Transactions of the American Fisheries Society 137:1389–1405, 2008
© Copyright by the American Fisheries Society 2008
DOI: 10.1577/T07-159.1

[Article]

Comparison of Reef Fish Catch per Unit Effort and Total Mortality between the 1970s and 2005–2006 in Onslow Bay, North Carolina

PAUL J. RUDERSHAUSEN*
Department of Zoology, Center for Marine Sciences and Technology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

ERIK H. WILLIAMS
National Oceanic and Atmospheric Administration, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

JEFFREY A. BUCKEL
Department of Zoology, Center for Marine Sciences and Technology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

JENNIFER C. POTTS
National Oceanic and Atmospheric Administration, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

CHARLES S. MANOOCH III
2900 Dogwood Lane, Morehead City, North Carolina 28557, USA

Abstract.—Stock assessments indicate many reef fish species have declined in size and abundance in the Atlantic Ocean off the southeastern coast of the United States. However, commercial fishers often state that stock assessments do not match their observations. We compared fishery-independent catch per unit effort (CPUE) and species composition data between the 1970s and 2005–2006 for reef fishes in the vicinity of Onslow Bay, North Carolina. Additionally, total mortality (Z) was estimated by means of a length-based catch-curve analysis. Effort (drops) by rod and reel focused on three sites, two inshore (30 m deep) and one offshore (125 m). The CPUE was compared between periods within each site and larger area (inshore, offshore). The CPUEs of red porgy *Pagrus pagrus*, vermilion snapper *Rhomboplites aurorubens*, black sea bass *Centropristis striata*, and gray triggerfish *Balistes capriscus* were greater in the 1970s than in 2005–2006 at specific capture sites. Conversely, the CPUEs of red grouper *Epinephelus morio*, white grunt *Haemulon plumieri*, and bank sea bass *C. ocyura* were greater in 2005–2006 than in the 1970s. The CPUEs of snowy grouper *E. niveatus*, blueline tilefish *Caulolatilus microps*, and gag *Mycteroperca microlepis* remained steady or increased between periods. Estimates of Z for snowy grouper, blueline tilefish, red porgy, white grunt, and vermilion snapper were generally greater in 2005–2006 than in the 1970s. Apex species caught in the 1970s but not in 2005–2006 included red snapper *Lutjanus campechanus*, silk snapper *L. vivanus*, warsaw grouper *E. nigritus*, and speckled hind *E. drummondhayi.* Catch rates and composition may have differed owing to differences in captains' skills and electronics despite efforts to standardize the fishing methods between periods. Estimates of total mortality are generally inconsistent with fisher observations and agree with recent stock assessments concluding that important reef species are overfished. Altogether, our results suggest that fishing and possibly other variables have affected the abundance and mortality of major species in this fishery.

The continental shelf waters off North Carolina represent the northern range of fisheries for groupers (Epinephelinae) and snappers (Lutjanidae) along the East Coast of the United States (Ulrich et al. 1977; Chester et al. 1984). Owing to slow growth, late maturity, high value, and ease of capture, some of these species are vulnerable to rapid depletion from localized habitat patches (Epperly and Dodrill 1995) and, therefore, at risk of being overfished (Huntsman et al. 1999). Additionally, since most groupers are protogynous hermaphrodites, size-selective fishing pressure may skew sex ratios. Evidence of this susceptibility has been documented through the decline in the proportion of male gag *Mycteroperca microlepis* (McGovern et al.

---

* Corresponding author: pjruders@unity.ncsu.edu

Received July 24, 2007; accepted February 3, 2008
Published online September 11, 2008

1998) and snowy grouper *Epinephelus niveatus* (Wyanski et al. 2000) in the South Atlantic Bight.

The North Carolina reef fishery is relatively young. Fishing operations were mostly exploratory until the mid-1960s and limited to headboats through the early 1970s (Huntsman 1976). Catch per unit effort (CPUE) and tag return data indicated groupers important to the fishery (gag, snowy grouper, scamp *M. phenax*, and speckled hind *E. drummondhayi*) could be rapidly overfished (Huntsman and Dixon 1976; Huntsman 1976). Huntsman et al. (1983) used yield-per-recruit estimates to determine that by 1975 fishing was already taking between 70 and 85% of the maximum sustainable yield of important species. The North Carolina fishery expanded in 1976 (Ulrich et al. 1977) with the development of trawling for snappers and groupers. In turn, effort and landings increased in the late 1970s (SAFMC 1982), resulting in declines in total length for gag, red porgy *Pagrus pagrus*, and red snapper *Lutjanus campechanus* (Low et al. 1985). Huntsman et al. (1990) determined by 1988 the spawning potential ratio was less than 0.30 for snowy grouper, scamp, speckled hind, and warsaw grouper *E. nigritus*; the South Atlantic Fishery Management Council (SAFMC) considers a species overfished when values drop below this level. Species currently considered overfished (NOAA 2005) include red porgy, red snapper, red grouper *E. morio*, black grouper *M. bonaci*, goliath grouper *E. itajara*, black sea bass *Centropristis striata*, and snowy grouper; these species (and others) have substantially contributed to commercial, recreational, and headboat landings in the North Carolina fishery.

Direct assessment techniques useful for other fisheries are partly ineffective for deepwater reef fishes (Low et al. 1985). Stakeholders and managers of this resource continue to disagree over the relative health of stocks despite reports describing overharvest (i.e., Coleman et al. 2000), increasingly skewed sex ratios (Huntsman et al. 1999), decreased spawning potential ratios (Huntsman et al. 1999), and rapid depletion of groupers at once-productive reef habitat (Epperly and Dodrill 1995). Commercial and recreational fishers have consistently questioned the data used to develop assessments for important reef fish species. The lack of fishery-independent data is cited as a concern in reef fish assessments (SAFMC 2006).

In 2005–2006, we used hook and line to collect reef fishes in Onslow Bay, North Carolina. We compared these data to fishery-independent collections made by the National Oceanic and Atmospheric Administration (NOAA) in the 1970s. In fisheries research, catch comparisons must be made cautiously because collection methods are not always closely duplicated. This interdecadal comparison afforded us an opportunity to try and match methods used in the 1970s, when substantial fishing for reef species was beginning in North Carolina. Our purpose was to determine whether changes in CPUE, species composition, size, and total mortality have occurred over the three intervening decades. We speculated that we would find decreasing catch rates, increasing mortality, and changes in numerically dominant species at each site—changes that would be consistent with assessments of species in this fishery. Findings from this study serve as a fishery-independent census of reef fish species and assist with interpretation of formal assessments.

Methods

Study site.—The most productive reef fish habitat in the Carolinas consists of discontinuous limestone and sandstone outcroppings of moderate (>1-m) height with intermittent sandy troughs (MacIntyre and Milliman 1970). Sites with this structure and relief are often called live bottom because the porous limestone supports infauna and epifauna important as food for large reef fishes. The 210 Rock (~34°14′N, 76°35′W; depth ≈ 30 m) and 2113 Rock (~34°10′N, 76°50′W; depth ≈ 30 m) are considered inshore sites, and were two of the three live-bottom sites fished in the 1970s and again in 2005–2006 (Figure 1). While 2113 Rock is almost the same distance from Beaufort Inlet, the bottom profile of this area is less conspicuous than 210 Rock. For this reason, 2113 Rock may have been fished less heavily than 210 Rock in the late 1970s. As relatively shallow sites, both 210 and 2113 rocks support two different assemblages of demersal fishes; a temperate group, represented chiefly by black sea bass, and a tropical group, represented by groupers, snappers, and porgies that occupy warm bottom waters year-round close to the Gulf Stream at the northern limit of their ranges (Huntsman 1976). The Snowy Edge (~34°15′N, 76°05′W; depth range, 100–150 m), the third site fished in both periods, lies along the edge of the continental shelf, where drowned limestone cliffs serve as habitat for species such as snowy grouper and blueline tilefish *Caulolatilus microps* (Huntsman et al. 1999). Scientific and common names of species collected in one or both periods are listed in Table 1. The Gulf Stream moderates water temperatures sufficiently so that habitat in the vicinity of the Snowy Edge supports a year-round population of subtropical reef species.

