# Spawning Locations for Atlantic Reef Fishes off the Southeastern U.S.

GEORGE R. SEDBERRY, O. PASHUK, D.M. WYANSKI,
J.A. STEPHEN, and P. WEINBACH
*South Carolina Department of Natural Resources*
*P.O. Box 12559*
*Charleston, South Carolina 29422-2559 USA*

## ABSTRACT

Spawning condition was determined for 28 species of reef fish representing 11 families (Balistidae, Berycidae, Carangidae, Centrolophidae, Haemulidae, Lutjanidae, Malacanthidae, Polyprionidae, Scorpaenidae, Serranidae, Sparidae) collected off the Carolinas, Georgia and east coast of Florida (including the Keys) in depths from 1 - 686 m. The presence of migratory-nucleus oocytes, hydrated oocytes and/or postovulatory follicles was used to indicate imminent or very recent spawning, and locations of capture of fishes in spawning condition were mapped using GIS. Reproductive behavior was observed from submersible for a few species. Most fishes were collected from fishery-independent sampling, with time and location of collection accurately recorded. Some specimens were sampled from fishery landings, and time and location data were approximate. Samples came from all months and throughout the region, but sampling effort was not equally distributed and was concentrated from May through September and in the middle of the region (South Carolina and Georgia). In spite of some temporal and spatial sampling limitations, we determined that several species such as small serranids, haemulids, sparids and lutjanids spawn over protracted periods and throughout the region. Other species such as *Helicolenus dactylopterus, Caulolatilus microps, Epinephelus niveatus, Lopholatilus chamaeleonticeps, Hyperoglyphe perciformis* and *Polyprion americanus* have specific habitat requirements and live and spawn in very restricted areas. Several species (*Mycteroperca microlepis, M. phenax*) appear to spawn at specific shelf-edge reef sites (50 - 100 m depth), and tagging indicated they may undertake migrations to those specific sites during the spawning season. Some of the shelf-edge sites are utilized by several species, including some with moderately protracted spawning seasons that peak during winter or summer months. These sites may be in nearly continuous use by spawning fishes year-round, and should be considered as no-take MPAs to protect spawning adults.

KEY WORDS: Essential Fish Habitat, Geographic Information Systems, Marine Protected Areas

# Sitios de Desove de Peces de Arrecife en el Atlántico Sudeste (USA)

Se determino la condición de desove de 28 especies de peces de arrecife representando a 11 familias (Balistidae, Berycidae, Carangidae, Centrolophidae, Haemulidae, Lutjanidae, Malacanthidae, Polyprionidae, Scorpaenidae, Serranidae, Sparidae). Los especímenes se obtuvieron en las aguas de las Carolinas, Georgia y de la costa este de la Florida (incluyendo los Cayos) en profundidades de 16 a 686 m. La presencia de ovocitos con núcleo migratorio, ovocitos hidratados y/o folículos postovulatorios se utilizo para acertar el desove inminente o muy reciente. Los sitios de captura de peces en condición de desove fueron trazados usando Sistemas de Información Geográfica (SIG). El comportamiento reproductivo de algunas especies fue observado desde un sumergible. La mayoría de los especímenes fueron obtenidos mediante muestreo independiente de la pesca, con el tiempo y el sitio de los muestreos registrados exactamente. Algunos de los especímenes se obtuvieron por medio de la industria pesquera, y la hora y los datos del sitio de captura son aproximados. Las muestras provinieron de todos los meses del año y de toda la región, pero el esfuerzo del muestreo no se distribuyo igualmente sino que se concentro de mayo a octubre y en el centro de la región (Carolina del Sur y Georgia). A pesar de los límites del muestreo, determinamos que varias especies tales como serranids pequeños, haemulids, sparids y lutjanids desovan durante períodos prolongados y por toda la región. Otras especies tales como *Helicolenus dactylopterus*, *Caulolatilus microps*, *Epinephelus niveatus*, *Lopholatilus chamaeleonticeps*, *Hyperoglyphe perciformis* y *Polyprion americanus* tienen requisitos específicos del habitat y viven y desovan en áreas muy restringidas. Aparentemente varias especies (*Mycteroperca microlepis*, *M. phenax*) desovan en sitios específicos de 50 a 100 m en el borde del continente, y de acuerdo con estudios de marqueo, estas especies emprenden migraciones a esos sitios específicos durante la estación de desove. Algunos de los sitios del borde del continente son utilizados por varias especies, incluyendo algunas con estaciones de desove moderadamente prolongadas que alcanzan su punto más alto durante los meses de invierno o verano. Los peces pueden utilizar estos sitios para el desove casi continuamente a lo largo del año, y por lo tanto estas áreas se deben considerar como Áreas de Conservacion Marinas donde no se permite la captura de ninguna especie para proteger el desove de peces adultos.

PALABRAS CLAVES: Áreas de Conservacion Marinas, hábitat esencial para peces, Sistemas de Información Geográficos

## INTRODUCTION

In the re-authorization of the Magnuson-Stevens Fishery Conservation and Management Act, through the Sustainable Fisheries Act, the U.S. Congress included provisions that required fishery management councils to identify essential fish habitat (EFH). Such EFH should include “those waters and substrate necessary to fish for spawning, feeding or growth to maturity” (Schmitten 1999). The Magnuson Act re-authorization also provided for recognition of Habitat Areas of Particular Concern (HAPC) for various fish stocks or assemblages (e.g., Murawski et al. 2000). HAPC are areas where some user activities (e.g., trawling, bottom longlining) are banned because of particularly sensitive habitats or species assemblages such as ivory tree coral (*Oculina varicosa*) and associated organisms (Reed 2000). In order to manage fisheries under EFH and HAPC provisions, it is necessary to recognize and map EFH and HAPC, and to more clearly define them in relation to the fishery management unit (e.g., the Snapper-Grouper Complex of the U.S. South Atlantic Fishery Management Council). Spawning grounds, by definition, are EFH. Likewise, spawning areas must certainly qualify as HAPC, as spawning habitats are important in the life history of fishes and, for reef fishes in particular, often contain sensitive species assemblages such as corals and sponges.

In tropical and warm-temperate zones, many reef fishes undergo migrations to spawn at particular reef sites that probably possess hydrographic regimes or biological assemblages that enhance survival of offspring. Many species of coral reef fish spawn in large aggregations, wherein large portions of a dispersed population migrate to specific sites at specific times of the year to spawn (Domeier and Colin 1997). Because of the physical and biological conditions that are apparently favorable for survival of eggs and larvae, many different species use the same sites on tropical coral reefs (e.g., Carter and Perrine 1994). As a first step in mapping EFH and HAPC it is essential to determine where fishes spawn, where fishes that aggregate to spawn gather in spawning condition, and what sites are important spawning locations for multiple species, so that these areas can be given further considerations for management, such as area closures, that protect spawning fish. Determination of precise spawning times is essential for establishing time closures that might protect spawners and enhance recruitment. For species with protracted spawning periods, or for areas used as spawning grounds by many species that spawn at different times of the year, permanent closure of the grounds may be needed to protect spawning assemblages of fishes. Of greatest priority is determining spawning grounds for exploited reef fishes, especially those that are exploited during the spawning season when they are aggregated at specific locations and times. Off the southeastern United States, such priority species and habitats include at least some of the 73 species of the Snapper-Grouper Complex (e.g., snappers, groupers, porgies, grunts, tilefishes) that are managed by the South Atlantic Fishery Management Council (SAFMC), and their hard-bottom and sponge-coral habitats.

The South Carolina Department of Natural Resources (SCDNR) has conducted research since 1973 on the continental shelf and slope off the southeastern U.S., in an area often referred to as the South Atlantic Bight (SAB), from Cape Hatteras to Cape Canaveral. Some surveys have extended south to the Florida Keys, and offshore to the Charleston Bump area of the Blake Plateau. Through cooperative programs with federal resource management agencies, the SCDNR has conducted basic descriptive faunal surveys, fishery assessment surveys, monitoring surveys, and studies directed at specific resource management problems. Surveys have included sampling of demersal fishes with a variety of fishing gear; and hydrographic, benthic and ichthyoplankton sampling (e.g., Wenner 1983, Mathews and Pashuk 1986, Collins and Stender 1987, McGovern, Sedberry and Harris 1998, Harris et al. 2001). Various cooperative state-federal projects at SCDNR have conducted detailed life history studies of many reef fishes. These have included descriptions of age and growth, reproduction, feeding habits, early life history, movements determined by tagging, and population genetics (e.g., Collins and Stender 1987, Sedberry and Cuellar 1993, Van Sant et al. 1994, Sedberry et al. 1999, McGovern et al. 1998). Ichthyoplankton (1973-1984), trawl (1973-1987) and trap (1978-2004) surveys have included region-wide annual sampling cruises. Studies of reproductive biology of reef fishes have included determination of spawning times and frequencies (e.g., Cuellar et al. 1996). Tagging studies have indicated movements to locations suspected to be spawning grounds (Van Sant et al. 1994).

Data from the published studies cited above, from monitoring and sampling that has continued since those publications, and a substantial database on other species of the region are available for additional analyses. Of particular interest in a re-analysis of the historical data is the goal of using recently developed spatial and geographic analysis tools unavailable or not considered when many of the original data analyses were performed. Spatial analysis tools such as Geographic Information Systems (GIS) can be used on these databases to determine areas that support greater abundance, biomass and/or diversity of fishes. The databases can also be examined to describe distribution of individual species in relation to bottom and hydrographic features. Importantly, the databases can be queried for locations of fish in spawning condition, locations where large numbers of juveniles are found (recruitment areas) and locations where early larvae of priority species are found (spawning areas). Mapping of EFH and HAPC for reef fishes off the southeastern U.S. Atlantic coast is of particular importance at this time, as increasing demands are placed on the resource (see Coleman et al. 2000 for review). The consumption of fishes by humans has increased dramatically in the last several decades because of increases in human population, per-capita consumption of seafood, and advances in fishing technology. Reef fishes such as those of the warm-temperate hard-bottom reefs in the SAB appear to be particularly at risk, and many species are undergoing overfishing, are overfished, or are in danger of being so (Coleman et al. 2000, NMFS 2004). Severe restrictions, including size limits, bag limits, closed seasons and limited entry have been imposed on a species-by-species basis by the SAFMC. More restrictions might be needed; for example, the fishery for red porgy in the U.S. Atlantic was closed in 1999 because of extremely low spawning potential. The economic value of the reef species complex makes protecting the sustainability of the fishery a critical consideration for this region. Commercial reef fish landings in the SAB from 1980-1996 were roughly 147 million lbs, with an ex-vessel value near $186 million (www.st.nmfs.gov/st1/commercial/landings/annual_landings.html).

Many economically important reef fish species share a suite of life history and behavioral characteristics that make them particularly susceptible to overexploitation. These characteristics include long life, large adult size, late maturity, protogyny, and spawning in aggregations or at sites that are predictable in time and space (Coleman et al. 2000). Predictable spawning aggregations are particularly well-documented in tropical reef fishes, and the negative impacts of fishing these aggregations are well-known (Craig 1969, Carter et al. 1994, Domeier and Colin 1997, Sala et al. 2001). Although some studies have presented evidence for spawning aggregations of gag (*Mycteroperca microlepis*) on temperate reefs of the Gulf of Mexico (Coleman et al. 1996), it is uncertain if such aggregations represent a major regional spawning ground, as has been documented for some tropical groupers (Carter et al. 1994), and what the effects might be of fishing such aggregations if they do represent the major reproductive output for a large region. There are few data available on spawning locations, times and behavior of reef fishes of the SAB, but there is some circumstantial evidence for aggregations of some species such as gag. Circumstantial evidence includes long-distance migrations that sometimes coincide with the spawning season, and are thought to be movements toward pre-spawning aggregations or movements to actual spawning sites (Van Sant et al. 1994, McGovern et al. in press). Additional circumstantial evidence for spawning aggregations of gag in the SAB includes capture of fish in spawning condition (presence of migratory-nucleus oocytes, hydrated oocytes or post-ovulatory follicles) at specific depths such as deep shelf edge reefs (MARMAP unpublished data). Such capture might represent spawning aggregations that should certainly be classified as EFH. If fishermen target these aggregations, additional HAPC consideration should be given to current management plans, so that such spawning sites can be protected during the spawning season. If such spawning sites are used by many species for much of the year, additional protection should be provided in the form of no-take MPA designation.

Spawning aggregations in reef fishes are believed to correspond spatially and temporally with hydrographic features that insure greatest survival of early life history stages. For this reason, many species utilize the same locations for spawning, often at different times of the year (e.g., Carter et al. 1994, Carter and Perrine 1994). These hydrographic features are often associated with prominent bottom features that influence circulation near (and downstream from) the spawning banks (Carter et al. 1994, Sedberry et al. 2001, Govoni and Hare 2001). Many reef fishes with pelagic eggs and larvae spawn in the vicinity of gyres near the shelf edge (Johannes 1978). Such topographically-produced gyres are implicated in removal of pelagic eggs from the spawning site, thus reducing predation, while retaining fish eggs and larvae for the ultimate return of larvae to the shelf at later developmental stages that can avoid some predation. Such gyres may carry eggs and larvae toward ideal post-larval settlement habitat, or toward areas of high larval fish food production. Along the continental shelf edge of the SAB, there are areas of gyres and upwelling that are associated with high nutrients and plankton productivity (Paffenhöffer et al. 1984, Mathews and Pashuk 1986). Small occasional frontal eddies and meanders that propagate northward along the western edge of the Gulf Stream provide small-scale upwellings of nutrients along the shelf break in the SAB (Miller 1994). Such intermittent upwellings might coincide with reef fish spawning times and locations. In addition to these intermittent upwellings, there are two more permanent upwelling areas in the SAB. One is located just to the north of Cape Canaveral and is caused by diverging isobaths (Paffenhöfer et al. 1984). The other much larger and stronger upwelling occurs mainly between 32°N and 33°N (Atkinson 1985, Mathews and Pashuk 1986) and results from a deflection of the Gulf Stream offshore by the topographic irregularity known as the Charleston Bump (Bane et al. 2001). Off of South Carolina and North Carolina, the large meander set up by the Charleston Bump forms the Charleston Gyre, an eddy with upwelled water at its core, and which moves shoreward across the edge of the shelf and may be important in reef fish recruitment.

The presence of high nutrients at the shelf edge, and a gyre mechanism to transport larvae from shelf-edge spawning to estuarine nursery habitats influences recruitment success in gag (Sedberry et al. 2001). Recruitment in gag and some other fishes is correlated with the location, strength, and persistence of the Charleston Gyre (Sedberry et al. 2001, Govoni and Hare 2001). It is likely that spawning of gag and other reef fishes off the Carolinas is timed and located to take maximum advantage of the hydrographic conditions created by the Charleston Bump complex from 32°N and 33°30’N (Sedberry et al. 2001, Govoni and Hare 2001). Other intermittent upwelling sites along the shelf edge of the SAB, and the more permanent upwelling north of Cape Canaveral might also be important spawning grounds. Life history and spawning strategies of reef fishes might be timed to coincide with different upwelling types, times and locations. For example, fishes that spawn in a few large aggregations might utilize areas of more permanent gyres, while fishes with protracted seasons (spawning many times) might use more intermittent upwelling areas. Such areas might be considered EFH or HAPC, and it is important to map prominent and persistent hydrographic features in relation to distribution of fish larvae, juveniles and adults to determine the spatial relationships among life history stages and hydrographic features.

As a result of overfishing and the apparent inability of traditional methods to reverse declines in abundance of deep reef fishes, the SAFMC has proposed a series of Marine Protected Areas (MPAs) that could include no-take marine reserves (SAFMC 2004). The SAFMC has recently gone through an exercise in siting MPAs that included obtaining input from user groups, interested parties, and the general public, along with some review of existing biological and habitat data. Of prime concern is protecting those spawning habitats and locations that are essential to completing the life cycles of overfished species. Also of concern is placement of MPA networks to maximize spawning potential and recruitment of larvae from protected areas to harvest areas and to other protected areas in order to provide fishing opportunities while conserving spawning stock biomass. Additional study of distribution of individual reef fish species and spawning sites in relation to bottom habitats and faunas, and the relationship of bottom features to hydrographic features and proposed MPA sites, is needed. These data are needed to maximize the effectiveness of severe management measures, such as no-take reserves, that are perceived to be an extreme burden on commercial and recreational reef fish fishermen. By strategic placement of MPAs in networks based on biological and oceanographic data, it is hoped that the maximum positive effect can be achieved with the minimum impact on fishermen. It is imperative to collect and summarize such biological and oceanographic data, particularly data on spawning locations and recruitment pathways.

We have utilized a 30-year fishery-independent database to build a GIS that has mapped distributions of species, and their abundance, biomass and diversity. We have also mapped data on gonad condition for several fishery species using this database and some fishery-dependent sampling. In this paper we will describe some of the results aimed at locating spawning grounds for reef fishes. We hypothesize that species that appear to form large aggregations do so at specific sites and times that are related to cyclical yet permanent hydrographic features. We also hypothesize that species that appear to have protracted spawning in small widely-distributed groups may use ephemeral features such as those that form intermittently during summer and fall. The purpose of this paper is to report on the results of a temporal and spatial analysis of the data available on reproduction in several species of reef fish, in order to determine locations of EFH and HAPC for spawning reef fishes, and sensitive areas that might need intensive management in the form of temporal, spatial or some combination of no-take Marine Protected Areas (MPAs).

## METHODS

### Study Area, Field Methods and Databases

The MARMAP (Marine Resources Monitoring, Assessment and Prediction) fishery-independent database that went into this analysis consisted of a variety of demersal fish surveys conducted from several research vessels (Figure 1, Table 1). Details of sampling can be obtained from the senior author. Briefly, fish surveys generally covered the region from Cape Fear, North Carolina to Cape Canaveral, Florida, with some stations outside that range. Surveys were conducted with bottom trawls (e.g., Wenner et al. 1979, Wenner 1983), baited fish traps (Collins 1990), bottom longlines and hook-and-line (Harris et al. 2004). MARMAP trawling was conducted from 1973 to 1987, in depths from 9 - 366 m. Trawl stations were established randomly within depth and latitude strata; along transects perpendicular to the coast; or at index monitoring sites in reef habitat. Those index stations were also sampled with fish traps from 1978 to the present; however, since 1987 the trap survey has been conducted at randomly chosen reef points (e.g., McGovern, Sedberry and Harris 1998), many of which are at or near the trap index stations sampled from 1978 - 1986.

