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

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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。**

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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

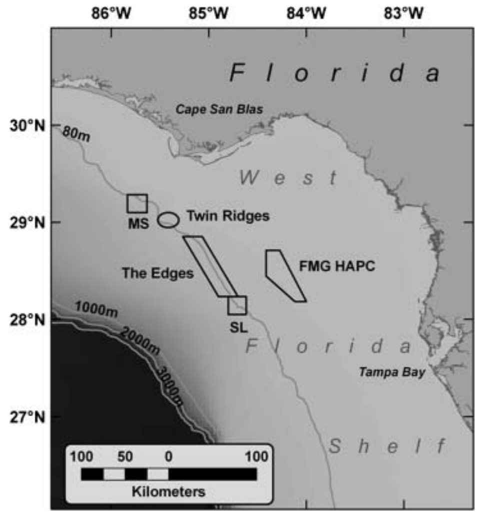

Figure 1 *Spawning habitats on the northern West Florida Shelf, Gulf of Mexico, including the Madison–Swanson Marine Reserve (MS), Steamboat Lumps Marine Reserve (SL), the Florida Middle Grounds HAPC (FMG HAPC), the Edges, and Twin Ridges.*

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.

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.

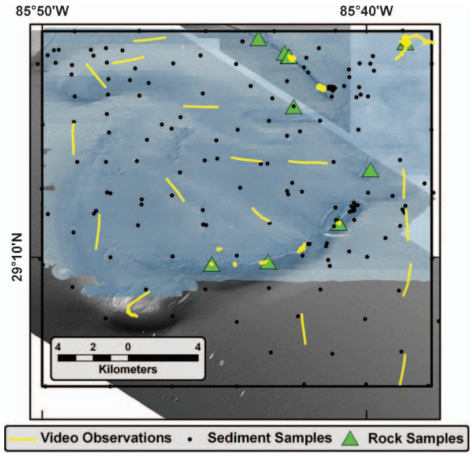

Figure 2 *Data collection sites within the Madison–Swanson Marine Reserve, including video transects conducted with remotely operated vehicles (ROVs), towed cameras, and stationary drop cameras; sediment samples collected using a van Veen grab, and rock samples collected by divers or with ROV manipulator 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 gray-head 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

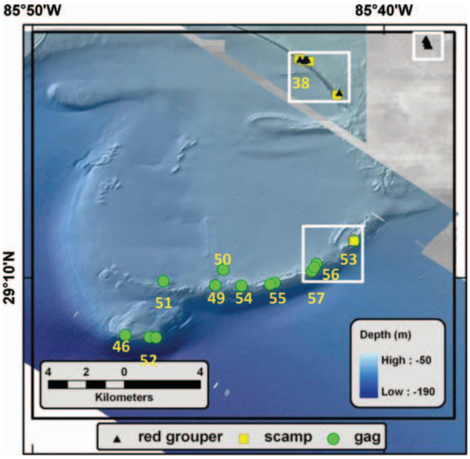

Figure 3 *Spawning sites in the Madison–Swanson Marine Reserve, West Florida Shelf, Gulf of Mexico. Sites overlay merged multibeam bathymetry data (Gardner, Dartnell, and Sulak 2002; D. Naar, University of South Florida) and side-scan sonar data (this study). Upper box: Red grouper spawning sites; middle 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

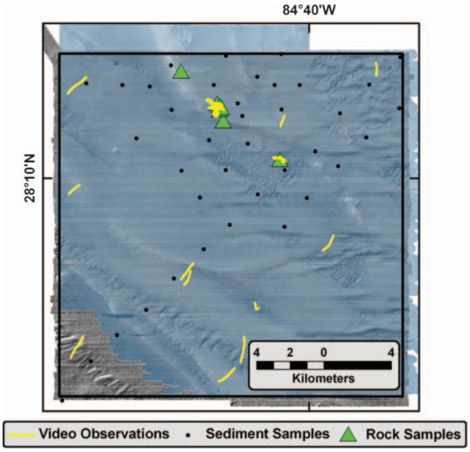

Figure 4 *Data collection sites within the Steamboat Lumps Marine Reserve, including video transects conducted with remotely operated vehicles (ROVs), towed cameras, and stationary drop cameras; sediment samples collected using a van Veen grab, and rock samples collected by ROV manipulator arm. Sites 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

