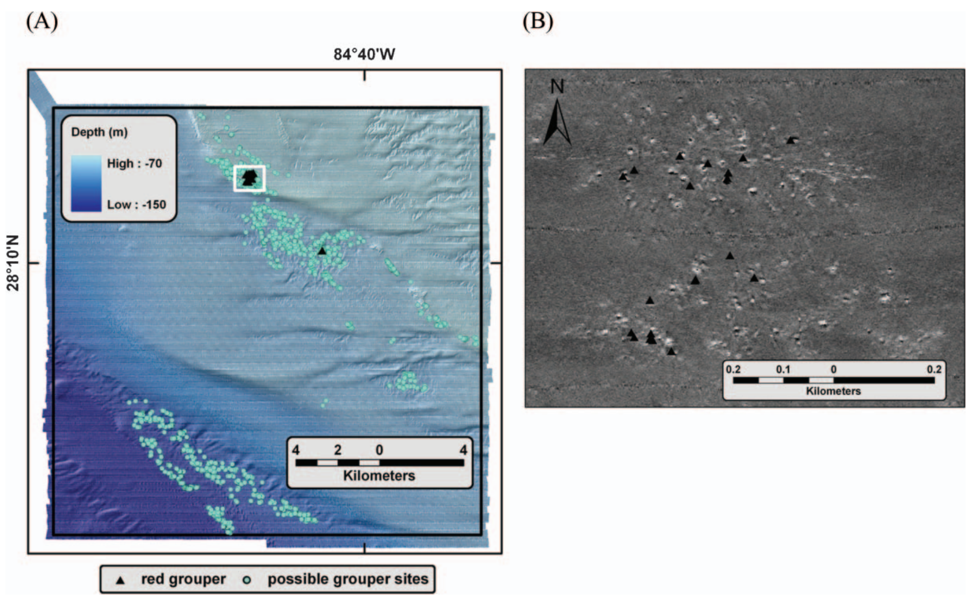


Figure 5 *Red grouper spawning sites within the Steamboat Lumps Marine Reserve (SLMR) superimposed on side-scan sonar mosaic images. (A) Ground-truthed (black marks) and presumed (blue marks) red grouper habitat based on geomorphologic features. (B) Blow-up of white block indicated in upper panel, red grouper habitat. (Color figure available online.)*

Table 2 *Movement of gag, scamp, and red snapper within the Madison–Swanson Marine Reserve, West Florida Shelf, Gulf of Mexico, based on transmitter data from telemetered fish*

					2003		2004		2005	
Species	**Size (TL, cm)**	**Sex**	**Tag date**	**Tag Site**	**Jan–June**	**July–Dec**	**Jan–June**	**July–Dec**	**Jan–June**	**Maximum distance (km)**
GA	95	M	4/16/2003	51	51	LR	51	51	51	0
GA	99	M	4/17/2003	50	50	LR	49, 50	49	50	0.9
GA	109	M	3/24/2003	54	ND	LR	ND	ND	ND	Lost
GA	107	M	4/4/2003	53	53	LR	53	53	53	0
GA	117	M	4/4/2003	53	ND	LR	ND	ND	ND	Lost
GA	126	M	5/10/2004	55	—	—	55	55	55, 57	1.8
GA	122	M	4/16/2003	53	55	LR	53	53	53	0
GA	122	M	5/4/2003	50	ND	LR	54, 49, 50	54, 49, 50	ND	1.3
GA	85	M	4/17/2003	49	49	LR	49	49	49	0
GA	121	M	6/29/2004	49	—	—	49	49	ND	0
GA	98	M	5/26/2005	51	—	—	—	—	51	0
GA	90	F	4/17/2003	50	ND	LR	ND	ND	ND	Lost
GA	91	F	5/4/2003	46	46	LR	46	46	46	0
GA	89	F	4/17/2003	50	50	LR	49, 50	49, 50	50	0.9
GA	94	F	1/13/2004	49	—	—	49	49	ND	0
GA	91	F	5/10/2004	53	—	—	53	ND	ND	0
GA	89	F	1/14/2004	52	—	—	ND	ND	ND	Lost
GA	92	F	1/14/2004	46	—	—	46	46	46	0
GA	106	F	4/18/2004	53	—	—	49, 51, 54, 57, 46	ND	ND	11.1
GA	91	F	3/20/2004	46	—	—	46	46	46	0
GA	98	F	10/20/2004	54	—	—		ND	ND	Lost
GA	86	F	1/9/2005	55	—	—			55, 57	1.8
RS	56	?	7/26/2003	55	—	LR	55	55, 51	55, 51	5.2
RS	70	?	1/13/2004	51	—	—	51	51	51	0
RS	78	F	3/13/2004	46	—	—	46	46	46	0
RS	73	?	4/18/2004	51	—	—	55, 46	55	55	7.4
RS	68	F	5/10/2004	54	—	—	49, 54	49, 54	ND	1.3
RS	63	M	6/29/2004	55	—	—	55	ND	ND	Lost
SC	54	M	4/15/2003	53	—	LR	53	53	53	0