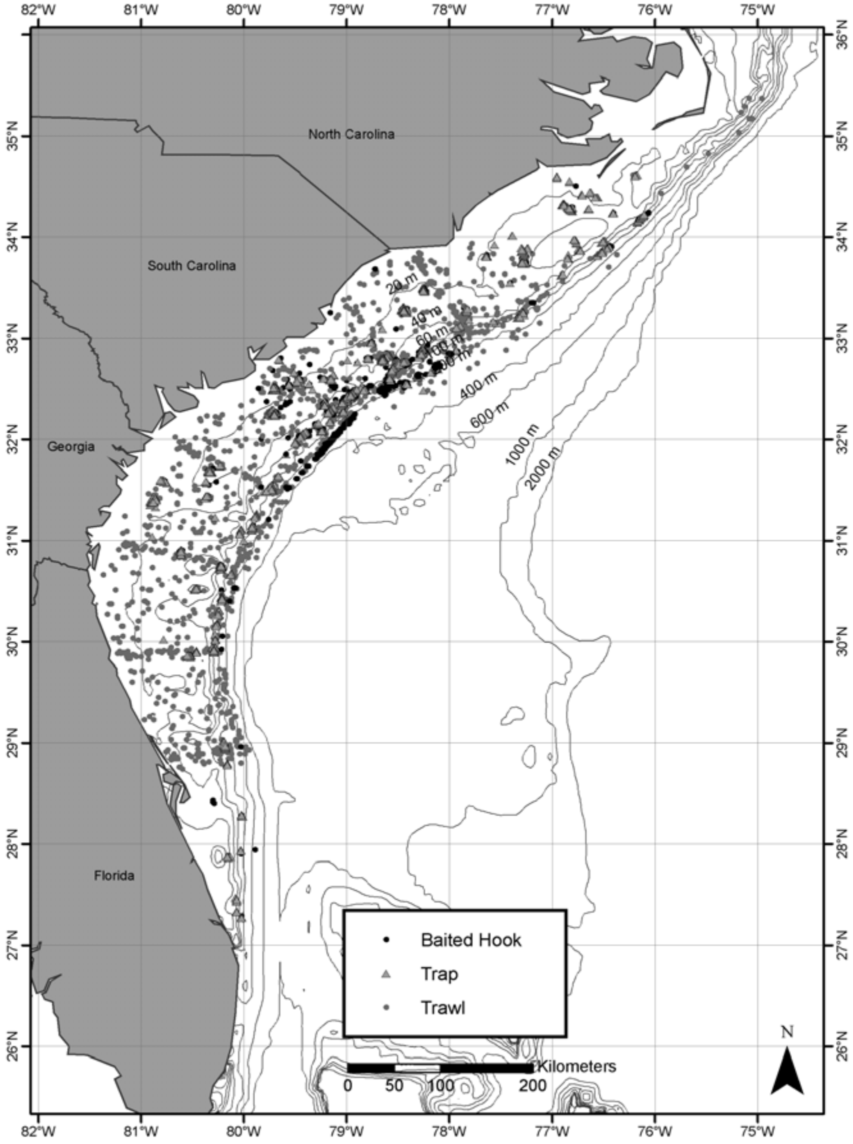

**Figure 1.** Sampling locations, by fishery-independent gear type, for specimens used in the spatial and temporal analysis of reef fish spawning.

**Table 1.** Summary of primary sampling gear used in collection of specimens; and months, years, latitude and depths of collections. Ind = fishery-independent samples; Dep = fishery-dependent samples.

| Gear | Number of Collections | Month Range | Year Range | Latitude Range (°N) | Depth (m) Range | Ind | Dep |
|---|---|---|---|---|---|---|---|
| Conductivity-temperature-Depth (CTD) cast | 1393 | Mar - Oct | 1987 - 2003 | 27.2 - 34.6 | 15 - 789 | X | X |
| Blackfish trap | 3298 | Jan - Dec | 1977 - 1999 | 30.7 - 34.3 | 15 - 65 | X | X |
| Chevron fish trap | 6185 | Mar - Dec | 1987 - 2003 | 27.2 - 34.6 | 13 - 218 | X | X |
| Florida snapper trap | 1710 | Feb - Sep | 1980 - 1989 | 30.4 - 34.3 | 15 - 196 | X | |
| Mini-Antillean S-trap | 157 | Jan - Feb<br>May - Sep | 1977 - 1980 | 30.7 - 33.7 | 19 - 75 | X | |
| Bottom longline | 502 | Jan - Dec | 1982 - 2003 | 27.9 - 38.7 | 15 - 500 | X | X |
| Kali pole bottom longline | 199 | May - Sep | 1982 - 1986 | 32.0 - 32.8 | 44 - 229 | X | |
| Vertical longline | 305 | Feb - Mar<br>May - Sep | 1979 - 2003 | 28.2 - 34.2 | 49 - 220 | X | X |
| Hook and line (rod & reel) | 369 | Jan - Dec | 1983 - 2003 | 26.0 - 34.4 | 1 - 234 | X | X |
| Snapper reel | 3226 | Jan - Dec | 1974 - 2003 | 18.2 - 34.7 | 11 - 256 | X | X |
| Wreckfish reel | 452 | Jan - Dec | 1989 - 2003 | 25.8 - 32.0 | 396 - 838 | X | X |
| Falcon net (23-m otter trawl) | 232 | Apr<br>Aug - Oct | 1986 - 1989 | 29.1 - 33.9 | 3 - 13 | X | X |
| Fly net (16-m bottom trawl) | 145 | Feb<br>Apr - Sep | 1980 - 1987 | 31.6 - 34.3 | 15 - 35 | X | X |
| Otter trawl (18-m semi-balloon) | 1071 | Jan - Dec | 1980 - 1987 | 28.7 - 34.9 | 4 - 20 | X | X |
| Yankee trawl (3/4 scale) | 1214 | Jan - Dec | 1973 - 2001 | 28.7 - 40.6 | 9 - 686 | X | |
| Spear gun | 38 | Feb - Aug<br>Oct, Dec | 1988 - 2002 | 26.0 - 32.5 | 17 - 52 | | X |

In order to sample deeper habitats, we employed experimental longline gear, directed at two habitat types: upper continental slope reefs (100 - 250 m) and mud-bottom tilefish grounds (175 - 225 m).

Data collected from each sampling gear included location, hydrographic parameters (measured with CTD), species composition, abundance, biomass, and length frequency of all fish species caught. Stations were located using LORAN-A, LORAN-C, or GPS, and the best available navigation technology was used at the time of fishery-independent sampling. All fish samples from fishery-independent sampling that were processed for reproductive studies were obtained using LORAN-C or differential GPS navigation.

Subsamples of certain priority species in the catches (Table 2) were dissected to obtain otoliths and gonad tissues. For those fishes, all appropriate lengths and weights were measured and the otoliths and gonads removed. Gonads were fixed in the field in 10% seawater formalin solution.

In addition to samples collected during the fishery-independent surveys, we sampled commercial catches to obtain a full size range of specimens or to obtain samples outside of the months (generally May through September) that fishery-independent sampling occurred. Samples were processed in the field and lab in the same manner as those collected during fishery-independent surveys; however, precise catch time and location were not always available. Catch location was often reported as a National Marine Fisheries Service (NMFS) Reef Fish Logbook statistical grid cell number. Those cells are one degree of latitude by one degree of longitude or about 10,440 km$^2$ for this region. Deficiencies in time and location data were noted in the data analysis.

## Laboratory Processing of Gonad Samples

Reproductive tissues were vacuum infiltrated and blocked in paraffin, and then sectioned (7 mm thickness) on a rotary microtome. Three sections from each sample were placed on a glass slide, stained with double-strength Gill's hematoxylin and counter-stained with eosin Y. Sections were viewed under a compound microscope at 40 - 400X and for most species two readers independently assigned sex and reproductive state with criteria from Harris et al. (2004) for gonochorists and from Wenner et al. (1986), Harris and McGovern (1997) and McGovern et al. (1998) for hermaphrodites. Date of capture, specimen length, and specimen age were unknown to the readers. If the assessments differed, both readers viewed the slide simultaneously and agreement was reached. Spawning females of all species had at least one of the following structures in histological sections:

i) Migratory-nucleus oocytes,
ii) Hydrated oocytes, or
iii) Postovulatory follicles.

**Table 2.** Species on which SCDNR has collected life history samples from which data on sex and reproductive state were obtained for spatial and temporal analysis.

| **Family**<br>**Scientific Name** | **Common Name** |
|---|---|
| Berycidae | |
| *Beryx decadactylus* | red bream |
| Scorpaenidae | |
| *Helicolenus dactylopterus* | blackbelly rosefish |
| Polyprionidae | |
| *Polyprion americanus* | wreckfish |
| Serranidae | |
| *Centropristis ocyurus* | bank sea bass |
| *Centropristis striata* | black sea bass |
| *Cephalopholis cruentata* | graysby |
| *Cephalopholis fulva* | coney |
| *Diplectrum formosum* | sand perch |
| *Epinephelus adscensionis* | rock hind |
| *Epinephelus drummondhayi* | speckled hind |
| *Epinephelus flavolimbatus* | yellowedge grouper |
| *Epinephelus morio* | red grouper |
| *Epinephelus nigritus* | warsaw grouper |
| *Epinephelus niveatus* | snowy grouper |
| *Mycteroperca interstitialis* | yellowmouth grouper |
| *Mycteroperca microlepis* | gag |
| *Mycteroperca phenax* | scamp |
| Malacanthidae | |
| *Caulolatilus microps* | blueline tilefish |
| *Lopholatilus chamaeleonticeps* | tilefish |
| Carangidae | |
| *Seriola dumerili* | greater amberjack |
| Lutjanidae | |
| *Lutjanus campechanus* | red snapper |
| *Rhomboplites aurorubens* | vermilion snapper |
| Haemulidae | |
| *Haemulon aurolineatum* | tomtate |
| *Haemulon plumieri* | white grunt |
| Sparidae | |
| *Calamus nodosus* | knobbed porgy |
| *Pagrus pagrus* | red porgy |
| Centrolophidae | |
| *Hyperoglyphe perciformis* | barrelfish |
| Balistidae | |
| *Balistes capriscus* | gray triggerfish |

### Data Manipulation, Standardization and GIS Analysis

Data from the surveys (fishery-independent and -dependent) and laboratory analysis were incorporated into a database that could be queried for species identification, collection data, sex and reproductive state. The database also included hydrographic measurements taken by CTD deployed at the same time as the fish collections (± 2 h), and within one kilometer of the fish collection sites. We queried the database for the priority species for which we had reproductive data (Table 2) and exported the data to ESRI ArcInfo ArcMap 9.0 for spatial analysis. We plotted location of capture of all specimens of each species, and overlaid location of capture of spawning females (as defined above) on the same map. Where relevant, we included on each map the location of proposed no-take (no bottom fishing) MPAs that are currently under consideration by the SAFMC (SAFMC 2004). We also analyzed occurrence of spawning females by month to define spawning season and temporal peaks in spawning activity. We calculated mean (± one standard deviation) and range of bottom temperatures recorded when spawning females of each species were collected. Data reported in tables were from fishery-independent sampling only, and depth, location, time and temperature data are accurate. Maps generated from the GIS analysis included approximate locations from some fishery-dependent samples, and those are differentiated on the maps.

## RESULTS AND DISCUSSION

Fishery-independent sampling effort was not equally distributed, either spatially or temporally (Figure 1, Table 1), and was concentrated from May through September and in the middle of the region (South Carolina and Georgia). Fishery-dependent samples provided accurate temporal information (± 5 days) on spawning times for those months not sampled during fishery-independent surveys, but location data, particularly those collected by NMFS, were often "rounded" to the nearest degree of latitude and longitude.

In spite of some temporal and spatial sampling limitations, we found that fish species examined exhibited a variety of spatial patterns of spawning activity, with respect to their general distribution, habitat features and in relation to other species. Several species such as small serranids, haemulids, sparids and lutjanids spawned over protracted periods and throughout the region (Table 3).

Black sea bass (*C. striata*), a small serranid, were distributed across the continental shelf throughout the region, generally in depths less than 60 m (range: 2 - 130 m). Of 30,170 examined to determine sex and reproductive state, 2251 were spawning females (Table 3). Spawning sites were located throughout the region in depths of 15 - 56 m (Figure 2), although most were found mainly in the middle of the SAB. Spawning females were collected during most months of the year (Table 4), with a major spawning period of February through April. In contrast, black sea bass north of Cape Hatteras spawn mainly from June through September (Able et al. 1995); however, spawning times here were similar to those found in the Gulf of Mexico

[December to April (Hood et al. 1994)]. Bottom water temperatures where spawning females were collected ranged from 11.45 to 26.57°C (Table 3, N = 898 independent measurements).

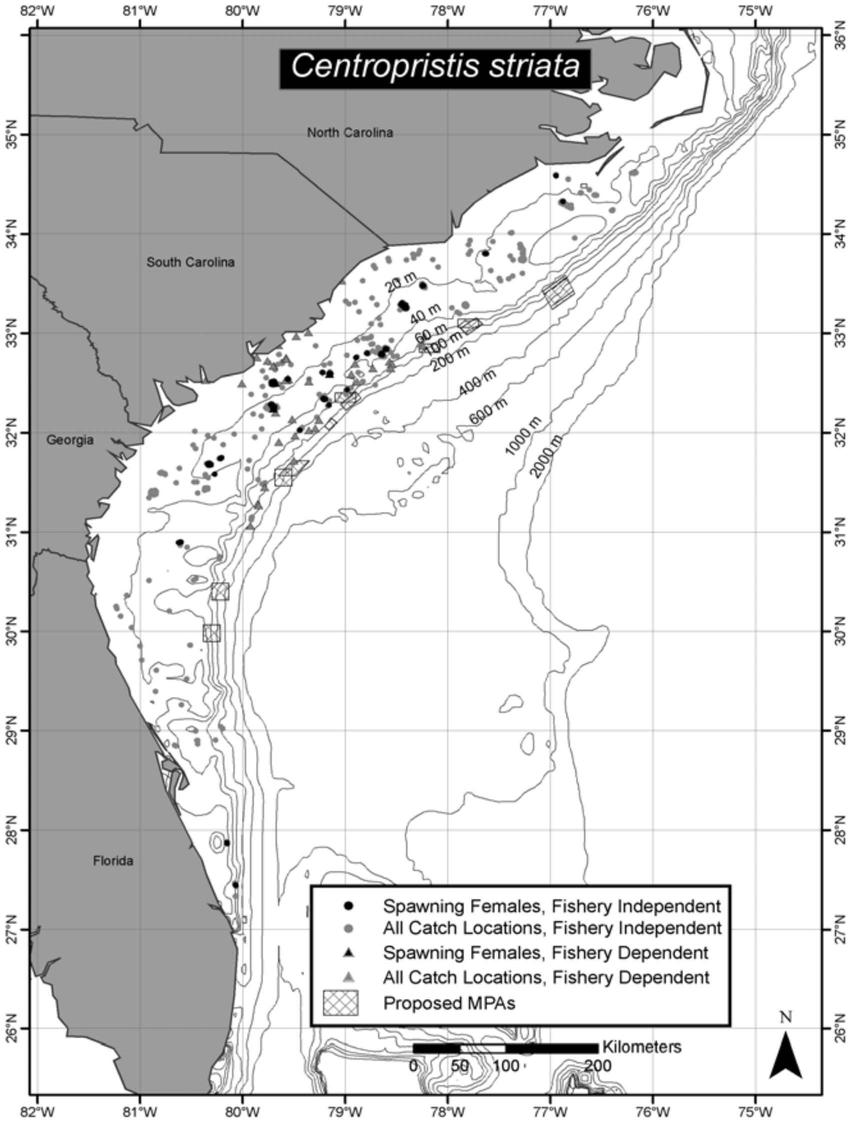

**Figure 2.** Locations of capture of black sea bass, including all captures and capture of spawning females, by survey type (fishery-independent vs. fishery-dependent). Sites proposed as MPAs that would prohibit bottom fishing are also shown.

**Table 3.** Collection data for species examined for spawning activity. Data include total number of specimens collected, number examined to determine sex and reproductive state, and number found to be spawning females; depth of capture of all specimens and of spawning females; latitude range (°N) of collections of spawning females; and bottom temperatures (mean, standard deviation and range) where spawning females were collected. Depth, latitude, and temperature data were from fishery-independent sampling. In some cases (-), data were not available.

| | Total Specimens | | | Capture Depth | Spawning Depth | Spawning Latitude | Spawning Temperatures (°C) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Collected | Exam | Spawning (m) | (m) | (°N) | Mean | sd | Range | |
| *B. capriscus* | 7582 | 4349 | 141 | 13 - 128 | 20 - 75 | 27 - 33 | 22.41 | 1.96 | 18.87 - 27.42 |
| *B. decadactylus* | 17 | 16 | 8 | - | - | - | - | - | - |
| *C. nodosus* | 3210 | 1181 | 88 | 21 - 155 | 45 - 60 | 31 - 32 | 21.92 | 0.68 | 20.10 - 22.67 |
| *C. microps* | 1344 | 1112 | 514 | 46 - 256 | 48 - 234 | 32 - 32 | 14.91 | 2.12 | 8.87 - 16.28 |
| *C. ocyurus* | 20754 | 2402 | 52 | 1 - 146 | 27 - 57 | 32 - 32 | 16.81 | 0.63 | 16.24 - 18.63 |
| *C. striata* | 118059 | 30170 | 2251 | 2 - 130 | 15 - 56 | 27 - 34 | 18.88 | 2.68 | 11.45 - 26.57 |
| *C. cruentata* | 11 | 7 | 0 | 30 - 50 | - | - | - | - | - |
| *C. fulva* | 24 | 18 | 1 | 39 - 58 | 39 | 33 | 23.80 | - | 23.80 - 23.80 |
| *D. formosum* | 12830 | 780 | 634 | 9 - 84 | 17 - 47 | 27 - 34 | 23.55 | 3.09 | 14.03 - 28.50 |
| *E. adscensionis* | 43 | 34 | 5 | 33 - 83 | 37 - 53 | 32 - 32 | 21.75 | 1.51 | 20.05 - 23.96 |
| *E. drummondhayi* | 427 | 274 | 5 | 28 - 114 | - | 32 - 32 | - | - | - |
| *E. flavolimbatus* | 1000 | 73 | 6 | 31 - 205 | 160 - 194 | 32 - 32 | 14.47 | - | 14.47 - 14.47 |
| *E. morio* | 2390 | 2223 | 46 | 22 - 95 | 30 - 90 | 32 - 34 | 21.01 | 2.09 | 16.97 - 24.08 |
| *E. nigritus* | 21 | 12 | 1 | 48 - 168 | 168 | | | | |

**Table 3.** Continued.

| Species | Total Specimens<br>Collected | Exam | Spawning (m) | Capture Depth (m) | Spawning Depth (°N) | Spawning Latitude Mean | Spawning Temperatures (°C)<br>sd | Range | |
|---|---|---|---|---|---|---|---|---|---|
| *H. dactylopterus* | 4280 | 1381 | 138 | 38 - 686 | 229 - 238 | 32 - 32 | - | - | - |
| *H. perciformis* | 353 | 102 | 12 | 181 - 520 | - | - | - | - | - |
| *L. chamaeleonticeps* | 3552 | 2431 | 324 | 62 - 311 | 190 - 300 | 31 - 32 | 13.02 | 1.96 | 10.16 - 14.90 |
| *L. campechanus* | 1225 | 778 | 80 | 7 - 240 | 24 - 67 | 27 - 33 | 23.16 | 2.02 | 18.05 - 27.59 |
| *M. interstitialis* | 29 | 18 | 9 | 27 - 84 | 49 - 51 | 32 - 32 | - | - | - |
| *M. microlepis* | 7329 | 5363 | 1848 | 15 - 117 | 24 - 117 | 26 - 33 | 17.26 | - | 17.26 - 17.26 |
| *M. phenax* | 3759 | 2467 | 351 | 17 - 113 | 33 - 93 | 29 - 32 | 21.18 | 1.84 | 15.60 - 24.08 |
| *P. pagrus* | 22732 | 15687 | 457 | 9 - 307 | 26 - 57 | 30 - 32 | 16.88 | 0.89 | 16.24 - 18.99 |
| *P. americanus* | 2067 | 1466 | 55 | 44 - 653 | 433 - 595 | 31 - 31 | - | - | - |
| *R. aurorubens* | 41455 | 11798 | 3280 | 14 - 163 | 18 - 97 | 27 - 34 | 23.37 | 2.01 | 16.01 - 28.09 |
| *S. dumerili* | 2797 | 2498 | 250 | 15 - 216 | 45 - 122 | 24 - 33 | 23.71 | 0.00 | 23.71 - 23.71 |