Collection methods.—Scientists from NOAA's Beaufort, North Carolina, laboratory collected fish from offshore waters between Cape Lookout and Cape Fear, North Carolina, from 1972 to 1979. Ninety-nine percent of the trips during this period were made over a

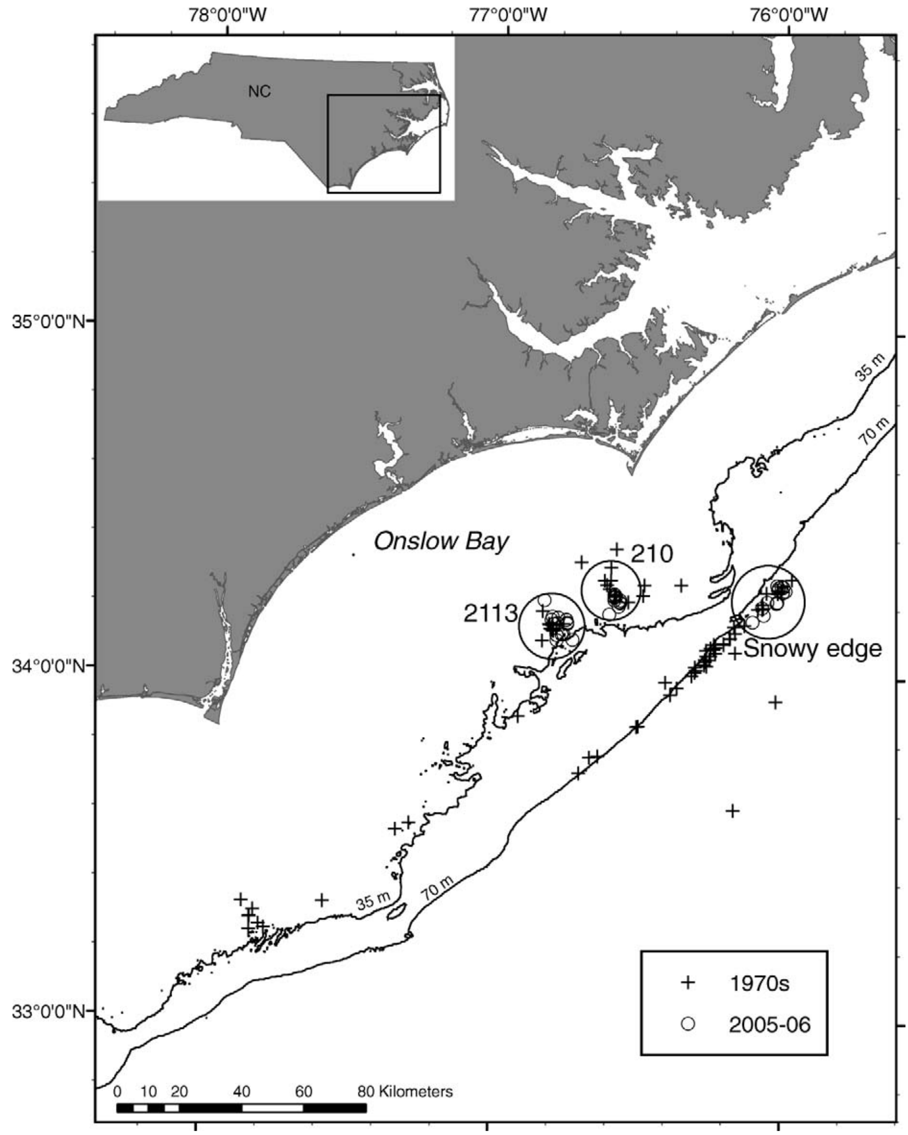

FIGURE 1.—Sites fished in the 1970s (plus signs) and 2005–2006 (small circles) in Onslow Bay. The specific sites considered in this study—210 Rock, 2113 Rock, and Snowy Edge—are denoted by large circles.

53-month span from May 1972 through September 1976. Collections during that period were made with rods and electric reels fished aboard the RV *Onslow Bay*, a vessel that measured 15.2 m long and 4.4 m wide and was powered by twin diesel engines. These 1970s research trips documented numbers and sizes of species captured. We consulted scientists and captains on the 1970s trips to develop our sampling protocol and design. A portion of the data from these collections described the reef fish community (Chester et al. 1984). The 1970s sampling occurred across a range of sites in Onslow Bay (Figure 1), but most regularly at three sites: 210 Rock, 2113 Rock, and Snowy Edge. Because of the frequency of trips to these three sites in the 1970s, they were selected for sampling in 2005–2006. For each season, roughly equal percentages of trips were taken between the two periods; in the 1970s, 31, 34, 19, and 17% of trips were taken in spring, summer, fall, and winter, while in 2005–2006, 33, 27, 23, and 17% of trips were taken during these four respective seasons.

The fishing techniques of the 1970s were duplicated

TABLE 1.—Reef fish species captured in Onslow Bay in the 1970s, 2005–2006, or both.

Species
Gray triggerfish *Balistes capriscus*
Whitebone porgy *Calamus leucosteus*
Knobbed porgy *Calamus nodosus*
Goldface tilefish *Caulolatilus chrysops*
Blueline tilefish *Caulolatilus microps*
Bank sea bass *Centropristis ocyurus*
Black sea bass *Centropristis striata*
Spottail pinfish *Diplodus holbrookii*
Speckled hind *Epinephelus drummondhayi*
Yellowedge grouper *Epinephelus flavolimbatus*
Red grouper *Epinephelus morio*
Misty grouper *Epinephelus mystacinus*
Warsaw grouper *Epinephelus nigritus*
Snowy grouper *Epinephelus niveatus*
Tomtate *Haemulon aurolineatum*
White grunt *Haemulon plumieri*
Squirrelfish *Holocentrus adscensionis*
Puffers *Lagocephalus* spp.
Red snapper *Lutjanus campechanus*
Silk snapper *Lutjanus vivanus*
Sand tilefish *Malacanthus plumieri*
Gag *Mycteroperca microlepis*
Scamp *Mycteroperca phenax*
Spinycheek scorpionfish *Neomerinthe hemingwayi*
Red porgy *Pagrus pagrus*
Vermilion snapper *Rhomboplites aurorubens*
Greater amberjack *Seriola dumerili*
Almaco jack *Seriola rivoliana*
Longspine porgy *Stenotomus caprinus*
Scup *Stenotomus chrysops*

as closely as possible in 2005–2006. Fishers during this latter period consisted of scientists, the boat's captain, and invited amateur anglers from the public. The captain was allowed to commercially sell a fraction of catch on some trips in 2005–2006, and a scientific observer was on board to ensure that the methods used in the 1970s were duplicated as closely as possible. Fishing in 2005–2006 was conducted aboard a 10-m center-console vessel equipped with two 250-hp (1 hp = 746 W) outboard engines. For both periods we separated a fishing day into two or more trips if effort was expended at multiple discrete sites. This determination was made in the former period when LORAN A coordinates were recorded in logbooks. Conversions from LORAN A used in the 1970s to latitude and longitude coordinates were made with LoranGPS 6.1 Software (Andren Software Co., Indiatlantic, Florida). Fishing consisted of using rods and electric reels spooled with dacron line in the former period and SpectraBraid in the latter period. Both types of line are preferred in the deepwater reef fishery because they have relatively little stretch compared with monofilament nylon line. Terminal tackle in both periods consisted of a two-hook, high–low bottom rig made from 90-kg-test monofilament nylon line, two three-way swivels equipped with a lead sinker ranging from 340 to 900 g, and J-hooks primarily of size 5/0 and 6/0. Hooks were baited with squid (*Ilex* and *Loligo* spp.), and to a lesser extent, cut fish.

While marine electronics are more advanced now than in the 1970s, we allowed cooperating commercial fishermen in the latter period to use sonar and positioning devices since these electronics were used in the former period. Fishing occurred during daylight hours primarily by drifting, and to a much lesser extent anchoring, over potentially productive bottom. On most trips in the 1970s, and all trips in 2005–2006, we recorded rod-hours and number of drops. We used drops of the baited terminal tackle as the standard unit of effort because of the subjectivity in defining time spent fishing (i.e., time spent handling fish and searching for productive bottom can bias actual time that gear is on bottom). We also used drops as the unit of effort because the number of drops per rod-hour on inshore (14.9 ± 4.9 [mean ± SD]) and offshore trips (6.1 ± 1.4) in 2005–2006 were significantly greater than those on inshore (6.2 ± 1.8) and offshore trips (4.6 ± 1.7) in the 1970s ($P < 0.001$ and $P = 0.002$, respectively). Since the number of drops was not recorded on 105 of 155 trips in the 1970s, we used the existing data on drops (dependent variable), rod-hours of fishing, depth, and catch of all specimens (independent variables) to produce a stepwise regression model ($\alpha = 0.05$ to enter model) that could be used to estimate the number of drops on remaining historic trips (model $r^2 = 0.589$). A subsample (21.4%) of the 8,937 fish caught in the 1970s were measured (total length [TL]; mm); for the species for which we estimated mortality (see later section), 100, 78.2, 16.7, 25.7, and 24.9% of the snowy grouper, blueline tilefish, red porgy, white grunts, and vermilion snapper were measured in the 1970s. All fish were measured in 2005–2006 (TL, mm). Depth (m) was recorded in both periods.

Species composition and comparisons of catch rates between periods.—We compared historic and present species composition, CPUE (number per drop), and size in two ways. One set of analyses focused on data collected from the three specific sites visited in both periods: 210 Rock, 2113 Rock, and Snowy Edge (Figure 1). The second set of analyses partitioned trips into two larger areas, inshore and offshore, which allowed us to use all the data collected in the 1970s on historic trips. Inshore versus offshore trips were identified by depth and the presence of one or more reef species unique to offshore catches—snowy grouper, blueline tilefish, and yellowedge grouper (Parker and Mays 1998). This change in species assemblage from inshore to offshore areas occurred in waters roughly 70 m deep. For the 2005–2006 data, trips to 210 and 2113 rocks were classified as inshore, while trips to Snowy Edge were classified as offshore.

The composition of reef species (percent abundance) was examined qualitatively for each period and site or area combination. This analysis was restricted to species in the SAFMC snapper–grouper management complex.