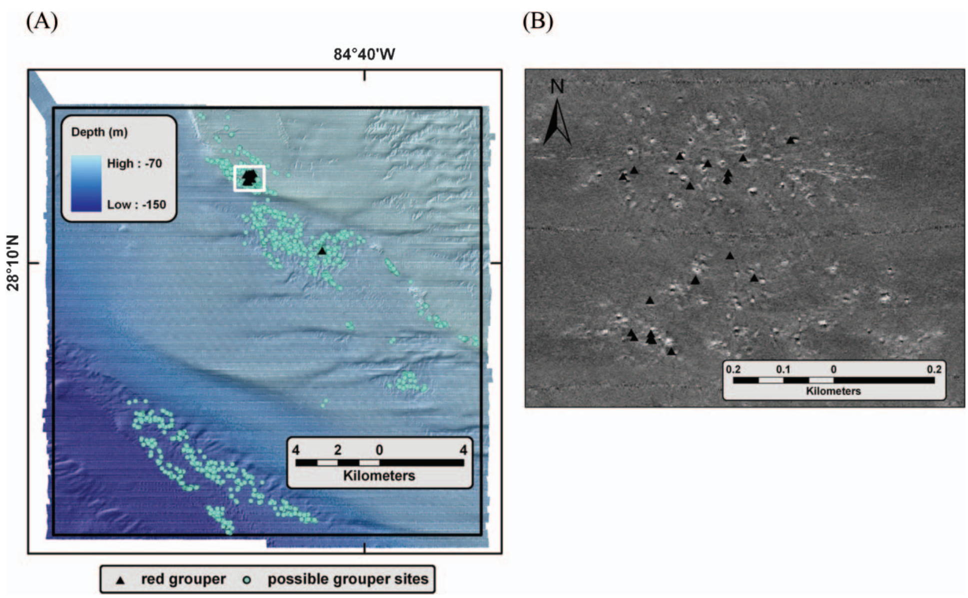

Figure 5 *Red grouper spawning sites within the Steamboat Lumps Marine Reserve (SLMR) superimposed on side-scan sonar mosaic images. (A) Ground-truthed (black marks) and presumed (blue marks) red grouper habitat based on geomorphologic features. (B) Blow-up of white block indicated in upper panel, red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