**Table 4.** Spawning periods for fishes examined. Spawning percentage = percent of female specimens in spawning condition. Dark gray indicates major spawning period. Light gray indicates months of spawning activity.

| Species | # Females | Spawning Percentage | Percentage in spawning condition by month | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sept. | Oct. | Nov. | Dec. |
| *B. capriscus* | 2259 | 6.24 | 0.0 | 0.0 | 0.0 | 0.0 | 2.7 | 10.0 | 13.0 | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| *B. decadactylus* | 11 | 72.73 | - | - | - | 0.0 | 0.0 | 100.0 | 100.0 | 100.0 | 100.0 | - | 0.0 | 0.0 |
| *C. nodosus* | 752 | 11.70 | 0.0 | 0.0 | 2.6 | 55.4 | 76.5 | 2.2 | 2.8 | 0.0 | 0.0 | 0.0 | - | 0.0 |
| *C. microps* | 619 | 83.04 | 0.0 | 100.0 | 66.7 | 68.8 | 89.4 | 84.2 | 92.7 | 75.7 | 91.1 | 86.4 | - | - |
| *C. ocyurus* | 1267 | 4.10 | 13.6 | 45.0 | 26.1 | 29.6 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 15.4 | 14.8 | 0.0 |
| *C. striata* | 19740 | 11.40 | 0.0 | 31.5 | 79.9 | 35.6 | 20.5 | 0.6 | 6.4 | 0.2 | 2.9 | 0.0 | 15.1 | 0.0 |
| *C. cruentata* | 4 | 0.00 | - | - | 0.0 | - | - | - | 0.0 | - | - | - | - | - |
| *C. fulva* | 8 | 12.50 | - | - | - | - | - | 100.0 | 0.0 | 0.0 | - | - | - | - |
| *D. formosum* | 779 | 81.39 | - | - | - | - | 100.0 | 95.8 | 78.4 | 77.0 | 64.1 | - | - | - |
| *E. adscensionis* | 12 | 41.67 | - | - | 100.0 | - | 100.0 | 20.0 | 0.0 | - | - | - | - | - |
| *E. drummondhayi* | 169 | 2.96 | - | 0.0 | 0.0 | 0.0 | 2.5 | 6.8 | 0.0 | 2.9 | 0.0 | - | - | 0.0 |
| *E. flavolimbatus* | 52 | 11.54 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7.7 | 27.8 | - | - | - |
| *E. morio* | 2058 | 2.24 | 0.0 | 2.8 | 3.5 | 13.3 | 2.3 | 3.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *E. nigritus* | 9 | 11.11 | - | 0.0 | - | - | 50.0 | 0.0 | 0.0 | - | - | - | - | 0.0 |
| *E. niveatus* | 533 | 18.01 | 0.0 | 0.0 | 0.0 | 3.1 | 28.7 | 7.1 | 19.0 | 31.3 | 15.0 | - | - | 0.0 |
| *H. aurolineatum* | 925 | 25.73 | - | 0.0 | - | 0.0 | 58.1 | 31.3 | 31.1 | 0.0 | 0.0 | - | - | - |
| *H. plumieri* | 1227 | 12.31 | 0.0 | 0.0 | 2.4 | 10.8 | 23.4 | 26.4 | 1.1 | 0.9 | 3.9 | 0.0 | 0.0 | 0.0 |
| *H. dactylopterus* | 548 | 25.18 | 38.5 | 57.8 | 77.1 | 37.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.1 |
| *H. perciformis* | 68 | 17.65 | 14.3 | - | - | - | 50.0 | - | 0.0 | - | - | 0.0 | 21.4 | 22.2 |
| *L. chamaeleonticeps* | 1161 | 27.91 | 1.4 | 1.3 | 40.0 | 76.2 | 85.6 | 66.1 | 18.8 | 1.7 | 0.7 | 0.0 | 1.3 | 0.0 |
| *L. campechanus* | 402 | 19.90 | 8.7 | 0.0 | 0.0 | 0.0 | 15.2 | 27.3 | 56.0 | 28.1 | 41.2 | 18.2 | 0.0 | 0.0 |
| *M. interstitialis* | 12 | 75.00 | - | 50.0 | 100.0 | 0.0 | - | 0.0 | - | 100.0 | - | - | - | - |
| *M. microlepis* | 4872 | 37.93 | 11.8 | 39.6 | 57.3 | 50.2 | 3.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 |
| *M. phenax* | 1988 | 17.66 | 0.0 | 1.1 | 39.2 | 53.0 | 64.1 | 8.8 | 3.6 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| *P. pagrus* | 10870 | 4.20 | 88.5 | 64.0 | 33.3 | 3.5 | 0.1 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 48.0 | 43.5 |
| *P. americanus* | 793 | 6.94 | 14.7 | 77.8 | 92.9 | 16.4 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 3.1 |
| *R. aurorubens* | 8666 | 37.85 | 0.0 | 0.0 | 0.0 | 8.6 | 24.0 | 41.9 | 59.7 | 40.2 | 34.6 | 0.0 | 0.0 | 0.0 |
| *S. dumerili* | 1363 | 18.34 | 1.9 | 5.7 | 14.1 | 49.1 | 53.5 | 4.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

Bank sea bass (*C. ocyurus*) were also broadly distributed across the shelf throughout the region (Figure 3), but appeared to prefer deeper waters than black sea bass (range 1 - 146 m). Of 2402 examined for sex and reproductive state, only 52 were spawning females, and all of those were collected in depths of 27-57 m off South Carolina in October through May (Tables 3-4). The major spawning period was February through April. Spawning females were collected in water temperatures that ranged from 16.24 to 18.63°C (n = 21).

Sand perch (*D. formosum*) were also widely distributed across the shelf (Figure 4), generally in depths less than 60 m (range 9 - 84 m). The sand perch appears to be much less dependent on reef habitat, and was often taken in trawl collections over sandy bottom (e.g., Wenner et al. 1979, Darcy 1985). More than 80% of the female sand perch examined were in spawning condition. Spawning females (n = 634) were collected throughout the region from May through September at depths of 17 - 47 m (Tables 3-4). Bottom temperatures at spawning sites ranged from 14.03 to 28.50°C (n = 596). A similar spawning season (April-October) was reported from the southern Caribbean (Obando and Leon 1989) and Bortone (1971) reported peak ovary maturation in May in the northern Gulf of Mexico.

Like sand perch, tomtate (*H. aurolineatum*) were found across the shelf throughout the region. Spawning females (n = 238 of 2412 examined) occurred on middle and outer-shelf reefs (Figure 5) and were collected from May through July in depths from 15-54 m (Tables 3-4). Bottom temperatures at spawning sites ranged from 20.16 to 28.04°C (n = 232).

Red snapper (*L. campechanus*) were also widely distributed across the shelf (Figure 6, Table 3), but appeared to spawn at mid- to outer-shelf depths (24 - 67 m). Of 778 red snapper examined for sex and reproductive state, 80 were spawning females. Spawning females were collected in January and May through October in the waters off South Carolina to Florida (Table 4). The major spawning period was June through September. Red snapper spawned at temperatures ranging from 18.05 to 27.59°C (Table 3; n = 41). Red snapper were reported to spawn in the northeastern Gulf of Mexico from April through October (Collins et al. 2001).

Vermilion snapper (*R. aurorubens*) were ubiquitous in collections on the middle and outer shelf, and were found in depths from 14 - 163 m (Figure 7, Table 3). Spawning females (n = 3280 of 11,798 fish examined) were found at nearly all depths and latitudes where vermilion snapper occurred. Vermilion snapper spawned in depths from 18 to 97 m and at temperatures from 16.01 to 28.09°C (n = 2511). Spawning occurred from April through September, with a major spawning period of May through September (Table 4). Spawning appears to be slightly more protracted than in the Gulf of Mexico [May to September (Hood and Johnson 1999)].