We used two-way analysis of variance (ANOVA) to test for effects ($\alpha = 0.05$) of period and site per area on catch-per-drop data for red porgy, vermilion snapper, black sea bass, white grunt, gag, and gray triggerfish. A *t*-test was used to test for a period effect on catch-per-drop data for snowy grouper and blueline tilefish since these two species are found only offshore. These eight species are important components in commercial or recreational catches of reef fishes, or both, in North Carolina (Huntsman 1976; Tester et al. 1983; Parker and Mays 1998). Two-way ANOVA was also used to test for effects of period and site on catch-per-drop data for red grouper and bank sea bass because the red grouper is a commercially important serranid in North Carolina (North Carolina Division of Marine Fisheries, unpublished data) and bank sea bass are a common bycatch when targeting the aforementioned species (P. J. Rudershausen, personal observation). Additionally, we used two-way ANOVA to test for effects of period and site on the catch-per-drop data for all reef species combined. Before performing two-way ANOVAs, we log transformed the CPUE data ($\log_e[x + 1]$) to better approximate a normal distribution. Post hoc multiple comparisons were performed with Tukey's honestly significant difference test.

Comparisons of median length and length-based estimates of total mortality.—For species with at least 15 individuals measured by site and period, we compared median lengths between periods using a median test. When enough data were available, median lengths were compared between periods for each of the three specific sites (210 Rock, 2113 Rock, and Snowy Edge) and two larger areas (inshore and offshore).

We estimated total mortality (Z) for those species for which enough length samples were collected in each period, namely, snowy grouper, blueline tilefish, red porgy, white grunt, and vermilion snapper. We estimated Z by two methods of length-based catch-curve analysis, each using two assumptions about selectivity for the historic and present length data. The first method converts lengths to ages using the rearranged von Bertalanffy equation, as follows:

$$a = \frac{\log_e\left(\frac{L_\infty}{L_\infty - L}\right)}{K} + t_0,$$

where a is the age of the fish, L is the observed length, and L_∞, K, and t_0 are the von Bertalanffy growth parameters (Pauly 1984, 1990; Quinn and Deriso 1999). The second method uses an extension of a method commonly used in stock assessment models (Quinn and Deriso 1999; Williams 2001; SEDAR 2004, 2006a). This method uses an age–length conversion matrix, which models mean length at age using the von Bertalanffy growth parameters and allows for normal probability of length at age. In this case, the matrix was simplified by assuming a constant coefficient of variation of length at age.

With the first method of catch-curve analysis, the converted age data were distributed into observed proportion at age and fitted to an equilibrium age-structured model that estimates total mortality and selectivity at age, as follows:

$$N_a = N_{a-1}e^{-Zs_a},$$

where N_a is the number at age (a) and s_a is the selectivity at age.

The selectivity at age was estimated with a two-parameter logistic function, as follows:

$$s_a = 1/[1 + e^{-\alpha(a-\beta)}],$$

where α is the slope parameter and β is the age at 50% selection. Before fitting the model predictions to the observed data, the number at age data were converted to predicted proportion at age, as above. The observed and predicted proportions were then fit by maximum likelihood assuming a multinomial distribution of the proportions.

For the second method of catch-curve analysis, an equilibrium age-structured model was used to compute a predicted length distribution. This length distribution was then fitted to the observed length distributions from the two time periods. The observed and predicted proportions were fitted by maximum likelihood, as was done in the first method with ages.

For both catch-curve analysis methods, we applied selectivity in two ways. In one case we assumed that the selectivity was the same between historic and present catches, requiring estimation of only one selectivity curve. In the second case, we assumed separate selectivity functions for the two time periods. This method of catch-curve analysis, which estimates selectivity and Z simultaneously, differs from methods described in the literature. It avoids the problem of choosing an age cutoff and allows for easy automation of fitting multiple length distributions.

Because of uncertainty in the growth parameters, a range of values from 0.5 to 1.5 times the literature-derived values for L_∞ and K were examined with both catch-curve methods. The value of t_0 is an age-adjustment parameter with little influence on the

TABLE 2.—Absolute (*n*) and percent catch for reef fish species in the South Atlantic Fishery Management Council's snapper–grouper management complex collected on 19 trips in the 1970s and 16 trips in 2005–2006 to 210 Rock, Onslow Bay. Trips = the number of trips on which each species was captured.

Species	*n*	%	Trips
1970s			
Black sea bass	715	68.1	18
Bank sea bass	95	9.0	15
Red porgy	85	8.1	13
White grunt	77	7.3	10
Gray triggerfish	26	2.5	8
Vermilion snapper	20	1.9	5
Whitebone porgy	11	1.0	5
Gag	7	0.7	4
Red snapper	6	0.6	1
Tomtate	4	0.4	2
Red grouper	2	0.2	2
Knobbed porgy	1	0.1	1
Scup	1	0.1	1
2005–2006			
Black sea bass	290	26.1	16
Bank sea bass	289	26.0	16
White grunt	286	25.8	16
Spottail pinfish	67	6.0	9
Vermilion snapper	52	4.7	8
Tomtate	49	4.4	9
Red grouper	27	2.4	12
Gag	26	2.3	9
Whitebone porgy	10	0.9	6
Red porgy	6	0.5	4
Gray triggerfish	4	0.4	3
Greater amberjack	2	0.2	1
Scamp	1	0.1	1
Scup	1	0.1	1

estimates of Z, making examination of sensitivity unnecessary.

To determine whether fishing mortality (F) was higher than the F at maximum sustainable yield (MSY), we compared the Z_{Ratio} estimates to Z_{Ratio} at MSY where

$$Z_{\text{Ratio}} \text{ at MSY} = (F_{\text{MSY}} + M)/M.$$

Fishing mortality rate (F_{MSY}) is a threshold level often used to describe overfishing.

Estimates of F_{MSY} were obtained from stock assessments on snowy grouper (SEDAR 2004) and red porgy (SEDAR 2006a); there were no estimates of F_{MSY} for white grunt or blueline tilefish. An estimate of F_{MSY} for tilefish *Lopholatilus chamaeleonticeps* was used as a surrogate for blueline tilefish. Owing to uncertainties about the level of F_{MSY} for vermilion snapper, the recommended proxy, F_{MAX}, from the stock assessment was used (SEDAR 2003). For a valid comparison of Z_{Ratio} at MSY to the current estimated ratio, we made the assumption that no fishing occurred in the historic time period (i.e., $Z = M$ for the historic time period), although there was reportedly some light fishing effort for these species in the early 1970s (Huntsman 1976).

TABLE 3.—Absolute (*n*) and percent catch for reef fish species in the South Atlantic Fishery Management Council's snapper–grouper management complex collected on 19 trips in the 1970s and 18 trips in 2005–2006 to 2113 Rock, Onslow Bay. Trips = the number of trips on which each species was captured.

Species	*n*	%	Trips
1970s			
Black sea bass	529	42.2	16
Red porgy	418	33.3	18
White grunt	135	10.8	15
Vermilion snapper	67	5.3	9
Bank sea bass	60	4.8	14
Gray triggerfish	23	1.8	11
Gag	9	0.7	5
Whitebone porgy	5	0.4	3
Greater amberjack	4	0.3	3
Longspine porgy	3	0.2	3
Knobbed porgy	1	0.1	1
2005–2006			
White grunt	433	37.9	17
Red porgy	256	22.4	17
Black sea bass	114	10.0	14
Bank sea bass	104	9.1	16
Red grouper	74	6.5	14
Vermilion snapper	71	6.2	9
Tomtate	43	3.8	7
Gag	16	1.4	8
Scup	12	1.1	6
Whitebone porgy	8	0.7	7
Scamp	5	0.4	4
Gray triggerfish	4	0.4	3
Greater amberjack	1	0.1	1

Results

Species Composition

The composition of reef species fluctuated between periods at each site (Tables 2–5). At 210 Rock, black sea bass was the most abundant species (>65% of catch) in the 1970s, but it decreased to 26% of catch in 2005–2006 (Table 2). The contribution of red porgy and gray triggerfish to the total catch also decreased at this site, but it increased for white grunt, bank sea bass, vermilion snapper, red grouper, and gag.

As at 210 Rock, black sea bass at 2113 Rock decreased in relative abundance from the 1970s to 2005–2006 (Table 3). The contribution of red porgy to the total catch declined by approximately 10% while for white grunt it increased by approximately 25%. Gag and vermilion snapper increased in relative abundance only slightly. Red grouper were not caught at 2113 Rock in the 1970s, but they represented 6.2% of the catch there in 2005–2006.

Changes in relative abundance for all inshore trips in the 1970s versus 2005–2006 were similar to the

TABLE 4.—Absolute (*n*) and percent catch for reef fish species in the South Atlantic Fishery Management Council's snapper–grouper management complex collected on 78 trips in the 1970s and 34 trips in 2005–2006 to inshore areas, Onslow Bay. (The 2005–2006 inshore areas were 210 Rock and 2113 Rock combined.) Trips = the number of trips on which each species was captured.

Species	*n*	%	Trips
1970s			
Black sea bass	2,234	42.3	64
Red porgy	1,603	30.3	63
White grunt	562	10.6	51
Vermilion snapper	270	5.1	33
Bank sea bass	262	5.0	54
Gray triggerfish	194	3.7	41
Gag	33	0.6	15
Scamp	27	0.5	7
Tomtate	27	0.5	10
Whitebone porgy	26	0.5	8
Knobbed porgy	10	0.2	6
Red snapper	9	0.2	4
Greater amberjack	8	0.2	6
Almaco jack	7	0.1	3
Speckled hind	5	0.1	2
Red grouper	4	0.1	3
Longspine porgy	3	0.1	3
Scup	1	0.0	1
2005–2006			
White grunt	719	32.9	33
Black sea bass	404	18.5	30
Bank sea bass	393	18.0	32
Red porgy	262	12.0	21
Vermilion snapper	123	5.6	17
Red grouper	101	4.6	26
Tomtate	92	4.2	16
Gag	42	1.9	17
Whitebone porgy	18	0.8	13
Scup	13	0.6	7
Gray triggerfish	8	0.4	6
Scamp	6	0.3	5
Greater amberjack	3	0.1	2

TABLE 5.—Absolute (*n*) and percent catch for reef fish species in the South Atlantic Fishery Management Council's snapper–grouper management complex collected on 77 trips in the 1970s to all offshore areas, 17 trips in the 1970s to Snowy Edge, and 20 trips to Snowy Edge in 2005–2006, Onslow Bay. Trips = the number of trips on which each species was captured.