Note: Tag sites (site location numbers on Figure 3) indicate original sites where fish were tagged. Subsequent locations of fish as determined by receivers are given for each of two seasonal periods (January–June, July–December) for each of three years. GA = gag; RS = red snapper; SC = scamp; F = female; M = male; TL = total length; LR = lost receiver, replaced receiver; ND = not detected; Lost = fish either left the area or died during the study.

clearly exhibited strong site fidelity, remaining on one or at most two spawning sites for extended periods of time (Table 2). Most males (including those tracked for about two years) rarely left a single spawning site. Activity patterns around those sites indicated that the tagged fish were alive (Figure 6). Others moved relatively short distances between two sites. This included one that moved 0.9 km between sites, remaining on the second site for five months before returning to the original site just prior to the spawning season and remaining there for the rest of the observation period, and one that moved 2.8 km between sites (the greatest movement observed). Female gag show a very different pattern. They tend to move more frequently among spawning sites, stopping at sites only briefly before moving on or just passing through sites (based on VR2 receiver records of only a few hits). Many of the females at the aggregations left the MSMR soon after the spawning season ended, but some unknown proportion remained.

Scamp. The single scamp (male) tagged with a transmitter displayed movement patterns similar to that of male gag and remained around the tagging site throughout the twenty-three-month observation period (Figure 7).

Red Grouper. Red grouper showed exceedingly strong site fidelity, based on nine separate dart-tag returns from fish at liberty for 100 to 300 days. Eight of these fish did not move at