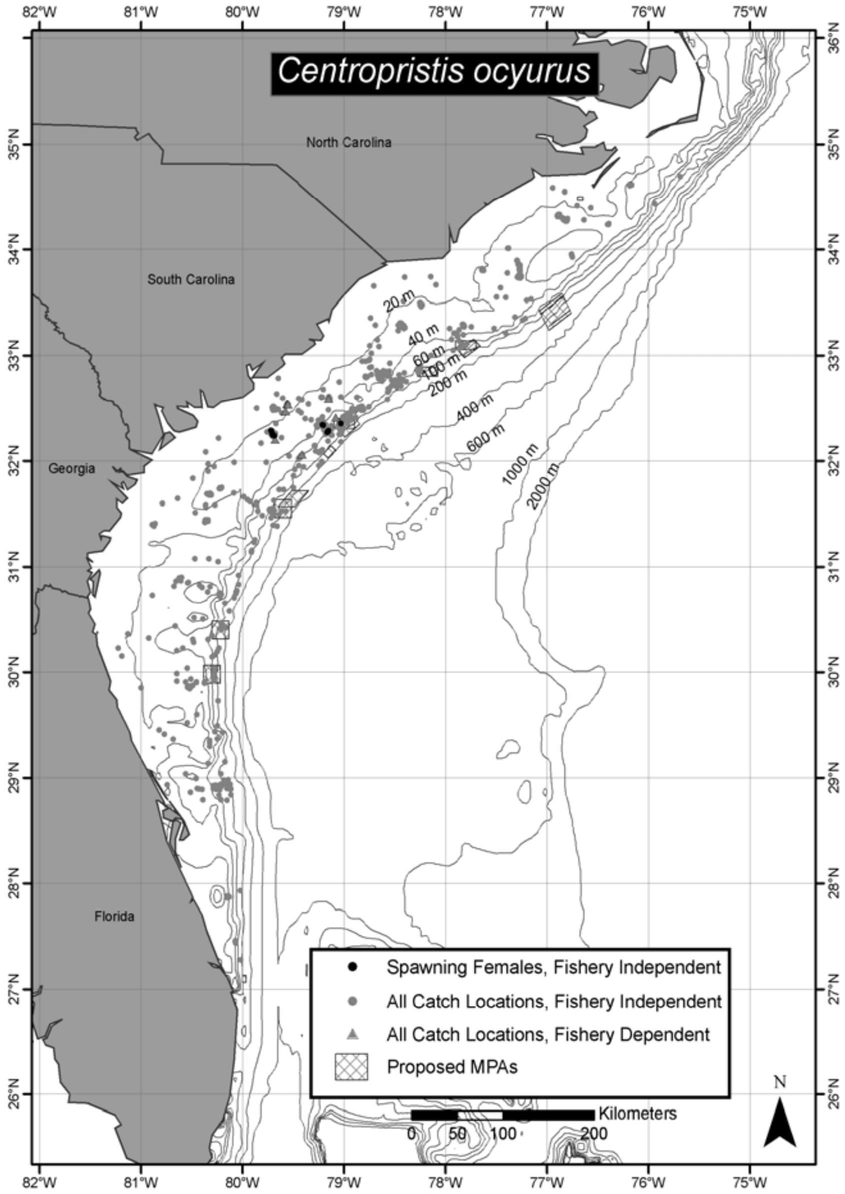

**Figure 3.** Locations of capture of bank sea bass. See Figure 2 for additional explanation.

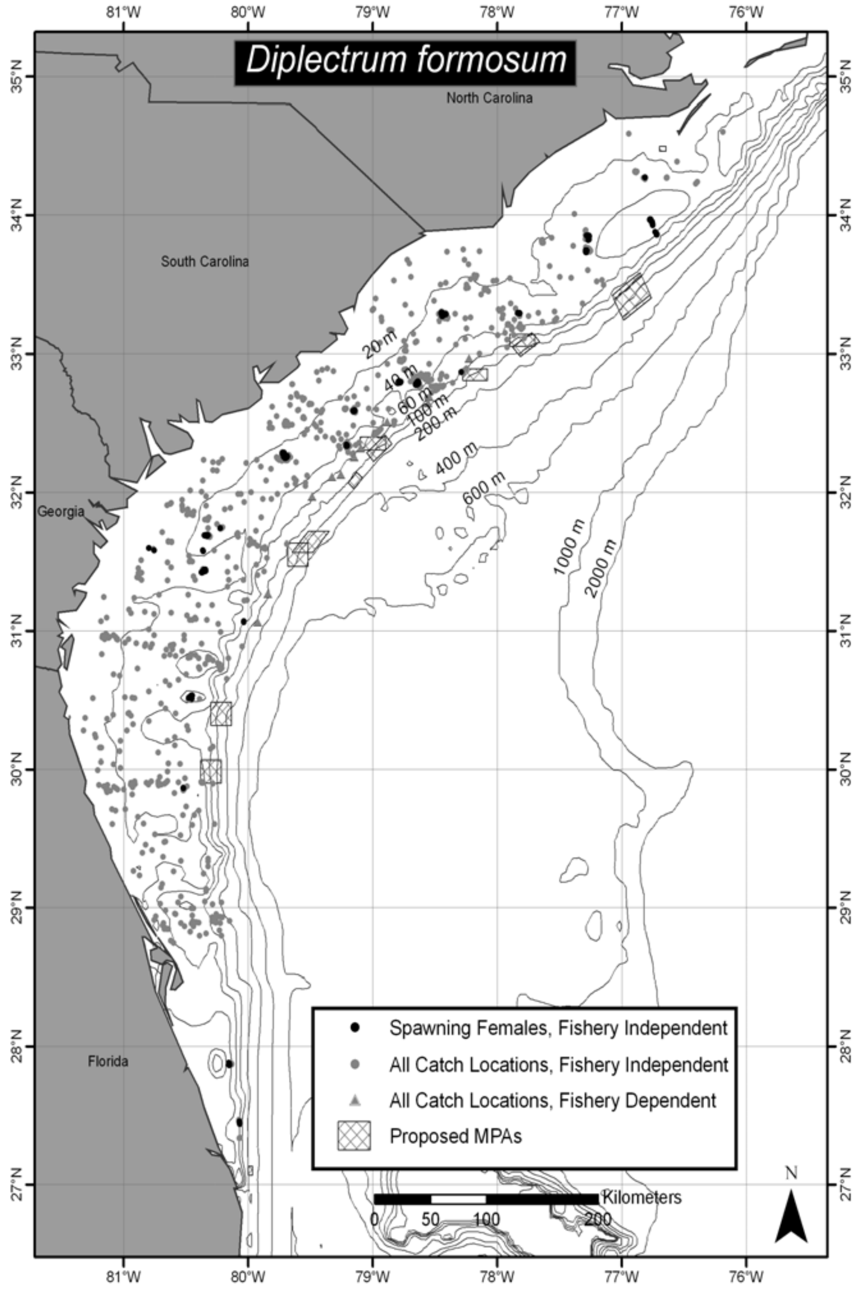

**Figure 4.** Locations of capture of sand perch. See Figure 2 for additional explanation.

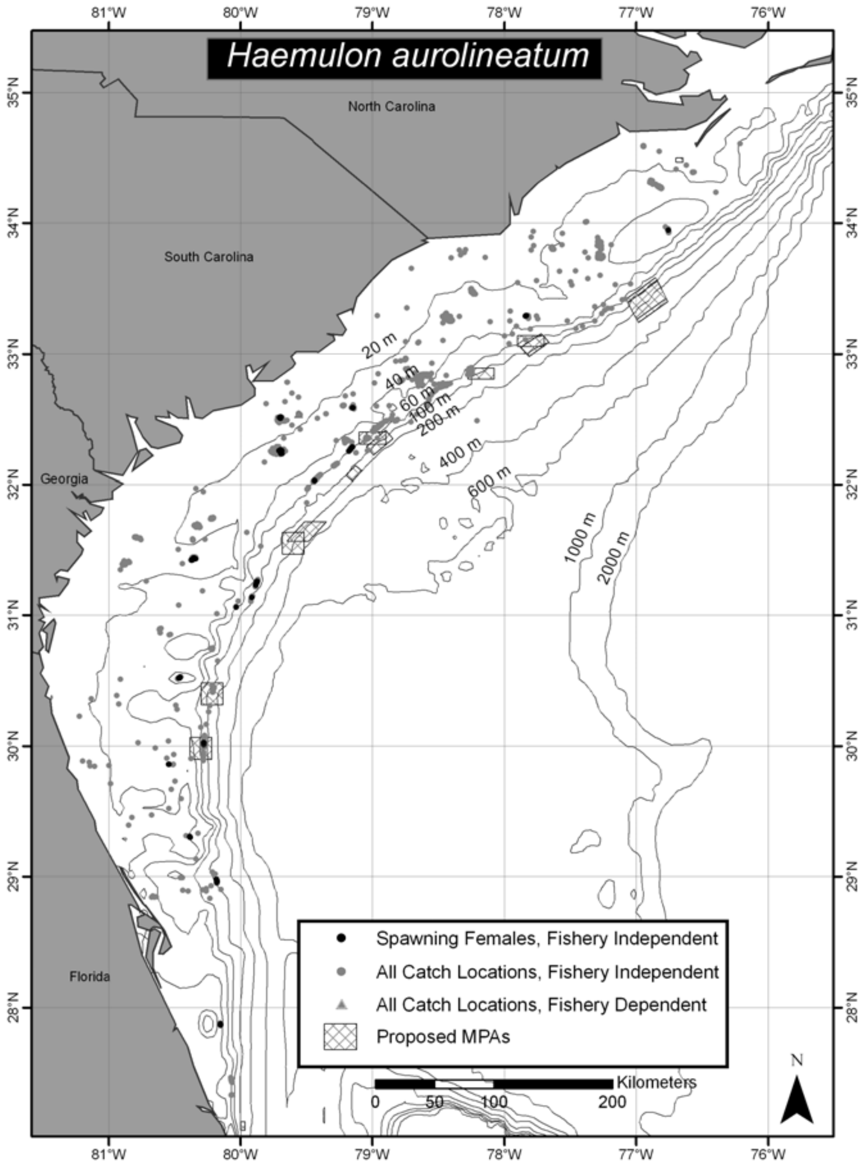

**Figure 5.** Locations of capture of tomtate. See Figure 2 for additional explanation.

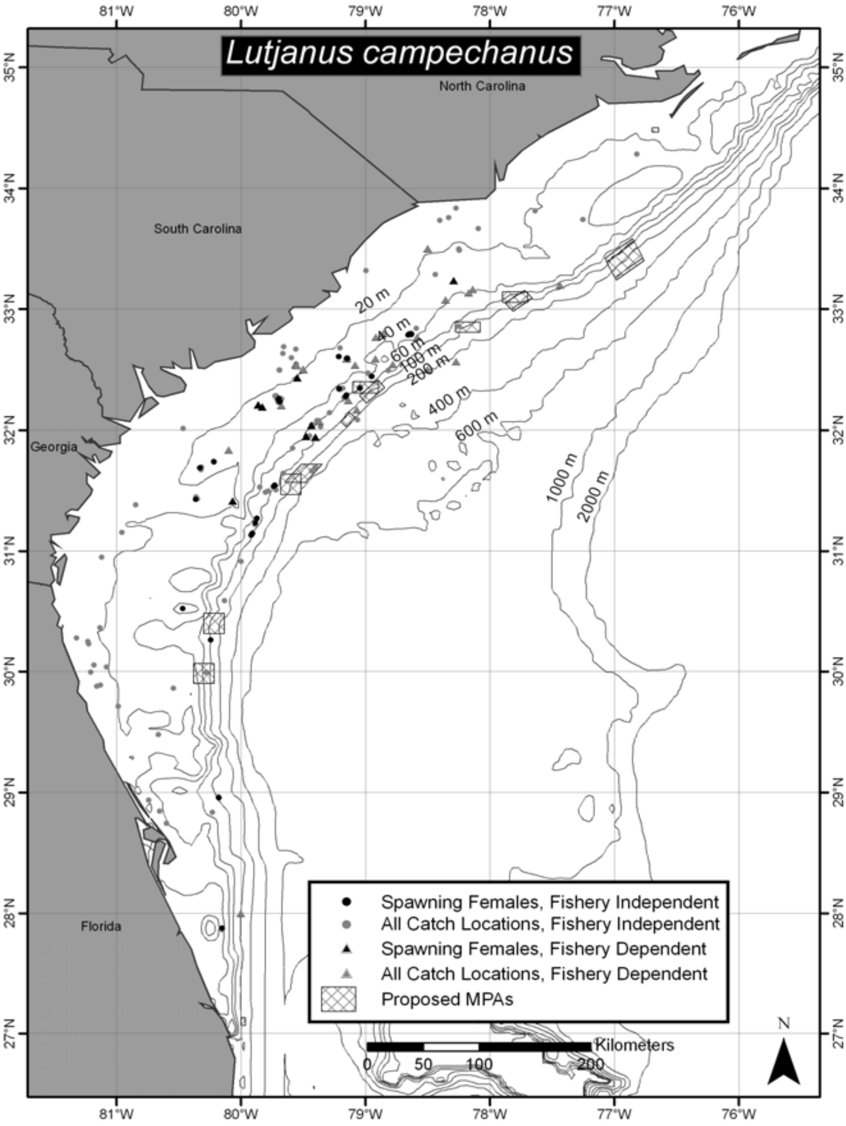

**Figure 6.** Locations of capture of red snapper. See Figure 2 for additional explanation

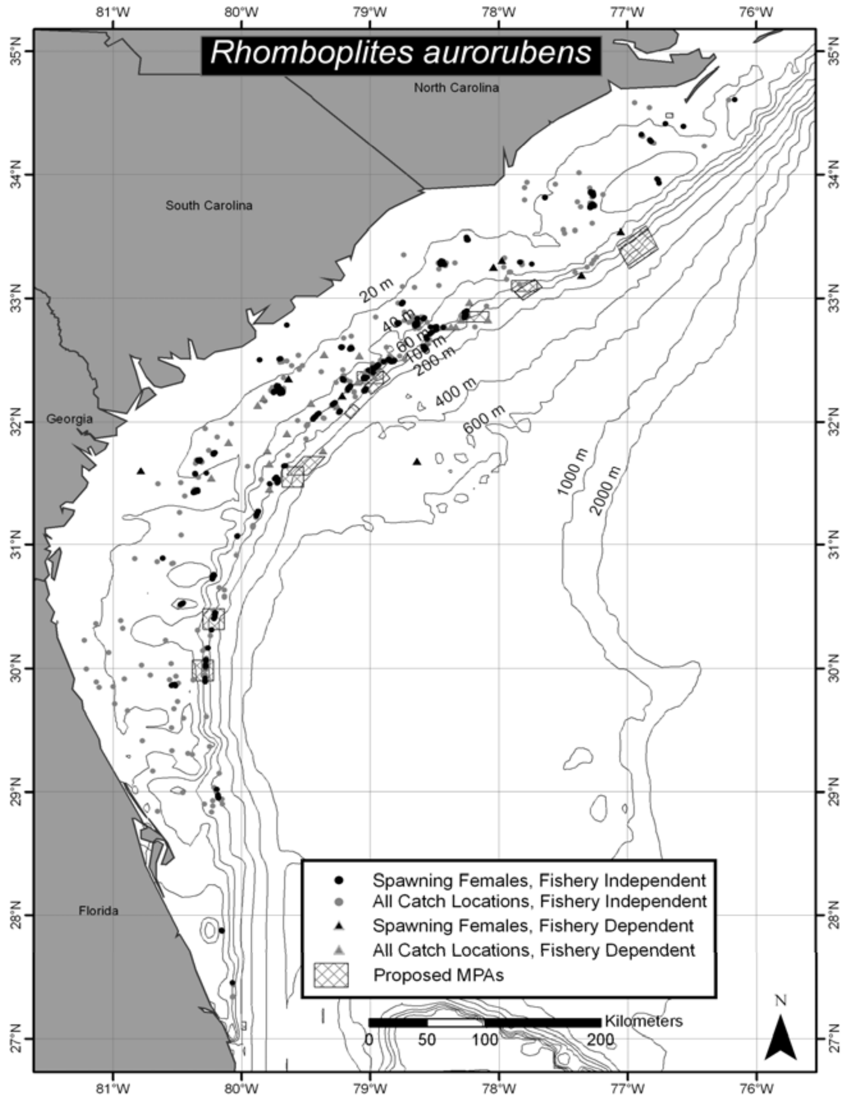

**Figure 7.** Locations of capture of vermilion snapper. See Figure 2 for additional explanation.

Several species (*Mycteroperca microlepis, M. phenax, Balistes capriscus, Calamus nodosus, Pagrus pagrus and Seriola dumerili*) appeared to spawn at specific shelf-edge reef sites (50 - 100 m depth) in spite of being generally distributed across the shelf. Gag (*M. microlepis*) were caught throughout the region (15 - 117 m) during fishery-independent sampling (Table 3, Figure 8).

Because gag are winter-early spring spawners (from December through May), few were collected during research cruises that sampled mainly from May through September. However, fishery-dependent sampling yielded many female gag in spawning condition from throughout the region. Of 5,363 gag obtained from all sampling, 1,848 were spawning females. Most fishery-dependent samples were landed under an emergency rule that required fishermen to land gag with the gonads intact so that researchers could determine sex ratios and other aspects of reproduction (McGovern et al. 1998). Unfortunately, the emergency rule did not require accurate location data and catch locations were often reported in NMFS sampling grid cells (Figure 8). In spite of the inaccuracy in location, it appears that gag spawn at shelf-edge reefs, in depths from 24 - 117 m, primarily from February through April (Table 4), at a bottom temperature of 17.26°C (only one measurement). Gag in the Gulf of Mexico spawn slightly earlier than we found here [December to May, with peak activity occurring during February and March (Hood and Schlieder 1992)].

Scamp (*M. phenax*) were found mainly on middle- and outer-shelf reefs throughout the region (Table 3, Figure 9). Spawning females (n = 351 of 2,467 examined) were found at shelf-edge reefs from northern Florida to South Carolina from February to August (Table 4), with a major spawning period of March through May. In the Gulf of Mexico, scamp spawning peaks from late February to early June (Coleman et al. 1996). Spawning females were collected at depths of 33 - 93 m and water temperatures from 15.60 - 24.08°C (Table 3; n = 131). We observed scamp engaged in courtship behavior like that described by Gilmore and Jones (1992) at shelf-edge reefs off northern Florida and South Carolina in summer of 2002 and 2004 (off St. Augustine, 28 July 2002, 29.9°N, 80.3°W, 60 - 61 m depth, 1000 EDT, 19.46 - 19.49°C; off St. Augustine, 29 August 2004, 30.0°N, 80.3°W, 59 m, 0912 EDT, 17.8°C; off Jacksonville, 30 July 2002, 30.4°N, 80.2°W, 56 - 85 m depth, 1923 - 1929 EDT, 20.90 - 20.94°C; ESE of Charleston, 1 August 2002, 32.3°N, 79.0°W, 56 - 61 m depth, 1818-1829 EDT, 20.47 - 22.03°C). These observations involved one gray-head (apparent) male scamp and one to a few apparent females. Courtship behavior was observed, but not any spawning. As described by Gilmore and Jones (1992), scamp occurred in various color phases; individual fish were constantly in motion, and changed rapidly between different color morphs. Apparent females (usually one or two, but up to five, courted by single apparent males) tended to remain in the "brown phase", whereas the apparent males switched between "gray-head" phase when pursuing females, and "cat's paw" phase when turning away from apparent females. These behaviors were observed in the morning and late afternoon. Spawning was not observed, but as in other groupers (Carter et al. 1994) that may occur after sunset (Harris et al. 2002), when we were not making observations. Bottom temperatures during our observations were similar to those observed by Gilmore and Jones (1992) during spawning activity in scamp.

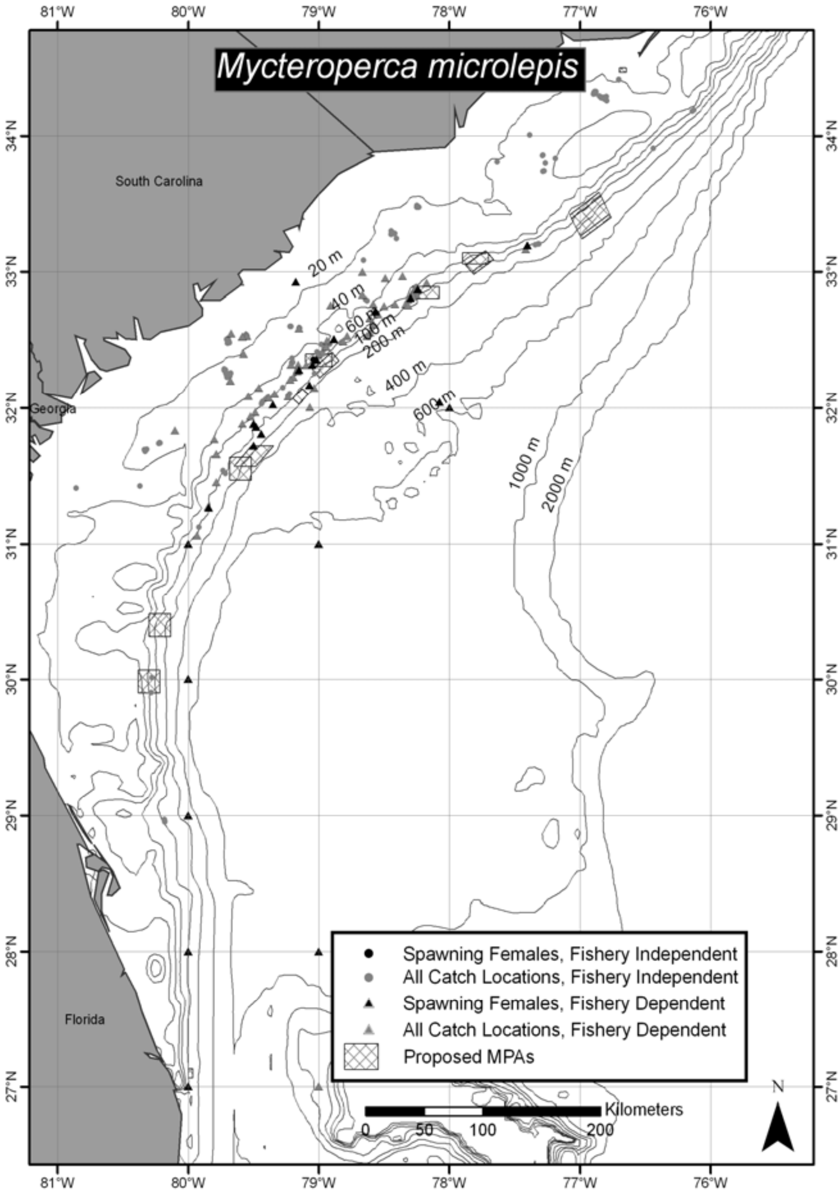

**Figure 8.** Locations of capture of gag. See Figure 2 for additional explanation. Note that all spawning locations deeper than 175 m are from fishery-dependent collections, reported from NMFS statistical areas (see Methods).

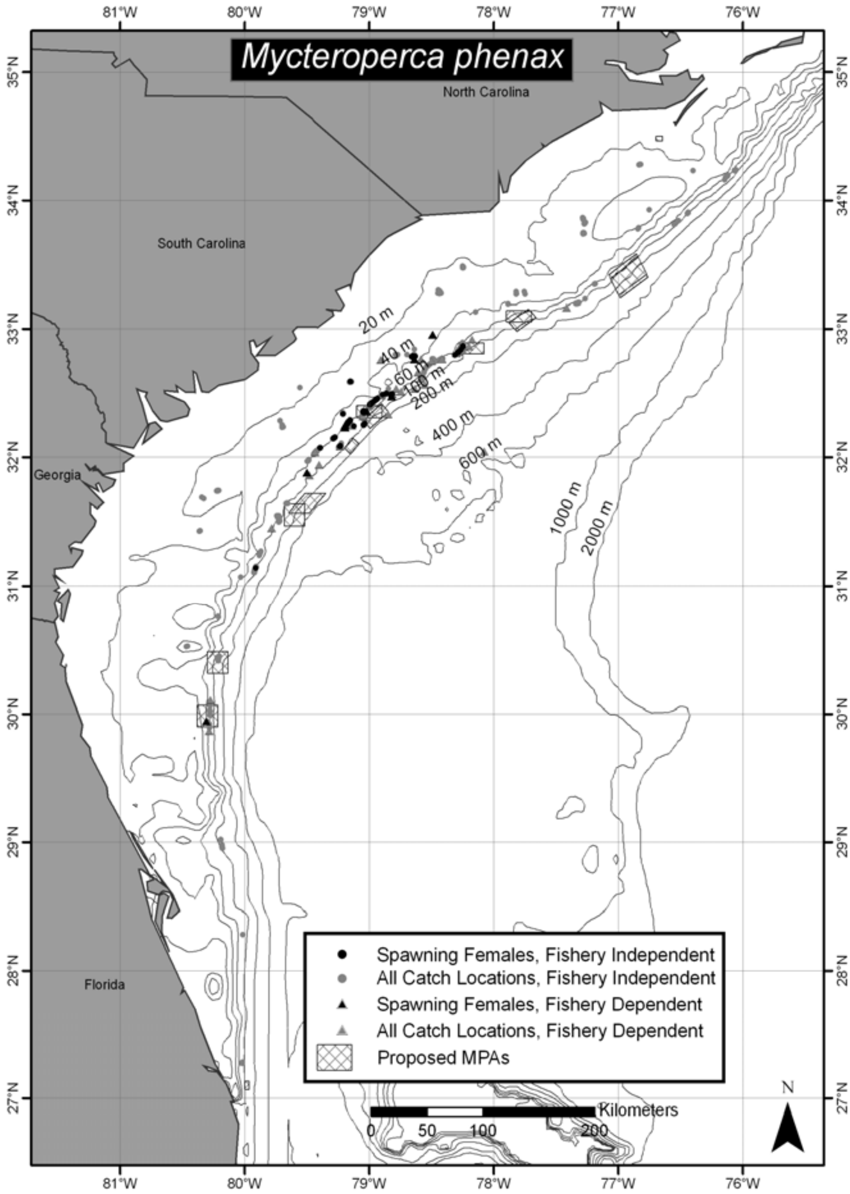

**Figure 9.** Locations of capture of scamp. See Figure 2 for additional explanation.

Greater amberjack (*S. dumerili*) occurred on middle- and outer-shelf and upper-slope reefs throughout the region and were captured at depths of 15 - 216 m (Table 3; Figure 10). We examined 2,498 gonads, 250 of which were from spawning females. Spawning females were collected from depths of 45 to 122 m. Only two spawning specimens were obtained from research cruises, and they were collected at a water temperature of 23.71°C. Spawning females were collected from January through June, with a major spawning period in April and May (Table 4). Most (88%) spawning greater amberjack were collected by commercial fishermen in the Florida Keys during a special effort aimed at obtaining gonads for determining fecundity, sex ratios and spawning season. Most (95%) spawning females were collected from waters south of 30°N latitude, although there is evidence for spawning off the Carolinas and Georgia too.

Knobbed porgy (*C. nodosus*) were more restricted to mid- and outer-shelf reefs off the Carolinas and Georgia (21 - 155 m, Figure 11). Spawning females were found almost exclusively at outer-shelf reefs and occurred at depths of 45 to 60 m (Table 3). Of 1181 specimens examined for sex and reproductive state, 88 were spawning females (Table 3). Knobbed porgy spawned over a narrow temperature range (49 measurements; range = 20.10 - 22.67°C). Spawning occurred from February through July, with a major spawning period of April through May (Table 4).

Red porgy (*P. pagrus*) were also distributed across the middle and outer shelf throughout the region, and spawning females were collected in depths from 26 - 57 m (Table 3, Figure 12). Of 15,687 examined for sex and reproductive state, 457 were spawning females. Females in spawning condition were found from September through May at bottom temperatures of 16.24 to 18.99°C (n = 18); however, the major spawning period was November through March (Table 4). In the Gulf of Mexico, red porgy spawn from January to April (Hood and Johnson 2000).

Gray triggerfish (*B. capriscus*) were broadly distributed across the shelf (13 - 128 m) throughout the region (Figure 13), but appear to concentrate spawning on middle-shelf to shelf-edge reefs (20 - 75 m). Of 4,349 examined for sex and reproductive state, 141 gray triggerfish were spawning females (Table 3). Gray triggerfish and other balistids construct nests by moving debris and fanning sediments on the bottom, creating a shallow cleared depression. These nests are guarded by either parent for 24 - 48 hours after spawning (Fricke 1980, Lobel and Johannes 1980). On 4 August 2002 (32.8° N, 78.3°W; 54 m; 20.58°C) we observed a large (~30 cm TL) gray triggerfish hovering over a cleared depression about 75 cm in diameter. An apparent egg mass could be observed in the bottom of the depression. Gray triggerfish spawned from May through August, with a major spawning period of June and July (Table 4), at temperatures of 18.87 - 27.42°C (N = 148; Tables 3. Gray triggerfish also spawn in warmer months (peak in November and December) in the southeastern North Atlantic [Ghana (Ofori-Danson 1990)].