Species	*n*	%	Trips
1970s, offshore			
Red porgy	1,860	57.7	71
Vermilion snapper	401	12.4	53
Blueline tilefish	329	10.2	55
Snowy grouper	261	8.1	35
Speckled hind	90	2.8	31
Gray triggerfish	67	2.1	18
Almaco jack	53	1.6	21
Greater amberjack	46	1.4	19
Silk snapper	24	0.7	14
Goldface tilefish	21	0.7	13
Yellowedge grouper	18	0.6	11
Red snapper	18	0.6	12
Sand tilefish	9	0.3	3
Gag	9	0.3	7
Warsaw grouper	8	0.2	7
Scamp	5	0.2	5
Bank sea bass	3	0.1	3
Knobbed porgy	3	0.1	3
Tomtate	3	0.1	1
White grunt	3	0.1	2
Black sea bass	2	0.1	2
Whitebone porgy	1	0.0	1
Misty grouper	1	0.0	1
1970s, Snowy Edge			
Red porgy	347	36.4	16
Vermilion snapper	216	22.7	14
Snowy grouper	155	16.3	13
Blueline tilefish	144	15.1	15
Almaco jack	24	2.5	7
Greater amberjack	19	2.0	7
Squirrelfish	10	1.1	1
Goldface tilefish	9	0.9	6
Sand tilefish	5	0.5	1
Silk snapper	5	0.5	3
Speckled hind	5	0.5	2
Yellowedge grouper	4	0.4	5
Black sea bass	2	0.2	2
Bank sea bass	2	0.2	2
Red snapper	2	0.2	2
Scamp	1	0.1	1
Gag	1	0.1	1
Warsaw grouper	1	0.1	1
2005–2006, Snowy Edge			
Snowy grouper	278	45.1	19
Blueline tilefish	242	39.2	17
Spinycheek scorpionfish	23	3.7	7
Goldface tilefish	20	3.2	11
Red porgy	15	2.3	8
Scamp	10	1.6	7
Yellowedge grouper	9	1.5	5
Vermilion snapper	8	1.3	2
Puffers	3	0.5	1
Bank sea bass	3	0.5	2
Misty grouper	2	0.3	2
Greater amberjack	2	0.3	1
Black sea bass	1	0.2	1
Whitebone porgy	1	0.2	1
Almaco jack	1	0.2	1

changes observed when examining 210 and 2113 rocks by themselves; the relative abundance of black sea bass, red porgy, and gray triggerfish decreased while that of white grunt, bank sea bass, and red grouper increased (Table 4). The percent contribution of vermilion snapper and gag to total catch remained constant. Red snapper and speckled hind comprised minor percentages of the catch inshore in the 1970s, but were not caught there in 2005–2006.

Dominant species also changed at Snowy Edge (Table 5). The percentage contribution of red porgy and vermilion snapper to total reef fish catch decreased by an order of magnitude while that of snowy grouper and blueline tilefish increased. These changes in species composition were similar for all offshore sites in the 1970s versus Snowy Edge in 2005–2006 (Table 5). Red snapper, silk snapper, speckled hind, and warsaw grouper comprised minor percentages of the catch at Snowy Edge and other offshore areas in the 1970s but were not caught in 2005–2006.

Comparisons of Catch Rates at 210 Rock, 2113 Rock, and Snowy Edge

The CPUE of several reef species declined between periods (Figure 2). The period and site effects and their interaction were significant for red porgy, vermilion snapper, black sea bass, gray triggerfish, red grouper, and white grunt. For the three specific sites, red porgy (2113 Rock and Snowy Edge), vermilion snapper (Snowy Edge), black sea bass (210 and 2113 rocks), and gray triggerfish (210 Rock) had a greater CPUE in the 1970s than in 2005–2006. Conversely, red grouper and white grunt at 2113 Rock had a greater CPUE in 2005–2006 than the 1970s. The period and site effects, but not their interaction, were significant for bank sea bass and all combined reef species. The CPUE of bank sea bass increased while CPUE of all combined reef species decreased between periods; both were caught at higher rates at 210 and 2113 rocks compared with Snowy Edge. There was no significant change in CPUE of gag between time periods, and the interaction between site and period was also not significant, although the site effect was significant. Gag had a greater CPUE at 210 Rock than at Snowy Edge. At Snowy Edge, there was no significant change in the CPUE of snowy grouper and blueline tilefish between periods.

Comparisons of Catch Rates at Inshore and Offshore Areas

The results of the CPUE comparisons for two larger areas (inshore and offshore; Figure 3) differed somewhat from the CPUE comparisons for the three specific sites. The period and site effects and their interaction were significant for black sea bass, red grouper, white grunt, and bank sea bass. Black sea bass had a greater CPUE inshore in the 1970s than in 2005–2006, but not offshore. The CPUE of red grouper, white grunt, and bank sea bass inshore was greater in 2005–2006 than in the 1970s. The period effect and the interaction between period and site were significant for red porgy, which had a greater CPUE in the 1970s than 2005–2006, but only offshore. The CPUE was also significantly greater in the 1970s for all reef species combined and that was true across all sites. Only the period effect was significant for vermilion snapper and gray triggerfish, which were caught at higher rates in the 1970s than in 2005–2006. Gag had a greater CPUE inshore than offshore; the period effect and interaction were not significant. At offshore areas, snowy grouper and blueline tilefish had a greater CPUE in 2005–2006 than the 1970s.

Comparisons of Median Length and Length-Based Estimates of Total Mortality

At each of the specific sites, median lengths were significantly greater for white grunt and vermilion snapper captured at 2113 Rock in the 1970s than in 2005–2006 (Figure 4). For two broad areas, median lengths were significantly greater for white grunt inshore and blueline tilefish offshore in the 1970s than 2005–2006 (Figure 5). While tests were not significant for eight other comparisons of median length, the frequency of catching the largest fish within each species was generally lower in 2005–2006 than in the 1970s.

For each species, a single site and a set of combined sites were used for the length-based catch-curve analysis to estimate total mortality. Owing to sample size limitations, the catch-curve analysis was limited to five species: snowy grouper, blueline tilefish, red porgy, white grunt, and vermilion snapper. The values of L_∞, K, and t_0 used for this analysis were obtained from relevant literature or recent stock assessments (Table 6).

The estimates of Z from the two catch-curve analysis methods are sensitive to L_∞ and K for all five species and both selectivity functions. Increases in L_∞ and K resulted in increases in the corresponding estimate of Z. However, the estimates of the ratio of total mortalities in 2005–2006 to those in the 1970s (present Z : historic Z, or Z_{Ratio}) are much less sensitive to changes in L_∞ and K, suggesting a robust measure for comparative purposes.

The estimates of Z_{Ratio} from the two methods of length-based catch-curve analysis using two separate selectivity assumptions indicate an increase in Z for all species and analysis combinations with the exception of vermilion snapper in one out of four analyses (Table 7). The Z_{Ratio} at F_{MSY} for snowy grouper, blueline tilefish, and red porgy is 1.42, 1.54, and 1.89, respectively. The F_{MSY} for blueline tilefish is taken from tilefish. No F_{MSY} estimates are currently available for white grunt. For vermilion snapper, Z_{Ratio} at F_{MAX} (2.40) was used instead of Z_{Ratio} at F_{MSY}. The range of Z_{Ratio} estimates for snowy grouper is from 84% to 265% of the estimate at MSY and the range of Z_{Ratio} estimates for blueline tilefish is from 100% to 171% of the estimate at MSY for tilefish. Depending on the type of analysis, the estimates of Z_{Ratio} suggest a two- to fourfold increase in Z for white grunt. The Z_{Ratio} estimates for red porgy and vermilion snapper suggest that mortality for each species is slightly below the MSY and MAX levels, respectively. For most species and sites, the estimates of Z_{Ratio} were generally similar between the two methods with the same selectivity assumption; however, the Z_{Ratio} estimates derived from