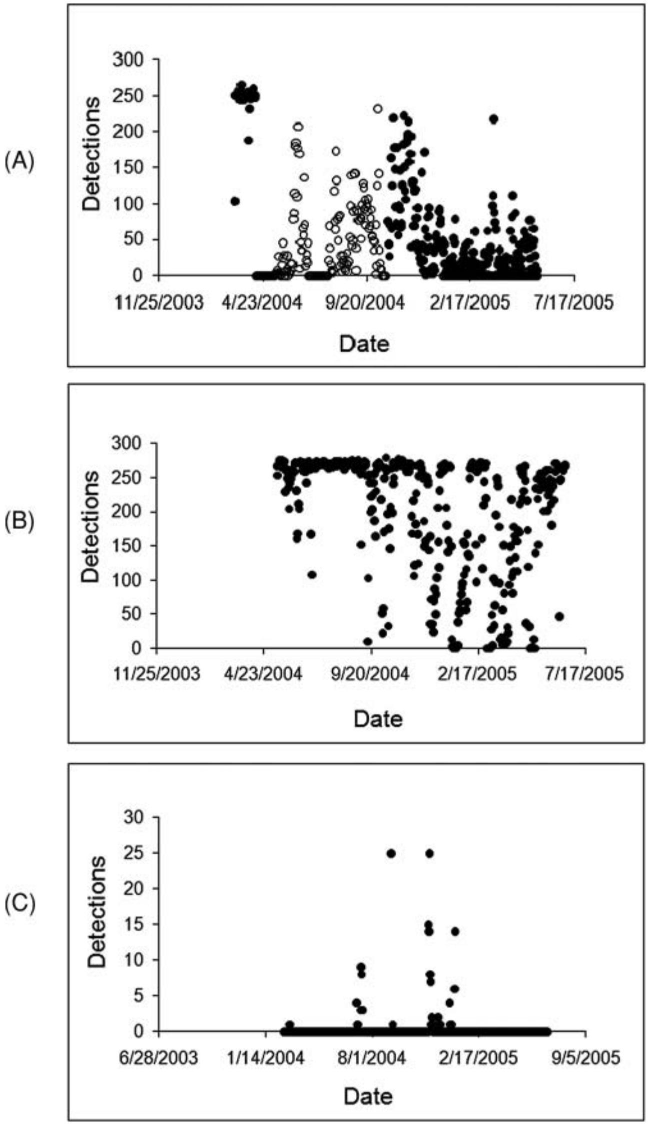


Figure 6 *Daily acoustic tag detections (circles, sum of detections per day) for gag (*Mycteroperca microlepis*) indicating movement patterns on spawning sites within Madison–Swanson Marine Reserve. (A) Male tagged 17 April 2003 on Site 50 (solid circles) moved 0.9 km to Site 49 (open circles), then back to Site 50. (B) Male tagged 16 April 2003 on Site 51 and remained near that site. (C) Female tagged on 14 January 2004, infrequently visited Site 46, then disappeared from the study.*

all from their original tagging site. This differs significantly from the aggregating behavior and movement patterns of gag and scamp.

Red Snapper. Although our study focused on groupers, we include movement data on red snapper because they exhibited spawning and movement patterns very similar to those of gag in that they spawned on gag spawning sites (as indicated by the presence of hydrated eggs in females) and tended to remain in the vicinity of these sites year round. Some fish moved among

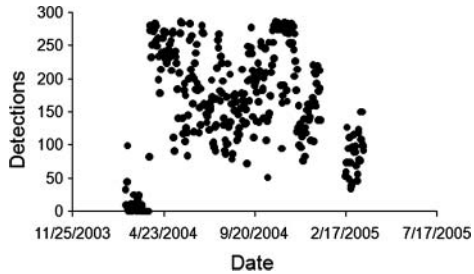


Figure 7 *Daily acoustic tag detections (circles, sum of detections per day) for scamp (*Mycteroperca phenax*) indicating movement patterns on spawning sites within Madison–Swanson Marine Reserve on the West Florida Shelf, Gulf of Mexico. Male tagged 15 April 2003 on Site 53, remained near the same site for nearly two years until 16 March 2005.*

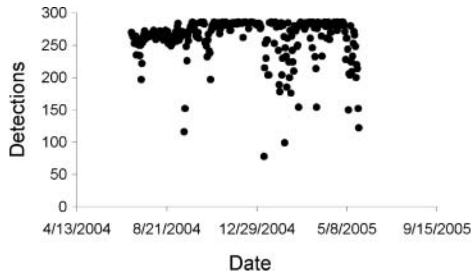


Figure 9 *Daily acoustic tag detections (circles, sum of detections per day) for control transmitter placed on the bottom (depth, 85 m) at spawning Site 54 within Madison–Swanson Marine Reserve, to determine the pattern of detections that would be produced by a dead fish within range of the receiver. Note that most of the detections are near the maximum daily value of 280.*

spawning sites, periodically revisiting alternate sites for extended periods, a characteristic reminiscent of male gag (Figures 8A, B).

Control. The radius of detection for VR2 transmitters was about 0.5 km, and the maximum number of detections per day ranged from about 280 to 1,100, depending on transmitter type (Figure 9).

Detection Problems. Two types of interference compromised detection of transmitters by VR2 receivers: intense meteorological events, such as severe storms, and the presence of operating echosounders on vessels. During Hurricane Ivan, which passed within 74 km of MSMR on 19 September 2004 producing 13 m waves (record from data buoy #42039, http://www.ndbc.noaa.gov/station_page.php?station=4203), transmitter detections declined by about two thirds. In the presence of a vessel with an operating echosounder, detection declined to zero.