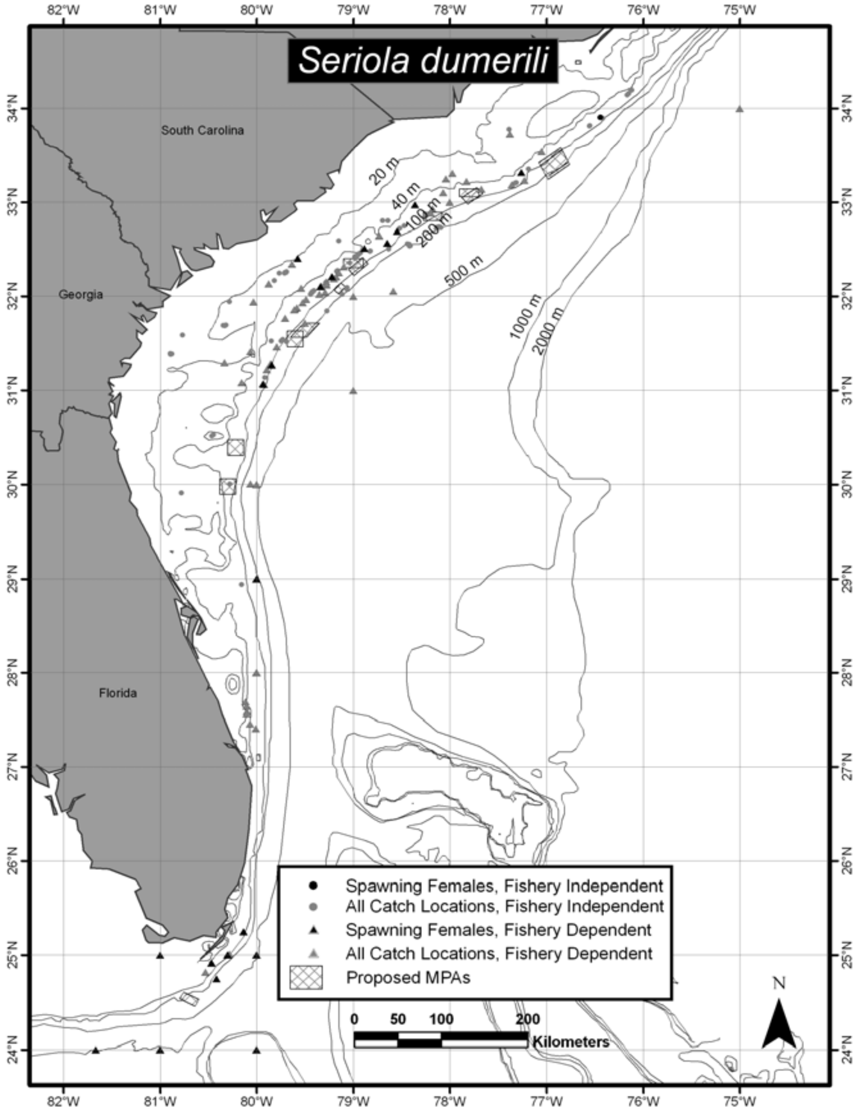

**Figure 10.** Locations of capture of greater amberjack. See Figure 2 for additional explanation. Note that some fishery-dependent collections in south Florida are as reported from NMFS statistical areas (see Methods).

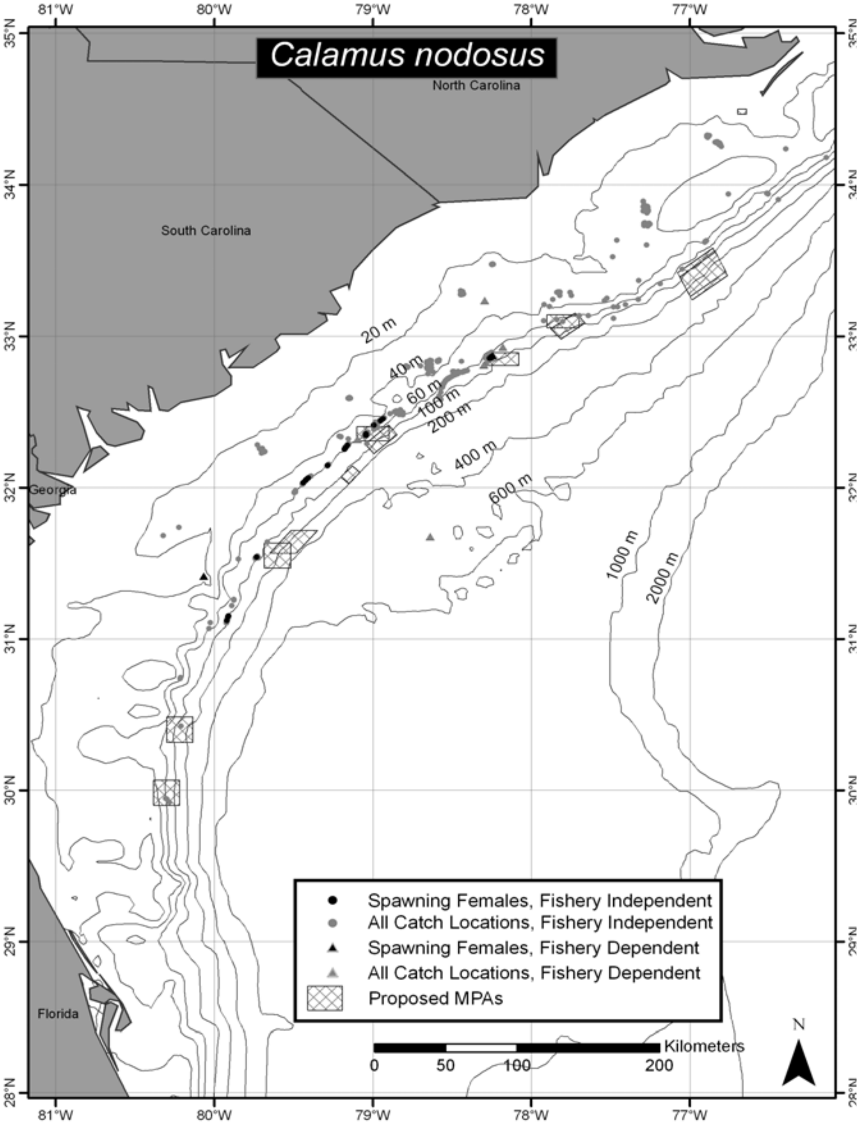

**Figure 11.** Locations of capture of knobbed porgy. See Figure 2 for additional explanation.

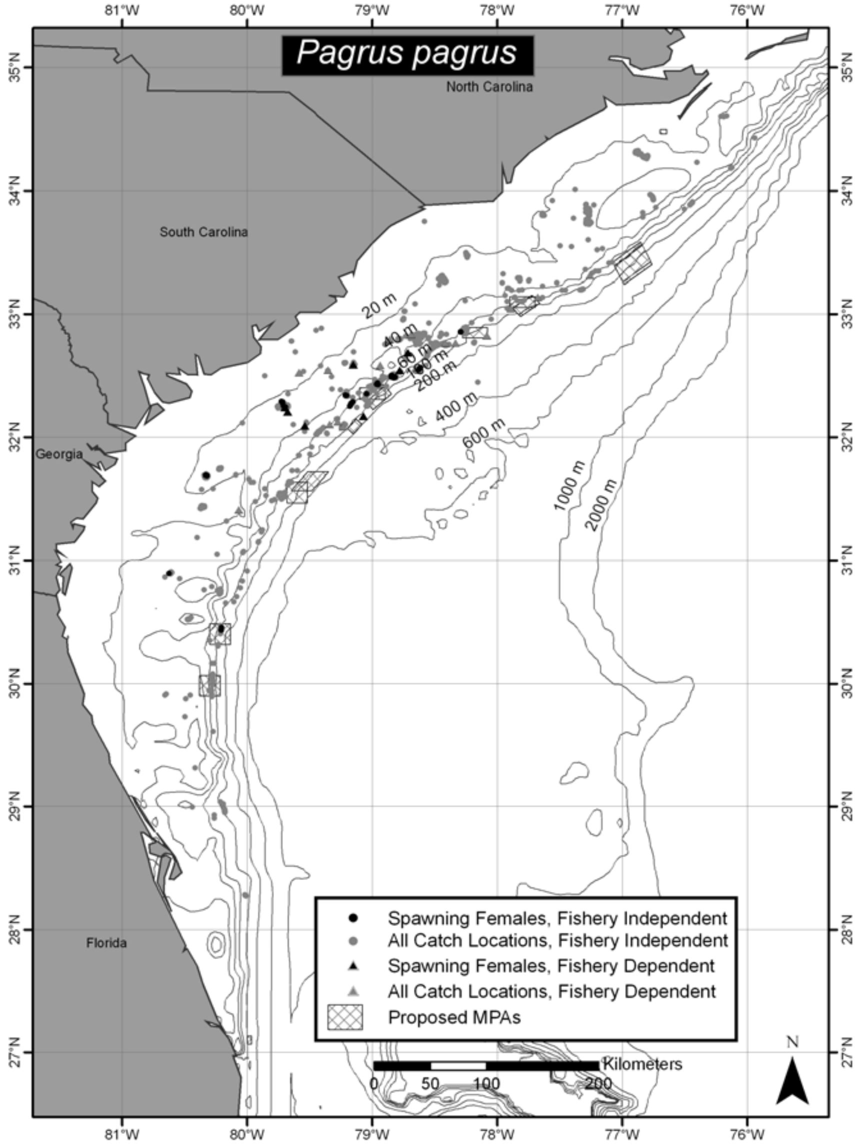

**Figure 12.** Locations of capture of red porgy. See Figure 2 for additional explanation.

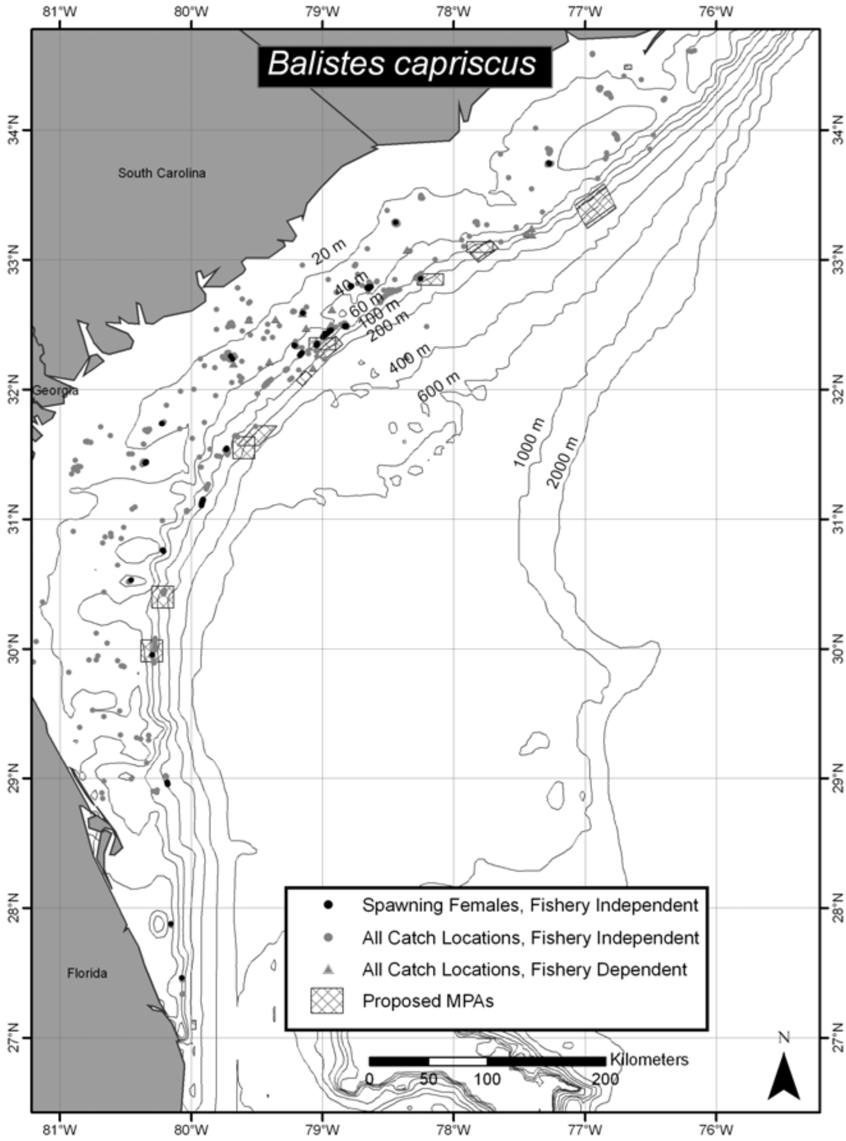

**Figure 13.** Locations of capture of gray triggerfish. See Figure 2 for additional explanation.

White grunt (*H. plumieri*) and red grouper (*E. morio*) had distributions that differed from most shelf species (Figures 14 - 15). Both species were caught on the middle and outer shelf, mainly in the northern part of the SAB, and apparently have a disjunct distribution (Zatcoff et al. 2004, Chapman et al. in prep.). They are abundant in the Caribbean and southern Florida, but are not common off northern Florida or Georgia. They appear to be more tropical species that are found only in the waters of the northern SAB, which are under the influence of the Charleston Gyre (see additional discussion below).

Of the 2,256 white grunt examined, 151 were spawning females. Spawning females were collected from March through September at most locations where white grunt occurred, with a major spawning period of April through June (Table 4). Spawning occurred in depths from 22 to 51 m (Table 3). White grunt spawned in warmer waters (20.23 - 27.42°C; n = 123) than other species examined, reflecting its preference for warmer waters.

Red grouper (*E. morio*) have a distribution similar to that of white grunt, although spawning is generally restricted to depths greater than 40 m (Figure 15). Spawning females (n = 46) represented 2.1% of the 2223 red grouper examined for sex and reproductive state (Table 3). Red grouper spawn in late winter and spring (February through June with a peak in April; Table 4) in depths from 30 to 90 m. In the Gulf of Mexico, peak spawning occurs in April (Coleman et al. 1996). Red grouper spawned in generally cooler waters than white grunt (range 16.97 - 24.08°C; n = 7).

Several species such as *Caulolatilus microps, Lopholatilus chamaeleonticeps, Epinephelus flavolimbatus, E. niveatus, Helicolenus dactylopterus, Polyprion americanus, Hyperoglyphe perciformis* and *Beryx decadactylus* have specific habitat requirements and were therefore collected and found in spawning condition in very restricted areas. They generally exhibited protracted spawning periods. Blueline tilefish (*C. microps*) were collected only off of South Carolina on shelf-edge and upper slope reefs between 46 and 256 m (Figure 16). Blueline tilefish (n = 1112 examined for sex and reproductive state) were found associated with hard bottom that occurs in that area (Sedberry et al. 2004). Females in spawning condition (n = 514) were collected from February through October, with a major spawning period of March through September (Table 4). Spawning females were collected at a temperature range of 8.87 - 16.28°C (n = 32).

Tilefish (*L. chamaeleonticeps*) also had a restricted depth and latitude range (Table 3, Figure 17); however, tilefish are found on soft-bottom habitat on the upper slope, where they construct burrows (Harris et al. 2001). Most tilefish were collected off South Carolina and Georgia, and spawning females were found in those areas. Spawning females ( 324 of 2431 fish examined) were collected in all months except October and December (Table 4), in depths from 190 to 300 m, at temperatures from 10.16 to 14.90°C (n = 9). The major spawning period was March through July. North of Cape Hatteras, most tilefish spawn from May to September (Grimes et al. 1988).