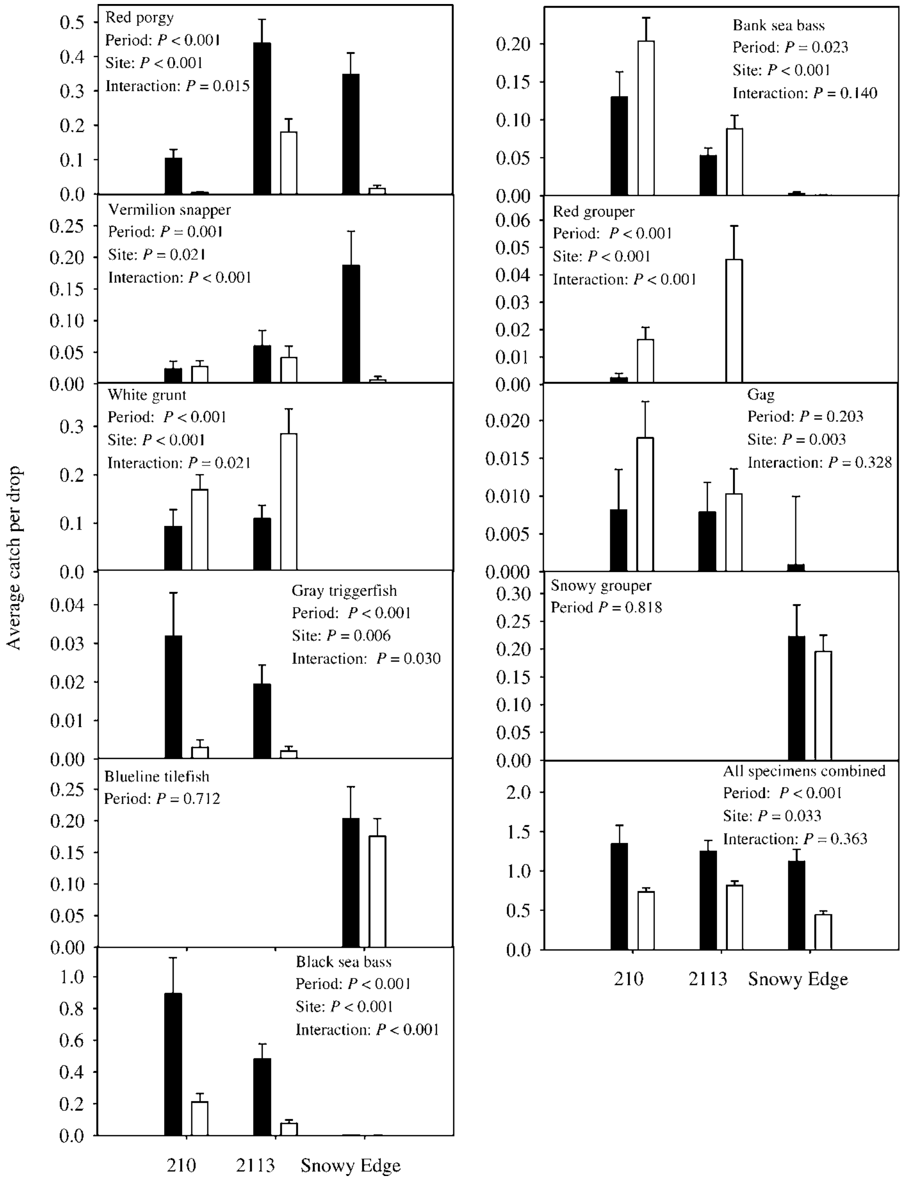

FIGURE 2.—Number caught per drop for 10 individual species and all reef species combined at 210 Rock, 2113 Rock, and Snowy Edge in the 1970s (black bars) and 2005–2006 (white bars). The error bars represent SEs; note the differences in the scale of the *y*-axis among panels. The sample sizes (number of visits to a site) in the 1970s were 19, 19, and 17 for 210 Rock, 2113 Rock, and Snowy Edge, respectively. The corresponding sample sizes in 2005–2006 were 16, 18, and 20. Probability levels for the period and site effects and their interaction are listed for each species except the snowy grouper and blueline tilefish (period effect only).

assuming equal selectivities for vermilion snapper were roughly double those assuming separate selectivities.

Discussion

In the three decades that have elapsed between the historic and present sampling, there have been striking changes in the fish community and mortality rates within Onslow Bay. We found declines in relative abundance between periods for some species, but increases for others; several species were present at specific sites in the 1970s but absent in 2005–2006. Catch-curve analysis revealed increased mortality for

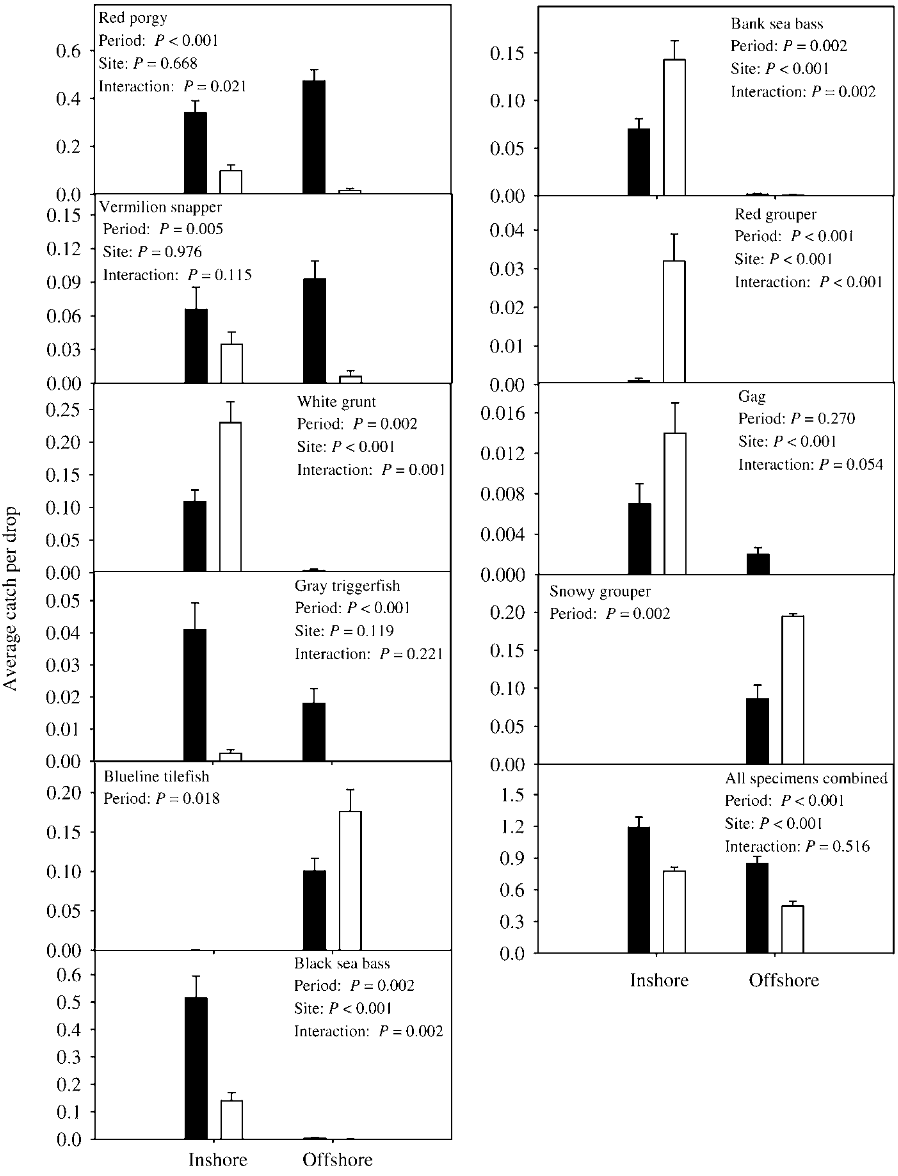

FIGURE 3.—Number caught per drop for 10 individual species and all reef species combined in inshore and offshore areas in the 1970s (black bars) and 2005–2006 (white bars). The error bars represent SEs; note the differences in the scale of the y-axis among panels. The sample sizes (number of visits to an area) in the 1970s were 78 and 77 for the inshore and offshore areas, respectively. The corresponding sample sizes in 2005–2006 were 34 and 20. Probability levels for the period and site effects and their interaction are listed for each species except the snowy grouper and blueline tilefish (period effect only).

almost all species and estimates of Z_{Ratio} suggest that values of F are too high (relative to MSY) for snowy grouper and blueline tilefish. In the analysis of the three sites, CPUE declined for four species, remained stable for three, and increased for three others. Differences in CPUE results between the three specific sites and two larger areas may have arisen because sites outside of 210 Rock, 2113 Rock, and Snowy Edge that were fished in the 1970s were not revisited in 2005–2006. However, among captains of commercial vessels and headboats, it is common knowledge that the depth ranges of red porgy, vermilion snapper, gag, and other reef species have contracted in Onslow Bay compared with the 1970s, when a detailed spatial census of