Echosounders (fathometers) record depth by emitting sounds that reflect off the bottom to a transducer on the hull of the vessel. These sounds are strong enough to mask transmitter

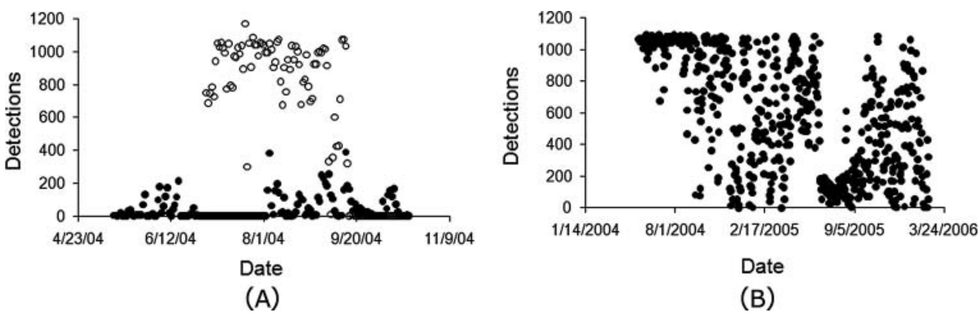


Figure 8 *Daily acoustic tag detections (circles, sum of detections per day) for red snapper (*Lutjanus campechanus*) indicating movement patterns on spawning sites within Madison–Swanson Marine Reserve on the West Florida Shelf, Gulf of Mexico. (A) Female tagged 10 May 2004 on gag spawning Site 54 (solid circles), moved 1.4 km to Site 49 (open circles), moved between the two sites frequently during the red snapper spawning season, then disappeared on 11 October 2004. (B) Red snapper tagged at Site 51 on 13 January 2004, remained on site through 16 February 2006, the last time receivers were checked. Sex unknown. Depth, 85 m.*

signals entirely. Vessels operating within the reserve include research vessels, fishers trolling at the surface for pelagic species, vessels operated by poachers, and vessels operated by the U.S. Coast Guard, the entity responsible for fisheries enforcement in federal waters. Intense poaching occurred in the MSMR following the hurricanes in 2004 (Ivan) and 2005 (Katrina and Rita) (C. Koenig, personal observation; U.S. Coast Guard, Mobile, AL, personal communication) largely because Coast Guard resources shifted to storm-related activities, leaving few assets for surveillance and enforcement of fishery regulations. Complete loss of signals from transmitter- implanted fish could have occurred in several ways: (1) fish swimming out of the area, (2) transmitter malfunction, or (3) fish being captured by mobile predators (including poachers, which was highly likely during this period). Given the unexplained transmitter loss, it was not possible to determine the relative proportion of females leaving or remaining on spawning sites after the spawning season.

Discussion

Many ecologically important reef fishes use continental shelf edges as spawning habitat (e.g., Claro and Lindeman 2003; Sedberry et al. 2006). They are particularly attracted to rock-covered areas, regardless of the type or shape (Colin and Clavijo 1988). Our studies in the Gulf of Mexico bear this out (Coleman, Koenig, and Collins 1996; Koenig et al. 2000, this study). We found that gag, red grouper, scamp, and red snapper all used shelf edge reef sites containing rocky substrate but that the characteristics varied considerably among sites and, therefore, in importance to different species.

Gag spawning sites had two critical features: (1) rocky ridges and (2) relatively steep delta terrace drop-offs. These are precisely the spawning site features described by fishers as *breaks*. Although gag did not distinguish markedly between high-relief rugose ridges or low-relief boulders, they apparently preferred drop-offs containing either of these rock features (e.g., at Madison Ridge) over those that did not (e.g., the southern rim of Twin Ridges,[4] described by Briere et al. 1999; Gardner et al. 2005). Scamp, on the other hand, tended to spawn on any high-relief rugose structure on the shelf edge, with or without a drop-off. For example, they were abundant on Twin Ridges (Figure 1; Briere et al. 1999) where no gag spawning aggregations occurred. Red grouper associated with two types of habitat: low-relief (<1 m) carbonate-rock hardbottom with a thin veneer of carbonate-derived sediments (MSMR) and cone-shaped solution holes embedded in a thick lens of carbonate-derived sediments (Coleman et al. 2010). In general, all three grouper species spawned in late winter to early spring. Red snapper, on the other hand, spawned during the late spring, summer, and early fall on the same sites as gag.

Movement Patterns of Aggregating Fishes

Sedentary species with limited home ranges are the best candidates for management using marine protected areas. Indeed, if large spawners remain within reserve boundaries, this dramatically enhances the reserve's value (Bohnsack 1996; Roberts et al. 2001; Berkeley, Chapman, and Sogard 2004; Berkeley et al. 2004).