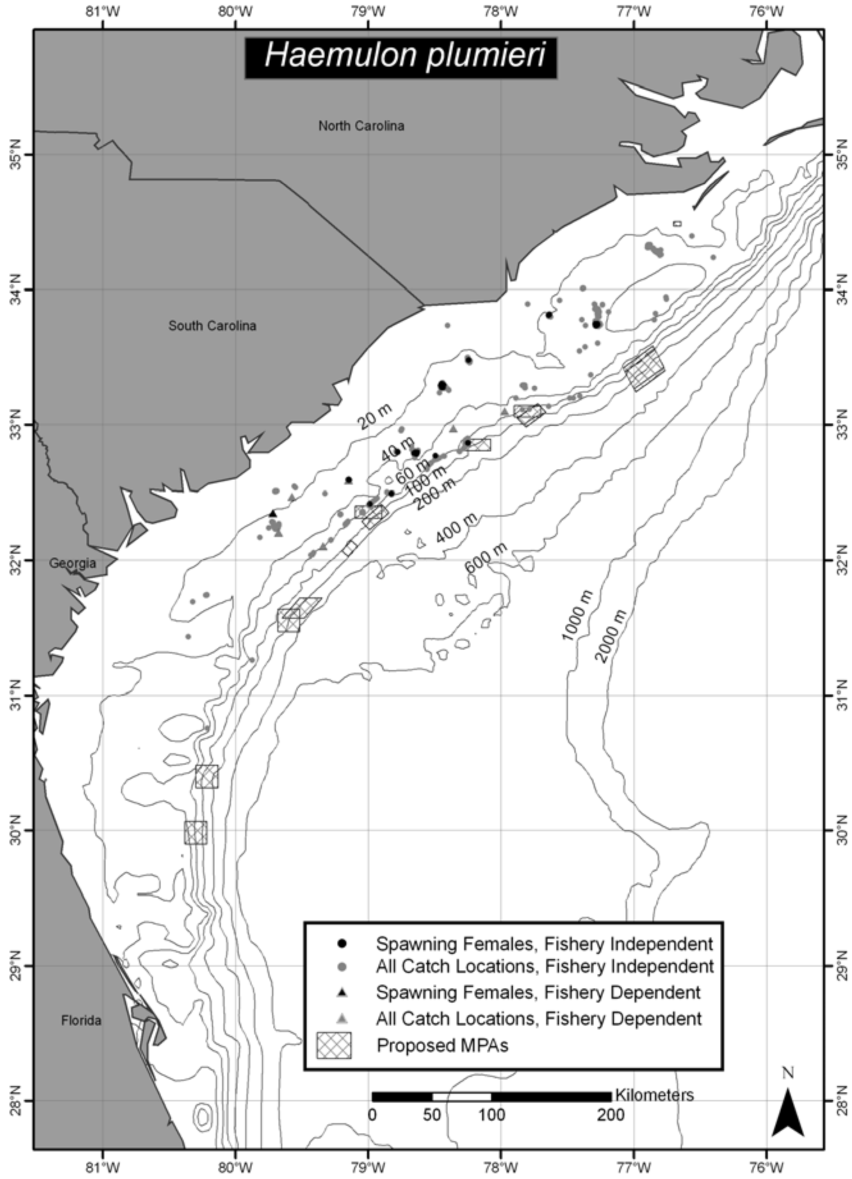

**Figure 14.** Locations of capture of white grunt. See Figure 2 for additional explanation.

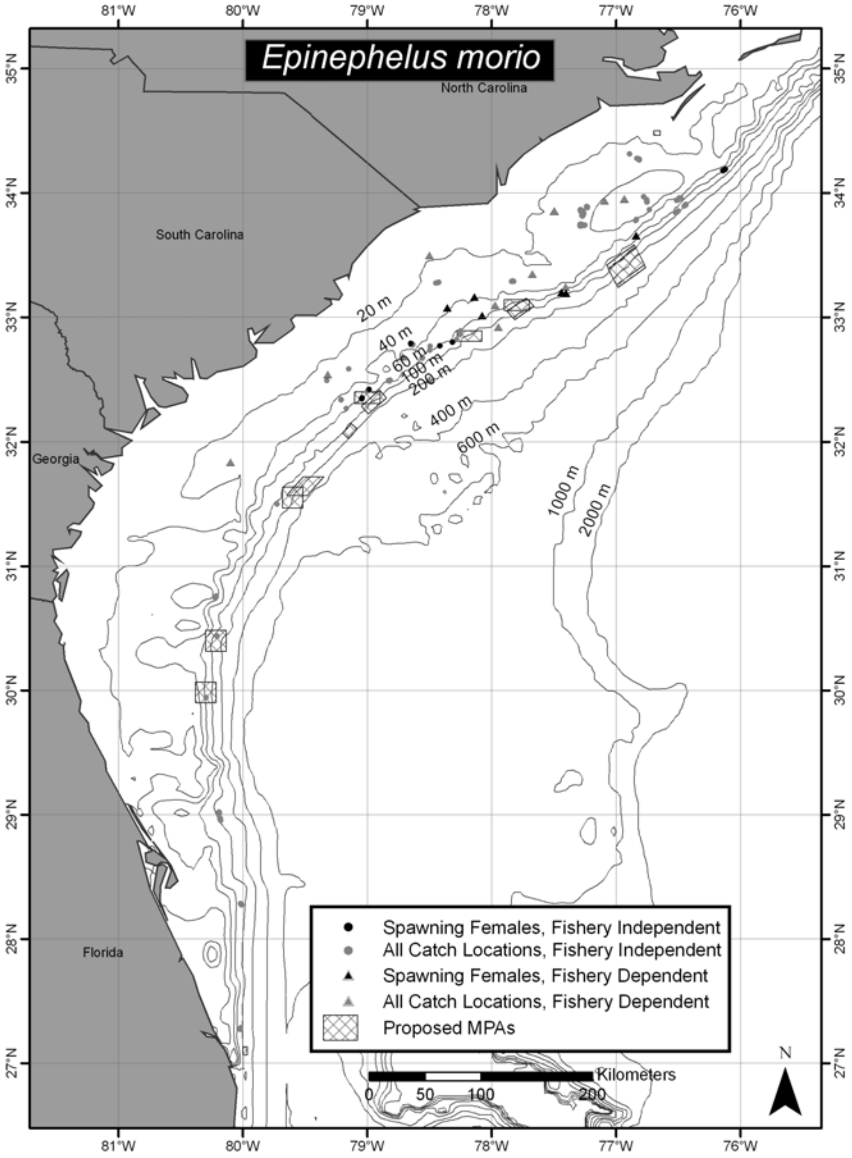

**Figure 15.** Locations of capture of red grouper. See Figure 2 for additional explanation.

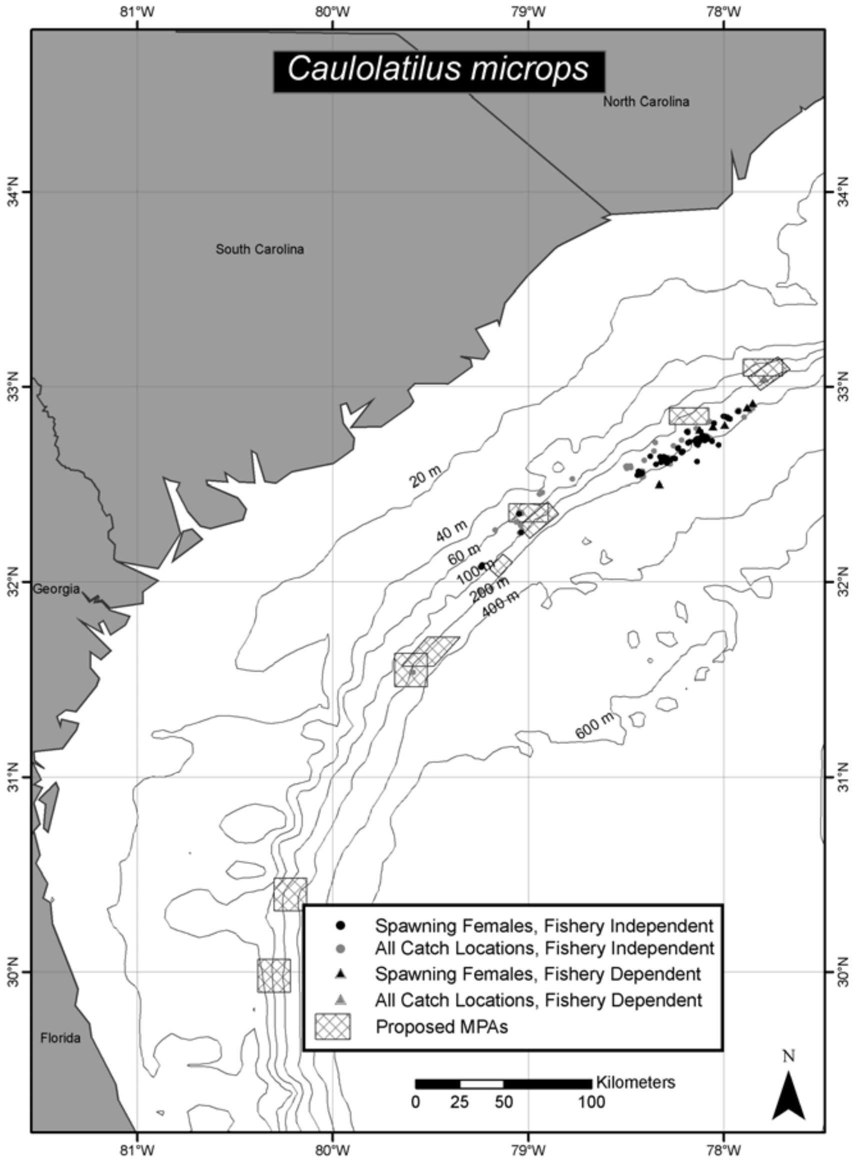

**Figure 16.** Locations of capture of blueline tilefish. See Figure 2 for additional explanation.

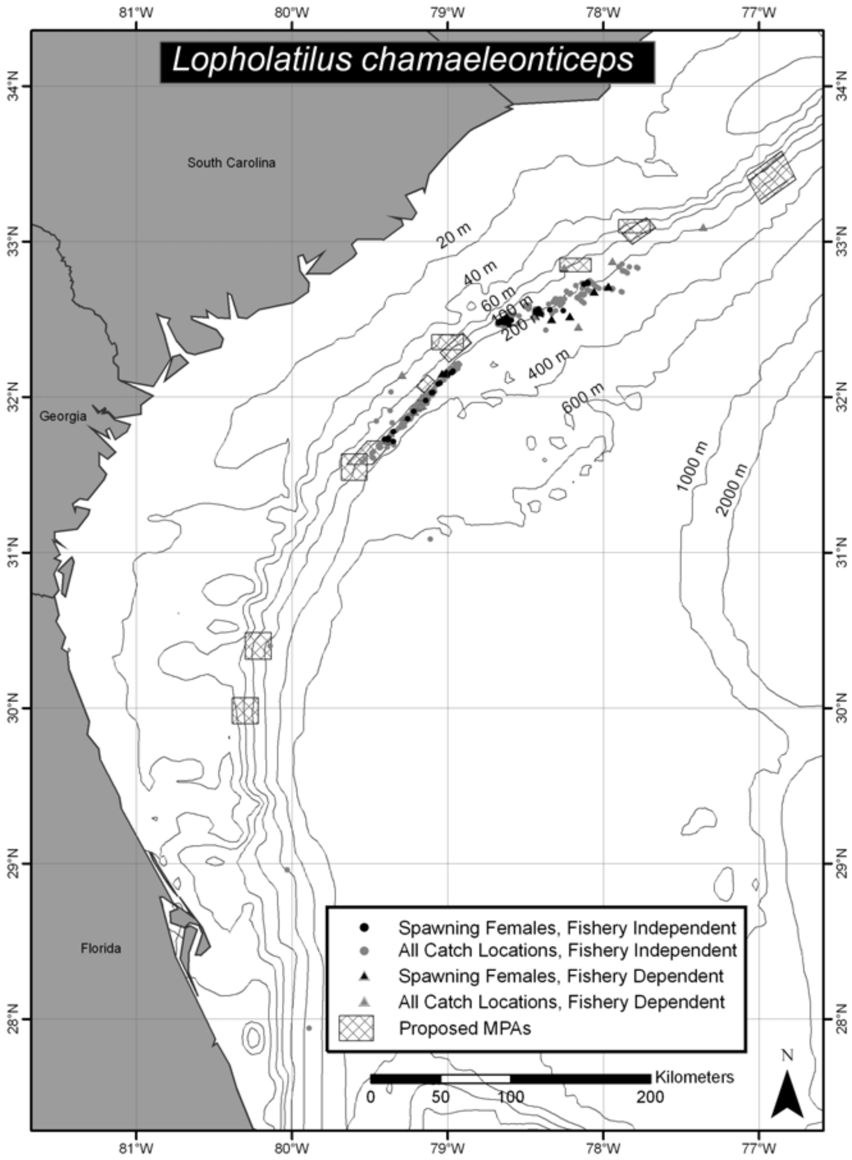

**Figure 17.** Locations of capture of tilefish. See Figure 2 for additional explanation.

Yellowedge grouper (*E. flavolimbatus*), like blueline tilefish, had a restricted depth distribution (Figure 18) and were also found mainly on shelf-edge and upper-slope reefs off of the Carolinas at depths of 31 to 205 m. Spawning females (six of 73 fish examined) were collected in August and September in depths from 160 to 194 m, at a temperature of 14.47°C (one measurement) (Tables 3-4). Yellowedge grouper spawn earlier (April to July) in the southern Caribbean (Manickchand-Heileman and Phillip 2000).

Snowy grouper (*E. niveatus*) were collected on shelf-edge and upper-slope reefs, mainly off the Carolinas (Figure 19). Spawning females (96 of 649 fish examined) were collected from April through September, in depths from 187 to 302 m (Tables 3 - 4). The major spawning period was May through August. No bottom temperature data were available for collections of spawning snowy grouper. During a submersible dive on snowy grouper habitat in August (2002) off South Carolina, a bottom temperature of 13.27°C was measured, although no spawning snowy grouper were observed during that dive (Sedberry et al. 2004).

Blackbelly rosefish (*H. dactylopterus*) were also found over a relatively restricted depth range over hard bottom, and were often caught along with snowy grouper (Figure 20). Blackbelly rosefish were collected between 38 and 686 m and spawning females were caught in depths from 229 to 238 m (Table 3). Of 1,381 specimens examined, 138 were spawning females. Females were in spawning condition from December through April, with a major spawning period of January through April (Table 4). In the western Mediterranean Sea, blackbelly rosefish spawn in January and February (Munoz et al. 1999). No bottom temperature data were available for collections of spawning blackbelly rosefish, and only one collection off South Carolina had location data (Figure 20).

Wreckfish (*P. americanus*) occurred only on the continental slope, on a feature known as the Charleston Bump (Sedberry et al. 2001). Of 1,466 wreckfish examined for sex and reproductive state, 55 were spawning females. Wreckfish were caught in depths from 44 to 653 m, and spawning females were caught in depths from 433 to 595 m (Table 3, Figure 20). Wreckfish on the Charleston Bump have been collected at temperatures ranging from 6.2 to 16.3°C (Sedberry et al. 1999), and observed from submersibles (September 2001; August-September 2003) at temperatures of 8.4 - 16.7°C in depths from 430 to 570 m. Females in spawning condition were collected from November to May and were most prevalent in samples from February and March (Table 4). The Charleston Bump is the only known spawning area for wreckfish in the western North Atlantic (Sedberry et al. 1999); wreckfish in the South Atlantic (Brazil) spawn in the austral winter [July to October (Peres and Klippel 2003)].

We obtained 325 barrelfish (*H. perciformis*) from commercial fishermen and conducted histological examination of 102 specimens. All samples, including spawning females, came from wreckfish fishermen fishing on the Charleston Bump (Sedberry et al. 2001). The distribution of adult barrelfish is similar to that of adult wreckfish and spawning locations and times are about the same. Of the 102 specimens examined, 12 were females in spawning condition (Table 3). Females in spawning condition were found from November through January and in May (Table 4).