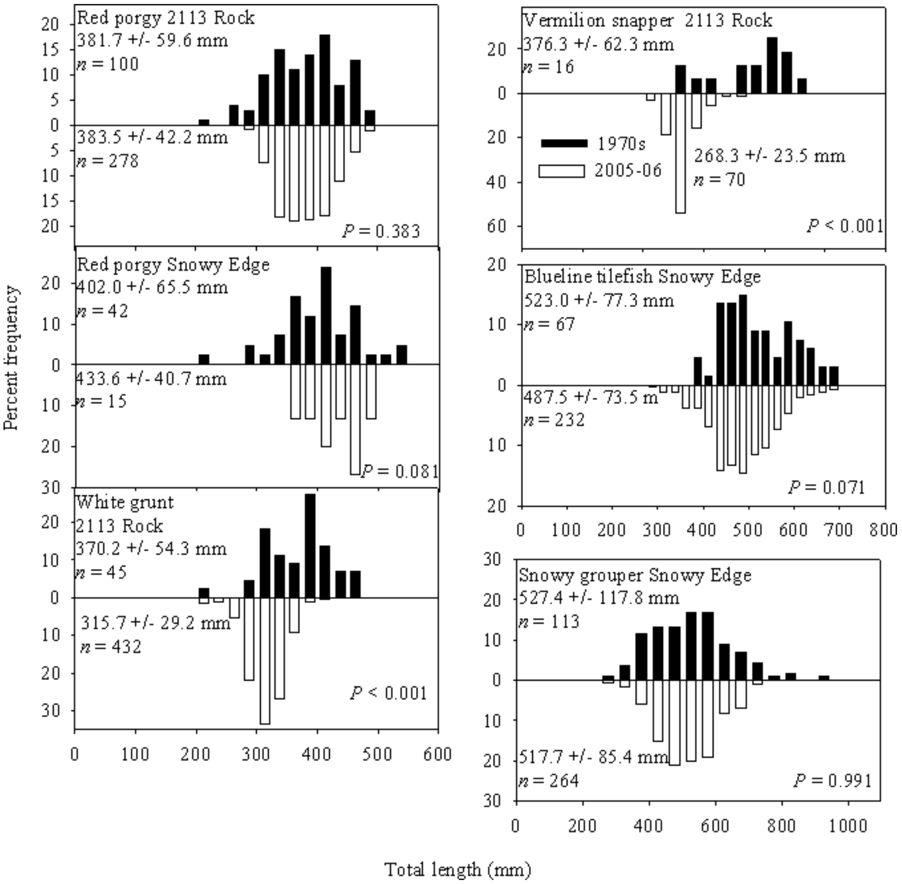

FIGURE 4.—Length frequency distributions for important commercial species caught at 2113 Rock and Snowy Edge in the 1970s (black bars) and 2005–2006 (white bars). At least 15 individuals were measured in each time period. The tick marks on the *x*-axes represent the midpoints of the total length (mm) bins. Probability values from median tests are shown in each panel.

headboat catches was conducted there (Tester et al. 1983). Our results are consistent with a contraction in the range of these species. The consistency between our mortality estimates and the findings of stock assessments contrasts with the common view of fishers that important species are not overfished.

The comparison of catch rates between periods may have been biased by the lack of drop data in the 1970s logbooks (the number of drops was not recorded on 68% of trips). We used stepwise regression to estimate drops for the 1970s trips where these data were missing. While using drops as a unit of effort may have introduced error in comparing catch rates between periods, we found similar results when comparing catch rates between periods by using hours as a unit of effort (P. J., Rudershausen, unpublished data). Comparisons of catch rates between periods could have also been biased by interannual fluctuations within period; sampling in the latter period was only over a single year while the majority of sampling in the 1970s was over an almost 5-year period.

Although substantial efforts were made to duplicate 1970s fishing methods in 2005–2006, we believe that the CPUEs in 2005–2006 are biased upward for several reasons. Firstly, productive live-bottom reef fish habitat in Onslow Bay is minimal in area and discontinuously distributed; modern sonar and navigation electronics make it much easier to find this habitat (Huntsman et al. 1999). Additionally, once over reef habitat, electronics can improve catch efficiency (Robins et al. 1998). The advantage of using electronics is probably most pronounced in deep water with current where present day chart plotters allow the captain to see the position of the boat relative to a marked fishing location. For example, the CPUE of snowy grouper was maintained or was higher in 2005–2006 than in the 1970s (Figures 2, 3); this contrasts with what would be expected based on the current stock assessment and

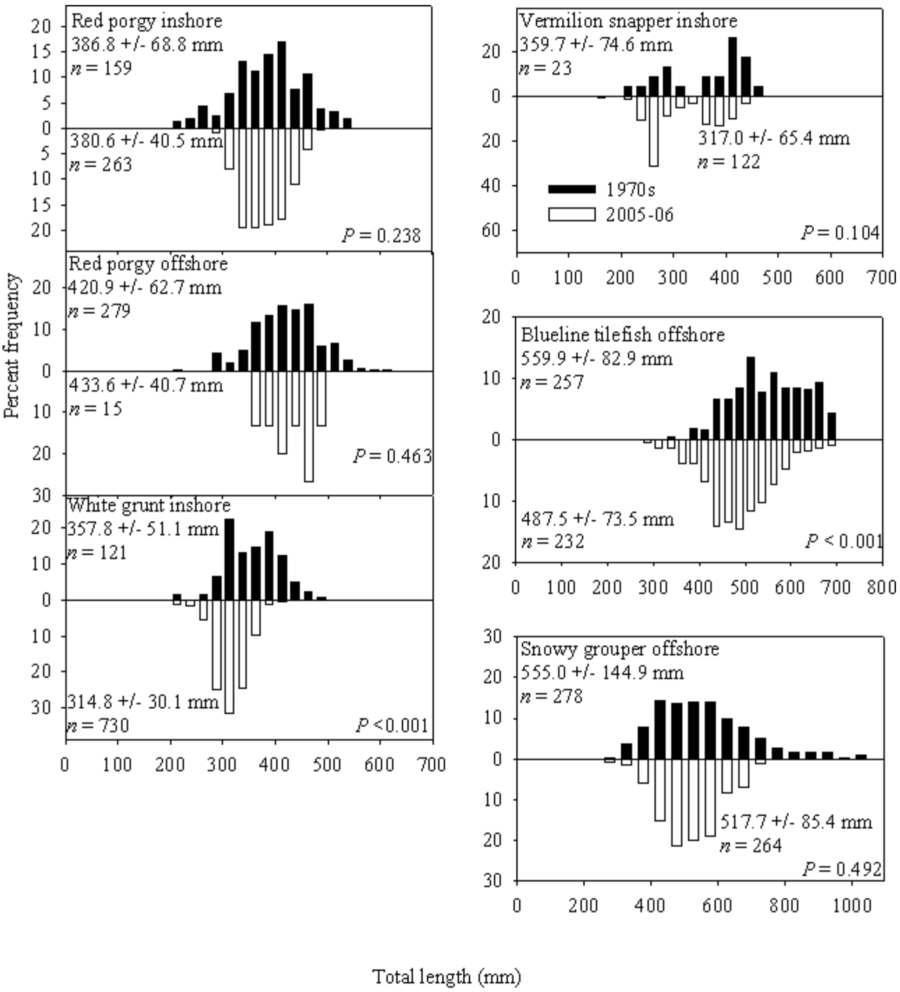

FIGURE 5.—Length frequency distributions for important commercial species caught in inshore and offshore areas in the 1970s (black bars) and 2005–2006 (white bars). See Figure 4 for additional details.

Z_{Ratio} comparisons for this species. While sonar (such as used for the 1970s trips) may have been available for use by the captains in 2005–2006, we decided that use of this outdated equipment in the latter period may have introduced its own biases to CPUE data by requiring captains to use electronics that they were not familiar with. The geographic positioning technology available in the 1970s, LORAN A, is no longer available and thus was not incorporated into the sampling design in 2005–2006.

TABLE 6.—Von Bertalanffy growth parameters applied to the length-based catch-curve analysis of 1970s and 2005–2006 collections of selected reef fish species (CV = coefficient of variation). A constant CV (100 • SD/mean) at age was used to estimate variance of length at age.

Species	L_∞ (mm)	$K(y^{-1})$	t_0 (y)	CV	Source
Snowy grouper	960	0.16	−0.5	0.1	SEDAR (2004)
Blueline tilefish	714	0.137	−1.03	0.05	Ross and Huntsman (1982)
Red porgy	510	0.21	−1.32	0.05	SEDAR (2006a)
White grunt	591	0.08	−4.21	0.05	Potts and Manooch (2001)
Vermilion snapper	650	0.144	−0.238	0.05	SEDAR (2003)

TABLE 7.—Estimates of total mortality (*Z*) for selected species captured at various sites during the 1970s and 2005–2006, along with the ratios of the latter to the former. The estimates were generated by two methods of age determination—a length-to-age conversion matrix and a von Bertalanffy growth equation—under two different assumptions about selectivity—that it was the same in both time periods and that it differed between periods. Thus four sets of estimates are presented. See the text for additional details.

		Z		
Species	Site or area	1970s	2005–2006	Ratio
	Conversion matrix, same selectivity			
Snowy grouper	Snowy Edge + offshore	0.46	0.75	1.62
	Snowy Edge	0.79	0.95	1.19
Blueline tilefish	Snowy Edge + offshore	0.16	0.42	2.62
	Snowy Edge	0.25	0.42	1.68
Red porgy	2113 Rock + Snowy Edge	0.39	0.51	1.31
	2113 Rock	0.45	0.56	1.25
White grunt	2113 Rock + 210 Rock	0.29	1.36	4.69
	2113 Rock	0.31	1.45	4.68
Vermilion snapper	All sites and areas	0.31	0.70	2.23
	Conversion matrix, different selectivities			
Snowy grouper	Snowy Edge + offshore	0.37	1.38	3.76
	Snowy Edge	0.56	1.38	2.46
Blueline tilefish	Snowy Edge + offshore	0.16	0.42	2.63
	Snowy Edge	0.24	0.42	1.76
Red porgy	2113 Rock + Snowy Edge	0.34	0.54	1.59
	2113 Rock	0.35	0.60	1.70
White grunt	2113 Rock + 210 Rock	0.56	1.45	2.59
	2113 Rock	0.54	1.71	3.17
Vermilion snapper	All sites and areas	0.44	0.52	1.18
	von Bertalanffy equation, same selectivity			
Snowy grouper	Snowy Edge + offshore	0.37	0.60	1.63
	Snowy Edge	0.58	0.68	1.18
Blueline tilefish	Snowy Edge + offshore	0.15	0.37	2.44
	Snowy Edge	0.24	0.37	1.54
Red porgy	2113 Rock + Snowy Edge	0.36	0.47	1.32
	2113 Rock	0.46	0.53	1.15
White grunt	2113 Rock + 210 Rock	0.29	1.06	3.68
	2113 Rock	0.30	1.12	3.70
Vermilion snapper	All sites and areas	0.26	0.54	2.08
	von Bertalanffy equation, different selectivities			
Snowy grouper	Snowy Edge + offshore	0.29	0.81	2.76
	Snowy Edge	0.47	0.81	1.71
Blueline tilefish	Snowy Edge + offshore	0.15	0.36	2.38
	Snowy Edge	0.24	0.36	1.54
Red porgy	2113 Rock + Snowy Edge	0.30	0.51	1.67
	2113 Rock	0.38	0.56	1.49
White grunt	2113 Rock + 210 Rock	0.58	1.11	1.92
	2113 Rock	0.58	1.24	2.13
Vermilion snapper	All sites and areas	0.47	0.45	0.96