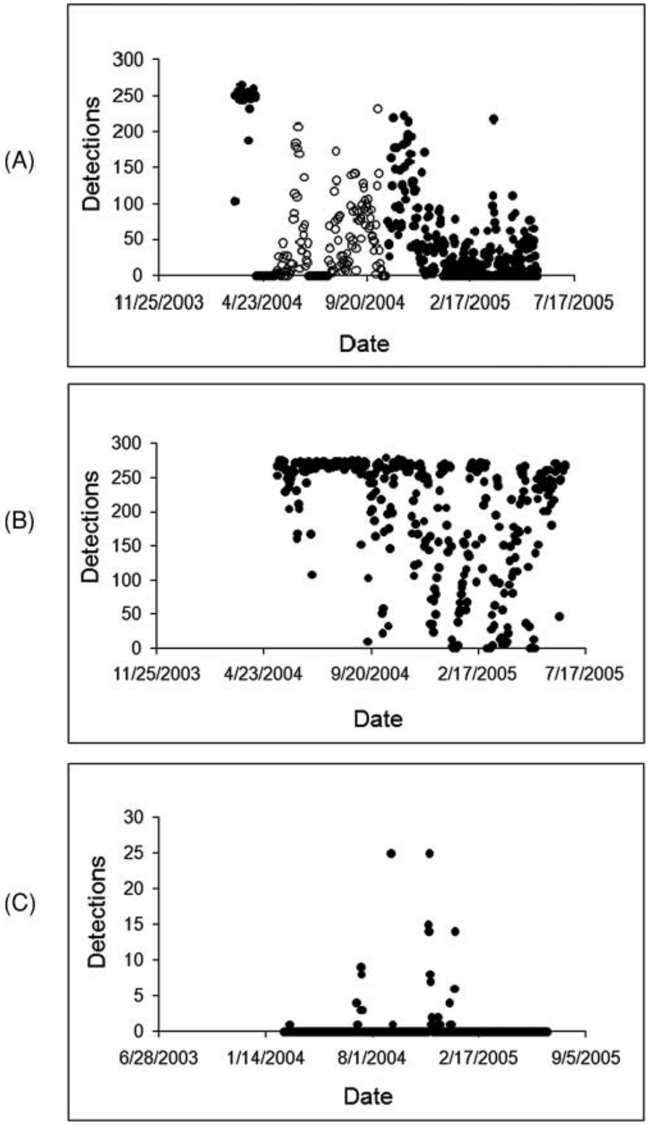

Figure 6 *Daily acoustic tag detections (circles, sum of detections per day) for gag (*Mycteroperca microlepis*) indicating movement patterns on spawning sites within Madison–Swanson Marine Reserve. (A) Male tagged 17 April 2003 on Site 50 (solid circles) moved 0.9 km to Site 49 (open circles), then 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

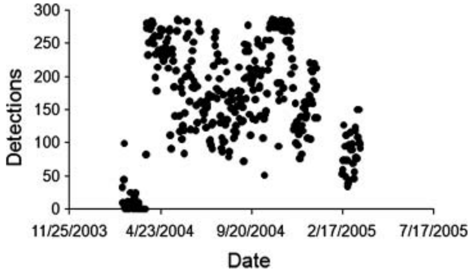

Figure 7 *Daily acoustic tag detections (circles, sum of detections per day) for scamp (*Mycteroperca phenax*) indicating movement patterns on spawning sites within Madison–Swanson Marine Reserve on the West Florida Shelf, Gulf of Mexico. Male tagged 15 April 2003 on Site 53, remained near the same site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

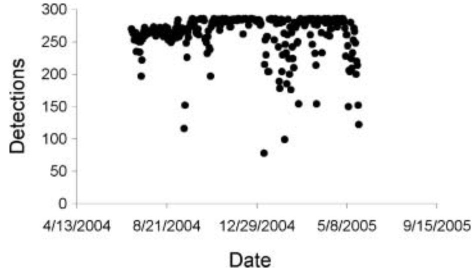

Figure 9 *Daily acoustic tag detections (circles, sum of detections per day) for control transmitter placed on the bottom (depth, 85 m) at spawning Site 54 within Madison–Swanson Marine Reserve, to determine the pattern of detections that would be produced by a dead fish within range of the receiver.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

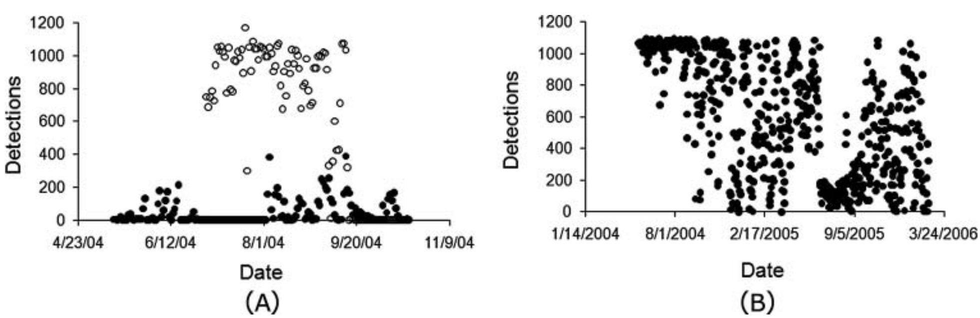

Figure 8 *Daily acoustic tag detections (circles, sum of detections per day) for red snapper (*Lutjanus campechanus*) indicating movement patterns on spawning sites within Madison–Swanson Marine Reserve on the West Florida Shelf, Gulf of Mexico. (A) Female tagged 10 May 2004 on gag spawning Site 54 (solid 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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