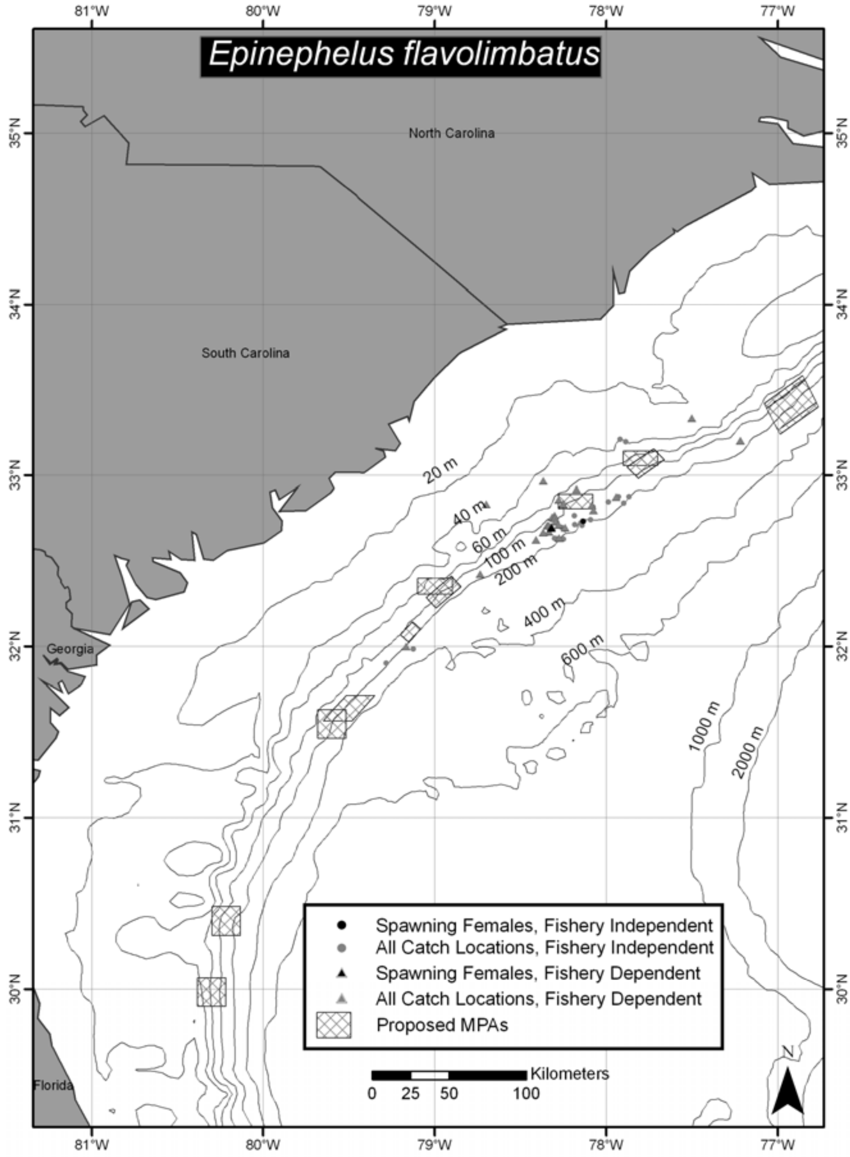

**Figure 18.** Locations of capture of yellowedge grouper. See Figure 2 for additional explanation.

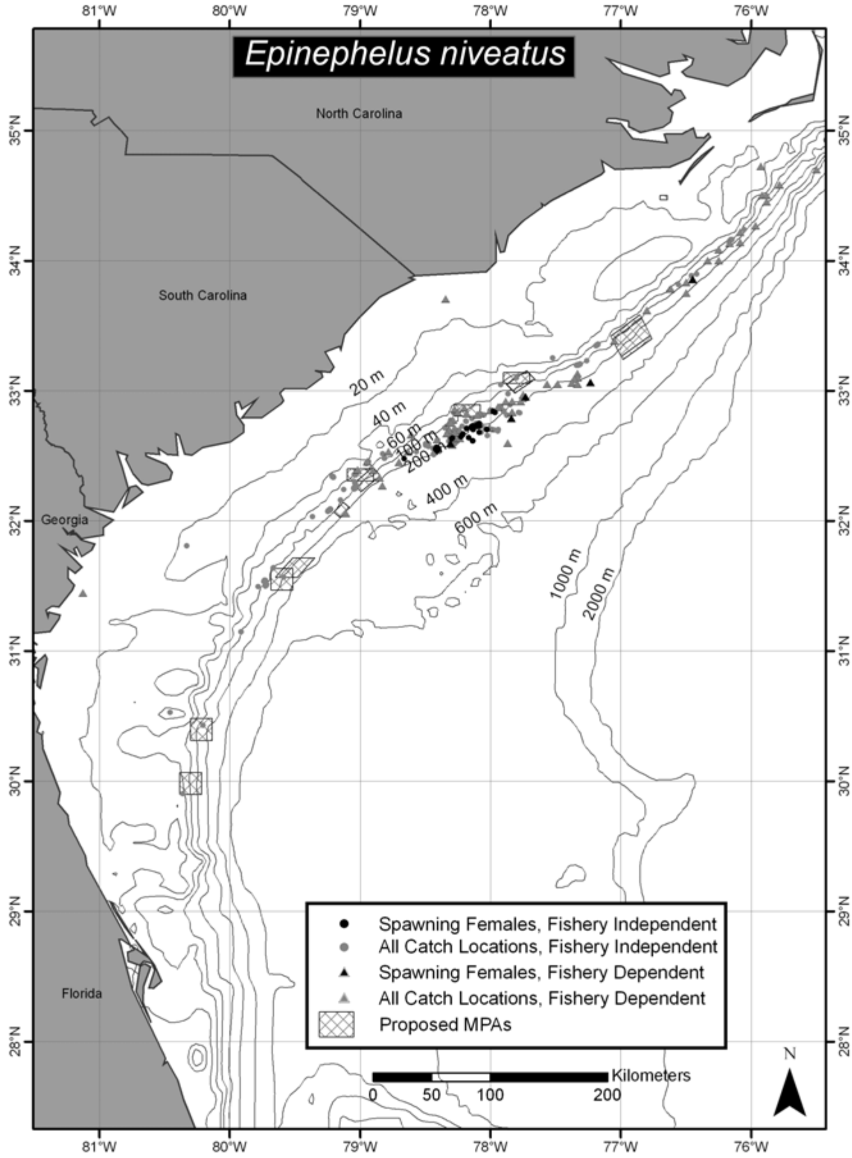

**Figure 19.** Locations of capture of snowy grouper. See Figure 2 for additional explanation.

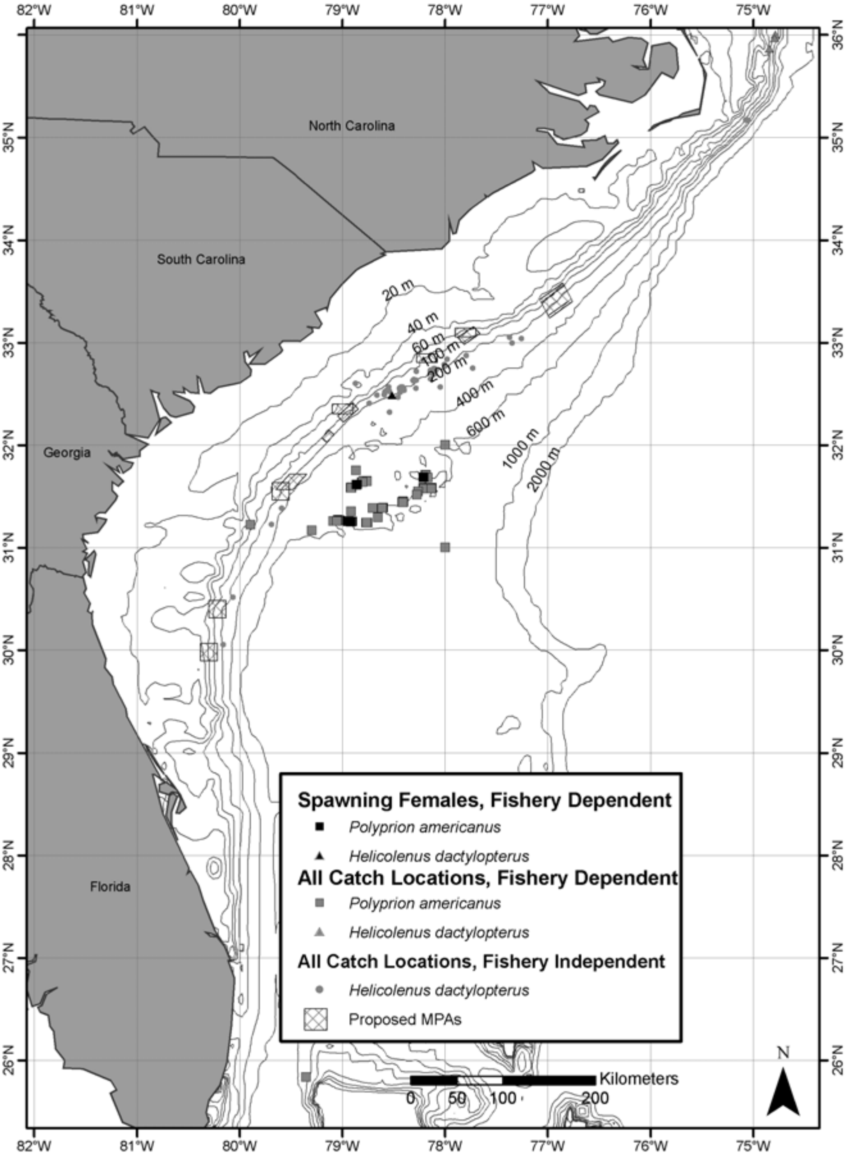

**Figure 20.** Locations of capture of blackbelly rosefish and wreckfish. See Figure 2 for additional explanation.

Red bream (*B. decadactylus*), like wreckfish and barrelfish, were collected by commercial wreckfish fishermen fishing on the Charleston Bump (Sedberry 2001). Of 16 specimens examined, eight were spawning females collected in June through September (Table 4). No spawning females were present in samples from April, May, November and December. No depth or temperature data were obtained from the commercial fishermen, but location and temperatures were similar to wreckfish catch locations.

Three additional species of grouper were also rarely collected in spawning condition. Yellowmouth grouper (*M. interstitialis*) was occasionally taken at middle- and outer-shelf reefs off of South Carolina (n = 18), where a few females (n = 9) were found in spawning condition in February, March and August off South Carolina at depths of 49 - 51 m (Tables 3-4, Figure 21). Only one bottom temperature was recorded at one spawning location (14.47° C). Rock hind (*E. adscensionis*) were collected mainly at shelf-edge reefs off of South Carolina and, of 34 examined for sex and reproductive state, five were spawning females collected during March, May and June from depths of 37 - 53 m (Tables 3-4, Figure 21). Bottom water temperatures for those collections were 20.05 - 23.96°C (n = 6). Speckled hind (*E. drummondhayi*) were distributed throughout the region on outer-shelf to upper-slope reefs in depths from 28 to 114 m, and were collected more frequently (274 examined) than rock hind (Table 3, Figure 22). Five spawning females were found off of South Carolina in May, June and September (Table 4).

In addition to the above species of grouper, we also examined gonads of seven graysby (*C. cruentata*), 18 coney (*C. fulva*) and 12 warsaw grouper (*E. nigritus*) collected throughout the region (Table 3). Several of the warsaw grouper were collected in proposed MPA sites off northern Florida and South Carolina. One spawning female was caught in May on the upper slope at a depth of 168 m (location unknown). An additional warsaw grouper examined from the database contained late vitellogenic oocytes, perhaps indicating potential spawning in the region. We collected one female coney in spawning condition in June (33.8°N, 76.8°N, 39 m), and one potential spawner in the same month with late vitellogenic oocytes. In Puerto Rico, coney spawn from December to March (Jimenez and Fernandez 2001). One female graysby examined also contained late vitellogenic oocytes, again perhaps indicating potential spawning in the region. We observed several running ripe male coney and graysby; however, male reef fishes are in spawning condition for much of the year and cannot be used to determine spawning location in the absence of females. In addition to the histological evidence of spawning cited above, we have observed courtship behavior in hogfish, *Lachnolaimus maximus*, at shelf-edge reef sites. Hogfish courtship was observed from submersible off Jacksonville, Florida on 30 July 2002 (30.4°N, 80.2°W, 56 m depth, 1846-1926 EDT) and off Charleston, South Carolina on 1 August 2002 (32.3°N, 79.0°W, 61 m depth, ~1000 EDT). Behavior was as described by Colin (1982), with the male displaying erect spines in the first dorsal fin, and rapid pelvic-fin agitations. This display was directed at one or two nearby females. Although Colin (1982) observed spawning from mid-afternoon to sunset, we did not observe actual spawning in hogfish during dives in morning and late afternoon. Bottom temperatures at the Florida site during the dive ranged from 20.90 - 20.94°C, considerably cooler than those reported by Colin (1982) in December to March in Puerto Rico (24 - 26°C). Bottom temperatures at the South Carolina site ranged from 20.47 - 22.03°C.

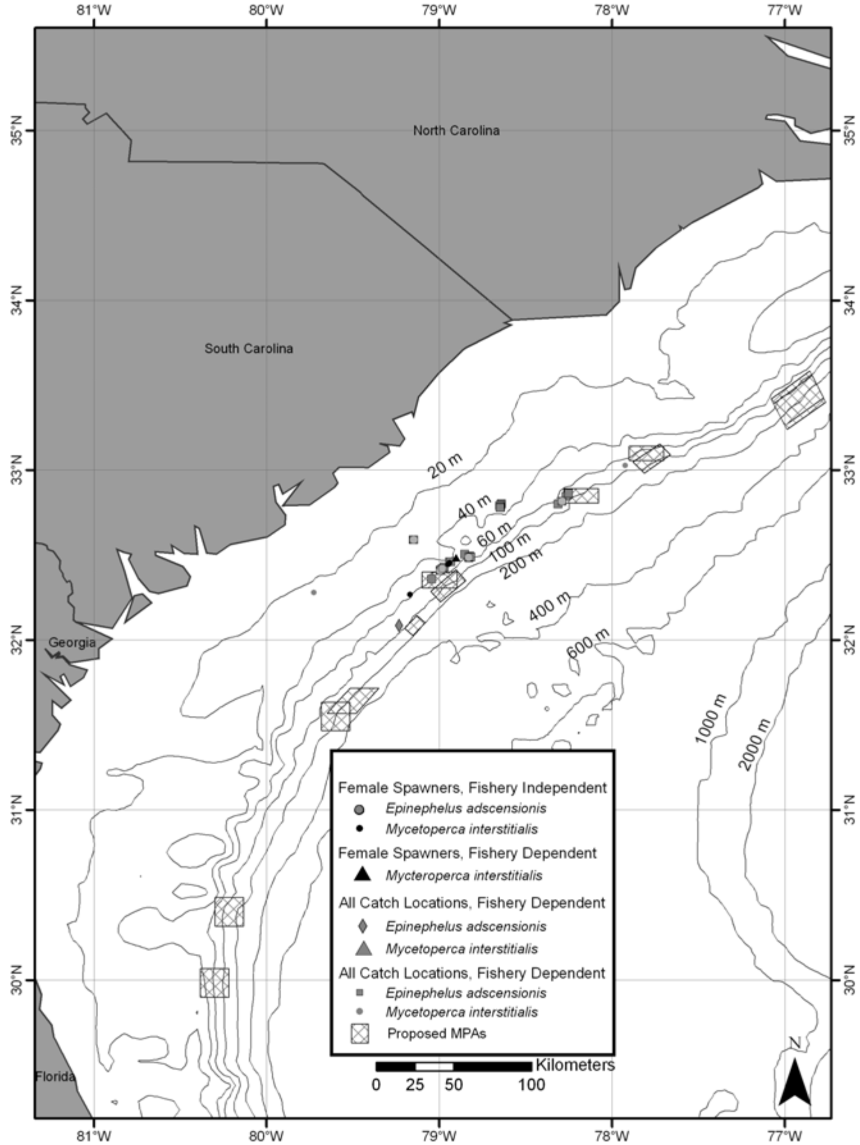

**Figure 21.** Locations of capture of rock hind and yellowmouth grouper. See Figure 2 for additional explanation.

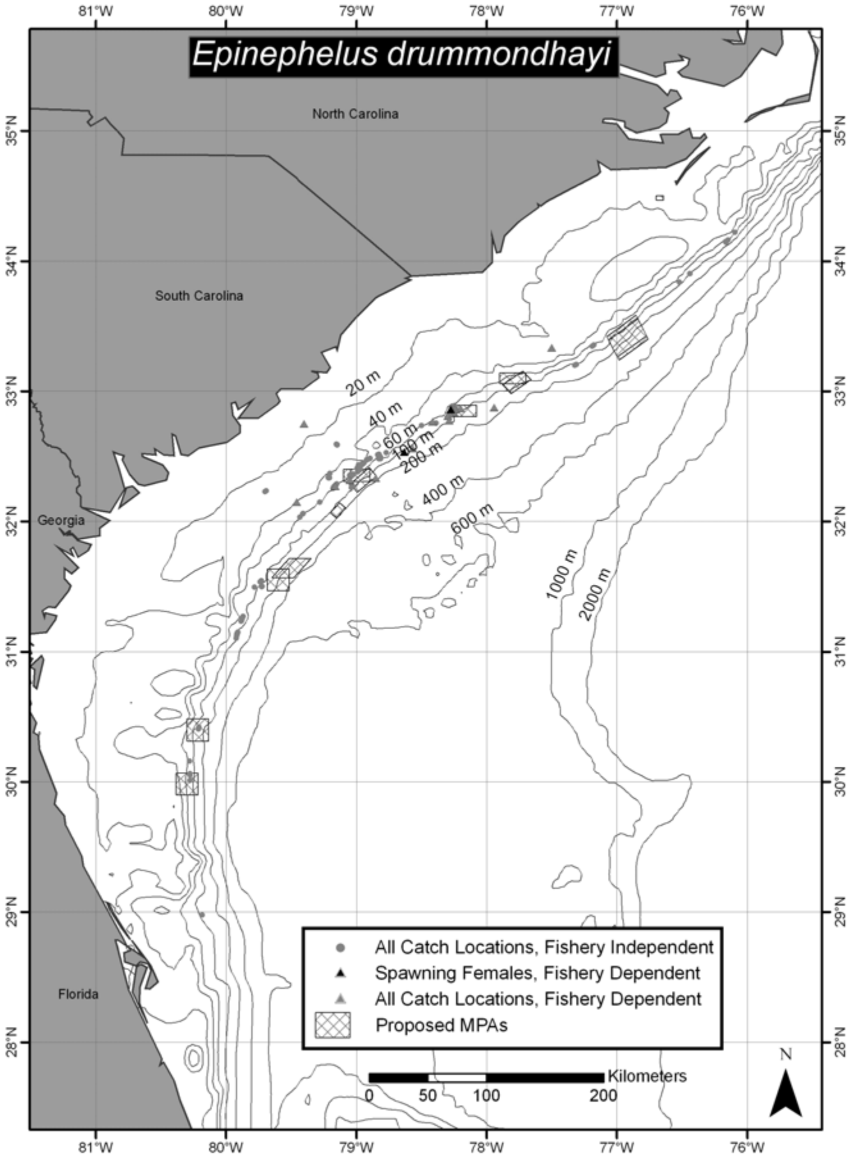

**Figure 22.** Locations of capture of speckled hind. See Figure 2 for additional explanation.

## CONCLUSIONS AND MANAGEMENT ISSUES

Spawning condition was determined for 28 species of reef fish at several phylogenetic levels, including Beryciformes (Berycidae), Scorpaeniformes (Scorpaenidae), Perciformes (Carangidae, Centrolophidae, Haemulidae, Lutjanidae, Malacanthidae, Polyprionidae, Serranidae, Sparidae) and Tetraodontiformes, and over a considerable depth and latitudinal range. In spite of some temporal and spatial sampling limitations, we determined that the species examined fall into a few groups of life history and spawning strategies.

Several species, such as small serranids, haemulids, sparids and lutjanids, spawned over protracted periods and throughout the region. Black sea bass, sand perch, tomtate, red snapper, and vermilion snapper were broadly distributed and spawned across the shelf, although vermilion snapper spawning activity seemed to be more concentrated at shelf edge reefs than the other species in this group.

Red porgy and bank sea bass also had broad distributions throughout the region, but spawning appeared to be more narrowly focused on deeper sites in the middle of the region. In the case of bank sea bass, and to a lesser extent red porgy, this may reflect sampling limitations as these both spawn in winter, when sampling is more difficult and was subsequently more confined to the waters near our laboratory.

Gag, scamp, red grouper, knobbed porgy and gray triggerfish spawned mainly at shelf-edge reefs. Gag use shallow coastal or estuarine waters as nursery areas, but make either an ontogenetic shift or spawning migration to the outer shelf. Tagging of gag has indicated a spawning migration (Van Sant et al. 1994, McGovern et al. In press). Gray triggerfish juveniles are pelagic or benthic in a variety of habitats (Martin and Drewry 1978), but apparently move to deep reefs with age and maturity. Knobbed porgy, red grouper and scamp appear to be more resident on outer-shelf reefs, where spawning occurs.

Tilefish, blackbelly rosefish, blueline tilefish, snowy grouper and yellowedge grouper are resident, at least as adults, on the upper slope. Spawning is restricted to reef (or mud in the case of tilefish) habitats on the upper slope.

Barrelfish, wreckfish and red bream live on the Charleston Bump, mainly in depths from 500 - 600 m (Sedberry et al. 2001, Popenoe and Manheim 2001, Weaver and Sedberry 2001). Spawning also occurs there, under the main axis of the Gulf Stream. Eggs, larvae and juveniles of wreckfish and barrelfish are pelagic, perhaps living at the surface for several months (Sedberry et al. 1999, Martin and Drewry 1978). It is uncertain how these fishes are recruited back to the Charleston Bump. Juvenile wreckfish are very common at the surface in the eastern North Atlantic in the months following spawning on the Charleston Bump, and wreckfish from the eastern North Atlantic are genetically identical to those from the Charleston Bump (Sedberry et al. 1999, Ball et al. 2000), indicating substantial gene flow between the regions, mediated by Gulf Stream flow.

White grunt, and to a lesser extent red grouper, were collected in spawning condition primarily in the northern part of the study area and apparently have a disjunct distribution (Zatcoff et al. 2004, Chapman et al. In prep.). They are abundant in the Caribbean and southern Florida, but are not common off northern Florida or Georgia. They appear to be more tropical species that are found only in the waters of the northern SAB that are under the influence of the Charleston Gyre. Because of the influence of Gulf Stream waters being transported onto shelf waters off northern South Carolina and southern North Carolina via the Charleston Gyre, many tropical species are recruited to this area (Powell et al. 2000).

Gag and greater amberjack appear to undertake spawning migrations to the south, with most spawning in greater amberjack apparently occurring off of southern Florida. Tagging of these species off South Carolina has indicated substantial movement to south Florida of large fish during the spawning season (Van Sant et al. 1994, McGovern et al. In press, Meister et al. In prep.).

Several rare tropical groupers (yellowmouth grouper, rock hind, speckled hind, graysby, coney, warsaw grouper) occur in the region, but it remains uncertain if spawning in most of these is occurring here or if recruitment of these fish comes from southern spawning locations. Groupers generally have long-lived larvae [31 - 66 days (Lindeman et al. 2000)], and it is certainly possible that periodic recruitment of these tropical species occurs. Some females examined appeared to be in, or approaching, spawning condition; however, it is unknown if population densities are high enough to induce spawning behavior (aggregation, harem formation) that often accompanies spawning in these tropical groupers (Jimenez and Fernandez 2001).

Although influenced by sampling limitations, there did appear to be areas within the region that are spawning grounds for several species. Shelf-edge reefs (40 - 60 m) in the middle of the SAB appeared to be particularly important. Some of these reefs coincide with areas proposed by the SAFMC as MPAs that will prohibit bottom fishing (SAFMC 2004). Proposed MPAs that encompass shelf-edge reefs off Charleston, South Carolina [SAFMC Proposed South Carolina-B MPA, Option 1 at about 32.3°N (SAFMC 2004)] included spawning grounds for bank sea bass, red grouper, gag, scamp, knobbed porgy, red porgy, vermilion snapper and gray triggerfish. Blueline tilefish were also caught in spawning condition in this proposed MPA site, but most were caught deeper, on upper slope reefs. Red snapper were also found spawning in this proposed MPA, but extensive spawning was found scattered across the shelf. Black sea bass and sand perch spawned near the South Carolina B sites, but most spawning in those two species was at scattered middle-shelf reefs. Rock hind spawned near this site and occurred in the proposed SC-B Option 1 MPA. Spawning in rock hind also occurred near Proposed South Carolina-A MPA, Option 2 at about 32.8°N, and rock hind were collected at that proposed shelf-edge MPA site. The two instances of courtship behavior observed in hogfish also took place in proposed MPA sites, one of which was South Carolina B (the other was Florida Option 1 off Jacksonville). The proposed MPA sites off South Carolina appear to be particularly important as spawning grounds for several species. Spawning occurred at one proposed South Carolina site (South Carolina-B Option 1) during all months of the year.

Gag and scamp spawning occurred in more than one proposed MPA site off South Carolina, and spawning scamp were caught in proposed MPA sites off Florida too (SAFMC Proposed North Florida MPA Option 2 at 30°N). Tomtate were found spawning at many mid- to outer-shelf sites, but only one proposed MPA site (the North Florida Option 2 site) had spawning tomtate. Vermilion snapper were found spawning in almost all of the proposed sites, the exceptions being deep (> 200 m) sites off North Carolina and Georgia.