For the most part, the species we evaluated fall into this category. In gag, males clearly exhibit strong spawning site fidelity year-round, whereas females that remain on the shelf edge show a much more varied pattern of site fidelity, and many apparently leave the shelf edge after the spawning season. Given that fishers fish spawning aggregations before, during, and after the spawning season (as suggested by their logs and by National Marine Fisheries Service data), their catch-per-unit effort is maximized during the spawning season but includes a higher proportion of males during the interspawning period (Collins et al. 1998). The latter presents a mechanism for fishing-induced erosion of the sex ratio to a heavily skewed female bias during the subsequent spawning season. The proportion of females remaining on site year-round is unclear, based on the limited returns of transmitter-tagged females. Our very limited data on scamp (derived from a single male tagged in the MSMR) indicating strong site fidelity (this study) coupled with data on erosion of the scamp sex ratio (Coleman, Koenig, and Collins 1996) suggest that male loss is a consequence of fishing. Red grouper do not show fishing-induced female bias in sex ratio (Coleman, Koenig, and Collins 1996), which is likely due to their very different mating system. Red grouper do not form spawning aggregations. Males and females remain tenaciously on excavated home sites year round where males spawn with females visiting from neighboring sites during the spawning season (Coleman et al. 2010). Under this mating system, one would expect males and females to be caught in the fishery with equal probability. This is supported by data in Coleman, Koenig, and Collins (1996) in which increased skewing of the sex ratio is absent.

For red snapper, we make two significant observations: that (1) they show a tight, long-term association with their spawning sites, confirming observations by longline fishers catching large spawners ("sows") offshore; and (2) they use the same spawning sites as gag, separated seasonally, supporting the idea that these sites are spawning "hotspots" (Colin and Clavijo 1988). This observation is highly significant as some of the first evidence that the suite of large commercially important groupers and snappers in the eastern Gulf might utilize multispecies reef fish aggregation sites as the similar suite of species from the grouper–snapper complex in tropical waters of the Caribbean and eastern Florida (Heyman this issue; Gleason, Kellison, and Reid this issue).

Connectivity Between Offshore Spawning Sites and In-Shore Nursery Habitats

One can reasonably assume that those geomorphologic features important to spawning couple with hydrographic features to ensure maximum survival of offspring. In the South Atlantic Bight, intermittent gyres and upwelling events contribute to larval retention and higher productivity near shelf edge spawning sites (Sedberry, McGovern, and Pashuk 2001; Sedberry et al. 2006) and might be important in the survival and transport of larvae into coastal areas, as occurs on the southwest Florida coast (Limouzy-Paris et al. 1997). In the northeastern Gulf, we suspect that upwelling on the shelf (He and Weisberg 2001, 2003) and seasonal outwelling of the Apalachicola River (Gilbes, Muller-Karger, and Del Castillo 2002) contribute to recruitment success of fish spawning on shelf edge reefs. The rationale is that the nutrients likely fuel benthic and pelagic food webs as they flow across these reefs during peak late-winter spawning (Morey, Dukhovskoy, and Bourassa 2009) and so might also contribute to the timing of spawning.

For gag in the northeastern Gulf, spawning must occur at a time and in a place consistent with enhancing the likelihood of delivering competent juveniles to highly productive seagrass habitat. It is no coincidence that the largest, most pristine seagrass bed in North America, the 3,000 km^2 Big Bend seagrass system of Florida (Zieman and Zieman 1989), is just in-shore of the dominant gag spawning sites on the WFS. Gag recruit to this habitat when seagrass productivity is increasing (May), and leave five to six months later (October) as productivity declines (Zieman, Fourqurean, and Iverson 1989; Koenig and Coleman 1998; Strelcheck et al. 2003).

Implications for Fisheries and Habitat Management

The activity of fishing on spawning sites is notoriously unsustainable because fish are vulnerable to capture due to their aggregating behaviors and strong site fidelity (Domeier and Colin 1997; Sadovy and Domeier 2005). A primary objective of effective fishery management should be protecting aggregating reef fish during their reproductive period. Because reef fish in the northeastern Gulf of Mexico are tightly linked to a particular habitat, shelf edges with rocky reefs as illustrated herein, management must include a strong spatial component (Coleman and Travis 2000; NRC 2001; Lubchenco et al. 2003; Coleman, Figueira, et al. 2004; Lorenzen et al. 2010).