Secondly, captain experience may influence catch rates in a reef fishery (Low et al. 1985). Experience may play a greater factor in fishing deep water near the edge of the continental shelf because a captain must continually assess a complex relationship between depth, current, and sonar settings when he tells his crew to drop their lines to the bottom. Each captain for trips in 2005–2006 had 25 years of experience commercially fishing for reef species in the vicinity of the three sites. In contrast, the captains on 1970s trips did not have this extensive experience because this fishery had just begun. The two commercial snapper–grouper captains on the 2005–2006 trips were restricted to visiting the areas considered—210 Rock, 2113 Rock, and Snowy Edge—but were under no other limitations as to where they fished. Within these three sites, they tended to revisit specific productive patches that they had fished in previous years or earlier in the 2005–2006 sampling. For example, despite being given an area of several square kilometers to fish at Snowy Edge, cooperating commercial fishers in 2005–2006 kept revisiting almost the same spot (as indicated by their chart plotter; Figure 1) because they knew from prior trips that it would yield a high catch. It is also likely that the smaller size and maneuverability of the vessel used in 2005–2006 allowed it to fish more precise areas than the vessel used in the 1970s.

In contrast to experience and electronics, it is unlikely that interdecadal differences (or lack thereof) would be due to terminal tackle such as hook size. Care was taken to match fishing gear, hook size, and bait types between periods. Furthermore, changes in hook size have been shown to have little influence on the sizes and catch rates of serranids (Bacheler and Buckel 2004). However, modern day braid lines may allow a fisher to feel a bite better than the dacron line that was used on the 1970s trips.

Despite the likely positive bias in CPUE for 2005–2006, we found declines in red porgy and vermilion snapper at Snowy Edge. Additionally, we found declines for black sea bass at each of the two shallow sites and for gray triggerfish at one shallow site. One explanation for the decline of red porgy and vermilion snapper at Snowy Edge is that the captains in 2005–2006 fished known snowy grouper aggregations and, therefore, did not fish a broad area as in the 1970s. However, the inshore sites showed the same pattern in decline of red porgy and vermilion snapper, suggesting that the numbers of these two species have declined over the three decades. Another explanation for the decline in CPUE of these two species at Snowy Edge is that the principal investigators on 1970s trips targeted red porgy and vermilion snapper on a portion of their trips to the offshore area (C. S. Manooch, personal observation). Despite the potential influence of fishing tactics on catch rates between periods, decadal declines in abundance are consistent with recent stock assessments for red porgy (SEDAR 2006a), vermilion snapper (SEDAR 2003), and black sea bass (SEDAR 2005).

Red grouper, white grunt, and bank sea bass often had a greater CPUE in 2005–2006; we are uncertain of the factors responsible for this change. The increase of red grouper is the most paradoxical. Groupers, which possess several *K*-selected characteristics, should be among the first reef species to be depleted from overfishing (Ault et al. 1998). While this pattern may explain the disappearance of speckled hind, warsaw grouper, and other apex species from catches in 2005–2006, it does not explain the increase in red grouper. Almost all of the red groupers caught in 2005–2006 were of sublegal size (i.e., below the legal limit of 508 mm TL), suggesting that the inshore sites may serve as nursery areas for this species; legal red grouper are caught in waters deeper than 210 Rock and 2113 Rock (P. J. Rudershausen, personal observation). Further evidence for lower CPUE of red grouper in the 1970s comes from headboat data in Onslow Bay; we caught more red grouper (27) on 16 trips to 210 Rock in 2005–2006 than were reported from 20 headboat trips to the same site during 1975–1977 (7 fish) (Parker and Dixon 1998), despite greater effort on a headboat trip than our trips involving 2–4 anglers. By scuba diving, Parker and Dixon (1998) found that several reef fishes with more tropical affinities, including red grouper, increased at their study site (210 Rock) and suggested that an interdecadal increase in water temperature could have caused this change. Such a temperature rise might also explain the increasing CPUE of white grunt at 210 Rock and decreasing CPUE of black sea bass with a more temperate distribution (Parker and Dixon 1998). Alternatively, or in conjunction with a thermally mediated range extension, red grouper, white grunt, and bank sea bass may be occupying a niche vacated by a species once more abundant at the same location, including red porgy, black sea bass, and vermilion snapper (Parker and Dixon 1998). Lastly, the rate of natural mortality of white grunt and bank sea bass may have decreased owing to declines in their fish predators. Ault et al. (1998) reported that grunts increased in relative abundance as groupers and snappers were overfished in the Florida Keys.

The findings of equal or greater catch rates of snowy grouper and gag in 2005–2006 than in the 1970s do not match the most recent assessments, which found that they are overfished (SEDAR 2004, 2006b). Catch rates of snowy grouper between periods also contrast with the Z_{Ratio} estimate. The differences may be that catches are inflated in 2005–2006 for reasons previously discussed. Epperly and Dodrill (1995) documented the rapid depletion of snowy grouper at one site off North Carolina; catch rates and sizes were reduced to levels comparable to those of nearby exploited sites over a period of months and had not recovered after 2 years. They concluded that overfishing in the reef fishery of the South Atlantic Bight is caused by a browsing pattern of fishers, such that, when aided by electronics, a discrete site is fished intensively and repetitively but never abandoned for enough time to allow recoveries in abundance. Although our between-decade comparisons of catch rates for snowy grouper do not agree with their findings, the change in size is apparent (Figures 4, 5).

Because the CPUEs for 2005–2006 may be inflated, estimates of Z derived from length data from historic and contemporary sources may provide better insight into population dynamics than comparisons of CPUE. The estimates of Z for both time periods are consistent with the most recent stock assessments for snowy grouper, red porgy, and vermilion snapper. Red porgies have been recovering from overfishing since 1999 with the implementation of various management regulations, including a brief moratorium and Amendment 12 (increased minimum size and decreased daily quota) to the snapper–grouper fishery management plan (SEDAR 2002).

The history of the reef fish fishery off North Carolina suggests that there was minimal fishing effort in the early 1970s. The fishery developed in the mid to late 1970s (Parker and Dixon 1998) and has experienced high effort since. Therefore, we expected to see a rise in total mortality (combination of natural and fishing mortality) from historic to present times. Our estimates of total mortality in the 1970s probably represent natural mortality (M) with little fishing mortality (F), while our estimates for 2005–2006 were a combination of M plus F. A small value for F in the 1970s would reduce the Z_{Ratio} estimate because $Z \neq M$. Our analysis suggests this may be the case because historic Z values appear higher than M estimates for these species (Table 7); estimates of M currently used in assessments are 0.12 for snowy grouper, 0.225 for red porgy, and 0.25 for white grunt and vermilion snapper. Therefore, the estimates of Z_{Ratio} presented in Table 7 should be treated as underestimates when compared with Z_{Ratio} at MSY. Even with this bias, Z_{Ratio} estimates were higher than Z_{Ratio} at MSY for blueline tilefish and most snowy grouper estimates (Table 7). For red porgy and vermilion snapper, Z_{Ratio} estimates were lower than Z_{Ratio} at MSY. Estimates of Z_{Ratio} suggest that blueline tilefish and white grunts could be experiencing unsustainable levels of mortality. For example, the estimate of Z for blueline tilefish during the 1970s in this study (Z = 0.15–0.25), and from Ross and Huntsman (1982) (Z = 0.22), are roughly one-half of the present day estimates and above Z_{Ratio} at MSY (Table 7).

The composition of the fish community changed between the two time periods examined. Several apex reef species caught in the 1970s were absent from catches in 2005–2006; this is the first fishery-independent evidence of the loss of these apex species at specific sites in North Carolina. Red snapper, silk snapper, speckled hind, and warsaw grouper, while infrequently caught in the 1970s, were not caught in 2005–2006. The total fishing effort in the 1970s was greater than 2005–2006, which could explain the absence of these species in the latter period. However, catch of these species remained relatively low when additional contemporary data were examined; from 2003 to 2007 two of this study's authors (P. J. Rudershausen and J. A. Buckel) participated in 60 fishery-independent, mid and outer shelf trips in Onslow Bay (separate from this study) and caught a total of two red snapper, one silk snapper, eight speckled hind, and no warsaw grouper (see 1970s data in Tables 4 and 5). The current rarity or absence of these species is consistent with the results of other recent investigations. Parker and Dixon (1998) estimated a density of 32 red snapper/ha at 210 Rock during 1975–1980, but found none there during 1990–1993. The gradual rise in water temperatures at one site in Onslow Bay (Parker and Dixon 1998) would not explain why a tropical species such as red snapper would decline over the three-decade period. Similarly, the speckled hind was noted as an indicator species of the fish community in the South Atlantic Bight by Miller and Richards (1979), and in the 1970s was considered an important component of headboat catches over some of the depths we fished in this study (Huntsman and Dixon 1976; Tester et al. 1983). Speckled hind were probably widely distributed at depths of 50–100 m and were captured on 28 of 33 historic trips on the RV *Onslow Bay* to the outer shelf (60–100 m depth) (Chester et al. 1984). Although management measures are in place for red snapper, silk snapper, speckled hind, and warsaw grouper, they are still vulnerable to depletion because of hooking mortality and barotraumas when captured as bycatch (Huntsman et al. 1999; Rudershausen et al. 2007).