Several species spawned mainly on upper-slope habitats. Blackbelly rosefish, snowy grouper, yellowedge grouper, and tilefish spawned on reef or mud habitat centered around 200 m. Although tilefish spawned near one of the proposed Georgia MPAs (SAFMC Proposed Georgia MPA Option 1), no spawning in any of these deepwater species was detected within the proposed MPA sites. Because protection and management of deepwater species is one of the primary objectives of the proposed MPA sites (SAFMC 2004), consideration should be given to locating a deepwater site to coincide with known spawning areas in deepwater species.

No spawning sites of greater amberjack coincided with proposed SAFMC MPA sites. However, two spawning locations were within the Florida Keys National Marine Sanctuary, but not within no-take zones in the Sanctuary. Tagging data (Meister et al. in prep.) indicate substantial movement of greater amberjack from the Carolinas to southern Florida during the spawning season. The commercial fishery for greater amberjack is closed in April (see SAFMC web site for regulations: www.safmc.net) and 56% of spawning fish were collected in April (most of those from southern Florida). This probably affords considerable protection to spawning greater amberjack.

Gag and red porgy are managed, in part, by a spawning season closure, with commercial catches limited to the recreational bag limit for gag in March and April (when 76% of spawning females were collected). Among several other restrictions, sale of red porgy is prohibited from January through April, when 88% of spawning females were collected. These closures during the peak spawning season probably afford some protection to spawning gag and red porgy.

Many species of reef fish spawn at shelf edge sites that are under the influence of the Charleston Gyre. Eggs and larvae of these species are probably entrained in this gyre. Gag larvae are most often collected in the Charleston Gyre, often several tens of kilometers offshore and over much deeper water (> 600 m) than their preferred (< 50 m) habitat (Sedberry et al. 2004). Spawning in the Charleston Gyre probably results in better survival, as early life history stages are carried off the shelf with its associated predators, and are retained in a cyclonic circulation (with upwelling at its core) that provides nutrients and eventual transported back onto the shelf toward shallow nursery areas. Such a strategy seems to be associated with the long larval period found in groupers that spawn at shelf edge sites (Lindeman et al. 2000) and that helps them utilize large gyres such as the Charleston Gyre.

Deep reef fishes of the Charleston Bump and Blake Plateau live and spawn in areas beyond those currently proposed as MPAs where bottom fishing would be prohibited. Wreckfish, however, are managed with gear restrictions (no longlines), an individual transferable quota with total allowable catch, and a spawning season closure (15 January through 15 April). Because barrelfish spawn at about the same place, and their spawning season extends into January (no data were available from February), it is likely that they are afforded some protection during spawning by regulations imposed on the wreckfish fishery. Red bream, however, spawn in summer on the Charleston Bump, when the wreckfish fishery is open and they are caught as bycatch. There is no evidence that the apparently small (but undocumented) bycatch is having a negative effect on spawning red bream, but this deserves further investigation. In addition to spawning demersal fishes on the Charleston Bump, there is some evidence that this is a spawning site for pelagic dolphin (*Coryphaena hippurus*) and swordfish (*Xiphias gladius*) as well (Govoni and Hare 2001, Sedberry et al. 2004).

Although many reef fishes important in commercial and recreational fisheries off the southeastern U.S. spawn across broad shelf areas, it is evident that some spawning is localized. Often, local spawning grounds are utilized by several species. In deciding among options for final MPA sites, consideration should be given to sites that are used as spawning grounds by several species. It is obvious that some options among the MPA sites proposed by the SAFMC contain more spawning sites for more species than do some of the other sites, and that by minor shifts in location or even orientation of the proposed closed areas, more spawning fishes could be protected. Consideration of known spawning areas and times should be an important criterion when planning time or area closures to ensure sustained fisheries.

## ACKNOWLEDGEMENTS

We thank scientists of the SCDNR-MARMAP program, past and present (especially C. Barans, W. Bubley, J. Burgos, N. Cuellar, E. Daniel, K. Filer, P. Harris, P. Keener-Chavis, D. Machowski, J. McGovern, S. Meister, J. Moore, S. Palmer, P. Powers Mikell, W. Roumillat, C. Sharp, S. Van Sant, W. Waltz, C. Wenner and B. White), for assistance in data collection and analysis. Personnel of the NOAA Fisheries Beaufort Laboratory assisted with collection of fishery-dependent samples. K. Grimball prepared most of the histological sections and C. Schobernd provided observations of courtship behavior observed during her analysis of submersible videotapes. M. Brouwer (SAFMC) assisted with translations. Funding was provided by grants from NOAA Fisheries, including MARFIN Grant NA17FF2874 (G. Sedberry, Principal Investigator) and Unallied Science Program Grants NA97FL0376, NA07FL0497 and NA03NMF4720321 (G. Sedberry, Principal Investigator). Submersible observations were supported with grants from the NOAA Office of Ocean Exploration (Grants NA16RP2697 and NA0ROAR4600055; G. Sedberry, Principal Investigator). NOAA Fisheries has supported the SCDNR since 1973 to collect the fishery-independent data used in this paper, under the SCDNR-MARMAP Program (current Grant 50WCNF106007-L0003; P. Harris, Principal Investigator).

## LITERATURE CITED

Able, K.W., M.P. Fahay, and G.R. Sheperd. 1995. Early life history of black sea bass, *Centropristis striata*, in the Mid-Atlantic Bight and a New Jersey estuary. *Fishery Bulletin* **93**:429-445.

Atkinson, L.P. 1985. Hydrography and nutrients of the southeastern U.S. continental shelf. Pages 77-92 in: L.P. Atkinson, D.W. Menzel, and K.A. Bush (eds.). *Oceanography of the Southeastern U.S. Continental Shelf.* American Geophysical Union, Washington, D.C. USA.

Ball, A.O., G.R. Sedberry, M.S. Zatcoff, R.W. Chapman, and J.L. Carlin. 2000. Population structure of the wreckfish *Polyprion americanus* determined with microsatellite genetic markers. *Marine Biology* **137**:1077-1090.

Bane, J.M.,Jr., L.P. Atkinson, and D.A. Brooks. 2001. Gulf Stream physical oceanography at the Charleston Bump: deflection, bimodality, meanders and upwelling. Pages 25-36 in: G.R. Sedberry (ed.). *Island in the Stream: Oceanography and Fisheries of the Charleston Bump.* American Fisheries Society Symposium 25, Bethesda, Maryland USA.

Bortone, S.A. 1971. Studies on the biology of the sand perch, *Diplectrum formosum* (Perciformes: Serranidae). *Florida Department of Natural Resources Technical Series* 65. 27 pp.

Carter, J., G.J. Marrow, and V. Pryor. 1994. Aspects of the ecology and reproduction of the Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43**:65-111.

Carter, J. and D. Perrine. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. *Bulletin of Marine Science* **55**:228-234.

Chapman, R.W., G.R. Sedberry, B.M. Eleby, and A.O. Ball. [In prep.]. Genetic structure of white grunt, *Haemulon plumieri*, populations: implications for gene flow and phylogeography.

Coleman, F.C., C.C. Koenig, and L.A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes* **47:**129-141.

Coleman, F.C., C.C. Koenig, G.R Huntsman, J.A. Musick, A.M. Eklund, J.C. McGovern, R.W. Chapman, G.R. Sedberry, and C.B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries* **25(3)**:14-20.

Colin, P.L 1982. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae). *Fishery Bulletin* **80**:853-862.

Collins, L.A., G.R. Fitzhugh, L. Mourand, L.A. Lombardi, W.T. Walling Jr., W.A. Fable Jr., M.R. Burnett, and R.J. Allman. 2001. Preliminary results from a continuing study of spawning and fecundity in the red snapper (Lutjanidae: *Lutjanus campechanus*) from the Gulf of Mexico, 1998-1999. *Proceedings of the Gulf and Caribbean Fisheries Institute* **52**:34-47.

Collins, M.R. 1990. A comparison of three fish trap designs. *Fisheries Research* **9**:325-332.

Collins, M.R. and B.W. Stender. 1987. Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*) and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973-1980. *Bulletin of Marine Science* **41**:822-834.

Craig, A.E. 1969. The grouper fishery of Cay Glory, British Honduras. *Annals of the Association of American Geographers* **59**:252-263.

Cuellar, N., G.R. Sedberry and D.M. Wyanski. 1996. Reproductive seasonality, maturation, fecundity and spawning frequency of vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States. *Fishery Bulletin* **94**:635-653.

Darcy, G.H. 1985. Synopsis of biological data on the sand perch, *Diplectrum formosum* (Pisces: Serranidae). *NOAA Technical Report NMFS 26*. 21 pp.

Domeier, M.L. and P.L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60**:698-726.

Fricke, H.W. 1980. Mating systems, maternal and biparental care in triggerfish (Balistidae). *Zeit. Tierpsychol.* **53**:105-022.

Gilmore, R.G.G. and R.S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. *Bulletin of Marine Science* **51**:83-103.

Govoni, J.J. and J.A. Hare. 2001. The Charleston Gyre as a spawning and larval nursery habitat for fishes. Pages 123-136 in: G.R. Sedberry (ed.). *Island in the Stream: Oceanography and Fisheries of the Charleston Bump*. American Fisheries Society Symposium 25, Bethesda, Maryland USA.

Grimes, C.B., C.F. Idelberger, K.W. Able, and S.C. Turner. 1988. The reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system. *Fishery Bulletin* **86**:745-762.

Harris, P.J. and J.C. McGovern. 1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994. *Fishery Bulletin* **95**:732–747.

Harris, P.J., S.M. Padgett and P.T. Powers. 2001. Exploitation related changes in the growth and reproduction of tilefish, and the implications for the management of deepwater fisheries. Pages 199-210 in: G.R. Sedberry (ed.). *Island In The Stream: Oceanography and Fisheries of the Charleston Bump*. American Fisheries Society Symposium 25, Bethesda, Maryland USA.

Harris, P.J., D.M. Wyanski and P.T. Powers Mikell. 2004. Age, growth, and reproductive biology of blueline filefish along the southeastern coast of the United States, 1982-1999. *Transactions of the American Fisheries Society* **133**:1190-1204.

Harris, P.J., D.M. Wyanski, D.B. White and L.L. Moore. 2005. Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979-1997. *Bulletin of Marine Science* **70:**113-132.

Hood, P.B., M.F. Godcharles, and R.S. Barco. 1994. Age, growth, reproduction, and the feeding ecology of black sea bass, *Centropristis striata* (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bulletin of Marine Science* **54**:24-37.

Hood, P.B. and A.K. Johnson. 1999. Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico. *Fishery Bulletin* **97**:828-841.

Hood, P.B. and A.K. Johnson. 2000. Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus*, from the eastern Gulf of Mexico. *Fishery Bulletin* **98**:723-735.

Hood, P.B. and R.A. Schlieder. 1992. Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bulletin of Marine Science* **51**: 337-352.

Jimenez, A.R. and M.F. Fernandez. 2001. Tag and recapture study of red hind and coney at three spawning aggregation sites off the west coast of Puerto Rico. *Proceedings of the Gulf and Caribbean Fisheries Institute* **52**:15-25.

Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* **3**:65-84.

Lindeman, K.C., R. Pugliese, G.T. Waugh, and J.S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of Marine Science* **66**:929-956.

Lobel, P.S. and R.E. Johannes. 1980. Nesting, eggs and larvae of triggerfishes (Balistidae). *Environmental Biology of Fishes* **5**:251-252.

Manickchand-Heileman, S.C. and D.A.T. Phillip. 2000. Age and growth of the yellowedge grouper, *Epinephelus flavolimbatus,* and the yellowmouth grouper, *Mycteroperca interstitialis*, off Trinidad and Tobago. *Fishery Bulletin* **98**:290-298.

Martin, F.D. and G.E. Drewry. 1978. *Development of Fishes of the Mid-Atlantic Bight, Volume VI, Stromateidae Through Ogcoephalidae*. U.S. Fish and Wildlife Service FWS/OBS-78/12.

Mathews, T.D. and O. Pashuk. 1986. Summer and winter hydrography of the U.S. South Atlantic Bight (1973-1979). *Journal of Coastal Research* **1**:311-336.

McGovern, J.C., G.R. Sedberry, and P.J. Harris. 1998. Status of stocks of reef fishes in the South Atlantic Bight, 1983-1996. *Proceedings of the Gulf and Caribbean Fisheries Institute* **50**:871-895.

McGovern, J.C., G.R. Sedberry, H.S. Meister, T.M. Westendorff, D.M. Wyanski, and P.J. Harris. [In press]. A tag and recapture study of gag, *Mycteroperca microlepis*, off the southeastern United States. *Bulletin of Marine Science.*

McGovern, J.C. D.M. Wyanski, O. Pashuk, C.S. Manooch II, and G.R. Sedberry. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976-1995. *Fishery Bulletin* **96**:797-807.

Meister, H.S., J.C. McGovern, and T.M. Westendorff. [In prep.]. A tag and recapture study of greater amberjack, *Seriola dumerili*, from the Southeastern United States.

Miller, J.L. 1994. Fluctuations of Gulf Stream frontal position between Cape Hatteras and Straits of Florida. *Journal of Geophysical Research* **99 (C3)**:5057-5064.

Munoz, M., M. Casadevall, and S. Bonet. 1999. Annual reproductive cycle of *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaeniformes) with special reference to the ovaries sperm storage. *Journal of the Marine Biological Association of the United Kingdom* **79**:521-529.

Murawski, S.A., R. Brown, H.-L. Lai, P.J. Rago and L. Henderson. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. *Bulletin of Marine Science* **66**:775-0798.

NMFS. 2004. Annual report to Congress on the status of U.S. Fisheries - 2003. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, Maryland USA. 24 pp.

Obando, E. and J.R. Leon. 1989. Reproducción del bolo, *Diplectrum formosum* (Linnaeus, 1766) (Pisces: Serranidae) en Punta Mosquito, Isla de Margarita, Venezuela. *Scientia Marina (Barcelona)* **53:**771-777.

Ofori-Danson, P.K. 1990. Reproductive ecology of the triggerfish, *Balistes capriscus* from the Ghanaian coastal waters. *Tropical Ecology* **31**:1-11.

Paffenhöfer, G.A., B.T. Wester, and W.D. Nicholas. 1984. Zooplankton abundance in relation to state and type of intrusion onto the southeastern United States shelf during summer. *Journal of Marine Research* **42**:995-1017.

Peres, M.B. and S. Klippel. 2003. Reproductive biology of southwestern Atlantic wreckfish, *Polyprion americanus* (Teleostei: Polyprionidae). *Environmental Biology of Fishes* **68:**163-173.

Popenoe, P. and F.T. Manheim. 2001. Origin and history of the Charleston Bump--geological formations, currents, bottom conditions, and their relationship to wreckfish habitats on the Blake Plateau. Pages 43-94 in: G.R. Sedberry (ed.). *Island in the Stream: Oceanography and Fisheries of the Charleston Bump.* American Fisheries Society Symposium 25, Bethesda, Maryland USA.

Powell, A.B., D.G. Lindquist, and J.A. Hare. 2000. Larval and pelagic juvenile fishes collected with three types of gear in Gulf Stream and shelf waters in Onslow Bay, North Carolina, and comments on ichthyoplankton distribution and hydrography. *Fishery Bulletin* **98**:427-438.

Reed, J.K. 2000. *Oculina* coral banks of Florida: conservation and management of a deep-water reserve. Pages 2-4 in: P. Hallock and L. French (eds.). Diving for Science in the 21st Century. Proceedings of the 20th Annual Symposium, American Academy of Underwater Sciences, Nahant Massachusetts USA.

SAFMC. [2004]. Informational public hearing document on marine protected areas to be included in Amendment 14 to the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, South Carolina USA. 46pp. Unpubl. MS.

Sala, E., E. Ballesteros, and R.M. Starr. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26(10)**:23-30.

Schmitten, R.A. 1999. Essential fish habitat: opportunities and challenges for the next millennium. Pages 3-10 in: L.R. Benaka (ed.). *Fish Habitat: Essential Fish Habitat and Rehabilitation.* American Fisheries Society Symposium 22, Bethesda, Maryland USA.

Sedberry, G.R., C.A.P. Andrade, J.L. Carlin, R.W. Chapman, B.E. Luckhurst, C.S. Manooch III, G. Menezes, B. Thomsen, and G.F. Ulrich. 1999. Wreckfish *Polyprion americanus* in the North Atlantic: fisheries, biology, and management of a widely distributed and long-lived fish. Pages 27-50 in: J.A. Musick (ed.). *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals*. American Fisheries Society Symposium 23, Bethesda, Maryland USA.

Sedberry, G.R., C.L. Cooksey, S.E. Crowe, J. Hyland, P.C. Jutte, C.M. Ralph, and L.R. Sautter. 2004. Characterization of deep reef habitat off the Southeastern U.S., with particular emphasis on discovery, exploration and description of reef fish spawning sites. Final Project Report, NOAA Ocean Exploration Project NA16RP2697.

Sedberry, G.R. and N. Cuellar. 1993. Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboplites aurorubens* (Teleostei: Lutjanidae). *Fishery Bulletin* **94**:699-709.

Sedberry, G.R., J.C. McGovern, and O. Pashuk. 2001. The Charleston Bump: an island of essential fish habitat in the Gulf Stream. Pages 3-24 in: G.R. Sedberry (ed.). *Island in the Stream: Oceanography and Fisheries of the Charleston Bump*. American Fisheries Society Symposium 25, Bethesda, Maryland USA.

Sedberry, G.R., O. Pashuk, J.K. Loefer, P. Weinbach, and J.C. McGovern. 2004. The role of the Charleston Bump in the life history of southeastern U.S. marine fishes, 2001-2003. Final report submitted to the National Marine Fisheries Service, Project Number NA07FL0497, by the South Carolina Department of Natural Resources, Charleston, South Carolina.

Van Sant, S.B., M.R. Collins, and G.R. Sedberry. 1994. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43**:417-428.

Weaver, D.C. and G.R. Sedberry. 2001. Trophic subsidies at the Charleston Bump: food web structure of reef fishes of the continental slope of the southeastern United States. Pages 137-152 in: G.R. Sedberry (ed.). *Island in the Stream: Oceanography and Fisheries of the Charleston Bump.* American Fisheries Society Symposium 25, Bethesda, Maryland USA.

Wenner, C.A. 1983. Species associations and day-night variability of trawl-caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. *Fishery Bulletin* **81**:537-552.

Wenner, C.A., C.A. Barans, B.W. Stender, and F.H. Berry. 1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight. I. Fall, 1973. *South Carolina Marine Resources Center Technical Report* **33**:79 pp.

Wenner, C.A., W.A. Roumillat, and C.W. Waltz. 1986. Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. *Fishery Bulletin* **84**:723-741.

Zatcoff, M.S., A.O. Ball, and G.R. Sedberry. 2004. Population genetic analysis of red grouper (*Epinephelus morio*) and scamp (*Mycteroperca phenax*) from the southeastern U.S. Atlantic and Gulf of Mexico. *Marine Biology* **144**:769-777.