Information about habitat characteristics is critical and highlights the importance of using coupled acoustic surveys and georeferenced videography (Tanoue et al. 2008). Having this information leads ultimately to informed and sometimes progressive management actions. Lacking it has contributed to rampant habitat destruction at the level of marine ecosystems. Indeed, gear impacts alone have destroyed spawning habitat and overall biological diversity on a global scale, from seamounts off New Zealand, Australia, and Namibia, to deep-water coral reefs off Florida's east coast. Fishing activity targeting orange roughy spawning aggregations around seamounts annihilated endemic benthic communities in its wake (Koslow and Gowlett-Holmes 1998; Koslow et al. 2000;

Koslow et al. 2001; Clark and Rowden 2009). Rock shrimp fisheries off Florida's east coast destroyed coral spawning habitat for grouper and many other reef-associated species (Koenig et al. 2005; Reed, Koenig, and Shepard 2007).

Only a small stand (~2 hectares) remains of the once extensive Oculina Banks, the deep-water shelf edge coral habitat off Florida's east coast (Koenig et al. 2005; Reed et al. 2005). Efforts to protect the habitat from gear impacts largely failed, despite regulations enacted in 1984 to protect the area from trawling and in 1994 to establish a no-take zone to protect the area from other types of bottom fishing. Trawling within the reserve did not effectively decline until 2003, when the advent of vessel monitoring systems in the southeastern United States allowed enforcement agencies to track trawler movements via satellite.

No similar impacts occur on the habitat described in this study, although highly vulnerable sites occur elsewhere on the WFS, including the Florida Middle Grounds (Figure 1) and Pulley's Ridge. The sites in this study are vulnerable to fishing practices that remove top-level predators or habitat engineers (e.g., Coleman and Williams 2002; Coleman et al. 2010) and other impacts that alter habitat structure or integrity, including oil and gas exploration and development, hypoxic events, and other forms of pollution (Allison et al. 2003).

The southeastern United States is making a concerted effort to protect spawning populations of reef fish because of the serious declines revealed in one stock assessment after another. Extensive closures for gag and scamp from 1 January through 30 April are proposed throughout the South Atlantic Bight, from Cape Hatteras, North Carolina, to Cape Canaveral, Florida, and in the Gulf of Mexico throughout the Edges (Figure 1), 1,338 km^2 on the shelf edge between MSMR and SLMR considered the heart of gag and scamp populations. These measures will protect major segments of the reproductive population of gag during part of the prespawning aggregation period of females and all of the spawning aggregation period. They will also protect scamp because their spawning seasons and habitat often overlap. No special provisions appear for red grouper, although the marine reserves in the Gulf of Mexico and the area-seasonal closures in both the Atlantic and Gulf will likely protect a considerable amount of red grouper spawning. Given the current knowledge base on spawning habitat and seasonality, these management measures are critical components of recovery for these heavily fished species. Additional year-round closures of shelf edge spawning habitat would protect protogynous species, given the vulnerability of males to capture during the interspawning period (Collins et al. 1998), and protect the age and size structure of both protogynous and gonochoristic species, given the importance of large, fecund females (Alonzo and Mangel 2004; Berkeley, Chapman, and Sogard 2004; Berkeley et al. 2004). Additional seasonal-area closures would help protect fish migrating to spawning sites. None of these measures is effective, however, if it results in intensified fishing on unprotected sites. This suggests that a more plausible approach is the coupling of spatial management with reduced fishing effort. ■

Notes

[1] Protogynous fishes are sequential hermaphrodites, in which all fish first mature as females and then some portion of the population changes sex to become males. Sex change is likely mediated through social interactions.

[2] Gonochoristic fishes have two distinct sexes in which the sex of an individual does not usually change throughout its lifetime.

[3] See the U.S. Geological Survey Web site, "Coastal and Marine Geology Program Internet Map Server: West Florida Shelf," at http://coastalmap.marine.usgs.gov/regional/contusa/gomex/flplatform/west_fl_shelf/data.html (last accessed 9 November 2009).

[4] Twin Ridges is a 9-km-long parallel set of high-relief rocky ridges located southeast of MSMR.

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