Removing larger individuals from a population of protogynous hermaphrodite fish such as the serranids in this study will result in skewed sex ratios. Protogynous stocks may be overfished more easily than dioecious stocks (Alonzo and Mangel 2004). Based on visual inspection of the gonads, male snowy grouper were absent from our 2005–2006 collections (TL range, 250–700 mm; Figure 5) at Snowy Edge. A study off the Carolinas by Wyanski et al. (2000) confirms our observations; the smallest male snowy grouper in their samples measured 767 mm TL. On the other hand, based on Wyanski et al.'s (2000) work and our historic length frequency information, we estimate that male snowy grouper comprised 3.5% of the samples from the Snowy Edge and 8.6% of all offshore samples during the 1970s. Currently, there are no harvest regulations specifically intended to protect male groupers in the South Atlantic Bight. With the exception of site closures, size-based regulations intended to reverse a skewed sex ratio in deepwater grouper would probably fail because they almost always suffer lethal barotraumas when reeled to the surface (Rudershausen et al. 2007).

These findings help clarify the changes in the abundance of species that have historically been important in the North Carolina reef fishery. While the results of the catch rate comparisons differ among species, the length-based total mortality comparisons generally parallel species-specific stock assessments and support recent conservation measures (e.g., SAFMC Amendment 13C) enacted to rebuild stocks to sustainable levels. For management measures already instituted to rebuild overfished stocks, Z_{Ratio} estimates for red porgy and vermilion snapper provide evidence that these regulations are having the desired effect on these species.

Acknowledgments

We thank anglers on the RV *Onslow Bay* during the 1970s, Doug Willis, Alex Ng, Anthony Ng, Andrew Flynt, and Jason Edwards for their assistance with collections. We also thank Doug Vaughan and Joseph Smith for comments on an earlier version of this manuscript. This project was funded through the North Carolina Fishery Resource Grant Program, Project 05-FEG-11.

References

Alonzo, S. H., and M. Mangel. 2004. The effects of size-selective fisheries on the stock dynamics of sperm limitation in sex-changing fish. U.S. National Marine Fisheries Service Fishery Bulletin 102:1–13.

Ault, J. S., J. A. Bohnsack, and G. E. Meester. 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. U.S. National Marine Fisheries Service Fishery Bulletin 96:395–414.

Bacheler, N. M., and J. A. Buckel. 2004. Does hook type influence the catch rate, size, and injury of grouper in a North Carolina commercial fishery? Fisheries Research 69:303–311.

Chester, A. J., G. R. Huntsman, P. A. Tester, and C. S. Manooch III. 1984. South Atlantic Bight reef fish communities as represented in hook-and-line catches. Bulletin of Marine Science 34:267–279.

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.

Epperly, S. P., and J. W. Dodrill. 1995. Catch rates of snowy grouper, *Epinephelus niveatus*, on the deep reefs of Onslow Bay, southeastern U.S.A. Bulletin of Marine Science 56:450–461.

Huntsman, G. R. 1976. Offshore headboat fishing in North Carolina and South Carolina. U.S. National Marine Fisheries Service Marine Fisheries Review 38(3):13–23.

Huntsman, G. R., and R. L. Dixon. 1976. Recreational catches of four species of groupers in the Carolina headboat fishery. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 29(1975):185–194.

Huntsman, G. R., C. S. Manooch III, and C. B. Grimes. 1983. Yield per recruit models of some reef fishes of the U.S. South Atlantic Bight. U.S. National Marine Fisheries Service Fishery Bulletin 81:679–695.

Huntsman, G. R., J. Potts, and R. W. Mays. 1990. A preliminary assessment of the populations of seven species of grouper (Serranidae, Epinephelinae) in the western Atlantic Ocean from Cape Hatteras, North Carolina, to the Dry Tortugas, Florida. Proceedings of the Gulf and Caribbean Fisheries Institute 43:193–213.

Huntsman, G. R., J. Potts, R. W. Mays, and D. Vaughan. 1999. Goupers (Serranidae, Epinephelinae): endangered apex predators of reef communities. Pages 217–231 *in* J. A. Musick, editor. Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society, Symposium 23, Bethesda, Maryland.

Low, R. A., Jr., G. F. Ulrich, C. A. Barans, and D. A. Oakley. 1985. Analysis of catch per unit of effort and length composition in the South Carolina commercial handline fishery, 1976–1982. North American Journal of Fisheries Management 5:340–363.

MacIntyre, I. G., and J. D. Milliman. 1970. Physiographic features on the outer shelf and upper slope, Atlantic continental margin, southeastern United States. Geological Society of America Bulletin 81:2577–2598.

McGovern, J. C., D. M. Wyanski, O. Pashuk, C. S. Manooch III, 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. U.S. National Marine Fisheries Service Fishery Bulletin 96:797–807.

Miller, G. C., and W. J. Richards. 1979. Reef fish habitat, faunal assemblages, and factors determining distributions in the South Atlantic Bight. Proceedings of the Gulf and Caribbean Fisheries Institute 32:114–130.

NOAA (National Oceanic and Atmospheric Administration). 2005. A message from the NOAA assistant administrator for fisheries. Available: www.nmfs.noaa.gov. (April 2007).

Parker, R. O., Jr., and R. L. Dixon. 1998. Changes in a North Carolina reef fish community after 15 years of intense fishing: global warming implications. Transactions of the American Fisheries Society 127:908–920.

Parker, R. O., Jr., and R. W. Mays. 1998. Southeastern U.S. deepwater reef fish assemblages, habitat characteristics, catches, and life history summaries. NOAA Technical Report NMFS 138.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. International Center for Living Resources Management, Manila.

Pauly, D. 1990. Length-converted catch curves and the seasonal growth of fishes. Fishbyte 8(3):33–38.

Potts, J. C., and C. S. Manooch III. 2001. Differences in the age and growth of white grunt (*Haemulon plumieri*) from North Carolina and South Carolina compared with southeast Florida. Bulletin of Marine Science 68:1–12.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Robins, C. M., Y.-G. Wang, and D. Die. 1998. The impact of global positioning systems and plotters on fishing power in the northern prawn fishery, Australia. Canadian Journal of Fisheries and Aquatic Sciences 55:1645–1651.

Ross, J. L., and G. R. Huntsman. 1982. Age, growth, and mortality of blueline tilefish from North Carolina and South Carolina. Transactions of the American Fisheries Society 111:585–592.

Rudershausen, P. J., J. A. Buckel, and E. H. Williams. 2007. Discard composition and release fate in the snapper and grouper commercial hook-and-line fishery in North Carolina, USA. Fisheries Management and Ecology 14:103–113.

SAFMC (South Atlantic Fishery Management Council). 1982.

Source document: fishery management plan for the snapper–grouper complex of the South Atlantic region. SAFMC, Charleston, South Carolina.

SAFMC (South Atlantic Fishery Management Council). 2006. Final: snapper–grouper amendment 13C. SAFMC, Charleston, South Carolina.

SEDAR (Southeast Data Assessment and Review). 2002. Stock assessment of South Atlantic red porgy. SEDAR, Charleston, South Carolina.

SEDAR (Southeast Data Assessment and Review). 2003. Complete assessment and review report of South Atlantic vermilion snapper. SEDAR, SEDAR2-SAR2, Charleston, South Carolina.

SEDAR (Southeast Data Assessment and Review). 2004. Stock assessment of the deepwater snapper–grouper complex in the South Atlantic. SEDAR, SEDAR4-SAR1, Charleston, South Carolina.

SEDAR (Southeast Data Assessment and Review). 2005. Report of stock assessment: black sea bass. SEDAR, Update Process 1, Charleston, South Carolina.

SEDAR (Southeast Data Assessment and Review). 2006a. Stock assessment of red porgy off the southeastern United States. SEDAR, Update Assessment, Charleston, South Carolina.

SEDAR (Southeast Data Assessment and Review). 2006b. South Atlantic gag grouper. SEDAR 10 Review Workshop Report, Charleston, South Carolina.

Tester, P. A., C. A. Wolfe, R. L. Dixon, and G. R. Huntsman. 1983. Reef fish distributions off North Carolina and South Carolina as revealed by headboat catches. NOAA Technical Memorandum NMFS-SEFC-115.

Ulrich, G. F., R. J. Rhodes, and K. J. Roberts. 1977. Status report on the commercial snapper–grouper fisheries off South Carolina. Proceedings of the Gulf and Caribbean Fisheries Institute 29:102–125.

Williams, E. H. 2001. Assessment of cobia, *Rachycentron canadum*, in the waters of the U.S. Gulf of Mexico. NOAA Technical Memorandum NMFS-SEFSC-469.

Wyanski, D. M., D. B. White, and C. A. Barans. 2000. Growth, population structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North and South Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 98:199–218.